

Phylogeny and diversity of the phantom crane flies (Diptera: Ptychopteridae)

by

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ABSTRACT

The species diversity and higher level classification of Ptychopteridae (Insecta: Diptera) is examined with cladistic methods using morphological and molecular datasets. The taxonomic status of *Ptychoptera contaminata* Linnaeus is discussed, and a neotype designation is proposed. The Afrotropical fauna is detailed as part of a larger reference work of Diptera in the region. The structure and homologies of male genitalia within the family are examined, and a new standardized terminology is proposed, supported with colorized illustrations. An illustrated key is provided for the Nearctic species of both subfamilies. The extant species of the subfamily Bittacomorphinae are revised, including redescriptions, illustrations, and a key. The extant species of Ptychopterinae are revised in a similar manner, and the subgeneric structure of the genus is reassessed in the first comprehensive classification of the taxon. In total four new species are described from North America and one from eastern Asia, and five new subgenera are erected.

CHAPTER ONE. INTRODUCTION

Ptychopteridae is a family of lower Diptera associated with saturated sediments as larvae (Mattingly 1987, Wolf & Zwick 2001), distributed across the northern hemisphere and the Afrotropical region. The first ptychopterid was “described” in 1758 by Linnaeus, and by the initiation of this research project there were 74 accepted species (Wagner *et al* 2008, Nakamura & Saigusa 2009) divided into three genera and two subfamilies. The current project examines the species diversity and classification of the family in a global context, with an emphasis in interpreting the morphological diversity and homologies within the group.

The genus *Ptychoptera* was described by Meigen in 1803, and was originally placed in Tipulidae. Westwood (1835) described the genus *Bittacomorpha* for the distinctive species “*Ptychoptera*” *clavipes*. Osten Sacken (1862) recognized that *Ptychoptera* and *Bittacomorpha* were not closely related to other Tipulidae and erected the subfamily Ptychopterinae. Hart (1895) elevated the subfamily to full family rank. In 1916 Alexander moved the species of *Bittacomorpha* without inflated tarsomeres into the new genus *Bittacomorphella*, and in 1919 erected the subfamily Bittacomorphinae for both genera. Also in 1919 Tonnoir described the genus *Parapteroptera* for some distinctive European *Ptychoptera*, but Alexander synonymized the genus in 1927 and it was largely ignored until Zwick & Stary resurrected it as a subgenus of *Ptychoptera* (Zwick & Stary, 2003). To date there has not been a cladistic examination of the classification of the extant taxa, and the current subfamily and generic structure of the group is based on only a limited character set.

Although new species had been sporadically described in the late 1700s and 1800s, most currently recognized species were described in the first half of the 20th century, over half by the prolific Charles P. Alexander, a crane fly specialist. Most species descriptions were brief, lacking detailed examination of most structures. Illustrations were rare, and those presented were often of wings, which

offer marginal diagnostic utility. Morphological homologies within the group, especially of the complex and character rich male genitalia, were essentially uninvestigated. Only cursory work had been undertaken with limited taxon sampling in larger surveys of lower Diptera (Wood 1991, Sinclair *et al* 2007, Sinclair *et al* 2014). Comprehensive species revisions or reviews have also been lacking, focusing on regional faunas and often without a comprehensive approach. The European fauna was most thoroughly surveyed by Peus (1958), and Krzeminski & Zwick (1993). The Japanese fauna was covered in detail by Nakamura & Saigusa (2009). The Afrotropics, Nearctic and mainland Asia have never had a comprehensive review or revision of the fauna, and do not have comprehensive keys.

The combination of sparse descriptions, few illustrations, and a poor understanding of the morphology of the group made identification of species outside of Europe and Japan difficult or impossible. A study was designed and executed with the purpose of understanding the diversity of Ptychopteridae on a global level and assessing the phylogenetic structure of the extant genera, especially the speciose *Ptychoptera*.

Dissertation Organization

The results of this study are presented here as six separate scientific journal articles. Chapter 2 is a proposal to stabilize the taxonomic status of the species *Ptychoptera contaminata*. *Ptychoptera contaminata* was described by Linnaeus in 1758 as a species of *Tipula*, and was placed by Meigen in his new genus *Ptychoptera* in 1803. Latreille (1810) fixed *P. contaminata* as the type species of the genus. Examination of the *P. contaminata* holotype has demonstrated that this specimen is a species of tipulid. It is proposed according to Article 75.6 of the International Code of Zoological Nomenclature that the holotype of *P. contaminata* be set aside and a neotype be designated to preserve common usage of the name and ensure higher level nomenclatural stability.

Chapter 3 is an invited submission to the Manual of Afrotropical Diptera, an international collaboration producing a two volume reference covering the biodiversity of all groups of Diptera in the region to the genus rank. This chapter consists of a diagnosis of the group, along with discussion of its biology, ecology, and diversity in the region.

Chapter 4 is a morphological examination of the structure of male genitalia throughout Ptychopteridae. Features within the family are homologized, and a consistent terminology is proposed for these structures. Colorized illustrations were created to facilitate recognition of these homologies. Species were placed into species groups, and a limited morphological phylogeny was recovered to polarize character states. The ground plan and potential evolutionary pathways of some characters are hypothesized.

Chapter 5 is an illustrated key to all the North American species of Ptychopteridae. Twenty five species are keyed, and four new species are described (three by the author). A consistent problematic series of misidentifications is also corrected, and the species *Ptychoptera lenis coloradensis* is elevated to full specific rank.

Chapter 6 is a revision of the subfamily Bittacomorphinae. Ten species are described in detail, and a key and illustrations are provided. Inferences about the life history and ecology of the Nearctic taxa are drawn. A morphological phylogeny is presented, examining the monophyly of Ptychopteridae, the subfamilies Bittacomorphinae and Ptychopterinae, and the relationships between species of Bittacomorphinae.

Chapter 7 is a revision of the diverse subfamily Ptychopterinae. Sixty one species are described, illustrated, and keyed. All species with non-fragmentary male genitalia available were included in a morphological phylogeny to assess the evolutionary relationship within the genus *Ptychoptera*. A molecular study of the Nearctic taxa was also performed, using both a mitochondrial and nuclear gene.

The results of these phylogenies were correlated to produce a new subgeneric classification of the genus.

Division of work among the authors of each chapter is as follows. Chapter 2, Fasbender: observational research, illustrations, writing, editing; Courtney: supervision, editing. Chapter 3, Fasbender: all aspects. Chapter 4, Fasbender: observational research, development of morphological dataset, phylogenetic analyses, illustrations, writing, editing; Courtney: supervision, editing. Chapter 5, Fasbender: observational research, field collections, development of the key, illustrations, descriptions of *Ptychoptera abbreviata*, *Ptychoptera espica* and *Ptychoptera lacrimiformis*; Copley: observational research, development of key, description of *Ptychoptera bilobata*; Cannings: observational research, development of key, description of *Ptychoptera bilobata*; Courtney: field collections, supervision of research, description of *Ptychoptera lacrimiformis*, editing. Chapter 6, Fasbender: observational research, field collections, development of morphological dataset, phylogenetic analyses, development of the key, illustrations, writing, editing; Courtney: field collections, supervision of research, editing. Chapter 7, Fasbender: observational research, field collections, development of morphological dataset, morphological and molecular phylogenetic analyses, development of the key, illustrations, writing, editing; Moulton: gene selection, DNA extraction and gene sequencing, sequence alignment; Courtney: field collections, supervision of research, editing. This project was supported in part by National Science Foundation grants (DEB-0933218 and EF-1115112) to G.W. Courtney and the National Institute of Food and Agriculture, Project No. 6693.

This dissertation should not be considered a published work for the purposes of Zoological Nomenclature per the International Code of Zoological Nomenclature Article 8.2 (ICZN 1999).

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**CHAPTER TWO: *TIPULA CONTAMINATA* LINNAEUS, 1758 (INSECTA, DIPTERA; CURRENTLY
PTYCHOPTERA CONTAMINATA): PROPOSED CONSERVATION OF PREVAILING USAGE THROUGH
DESIGNATION OF A NEOTYPE**

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Abstract. The purpose of this application under Article 75.6 of the Code is to conserve the universal usage of *Tipula contaminata* Linnaeus, 1758 by suppressing the holotype and designating a neotype. *T. contaminata* is the type species of the genus *Ptychoptera* Meigen, 1803, itself the type genus of the family Ptychopteridae Osten Sacken, 1862. This species is found over much of Europe, and all authors subsequent to Meigen (1803) have utilized his concept of the species. However, the holotype is a member of Tipulidae. It is proposed that a neotype be designated for *Tipula contaminata* to preserve two hundred years of common usage and ensure nomenclatural stability at the genus and family rank.

Keywords. Nomenclature; taxonomy; Insecta; Diptera; Ptychopteridae; *Ptychoptera*; *Tipula*; *Ptychoptera contaminata*; Phantom Crane Fly; Palaearctic; Europe.

1. Linnaeus described the species *Tipula contaminata* in the tenth edition of his *Systema Naturae* (Linnaeus, 1758, p. 586). The holotype is a member of the family TIPULIDAE Latreille, 1802. The specimen is an adult male mounted by a pin through the dorsal surface of the thorax. The complete head and abdomen remain complete and attached to the thorax, as does one wing. All legs are detached, with

only one leg glued to the determination label, on which is written “*T. contaminata*” in cursive script. No other labels are present. The material is housed at the Linnean Society of London, and the authors examined photographic images of the specimen.

2. Fabricius provided a diagnosis of *Tipula contaminata* in his *Systema Entomologiae* (1775, p. 749-750), *Species Insectorum* (1781, p.402), *Mantissa Insectorum* (1787, p. 322) correctly referencing Linnaeus as the originator of the name. The species is also diagnosed in *Mantissa Insectorum* (1787, p. 322), but no citation to Linnaeus is provided.

3. Meigen (1800) proposed several dozen new genera of Diptera in his *Nouvelle Classification des Mouches à deux Ailes*, with the description of the genus *Liriope* Meigen, 1800 closely corresponding to his later (Meigen, 1803) description of the genus *Ptychoptera*. The 1800 publication was suppressed in 1960 by the Commission (ICZN, 1963).

4. In *Versuch einer neuen Gattungs-Eintheilung der europäischen zweiflügligen Insekten* (Meigen, 1803, p.262-283), Meigen listed “*Tipula contaminata* Fabr.” and *Tipula albimana* Fabricius, 1787 as members of the genus *Ptychoptera* Meigen, 1803. *Tipula contaminata* Fabr. clearly refers to *Tipula contaminata* Linnaeus, 1758 as presented in Fabricius’ works. Meigen’s generic description (diagnostic based on the elongate first antennal flagellomere/third antennal segment) does not fit the holotype of *Tipula contaminata* Linnaeus, 1758. Specifically, “PTYCHOPTERA. Die Fühlhörner vorgestreckt, sechszehn gliederig: das erste Glied walzenförmig, kurz; das zweite becherförmig; das dritte walzenförmig, lang; die folgenden länglicht, dünnhaarig. Die Flügel halb offen.” (PTYCHOPTERA. Elongate antennae, sixteen segments: the first segment cylindrical; short, second cup-shaped, while the third cylindrical, long; the following oblong, fine setae. The wings half open.) In the Linnaean type specimen the first flagellomere/third antennal segment is round, and not significantly longer than the succeeding flagellomeres.

5. Pierre A. Latreille subsequently designated "*Ptychoptera contaminata*, Fab." as the type species of *Ptychoptera* in *Considerations generales sur l'ordre naturel des animaux* as a first reviser action (Latreille, 1810, p.442). According to Article 67.7 the incorrect citation of "*Ptychoptera contaminata* Fabr." is considered to refer to *Tipula contaminata* Linnaeus, 1758, and is a valid designation. Based on Article 69.1 and the Commission's Opinions 11 and 136 Latreille's (1910) citation is to be accepted as a designation of *Tipula contaminata* Linnaeus, 1758 as the type of the genus.

6. Carl R. Osten Sacken described the subfamily Ptychopterina (later emended to PTYCHOPTERINAE) within TIPULIDAE in 1862 in his collaboration with Hermann Loew in *Monographs of Diptera of North America Part I* (Osten Sacken, 1862, p. 12). The genera *Bittacomorpha* Westwood, 1835, *Macrochile* Loew, 1850, *Protoplasa* Osten Sacken, 1860 and *Ptychoptera*, were included; the type genus can be inferred as *Ptychoptera*.

7. Charles A. Hart elevated PTYCHOPTERIDAE to full family rank in *On the Entomology of the Illinois River and Adjacent Waters* (Hart, 1895, 189-190).

8. A combination of the Linnaean and Fabrician species descriptions with Meigen's genus description has resulted in all subsequent authors determining a common, currently unnamed species of *Ptychoptera* (*Ptychoptera* sp.) found across Europe as *Ptychoptera contaminata*. Publications include: Handlirsch, 1909 p. 269, 271-272; Tonnoir, 1919 p. 115, 119; Grünberg, 1920 p. 76-77; Reidel, 1921 p. 147; Séguy, 1925 p. 8-9, 11-14; Audcent, 1934 p. 106-109, 111, 116-119; Peus, 1958 p. 11, 15-21, 26, 28, 30, 32, 34; Brindle, 1962 p. 212-216; Tjeder, 1968 p. 73-75; Zitek-Zwyrtek, 1971 p. 416, 418, 420-423; Zwyrtek, 1971 p. 36-38; Hansen, 1981 p. 59-63; Theischinger, 1978 p. 26; Draskovits, 1983 p. 80, 82-83, 85; Krzeminski, 1986 p. 105, 107-108, 117-119; Zwick, 1988 p. 123, 128-129; Podenas, 1991 p. 155; Krzeminski & Zwick, 1993 p. 80, 85-86; Stubbs, 1993 p. 7, 9, 12, 25, 28; Rozkošný, 1997 p. 294-295; Pârvu, 2004 p. 190; Ujvárosi et al, 2011 p. 40, 42-43.

9. The authors cannot find a single instance of the usage of *Ptychoptera contaminata* definitively referable to the species represented by the Linnaean type material since the works of Fabricius, and the descriptions provided by Linnaeus or Fabricius are not sufficiently detailed to distinguish between the Linnaean type specimen of *Tipula contaminata* and the current usage of the name for *Ptychoptera sp.*

10. The consequences of maintaining the current species type designation for *Tipula contaminata* would be placing *Ptychoptera* as a synonym of an undetermined tipulid genus and PTYCHOPTERIDAE as a subjective junior synonym of TIPULIDAE. The current concept of the taxa *Ptychoptera* and Ptychopteridae would require new names, and *Ptychoptera sp.* would be assigned a different name than which it has historically been referred.

11. The authors propose that the Commission, using its powers as defined in Article 75.6, set aside the current holotype of *Ptychoptera contaminata* in the Linnean Collections of the Linnean Society of London, and designate a specimen of the currently unnamed species from the collection of the Natural History Museum of Denmark as the neotype. The neotype was chosen because it is representative of the current usage of the name *Ptychoptera contaminata*, for the state of preservation of the specimen and the locality in northern Europe where Linnaeus' specimen was likely collected. This neotype designation would preserve over two centuries of common usage of *Ptychoptera contaminata*, and preserve the established usage of the genus- and family-rank names *Ptychoptera* Meigen, 1803 and Ptychopteridae Osten Sacken, 1862.

12. An alternative proposal would be to avoid invoking Article 75.6, but instead treat Meigen's 1803 inclusion and Latreille's subsequent 1810 fixation of *Tipula contaminata* as the type species of *Ptychoptera* as a misidentification according to Article 70.3. Article 70.1, states that authors should be assumed to have made correct identifications of their type species, but as presented above there is substantial evidence that *Tipula contaminata* Linnaeus, 1758 was incorrectly referred to the genus

Ptychoptera by Meigen in his 1803 publication. Following Article 70.3.2 it is possible to designate the unnamed *Ptychoptera* species as type of the genus after giving it a name. However, the authors feel that this course of action is undesirable as it would require a new name for the unnamed *Ptychoptera* species and obliterate two hundred years of usage of *Ptychoptera contaminata*.

13. The authors do not anticipate any opposition among ptychopterid or tipulid taxonomists, as this measure is essentially conservative and avoids any nomenclatural changes in either taxon.

xv. The International Commission on Zoological Nomenclature is accordingly asked:

(1) to use its plenary power (under Article 75.6) to set aside all type fixations for the nominal species *contaminata* Linnaeus, 1758, as published in the binomen *Tipula contaminata*, and to designate the specimen from the Natural History Museum of Denmark (ZMUC) with the locality label data “Dania, Lolland, Saxkøbing Sómosø 20-6-1966 Bo Vest Pedersen,” and a second label reading “NEOTYPE: *Tipula contaminata* Linnaeus 1758, det. A Fasbender” as the neotype;

(2) to place on the Official List of Specific Names in Zoology the name *contaminata* Linnaeus, 1758, as published in the binomen *Tipula contaminata* and as defined by the neotype designated in (1) above.

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Figures

Figure 1: Habitus of the proposed neotype of *Tipula contaminata* Linnaeus, 1758. Scale bar 1mm.

Figure 2: Locality label of the proposed neotype of *Tipula contaminata*. Scale bar 1mm.

Figure 3: Male genitalia of the proposed neotype of *Tipula contaminata*: a. Overall lateral view; b. Epandrium lateral view; c. Epandrium dorsal view; d. Aedeagus anterior view; e. Aedeagus lateral view; f. Hypandrium posterior view; h. Gonopod dorsal view; i. Gonopod dorsal view; j. Paramere posterior view; k. Paramere dorsal view. Scale bars a.-i. 0.5mm, j&k 0.25mm.



Figure 1.



Figure 2.

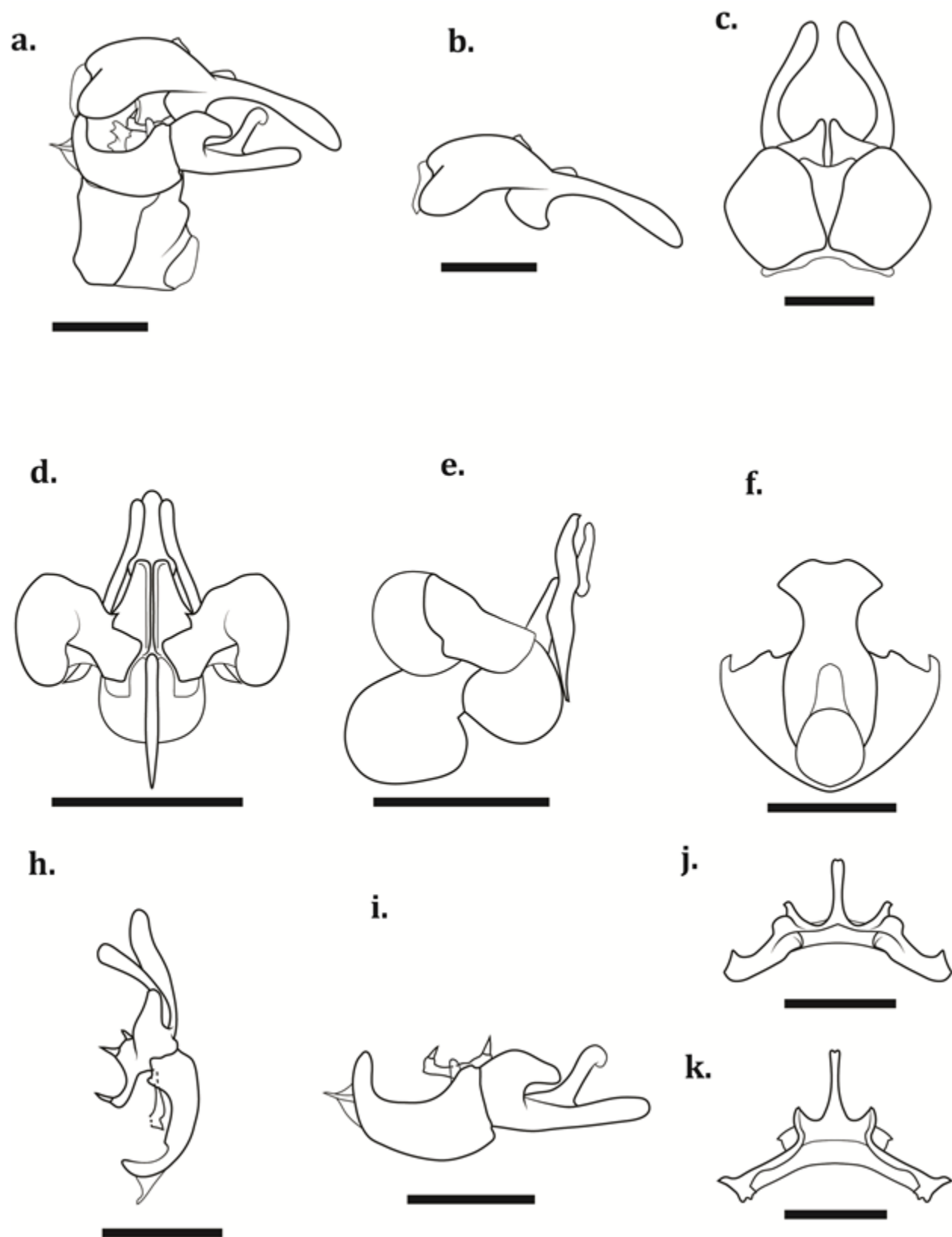


Figure 3.

CHAPTER THREE: PTYCHOPTERIDAE (PHANTOM CRANE FLIES OR FOLD-WINGED CRANE FLIES)

Accepted into the *Manual of Afrotropical Diptera*

Andrew Fasbender

Diagnosis

Medium to large (body length: 7–35 mm) crane fly-like nematoceran flies (Fig. 1).

Head roughly triangular; ocelli absent; compound eyes hemispherical, forming the lateral margins of the head capsule; antennae with 13–14 flagellomeres (in Ptychopterinae), or 18–21 flagellomeres (in Bittacomorphinae); labrum triangular; mouth-parts simple, with prominent labella; maxillary palpus 5-segmented, terminal segment often elongate.

Thorax box-like, higher than broad, with prominent prescutal suture ending in a triangular posterior point in Ptychopterinae, indistinct in Bittacomorphinae; pleural sclerites with indistinct, or absent, anepisternal suture; meron fused with epimeron, metapleural suture absent in Ptychopterinae. Wing (Fig. 4) with 4 radial branches reaching wing margin, 3 branches of medial vein reaching wing margin in Ptychopterinae (2 in Bittacomorphinae), and 2 branches of cubital reaching margin; wings often with infusate banding in Ptychopterinae; halter with distinctive polyp-like lobe anteriorly at base (termed prehalter). Legs elongate, longer than overall length of rest of body.

Abdomen elongate; abdominal segment 2 extended; sternite 3 with accessory copulatory organ in some male *Ptychoptera* Meigen, posterior abdominal segments slightly telescoping in Ptychopterinae; female terminalia (Fig. 9) with tergites 8–9 concealed by tergite 7 in Ptychopterinae, exposed in Bittacomorphinae; cerci heavily sclerotised and modified into ovipositor in Ptychopterinae, shorter and more membranous in Bittacomorphinae; male terminalia unrotated, with bilobate epandrium forming distinct epandrial claspers (Fig. 6), not fused with hypandrium (Fig. 5); parameres separate and stylate, or fused to form bridge, in Ptychopterinae base of paramere shifted posterior on dorsal surface of

gonocoxite; gonopods (Fig. 5) simple, or complex, free of hypandrium; hypandrium (Fig. 5) separated into distinctive basal and terminal divisions, often with articulated spathate lobes on basal division; aedeagus (Figs 7, 8) rotated dorsally in Ptychopterinae, with large sperm sac, well-defined ejaculatory apodeme, prominent lateral ejaculatory processes and variable subapical sclerite ventral to phallotrema.

Adult Ptychopteridae superficially resemble several other families of lower Diptera (*i.e.*, Tipuloidea, Tanyderidae (see Chapter 15), Sciarioidea, and non-Afrotropical Trichoceridae), based on the compact thorax and elongate legs and abdomen. Adults can be readily distinguished from all other Diptera by the prehalter. Wing venation is also distinctive, lacking the anal vein of Tipuloidea and Trichoceridae, with less than four branches of the medial vein reaching the wing margin (unlike Tanyderidae). Sciarioidea have three, or fewer, branches of the radial vein reaching the wing margin, compared to the four of Ptychopteridae.

Larva vermiform in shape (Fig. 2), metapneustic, with distinctive retractile respiratory siphon; eucephalous, cranium with well-defined subgenal sclerite; labrum with prominent brushes; mandible broad, divided into molar and incisor lobes, with mandibular comb; maxilla with lateral and medial setal brushes; maxillary palpus peg-like; prementum with circular apex, with ring of dentitions; postmentum serrated and bridge-like in Ptychopterinae, simple and fused to subgenal sclerite in Bittacomorphinae; thoracic segments short, slightly nodiform; abdominal segments 1–6 cylindrical, each with posterior annular creeping welt in Ptychopterinae; integument smooth and glabrous with sparse chaetotaxy in Ptychopterinae, with prominent tubercles present in Bittacomorphinae; ventral pair of prolegs weakly-developed on abdominal segments 1–3, with single sickle-shaped claw on each; abdominal segments posterior to segment 6 developed into conical anal division, housing respiratory siphon and 2 retractile anal papillae.

Pupa fusiform (Fig. 3), propneustic, thoracic respiratory organs unevenly developed: right organ hypertrophied in Ptychopterinae and *Bittacomorpha* Westwood, left organ hypertrophied in *Bittacomorphella* Alexander; Ptychopterinae with tarsi parallel, Bittacomorphinae with fore tarsomere lying over mid tarsomere; abdominal segments with numerous rows of tubercles, ringed with apical dentitions and elongate trichoid sensilla; posterior margins of segments with creeping welts in Ptychopterinae; male terminalia primordium readily apparent, morphology variable between species-groups.

Biology and immature stages

Larval Ptychopteridae reside in saturated organic sediments, such as groundwater seepages and the depositional areas of small to medium streams. The larvae use brushes of macrotrichia on the labrum and maxillae to sift fine organic particles from the sediment (Mattingly 1987; Wolf *et al.* 1997). The characteristic respiratory siphon is extended into oxygenated water above the substrate (Alexander 1920; Hodkinson 1973; Peus 1958; Wolf & Zwick 2001). Larvae experience significant mortality (Wolf & Zwick 2001), with predation by larval Tabanidae and Limnephilidae (Trichoptera) observed in the Nearctic Region (G.W. Courtney, pers. comm. 2013). Pupation occurs in the larval habitat, with mature pupae travelling to the surface of the substrate for eclosion. Adults remain near the natal habitat, typically resting on the upper surface of emergent vegetation and fly in a straight, direct manner between different perches. Males copulate with recently emerged females, which oviposit in the same habitat. Adults retain functional mouth-parts (including a well-developed cibarium) and have been recorded feeding on honeydew (Scherbakov & Lukashevich 2005). Wolf & Zwick (2001) found the Palearctic species *Ptychoptera* (*Parapteroptera*) *paludosa* Meigen, 1804, to be univoltine, with an emergence of eight weeks. The Nearctic taxa *P. (Ptychoptera) quadrifasciata* Say, 1824 and *Bittacomorpha clavipes* F., 1781, however, have an extended emergence of over four months and

probably have multiple generations during the summer months (Bowles 1998; Rogers 1942). In more thoroughly studied regions, multiple *Ptychoptera* spp. have been found in sympatric association, often facilitated by partitioning microhabitats, such as standing *versus* flowing water (Fasbender, pers. obs.; Harris & Carlson 1978; Stubbs 1993: 24–30).

Ecological information for Afrotropical taxa is severely lacking. Stuckenberg (1983) provides a brief synopsis of habitats of the Afrotropical fauna. He notes that most *Ptychoptera* spp. are associated with montane forests, including gallery forest, and tend to reside in shaded pools. An exception is *P. (Pt.) kosiensis* Stuckenberg, 1983, which is found in coastal “swamp-forest” in eastern South Africa. Previous workers have hypothesised that Ptychopteridae is a group associated with temperate montane environments (Alexander 1927; Hancock *et al.* 2006; Stuckenberg 1983). The extensive species diversity of the Oriental Region and the discovery of both *Ptychoptera* and *Bittacomorpha* in Central America as far south as Costa Rica (Fasbender, pers. obs.), seem to contradict this view. Rather, the absence of Ptychopteridae in South America and its comparatively poor diversity in the Afrotropics is more likely due to historical biogeographic processes than current climatic conditions.

Economic significance

No species of economic significance are currently known.

Classification

The placement of Ptychopteridae within the wider context of Diptera has been problematic. The family is very ancient, with fossils that can be definitively assigned to the group dating to at least the Early Jurassic (Lukashevich 2008) and potentially the late Triassic (Barth *et al.* 2011). Fossil evidence of the extant subfamilies is known only from Eurasia until past the separation of Laurasia and Gondwana (Lukashevich 2008). No Afrotropical fossils of the family have been described.

Most cladistic morphological hypotheses have placed Ptychopteridae as sister-group to the Tanyderidae, forming the infraorder Ptychopteromorpha (Hennig 1973: 24; Oosterbroek & Courtney 1995; Wood & Borkent 1989: 1358). The characters associating ptychopterids with tanyderids are either plesiomorphic or of problematic assessment; the sole “synapomorphy” of a foldable fifth tarsomere is not consistently distributed in Ptychopteridae. Furthermore, molecular analyses have not supported this morphological hypothesis, placing Tanyderidae closer to Psychodidae (Curler & Moulton 2012; Wiegmann *et al.* 2011). Culicomorpha has been suggested as sister-group to Ptychopteromorpha (Oosterbroek & Courtney 1995), but the evidence is equivocal.

Ptychopteridae comprises two extant subfamilies: Bittacomorphinae and Ptychopterinae. Bittacomorphinae is found in the Nearctic and Oriental Regions. Ptychopterinae has a Holarctic distribution, extending into the Afrotropical Region (including Madagascar). Currently, Ptychopterinae comprises the single genus *Ptychoptera*, with *ca.* 70 species globally. *Ptychoptera* (*Parapteroptera* Tonnoir) is represented by *P. (Pa.) surcoufi* Séguy, 1925, in Algeria, but does not enter the Afrotropics. *Ptychoptera* (*Ptychoptera*) is a heterogenous collection of species (Zwick & Starý 2003) and will be subdivided as part of an ongoing revision (Fasbender & Courtney, in prep). One author suggested that *P. (Pt.) capensis* Alexander, 1920, was related to the European *P. (Pt.) albimana* F., 1787 (Freeman 1959). The characters cited to support this hypothesis are, however, rather superficial and probably represent symplesiomorphies. Afrotropical *Ptychoptera* do not exhibit a strong association with the *Ptychoptera* spp. of North Africa and the western Palaearctic, but more closely resemble taxa from the Oriental Region, especially the Malay Archipelago. Further examination is required to determine the phylogenetic affinities and establish a biogeographic context for the Afrotropical species.

Identification

Unfortunately, there is currently no functional key for all Afrotropical species of *Ptychoptera*. The two best works are Freeman (1959) and Alexander (1928), of which only Freeman's contains illustrations. The three Malagasy species are keyed by Alexander (1957), including illustrations. Hutson (1980) catalogues the Afrotropical taxa, although no identification keys or diagnoses are provided. There has been very little taxonomic work on larvae of the family, with the only works useful for distinguishing species limited to the western Palaearctic fauna (Hansen 1981; Stubbs 1993: 18). There are no recorded larval collections of the group from the Afrotropical Region. The state of pupal taxonomy is even more rudimentary than that of the larvae and it is only possible to distinguish between genera (Alexander 1920, 1927, 1981: 327–328).

Synopsis of the fauna

***Ptychoptera* Meigen.** A genus of *ca.* 70 described species, occurring in the Afrotropical, Nearctic, northern Neotropical, Oriental and Palaearctic Regions. Eight recognised species occur in the Afrotropical Region; five widely distributed continental species and three confined to Madagascar. Five additional species were described in the first half of the 20th century, but were synonymised by Freeman (1959). This work is in need of review however, as at least one name, *P. (Pt.) schoutedeni* Alexander, 1956, was synonymised under the wrong species. Species of the genus are similar in habitus to large fungus gnats, with most Afrotropical species displaying bright banding on the body and patterned wings. Thorough sampling for this genus has occurred in only a few areas, primarily the Albertine Rift and coastal South Africa. West Africa is particularly poorly sampled, with known species recorded from only a single specimen (*P. (Pt.) camerounensis* Alexander, 1921), or a limited number of localities (*P. (Pt.) africana* Alexander, 1920). The three species known from Madagascar are also recorded only from the type localities and are of questionable phylogenetic association with the mainland fauna. Recent

investigations of the more thoroughly studied faunas of the Nearctic and western Palaearctic have revealed multiple new species (Fasbender pers. obs.; Krzeminski & Zwick 1993; Ujvárosi *et al.* 2011; Zwick & Starý 2003) and it appears likely that there are additional species awaiting discovery in the Afrotropical Region. Indeed, there is evidence that some of the disjunct populations of *P. (Pt.) africana* and *P. (Pt.) uelensis* Alexander, 1928, represent distinct species, contrary to the findings of Freeman (1959). Further collecting is required, however, before drawing definitive conclusions, as many of the species synonymised with *P. (Pt.) uelensis* were described from female holotypes.

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Figure Captions

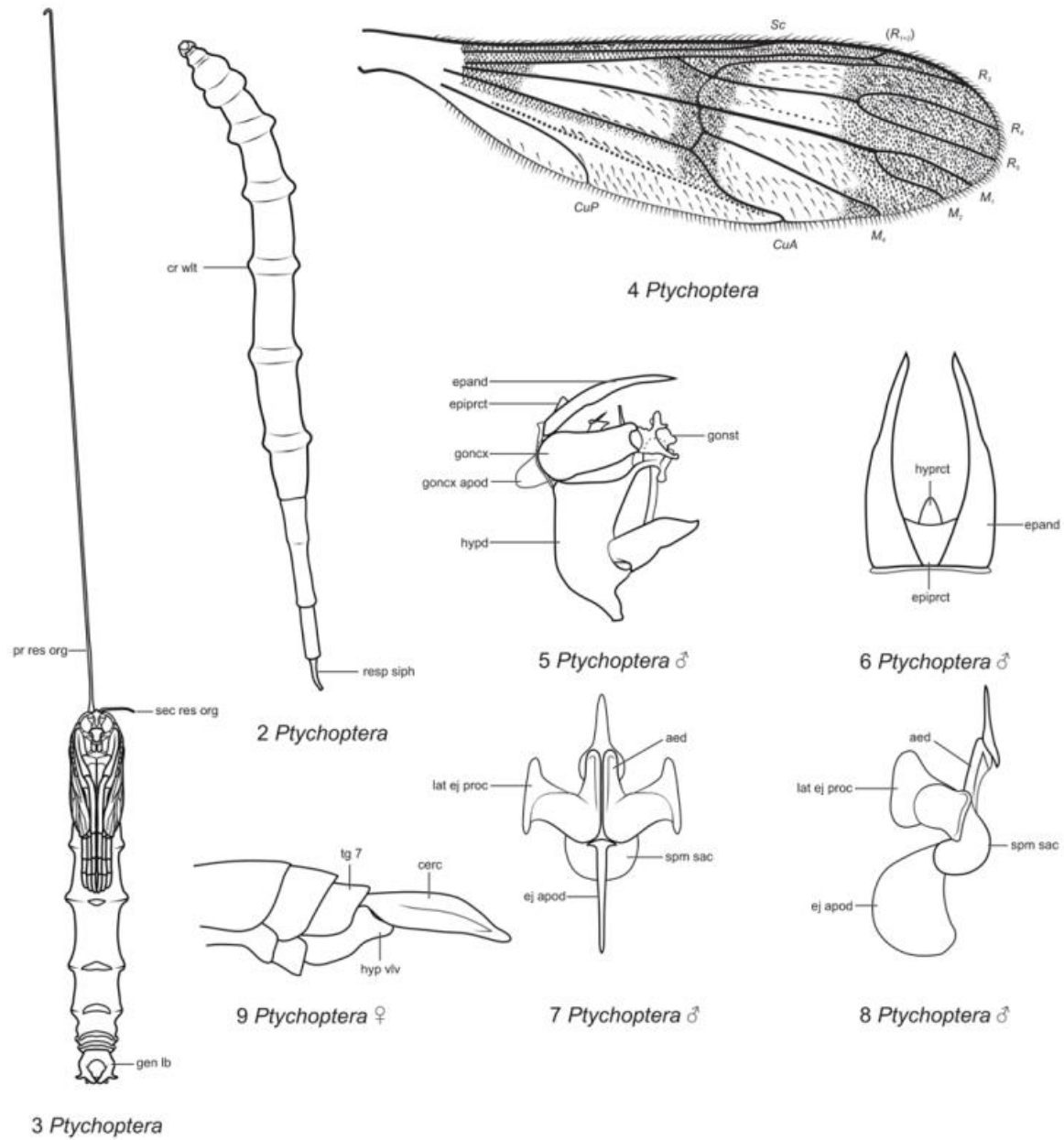
Fig. 27.1. Male of *Ptychoptera quadrifasciata* Say (non-Afrotropical) (photograph © S.A. Marshall).

Figs 27.2–9. Larva, pupa, wing and terminalia of Ptychopteridae: (2) larva of *Ptychoptera sculleni* (Alexander), dorsal view (non-Afrotropical); (3) same, male pupa, ventral view; (4) wing of *P. africana* (Alexander), dorsal view; (5) same, male terminalia, lateral view; (6) same, epandrium, dorsal view; (7) same, aedeagus, anterior view; (8) same, lateral view; (9) female terminalia of *P. africana*, lateral view. Fig. 3 (courtesy R.I. Madriz).

Abbreviations: aed – aedeagus; cerc – cercus; cr wlt – creeping welt; *CuA* – anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; ej apod – ejaculatory apodeme; epand – epandrium; epiprct – epiproct; gen lb – genital lobe; goncx – gonocoxite; goncx apod – gonocoxal apodeme; gonst – gonostylus; hyp vlv – hypogynial valve; hypd – hypandrium; hypprct – hypoproct; lat ej proc – lateral ejaculatory process; M_1 – first branch of media; M_2 – second branch of media; M_4 – third branch of media; pr res org – primary respiratory organ; R_{1+2} – anterior branch of radius; R_3 – lower branch of second branch of radius; R_4 – upper branch of third branch of radius; R_5 – lower branch of third branch of radius; resp siph – respiratory siphon; Sc – subcosta; sec res org – secondary respiratory organ; spm sac – sperm sac; tg – tergite.



Figure 27.1.



Figures 27.2-9.

CHAPTER FOUR: HOMOLOGIES OF THE MALE GENITALIA OF PTYCHOPTERIDAE (INSECTA: DIPTERA)

Submitted to *The Canadian Entomologist*

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Abstract

The male genitalia of Ptychopteridae are complex and highly apomorphic structures which have never been comprehensively surveyed across the group. Ingroup homologies are identified and described, and colorized illustrations of all major species groups of Ptychopterinae and Bittacomorphinae are provided. Species groups of Ptychopterinae are cataloged and diagnosed, and a phylogeny of these species groups is used to provide polarity to character evolution in the subfamily. A standardized terminology for the apomorphic structures of the family is proposed, and interpretations in previous studies are clarified. *Ptychoptera ressl*i Theischinger is placed in the subgenus *Paraptychoptera* Tonnoir based on characters of the male genitalia.

Introduction

The Ptychopteridae are a fascinating group within lower Diptera which have never had comprehensive morphological study. Although all life stages exhibit many interesting characters, the structure of the male genitalia is one of the most intriguing aspects of the group's morphology due to the intricate and highly apomorphic structure. Combined with the uncertain phylogenetic placement of

the group examination of these character systems may provide broader insights into the wider development of Diptera.

Most work on the structure of male genitalia in Ptychopteridae has been undertaken in the process of describing new species. Unfortunately, much of this work is highly fragmentary, typically consisting of only what characters were considered diagnostic for the species in question with limited or no attempts to compare the homologies between species. The most formal and intensive examination of the genitalia of Ptychopteridae was undertaken by Just (1973), a work which discussed the sclerotized structure and musculature of *Ptychoptera (Parapteroptera) lacustris* Meigen in the context of homologies shared with the species *Sergentomyia garnhami* Heisch, Guiggsberg & Teesdale and *Satchelliella palustris* Meigen of Psychodidae. Though the work is extremely thorough, over the intervening years there have been significant advancements in the understanding of the interfamilial homologies of Dipteran genitalia leading to the obsolescence of many of the inferences drawn. Furthermore, other ptychopterid taxa were noted only briefly, primarily as a reference taxon for the psychodid species, resulting in few intrafamilial inferences being drawn.

Krzeminski (1986), Krzeminski & Zwick (1993) and Nakamura & Saigusa (2009) illustrated the male genitalia of many of the Palaearctic Ptychopteridae, but descriptions of the genital structures utilize somewhat outdated terminology, and provide few inferences about homology between taxa. Zwick & Starý (2003) illustrated and labelled the male genitalia of *Ptychoptera (Parapteroptera) delmastroi*, utilizing largely modern terminology, but did not examine other ptychopterid taxa.

The most important publication in establishing the basic genitalia homologies of Ptychopteridae is Wood (1991). The colorized illustrations of *Bittacomorpha clavipes* Fabricius present five basic homologies (epandrium, gonopod, paramere, hypandrium, aedeagus) to the overall structure of the

genitalia. A final significant work on the male anatomy of Ptychopteridae is Sinclair *et al* (2007), which examined the soft tissue male genital tract of several lineages of lower Diptera. The key finding of this work was that ptychopterids have a multi-chambered accessory gland complex, also found in Bibionomorpha and Culicomorpha, and indicative of the production of spermatophores.

Wood (1991), Sinclair *et al* (1994), and Cumming *et al* (1995) provided a basis for understanding the structure and homologies of the male genitalia across Diptera, which have been expanded by Sinclair (2000), Sinclair *et al* (2007), and Sinclair *et al* (2013). While these works have extensively examined interfamilial characters, there remain gaps in our understanding of the intrafamilial morphology of many taxa. Further, broader sampling within taxonomic groups has uncovered unforeseen morphological diversity which challenges previous hypotheses about the distribution and polarity of certain characters. Although Wood (1991) examined and illustrated *Bittacomorpha clavipes* Fabricius, there have remained a number of aspects of the structure and homologies of Ptychopteridae that have remained ambiguous or unresolved.

In the published work on Ptychopteridae there has been essentially no consideration of ingroup homologies of the male genitalia, or the polarity of these characters. Further, much of the existing literature is limited to the fauna of localized areas, or at most a single biogeographic region (Krzeminski & Zwick 1993). The current study has examined ptychopterid taxa from all regions with an extant fauna, with special emphasis on the diverse Ptychopterinae, and correlated the morphological diversity of these taxa into species groups. Using a representative from each species group, phylogenies were constructed based on characters scored from the male genitalia, allowing character polarity and likely ancestral states of Ptychopterinae to be examined. Examination of these phylogenies and associated

structural data has provided broader insight into the development of alternative clasping functions, spermatophore production and transfer, and other evolutionary paths with application outside of the family.

Taxonomic Notes

A primary consideration in interpreting the characters of Ptychopteridae is the monophyly of the two extant subfamilies. Bittacomorphinae consistently occurs as a strongly supported monophyletic clade in all morphological phylogenetic analyses executed to date (Fasbender & Courtney unpub. data). Ptychopterinae is more contentious based on morphological evidence, typically being recovered as a monophyletic group in Maximum parsimony analyses with fairly robust support, often collapsing to a polytomy in analyses using Bayesian Inference algorithms. There are several morphological characters of varying subjective strength that are apomorphies of Ptychopterinae: 1. Prominent stout trichoid sensillae arranged in verticils on antennal flagellomeres, 2. Posterior apex of prescutum triangular, 3. Aedeagus and terminal division of hypandrium rotated dorsally at least 45° dorsally, 4. Epandrial collar present 5. Tubercles present at base of lateral ejaculatory process, 6. Aedeagus shortened, less than 2x length vs. width, 7. Gonostylus with basal lobe. Additionally, molecular analyses run by Chen W. Young (pers. comm.) and John K. Moulton (pers. comm.) on samples of ptychopterid species have delivered topologies that support both subfamilies as monophyletic. Based on these arguments the remainder of this document will treat Ptychopterinae as a monophyletic clade.

Several informal groupings within Ptychopterinae are discussed: these are based on morphological similarity and should not be interpreted as true clades. A future analysis will deal with the phylogenetic relationships within Ptychopterinae at the species level. A list details the species composition of each these groups, as well as the distinguishing characters of the male genitalia that unite them. In particular, the Southeast Asian species of Ptychopterinae are highly problematic,

probably representing an early radiation of the clade within the lineage containing species with spathate lobes and an articulated basal division of the hypandrium. Many of the character states shown in these Southeast Asian species are likely plesiomorphic or homoplastic based on the phylogeny constructed here. The difficulty in assessing this material is further compounded by the fact the many of the species were described from limited series, often only a single specimen. The genitalia of many of these specimens were mounted on slides by previous workers, typically to visualize diagnostic features of the gonopods and epandrium. In the mounting process the aedeagus and hypandrium were often torn or otherwise damaged, making character assessment difficult or impossible.

The Afrotropical species have similar issues to the Southeast Asian taxa, with very few specimens collected and most slide preparations being problematic. Much like the Southeast Asian fauna, the Afrotropical Ptychopterinae exhibit spathate lobes on the hypandrium and an articulated terminal division. However, much like the Southeast Asian fauna there is currently no convincing evidence to suggest that the Afrotropical fauna represents a monophyletic group.

A final classification problem is the paraphyly of *Bittacomorphella*. Unpublished phylogenetic analyses by the authors have demonstrated that *Bittacomorphella* is essentially an artificial grouping of bittacomorphine species that do not share the apomorphies of *Bittacomorpha*. The authors will thus refrain from using *Bittacomorphella*, and instead refer to species except for use in illustrating probable plesiomorphies in Bittacomorphinae.

A future species level revision of Ptychopterinae is in preparation by the authors, which is intended to elucidate some of these issues. For the purposes of establishing the homologies and character polarities in Ptychopterinae the authors feel that the current taxonomic coverage is sufficient.

The inferences that can be made about modern ptychopterid genital homologies based on the fossil record are few. Although the family has a fossil lineage that can be concretely traced back to the

early Jurassic (Lukashevich, 2008), the few reconstructions of ancestral genitalia provide only external characters and have very limited taxonomic coverage making it tenuous to draw strong conclusions. There are illustrations of fossil ptychopterid male genitalia sufficiently detailed for some inference: *Proptychopterina gracilis* Lukashevich, *Proptychopterina opinata* Lin & Lukashevich, *Leptychoptera diminika* Lukashevich & Azar, and *Crenoptychoptera defossa* Kalugina. An additional issue that arises from examining these taxa is that it is unlikely they represent stem taxa of extant ptychopterids, but rather arise from divergent branches that terminated before the present era (Lukashevich 2012). That being said, each of these taxa provide some inferences at different points of ptychopterid evolution, with *Proptychopterina* representing the middle Jurassic, *Leptychoptera* the early Cretaceous and the most recent probable outgroup to both extant subfamilies, and *Crenoptychoptera* a potential (if tenuous) sister group to Bittacomorphinae. At the end of each subsection a review of the fossil evidence is provided.

Materials and Methods

Specimens used in this study were provided by the following institutions: Institut Royal des Sciences Naturelles de Belgique (IRNSB), Royal British Columbia Museum (RBC), Carnegie Museum of Natural History (CMNH), Royal Museum of Central Africa (MRAC), Clemson University Arthropod Collection (CUAC), Colorado State University C. P. Gillette of Arthropod Diversity (CSU), Natural History Museum of Denmark (ZMUC), the Field Museum of Chicago (FMNH), Harvard Museum of Comparative Zoology (MCZ), Illinois Natural History Survey (INHS), Iowa State Insect Collection (ISIC), University of Kansas Snow Entomological Museum (KU), Natural History Museum London (NHM), Michigan State University Arthropod Research Collection (ARC), University of Michigan Museum of Zoology (UMMZ), Oregon State University (ORSU), University of Minnesota Insect Collection (UMSP), Mississippi Entomological Museum (MEM), Moravian Museum, Brno (MMB), North Carolina State University Insect

Collection (NCSU), Pacific Northwest Diptera Research Lab (PNDL), Purdue University Entomology Research Collection (PERC), Smithsonian National Museum of Natural History (USNM), Washington State University James Entomological Collection (WSU). Material collected by the authors is deposited in the Iowa State Insect Collection.

General Methods

Specimens were examined using Olympus SZX12 and SZX9 dissecting microscopes, and a Nikon E-800 compound microscope. Microscopes were fitted with apertures for a Nikon DS-Fi1 digital camera for photomicrography, and a camera lucida for drawings. Drawings were rendered by a combination of freehand work using the camera lucida, and proportional tracing using photomicrographs. Final illustrations were composed and colorized using Adobe Illustrator CS5.

Dissected specimens were cleared using a heated KOH solution. The apex of the abdomen was removed using microscissors, and dry specimens were hydrated for 18-24 hours in DI water before clearing. For each specimen a 1-Dram shell vial was half-filled with DI water, and a single KOH pellet added. The pellet was allowed to completely dissolve, and then capped and shaken to homogenize the solution. Vials were then placed on a warming plate and heated to 65°C and the genitalia added. Every five minutes each specimen was examined, and when fully cleared was rinsed twice in clean DI water for ten minutes, then brought through a series of 30%-50%-70%-95% ethanol solutions and mounted in glycerin. Select specimens were mounted from 95% ethanol to Euparal mounting media on slides.

The morphological terminology used here is that of Cumming & Wood, 2009.

Phylogenetic Methods

Characters were identified and scored using the microscopy equipment described above. Data was recorded into an Excel spreadsheet, which was then converted to a Nexus file using MacClade 4.08

(Maddison & Maddison 2005). This data matrix is presented in Supplemental Material I. Phylogenies were reconstructed using both the “New Technology” (Heuristic) Maximum Parsimony analysis in TNT (Goloboff *et al* 2008) and Bayesian Inference via MrBayes 3.1 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003). TNT was run using the “New Technology” search with the “Driven Search” option with parameters “Init. Adseqs.” set at five and “Find min. Length” set at thirty. Bootstrap values were calculated using a “Standard Search” with 100 replicates. Bremer support was calculated using TBR from existing trees. The MrBayes MCMC was run for 5,000,000 generations with two runs with four chains each, with the temperature set to 0.2, sample frequency was set at 100, swap frequency was set to one and the number of swaps set to two. The initial burn-in for the analysis was set using the “burninfrac” parameter to 0.15. After the analysis was complete the sampled trees were compiled into a consensus tree using the “sumt” function with a burn-in of 12500. Trees were visualized using MacClade and FigTree 1.3.1, and final figures were prepared using Adobe Illustrator CS5.

Results

Figures: 1-4

Phylogenetic Discussion

Due to the long divergence of Ptychopteridae (Lukashevich 2008, Lukashevich 2012), and its isolated position within the phylogeny of lower Diptera (Bertone *et al* 2008, Wiegmann *et al* 2011), several outgroups were selected for the phylogenetic analysis. *Tricyphona inconstans* Osten Sacken (Pediidae) was utilized to root the tree, based on the divergent position of Tipulomorpha in Wiegmann *et al* (2011) and the lack of tipuloid autapomorphies (Petersen *et al* 2010). *Edwardsina gigantea* Zwick (Blephariceridae) was selected as a representative of Psychodomorpha sensu Wiegmann *et al* (2011), while *Culicoides crepuscularis* Malloch (Ceratopogonidae) and *Dixa modesta* Johannsen (Dixidae) represent the two major subfamilies of Culicomorpha: Chironomoidea and Culicoidea respectively.

Finally, two species of Tanyderidae (*Araucoderus gloriosus* Alexander and *Protoplasa fitchii* Osten Sacken) were included based on prior hypotheses that Ptychopteridae and Tanyderidae shared a sister group relationship (Hennig 1973, Wood & Borkent 1989, Oosterbroek & Courtney 1995). More recent analyses utilizing molecular datasets have contradicted this hypothesis (Bertone *et al* 2008, Wiegmann *et al* 2011). Morphological characters of the male genitalia suggest Tanyderidae belong in Psychodomorpha (G.R. Curler & R.I. Madriz, pers. comm.), and reanalysis using a wider morphological character set finds that the morphological characters proposed to place the family in Ptychopteromorpha are of questionable polarity or are not consistently distributed with the two taxa (Griffiths 1990, Oosterbroek & Courtney 1995, Fasbender & Courtney unpub. data).

Maximum Parsimony analysis of the data recovered a large number (19) of equally parsimonious trees. The structure of these differs primarily in the placement of individual taxa within three broader categories: a grade of species identified by a bittacomorphine-like sperm pump, a cluster of species groups with a hypandrial eversible sac and poorly articulated terminal division which is split ventrally, and a well-supported clade with a hypandrium exhibiting spathate lobes and a highly articulated terminal division. The Bayesian analysis exhibits a similar topology, although much of the structure within Ptychopterinae collapsed, with early divergences of the subfamily especially poorly resolved. Some taxa have proved problematic in their placement, such as *Ptychoptera yasumatsui* (which lacks the hypandrial spathate lobes, yet has a terminal division similar to that seen in the spathate lobe clade), and several Southeast Asian and African species which are known from slide mounts that make assessment of certain characters problematic or impossible. Overall Bootstrap values are very poor: only the clade of Ptychopteridae, Ptychopterinae, and the spathate lobed Ptychopterinae are well supported.

Classification

The species of Ptychopterinae in the analyses were strongly supported as a monophyletic group. The three species of Bittacomorphinae included in the analysis as an outgroup were not recovered as a monophyletic group in either the Bayesian or Maximum Parsimony analyses, which is consistent with more comprehensive analyses of Bittacomorphinae that have found that the subfamily is a well supported monophyletic lineage defined primarily by non-genital adult characters (Fasbender & Courtney, unpub. data).

Detailed examination has provided preliminary synapomorphies for the proposed species groups of Ptychopterinae, which are recorded in Appendix I. This examination has also found that the species *Ptychoptera ressl*i Theischinger, 1978 exhibits the character suite associated with the subgenus *Ptychoptera* (*Parapteroptera*) (Male auxilliary sexual organ present on abdominal sternum III; epandrium with epandrial claspers well articulated and poorly sclerotized; parameres and medial gonocoxal lobes fused to membrane over hypandrium; basal lobe of gonostylus with ventral portion formed to narrow scythe-like structure curved medially; terminal division divided basally, poorly articulated; eversible sac present; basal scale present). Based on these similarities *Ptychoptera ressl*i is transferred to *Ptychoptera*(*Parapteroptera*).

A species level revision and phylogenetic analysis of Ptychopterinae is in progress and will be published at a later date which will explicitly examine the monophyly of the species groups.

General Morphology

Due to a combination of the complexity of the male genitalia of Ptychopteridae and the number of authors who have worked on the group the terminology and language used to describe structures has not been consistent. This is exacerbated by the changes in the standard terminology of Dipteran

morphology as more has been learned about the group. The terminology used here attempts to conform to Cumming & Wood (2009) as closely as possible, but there are numerous apomorphic structures in the male genitalia of Ptychopteridae. As a result it has become necessary to coin novel terms for these conditions. Such novel terms are highlighted in **bold** through the text. Table 1 provides a comparison chart between the terminology used in this manuscript and that of earlier revisionary studies.

Ptychopteridae demonstrates a fairly typical lower Dipteran body plan, with a compact thorax and head, thread-like antennae, and long legs. The pregenital abdomen is elongate, consisting of seven segments with Segment II longest and Sternite II subdivided. Some species of Ptychopterinae show development of an auxiliary sexual organ on Sternite III, most prominent in the subgenus *Paraptychoptera* Tonnoir although also present in some species of the *Ptychoptera contaminata* species group (Tonnoir, 1919; Freeman, 1950; Peus, 1958; Zwick & Stary 2003). Abdominal segments beyond III become increasingly attenuated, particularly in many Ptychopterinae where there is some telescoping the anterior of the posterior abdominal sclerites under the previous segment. There is no permanent rotation in any portion of the abdomen, although the abdomen is readily rotated to invert the genitalia in copula. The hypopygium is prominent and not retracted or telescoped into the previous segment; the epandrium, gonopods, and hypandrium are readily recognizable and all are unfused. In Bittacomorphinae the hypopygium is similar in diameter to the preceding abdominal segments, while many Ptychopterinae have a hypopygium much wider than the rest of the abdomen. However, this character is weakly developed in some Ptychopterinae (such as *Ptychoptera alexanderi* Hancock).

Fossil Ptychopteridae lack the extension of abdominal segment II and have the same general length of abdominal segments with the exception of *Crenoptychoptera*. *Crenoptychoptera* exhibits the elongate second segment, but appears to lack the extensive telescoping of Ptychopterinae, which has

been used (Lukashevich, 2012) to place it as sister to the Bittacomorphinae. However, the extent of abdominal telescoping is difficult to interpret based on the partial disarticulation which seems to be indicated by the illustrations, and as stated above the character of hypopygium width is based on a limited sampling of Ptychopterinae. Lukashevich additionally cites a ringlike abd. seg. VII as a synapomorphy of the *Crenoptychoptera* + Bittacomorphinae clade, but segment VII in Bittacomorphinae is no different from its counterpart in Ptychopterinae with the exception of reduced anterior telescoping.

Epandrium

The epandrium is composed of Tergites VIII-XI with Tergite VIII forming a collarlike apodeme at the posterior margin (Just, 1973). In all Ptychopterinae and the Asian *Bittacomorphella*, as well as *Bittacomorphella fenderiana* of the Nearctic, the epandrium is completely bilobate, with at minimum a medial suture completely subdividing the sclerite into distinct **epandrial lobes**. In *Bittacomorpha* the epandrium externally appears as an undivided plate, but in some cleared specimens a weak internal suture is present. The only species within Ptychopteridae without any evidence of a medial division are the *Bittacomorphella sackenii* species group and *Bittacomorphella jonesi*, all found in the Nearctic. Based on these observations and preliminary phylogenetic analyses that have placed neither the *Bittacomorphella sackenii* group nor *Bittacomorphella jonesi* as a basally diverging clade within Bittacomorphinae, the state of an undivided epandrium is probably an apomorphic condition within Bittacomorphinae. The fossil genus *Leptychoptera* also demonstrates a clearly divided epandrium, suggesting that the condition was present before the divergence of the contemporary subfamilies. It seems reasonable to assert that the condition of a bilobate epandrium is part of the ground plan of the extant Ptychopteridae.

The females of Ptychopterinae and some species of Bittacomorphinae exhibit a bilobate structure of the epigynum which may be correlated with the bilobate epandrium of the male (Figs. 20e, 21b&e), while species of Bittacomorphinae with a plate-like epandrium do not exhibit a bilobate epigynum (Fig. 20). However, there is a distinct differentiation between the epigynum of all Bittacomorphinae and Ptychopterinae, in that Bittacomorphinae is distinguished by a broad, subquadrate epigynum (probably plesiomorphic based on outgroup character states), while in Ptychopterinae the medial region of the epigynum, especially the epiproct, is highly reduced to a heavily sclerotized band, perforated medially by the anus. The 7th tergite covers the surface of the epigynum in Ptychopterinae, while the epigynum is exposed in Bittacomorphinae. *Bittacomorpha* often show a weakly developed epiproct between the base of the cerci and apex of the epigynal lobes. The cerci are developed at posterolateral corners, which is in bilobate species the apex of the epigynal lobes. There is a distinct point of articulation between the cercus and the epigynal lobe, which has implications for the origin of the epandrial claspers of males.

The anterolateral corners of the epandrial collar ("Tergite VIII") are formed into a triangular to bandlike **epandrial apodeme** in many ptychopterine taxa; it is closely associated with and articulates on the gonocoxal lobe, and in most the anterolateral apex of the basal division of the hypandrium. The epandrial apodeme appears to facilitate bowing of the epandrium in the dorsoventral plane, apparently to enhance the clasping function of the structure. This function is most developed in the *Ptychoptera lenis* and *Ptychoptera tibialis* groups. In both of these groups the epandrial claspers are massive, composite structures which are articulated in the transverse plane, and the epandrial apodeme opens and closes the structure.

In other ptychopterine taxa there are often breaks in the epandrial apodeme near the posteroanterior corner of the epandrial lobe. This break appears to allow the epandrium a wider arc of

motion in the dorsoventral plane, and is especially well developed in *Parapterychoptera* and the *Ptychoptera quadrifasciata* and *Ptychoptera pendula* groups.

Epandrial Claspers

The overall structure of the epandrium of most extant Ptychopteridae is dominated by a pair of accessory copulatory styli, termed here **epandrial claspers**. The epandrial clasper can be articulated (as in Bittacomorphinae and the *Ptychoptera contaminata* group), or contiguous with the epandrial lobe (as in much of the remainder of Ptychopterinae). The form of the epandrial clasper is fairly homogenous in Bittacomorphinae, being a cylindrical stylus curved weakly to strongly medially and tapering to its apex. The epandrial clasper forms found in Ptychopterinae are far more diverse, most distinctive as the dorsoventrally flattened stylus of the *Ptychoptera contaminata* group. Depending on the interpretation of homology between the *Ptychoptera contaminata* group and the remainder of Ptychopterinae, the poorly articulated stylus and lobes may also represent epandrial claspers. These range from the weakly sclerotized stylus of subgenus *Parapterychoptera* to the massive claw-like composite structure of the *Ptychoptera lenis* group, while in some taxa the epandrial claspers are extremely reduced and largely indistinguishable from the apex of the epandrial lobes as in the *Ptychoptera quadrifasciata* and *Ptychoptera pendula* groups. The character state of elongate nematoform stylus extending directly posterior from the epandrial lobes is widely distributed in Ptychopterinae, and will be discussed in greater depth below.

The authors distinguish between the epandrial lobe and epandrial clasper in Ptychopteridae based on whether the structure is closed ventrally with sclerotized cuticle (the epandrial clasper), or is “open” with membranous tissue ventrally (the epandrial lobe). All ptychopterine species exhibit this closed region forming an epandrial clasper except the *Ptychoptera quadrifasciata* and *Ptychoptera pendula* groups, where the remnants of the epandrial clasper are present as slight invagination at the

apex of the epandrial lobe. **Articulated epandrial clasper** is applied to epandrial claspers with a distinct break in sclerotization or other point of articulation with the epandrial lobe (currently applied to Bittacomorphinae and the *Ptychoptera contaminata* group, *Parapterychoptera* and *Ptychoptera bellula*) (Figs. 5a&b, 6a&b, 7a&b, 12a&b, 13a,b&c). **Contiguous epandrial clasper** will be used for the epandrial claspers found throughout much of Ptychopterinae, lacking a distinct point of articulation (Figs. 8a&b, 9a&b, 10a&b, 16a&b, 18a&b, 19a&b). In species with contiguous epandrial claspers there is sometimes a marked division between the epandrial lobe and the epandrial clasper (Fig. 18b). The *Ptychoptera quadrifasciata* and *Ptychoptera pendula* groups will be referred to only with the term epandrial lobe, as they have extremely reduced or absent epandrial claspers (Figs. 14a&b, 15a&b).

The epandrial clasper has received many different labels in the literature of Ptychopteridae. These include tergal horn (Alexander, 1981) surstylus (Peus, 1958; Alexander, 1981; Krzeminski & Zwick, 1993; Zwick & Sary, 2003) and cercus (Just, 1973). It is difficult to ascertain the primordial structure from which the epandrial clasper is derived from, and all of the previously cited terminology infers homologies that are not necessarily correct. Tergal horn is probably in reference to the epandrial lobe/epandrial clasper complex displayed by the *Ptychoptera lenis* group which is a specialized condition within Ptychopterinae and is not applicable outside that assemblage. The broad definition of surstylus (Sinclair, 2000) certainly applies to the Ptychopteridae (a clasping organ of the epandrium articulated by a subepandrial sclerite), but the term has been limited to epandrial claspers found in Eremoneura (Cumming & Wood, 2009). These are independently derived despite the superficial similarity to the epandrial claspers of Ptychopteridae, thus the application of “surstyli” is inadvisable.

An alternate interpretation of the epandrial clasper is as a modified cercus, but any evidence is equivocal. Just (1973) offers the term without in-depth interpretation, merely stating that the “cerci” of *Ptychoptera* (*Parapterychoptera*) *lacustris* do not have any associated musculature. The placement of the

epandrial clasper in many ptychopterids supports the cercal origin hypothesis, emerging laterally to the epiproct. Additionally, in female Ptychopterinae the cerci emerge from the apex of two widely separated epigynal lobes, suggesting that the apex of the epandrial clasper may be derived from cercal tissue.

However, there are several taxa where the epiproct is inevident or the epandrial clasper is not contiguous with the epiproct, particularly in Bittacomorphinae. In *Bittacomorphella fenderiana* the epandrial clasper is displaced far lateroposteriorly along the margin of the epandrial lobe, a characteristic seen to a lesser degree in other Bittacomorphinae. Furthermore, Bittacomorphinae and the *Ptychoptera contaminata* group articulate the epandrial clasper with the assistance of sclerotizations of the subepandrial membrane (the “subepandrial sclerite”), which does not appear to be derived from the proctiger. A final complication with the cercal hypothesis is the presence of a “posteriomedial stylus” on the posterior margin of the epandrium between the epandrial clasper and the epiproct in some species of both Bittacomorphinae and Ptychopterinae, which may represent the remnants of a cercus.

The favored interpretation of the authors is interpretation of the origin of epandrial claspers as the elongation and articulation of the epandrial lobe. A hypothesis can be formed based on changes in clasping function that suggest a possible evolutionary path from an initial ancestral character state (still present in many extant taxa) to all of the more specialized epandrial claspers. Several unrelated groups of Ptychopterinae have long, rod-like composites of the epandrial lobe (referred to as **nematoform epandrial claspers** and described in detail below) (Figs. 8a&b, 10a&b, 16a&b, 18a&b, 19a&b), and subdivision and articulation of this structure would promote clasping function, suggesting this is the groundplan state. Many species with a nematoform epandrium have the bases of the epandrial lobes expanded, suggesting intermediate stages between a true nematoform epandrium and the more specialized forms of epandrial lobe (ex. *Ptychoptera albimana*) (Fig. 9a&b).

One of the most pressing matters in interpretation of the epandrial clasper is whether the well-articulated state expressed in Bittacomorphinae and the *P. contaminata* group is homologous or independently derived. The polarity of this character state influences the interpretation of the poorly articulated extensions of the epandrial lobe found in many ptychopterines as reduced epandrial claspers or merely extensions of the epandrial lobe. Examination of the distribution of the nematoform lobe character state in Ptychopterinae provides resolution of this issue. The nematoform state is widely expressed across the subfamily, including many early diverging taxa. Species expressing the nematoform character state can be found in all bioregions inhabited by Ptychopterinae: several species in the eastern Palearctic, numerous species in the Oriental region, all of the Afrotropical fauna, *Ptychoptera sculleni* of the western Nearctic, and *Ptychoptera alexanderi* of the Central American Neotropics. In other aspects of the male genitalia these species are not homogenous, often showing affinities to taxa with different epandrial structures. This has been borne out by the phylogenetic analyses presented here, which show the nematoform character state distributed across the tree, including basally divergent taxa.

Ptychoptera albimana probably represents an intermediate stage in the development of opposing composite clasping structures (Fig. 9a&b): it exhibits superficial similarity to the nematoform epandrial configuration while other characters show affinities to the *Ptychoptera lenis* and *Ptychoptera tibialis* groups, such as the configuration of the posteromedial stylus and the presence of a ventromesal lobe. Preliminary morphological analysis has placed *Ptychoptera albimana* in a clade with these two groups. Based on these features it appears that the nematoform state of epandrial lobes is probably the ancestral character state of the extant Ptychopterinae. It appears that the well-articulated form of epandrial clasper developed by the *Ptychoptera contaminata* group is not a homologous character state with that found in Bittacomorphinae.

However, this still leaves the problem of interpretation of these structures as an epandrial clasper versus an extension of the epandrial lobe open to debate. There are two criteria which can be used to evaluate the presence of epandrial claspers: the extension and invagination of the epandrial lobe to form a closed, tubular structure, and the presence of a sclerotized subepandrial membrane (the “subepandrial sclerite”) to articulate the structure. The elongate stylus found in all Bittacomorphinae can undoubtedly be labeled as epandrial claspers, but there is not a clear concept of what constitutes an epandrial clasper in Ptychopterinae. While the lobes found in the *Ptychoptera contaminata* group are well articulated the weakly sclerotized lobes found in *Paraptychoptera* are very similar in overall structure, though evidently lacking musculature (Just, 1973). One of the defining characteristics of surstyli is the presence of an articulating subepandrial or bacilliform sclerite (Cumming & Wood, 2009): this condition is found in the Bittacomorphinae and the *Ptychoptera contaminata* group, but is lacking in *Paraptychoptera* and most other groups of Ptychopterinae. A heavily sclerotized and divided subepandrial sclerite is not necessarily associated with articulate epandrial claspers: the *Ptychoptera pendula* group has a quite distinct subepandrial sclerite, which is even divided medially and is much more prominent and heavily sclerotized than even that found in the *Ptychoptera contaminata* group.

Other ptychopterines have developed lateroanterior extensions of the sclerotized portion of the hypoproct, in some cases resulting in most of the subepandrial membrane becoming sclerotized, most prominently in *Ptychoptera sculleni*. It appears that in these taxa the hypoproct is developed anteriorly into a large plate that to serve as an attachment point for muscles to articulate the epandrium. One of the central unresolved issues about nematoform epandrial claspers is if the lobes grasp the female using a discrete clasping action, i.e. are apices of the lobes articulated outside the movement of the remainder of the epandrium. Detailed studies of uncleared specimens with intact musculature are necessary to answer this question. In *Ptychoptera sculleni* a muscle extends partway down the extension of the epandrial lobe, suggesting that there is some degree of movement in the structure, even if there is not a

discrete point of articulation. Additionally, if there is a discrete clasping action present along a dorsoventral arc, the degree to which there is an opposing component in clasping between the individual lobes is unclear. Unfortunately, the stiffening effects of alcohol on whole specimens make direct observation of motion difficult to ascertain.

Based on the distribution of the nematoform epandrial lobes and the placement of the *Ptychoptera contaminata* group in preliminary phylogenetics, it seems reasonable to assert that the *Ptychoptera contaminata* group's epandrial clasper developed from the nematoform structure. It is relatively simple to derive the articulated epandrial clasper from the nematoform prototype: the external portion of the hypoproct is reduced, becoming two sclerites in the subepandrial membrane, the posterior apex of the epandrial lobe thickens and develops a point of articulation at the base, and the basal portion of the epandrial lobe thickens and expands to a semi-hemispherical form.

This transition between the nematoform state and articulated epandrial claspers is reinforced by the configuration of the epandrium of *Ptychoptera bellula* Alexander, 1937. *Ptychoptera bellula* has a nematoform epandrium, with a distinct band of sclerotization near the subapical spine, which provides a point of articulation of the structure. The hypoproct of *Ptychoptera bellula* is a bar which appears to articulate the epandrial claspers. The phylogenetic position of *Ptychoptera bellula* and the *Ptychoptera contaminata* group again indicates that this well-articulated character state is has arisen multiple times, and that the transition from the nematoform to the articulated state is a viable evolutionary pathway.

There seems to be correlation between reduced epandrial lobes and a change in the degree of epandrial clasping against the gonopods. The *Ptychoptera pendula* group has developed an epandrium with a wide arc of dorsoventral motion, a state shared by the subgenus *Parapteroptera* and the *Ptychoptera quadrifasciata* group. In both the *Ptychoptera pendula* and *Ptychoptera quadrifasciata* groups the the epandrial claspers are highly reduced, while they remain prominent in *Parapteroptera*.

Again, the similarities between *Paraptychoptera* and the *Ptychoptera contaminata* group are intriguing: the epandrial claspers of *Paraptychoptera* resemble reduced versions of those found in *Ptychoptera contaminata* and its allies, suggesting that differences in dorsoventral clasping can drive the development or reduction of epandrial claspers. Additionally, there is an interesting analogue to the reduced form of the *Ptychoptera pendula* and *Ptychoptera quadrifasciata* groups in *Ptychoptera malaisei*, a southeast Asian species which is closely allied with two species with nematoform epandrial lobes based on the structure of the gonostylus, but the length of the epandrial lobes is reduced to an approximation of that found in the aforementioned groups. However, *Ptychoptera malaisei* still exhibits distinct invagination of the apices of the epandrial lobes, which is extremely reduced in the *Ptychoptera pendula* and *Ptychoptera quadrifasciata* groups.

While both *Paraptychoptera* and the *Ptychoptera pendula* group exhibit heavily modified, highly complex gonostyli, the *Ptychoptera quadrifasciata* group retains a simple gonostylus. There is some degree of epandrial clasping against the gonopods in all ptychopterines, but it is not developed nearly to the extent of these groups in other members of the subfamily.

The epandrium of *Bittacomorpha* does not appear to exhibit a dorsoventral clasping function; rather, the emarginate portion of the posterior margin of the epandrium is pressed against the ventral portion of the female abdomen by the epandrial claspers. A similar functionality is illustrated by Peus (1958) for *Ptychoptera contaminata*, with the epandrial claspers grasping the ventral portion of the female abdomen and again pressing it against the posterior margin of the epandrium. Most of *Bittacomorphella* probably clasp with the epandrium in a similar way. However, the *Bittacomorphella sackenii* group (and to a lesser extent *Bittacomorphella jonesi*) show a longer epandrium that has a greater arc of dorsoventral motion; it seems probable that these species have more developed clasping

functions between the epandrium and the gonopods. Unfortunately *Bittacomorpha clavipes* and *Ptychoptera contaminata* are the only species for which concrete evidence is available.

A final alternate development of epandrial clasping function is the **composite epandrial clasper** of the *Ptychoptera lenis* and *Ptychoptera tibialis* groups (Figs. 11a&b, 17a&b). In these species the each epandrial lobe is modified into a medially directed knuckle or claw-like structure which move in the lateromedial plane, articulated at the hypoproct. In both species groups epandrial apodeme is broad and especially prominent, forming a triangular structure without a dorsal break which narrowly interfaces with the anterolateral apex of the hypandrium. In the *Ptychoptera lenis* group the dorsal spur of the gonocoxal apodeme is further modified to enhance the mechanical association between the epandrial apodeme and the gonocoxite, linking the clasping motion of the epandrium with that of the gonopods, which can be observed in whole specimens. The *Ptychoptera tibialis* group has reduced the dorsal spur of the gonocoxal apodeme, which may be correlated with the reduced apex of the epandrial clasper. This reduction reduces the arc required to clasp the female hypogynium; the medial surface of the epandrial clasper apex is roughened in the *Ptychoptera tibialis* group which may enhance clasping with the reduced epandrial clasper apex.

Posteromedial Stylus

As mentioned previously, there is a **posteromedial stylus** associated with the margin of the epiproct in many species. In all species of Bittacomorphinae except *Bittacomorphella jonesi* the stylus can be identified, although it is modified into a triangular knob in the *Bittacomorphella sackenii* group and formed into a triangular downward directed lobe in *Bittacomorpha* (Figs. 5a&b, 6a&b, 7a&b).

The posteromedial stylus is more difficult to interpret and less evenly distributed in Ptychopterinae. Many taxa show no evidence of a posteromedial stylus, and this absence has no clear correlation to the overall form of the epandrium (Figs. 8b, 10b, 12b, 15b, 16b, 18b, 19b). Most species

with a nematoform epandrium do not have an obvious analog to the posteromedial stylus, though several species of Afrotropical and Southeast Asian ptychopterines have a small convex spot with a cluster of several setae, which perhaps is the remnant of a reduced posteromedial stylus. There is one exception to the lack of posteromedial stylus in the species exhibiting the nematoform epandrium: *Ptychoptera albimana* exhibits a distinct posteromedial stylus associated with the base of the epandrial lobe (Fig. 9b).

In ptychopterines exhibiting a posteromedial stylus the form of the structure is highly variable. The *Ptychoptera pendula* group (Fig. 14b) and *Ptychoptera albimana* have similar triangular lobes at the margin of the epiproct. A flattened structure at the base of the epandrial clasper in the *Ptychoptera contaminata* group may represent the posteromedial stylus (Fig. 15c), though if true it has been heavily modified. The placement on the epandrial clasper is not shared with any other ptychopterid, suggesting it is not homologous. However, the evidence either way is equivocal.

As the probable ancestral character state of the ptychopterine epandrium is the nematoform type, the homology of the posteromedial stylus within the group and comparison with Bittacomorphinae is problematic. The posteromedial stylus is located at the apex of the epandrial lobe or base of the epandrial clasper in Bittacomorphinae, with the epandrial clasper placed subapically (or at the lateral apex of *Bittacomorphella fenderiana*). Based on these observations the homology of the posteromedial stylus between the subfamilies is tenuous. These structures may represent the remnants of cerci, though their close association with the epandrial lobe and lack of contiguity with the lateral membrane of the hypoproct in most taxa suggests they are not. However, in the *Ptychoptera tibialis* group the posteromedial stylus is an articulated process, and the association with the epiproct is readily apparent, greatly resembling a true cercus (Fig. 17b). It is possible that the cercus has been integrated

into the epandrial lobe in most Ptychopteridae, and that the condition in the *Ptychoptera tibialis* group is a reversal to a more plesiomorphic articulated position.

Ventromesal Lobe and Subapical Spine

One of the most distinctive characters of the *Ptychoptera lenis* group is a flattened, leaf-like structure associated with the medial margin of the epandrial clasper. This character is also found in *Ptychoptera albimana* and the *Ptychoptera tibialis* group. It is suggested that the **ventromesal lobe** (*sensu* Alexander, 1937) (Figs. 9b, 11a&b, 17b) represents a synapomorphy uniting these three groups. The morphology of this structure is highly variable and often diagnostic to species, suggesting that it serves to facilitate species recognition during mating.

Another characteristic of the *Ptychoptera lenis* and *Ptychoptera tibialis* groups is the presence of a small spine on the lateroventral apex of the epandrial clasper (the **subapical spine** *sensu* Alexander 1937) (Figs. 9a&b, 13b, 14a, 16a&b, 17b). The form is highly variable (sometimes within a particular species), ranging from an acute spine to a broader, cone-like structure. There is also some variability of the placement of this spine in the *Ptychoptera lenis* group. There are potential analogues to the subapical spine in *Ptychoptera albimana*, *Ptychoptera bellula* and *Ptychoptera sculleni*, consisting of lobes on the ventral surface of the distal half of the epandrial clasper. In *Ptychoptera albimana* the lobes are filiform, *Ptychoptera bellula* while in *Ptychoptera sculleni* they are tapered knobs. The homology of these structures is problematic, for neither form closely resembles a spine, and while *Ptychoptera albimana* is related to the *Ptychoptera lenis* and *Ptychoptera tibialis* groups, *Ptychoptera sculleni* is closely related to the *Ptychoptera pendula* group.

Proctiger

The epiproct is prominent in most Ptychopterinae, and in the East Asian *Bittacomorphella*. In the remaining Bittacomorphinae the epiproct is inevident due to the fusion of the epandrial lobes, with the likely intermediate state demonstrated by *Bittacomorphella fenderiana*, which has a distinct division of the epandrial lobes, but they remain in close contact to the posterior margin of the epandrium. All Ptychopterinae demonstrate an identifiable epiproct, even if it is highly reduced. In Ptychopterinae and the East Asian *Bittacomorphella* the epiproct forms a web medially between the epandrial lobes.

As stated above, the presence of cerci in Ptychopteridae is difficult to evaluate. Both the epandrial claspers and the posteromedial stylus appear to be epandrially derived structures, despite their proximity to the proctiger. Based on these observations Ptychopteridae is presumed to have lost the cerci in the male genitalia.

The hypoproct is readily discerned in both subfamilies of Ptychopteridae. In most Bittacomorphinae the hypoproct consists of a small ovoid sclerite suspended in a poorly-sclerotized membrane beneath the aedeagus, drawn up on the underside of the epandrium. The sole exception to this is *Bittacomorphella jonesi*, where the hypoproct forms a short, tongue-like structure extending beyond the posterior margin of the epandrium. Ptychopterinae display a similar tongue-like hypoproct extending posterior from the underside of the epandrium, with the exception of the *Ptychoptera contaminata*, *Ptychoptera pendula*, and *Ptychoptera takeuchii* groups. In the *Ptychoptera contaminata* group the hypoproct is largely membranous, with paired subepandrial sclerites suspended in the subepandrial membrane which may represent the remnants of a highly modified hypoproct (probably helping to articulate the epandrial claspers). In the *Ptychoptera pendula* and *Ptychoptera takeuchii* group the hypoproct resembles the ovoid sclerite suspended in the subepandrial membrane seen in Bittacomorphinae.

The structure of the proctiger is quite different between the subfamilies in the female genitalia. In Bittacomorphinae the epiproct appears to be largely indistinguishably fused to the epigynum (though it is often discernable at the base of the cerci), and a distinctive triangular hypoproct is present. In female Ptychopterinae the proctiger is extremely reduced, essentially only consisting of the anus, with no epiproct developed. The remnants of the hypoproct are probably represented by a web between the bases of the cerci.

Subepandrial Sclerite

In Eremoneura the subepandrial sclerite articulates the surstyli (Cumming & Wood, 2009). As alluded to previously, the subepandrial sclerite in Ptychopteridae is highly variable in presence/absence and form. There are two broad configurations of the subepandrial sclerite in Bittacomorphinae. In *Bittacomorpha*, *Bittacomorphella fenderiana*, and the East Asian *Bittacomorphella* the subepandrial sclerite is divided into paired bacilliform sclerites seamlessly fused to the medial base of the epandrial clasper. In *Bittacomorphella jonesi* and the *Bittacomorphella sackenii* group the subepandrial sclerite forms a V-shape, fused medially at the anterior margin and extending posterolaterally to articulate the epandrial claspers from the medial base, with a distinct point of articulation between the epandrial clasper and the subepandrial sclerite. It is difficult to determine which character state is plesiomorphic in Bittacomorphinae based on the limited resolution of the phylogenetic position of each species group of *Bittacomorphella*.

The structure of the subepandrial sclerite is also diverse in Ptychopterinae. Several taxa show limited no evidence of sclerotization of the subepandrial membrane except for the external portion of the hypoproct. These include *Paraptychoptera*, the *Ptychoptera quadrifasciata* group, the *Ptychoptera lenis* group, and *Ptychoptera albimana*. An extension of the sclerotized portion hypoproct anterior to form an analog to the subepandrial sclerite is apparent in *Ptychoptera sculleni*, *Ptychoptera alexanderi*,

most of the Afrotropical and Southeast Asian Ptychopterinae, and the *Ptychoptera japonica* group. Indeed, many of the taxa with a nematoform configuration of the epandrium show sclerotization of the subepandrial membrane, probably to provide support for muscles articulating the epandrial claspers. The *Ptychoptera takeuchii* group and *Ptychoptera bellula* show limited sclerotization of the hypoproct, similar to Bittacomorphinae, but the subepandrial membrane is well sclerotized and show weak evidence of a suture posteriorly.

A divided subepandrial sclerite is demonstrated in the *Ptychoptera tibialis*, *Ptychoptera pendula* and *Ptychoptera contaminata* groups. In the latter two taxa there is a reduction in the external portion of the hypoproct (a bittacomorphine-like plate in the *Ptychoptera pendula* group; in the *Ptychoptera contaminata* group completely membranous). As mentioned previously, the subepandrial sclerite of the *Ptychoptera pendula* group is extensive, comprising almost the entire subepandrial membrane. With the complete reduction of the epandrial clasper in this group it seems likely that these extensive sclerites may facilitate lateral folding of the epandrial lobes to enhance clasping against the gonopods. In the *Ptychoptera contaminata* group the subepandrial sclerites probably facilitate articulation of the epandrial claspers, and may either represent a sclerotization of the subepandrial membrane, or a highly modified and reduced hypoproct. The configuration of the hypoproct and subepandrial sclerites of the *Ptychoptera tibialis* group may support the hypothesis that the subepandrial sclerite is derived from the hypoproct, as there are elongate paired sclerites that extend posterior from the base of the hypoproct in a similar position to the subepandrial sclerites of the *Ptychoptera contaminata* group.

Fossil Evidence

Early fossil Ptychopteridae (*Proptychopterina*) show some evidence of a bilobate epandrium (Lukashevich, 1993; Lin & Lukashevich, 2006). By the early Cretaceous it is clear that *Leptychoptera* has a distinctly bilobate epandrium (Lukashevich & Azar, 2003). Based on this character state distribution it

can safely be asserted that the bilobate epandrium is a ground plan character for the extant taxa.

Evidence for epandrial claspers is much more difficult to interpret: in *Proptychoptera* there is evidence for stylus-like structures associated with the epandrium (Lukashevich, 2008; Lukashevich, 1993), but illustrations of the specimen are insufficiently detailed to ascertain from what part of the epandrium this structure is derived, much less homologies with other groups. Indeed, the overall structure of the epandrium in illustration of the *Proptychoptera yenisica* specimen is not readily reconstructed, and the “surstylus” may just be a fragment of a damaged larger structure. *Leptychoptera* shows no evidence of epandrial claspers or other accessory copulatory structures associated with the epandrium (Lukashevich & Azar, 2003), again suggesting that interpretations of the *Proptychoptera* structures should be treated circumspectly. *Crenoptychoptera* is interpreted by Lukashevich (2008) to have articulated epandrial claspers homologous with Bittacomorphinae. The *Crenoptychoptera defossa* specimen which retains the male genitalia has the hypopygium exposed from a ventral view: the hypandrium dominates visible genitalia and completely obscures the epandrium. Lukashevich (2008) acknowledges that an alternate interpretation of a complex gonostylus cannot be disproved, thus using fossil taxa to interpolate historical development of the epandrial claspers does not provide definitive answers.

Parameres

The interpretation of parameres in Ptychopteridae is problematic because alternate hypotheses of the structure in other families of lower Diptera. Cumming and Wood (2009) refer to the parameres as a paired set of structures associated with the base of the gonocoxite, which become fused in many taxa. The evolutionary trend to a parameral bridge is illustrated by the development of the parameres in Ptychopteridae, particularly in Ptychopterinae.

In Bittacomorphinae the base of the paramere extends anterior to the gonocoxal apodeme, relatively parallel to the gonopod (*Bittacomorphella fenderiana*, with its arced parameres being an

exception). In most bittacomorphines the parameres have membranous webbing between them at the base, but are separate apically. The general structure of the paramere is a well sclerotized rod, sometimes bent (*Bittacomorphella fenderiana*) or bifurcate (*Bittacomorphella jonesi*, *Bittacomorphella* sp. nr. *pacifica*). *Bittacomorpha clavipes* is an exception, with the medial webbing of the paramere extending nearly to the apex, and a prominent ventrolateral spine subapically which supports an additional membrane associated with the gonocoxite along the lateral margin of the paramere. *Bittacomorpha occidentalis* shows a paramere configuration similar to that found in *Bittacomorphella*, suggesting the state found in *Bittacomorpha clavipes* is an autapomorphy.

The configuration of the parameres is more variable in Ptychopterinae. One of the most noticeable differences with the bittacomorphines is that the parameres are fused into a bridge over the aedeagus in most members of the subfamily. An exception is the *Ptychoptera lenis* group, where the individual parameres are clearly distinguishable (Fig. 11h). In most members of the group there is a lightly sclerotized bridge connecting the parameres at the base of the dorsally directed section, though this is not apparent in *Ptychoptera lenis* or *Ptychoptera byersi*. A similar configuration of weakly fused parameres is found in the *Ptychoptera tibialis* group (Fig. 17 h&i). *Ptychoptera bellula* also has medially separate parameres, although the parameral membrane extends nearly to the apex and the base of the paramere is shifted further anterior and somewhat ventrally compared to the aforementioned taxa. Much like Bittacomorphinae, the base of parameres in these groups has an associated medial membrane. In taxa exhibiting a bridge-like paramere configuration, the medial membrane remains present and is adhered along the medioanterior margin. It is difficult at this preliminary point of phylogenetic investigation in Ptychopterinae to assign a ground-plan interpretation of the paramere character state, based on the separation of the parameres in Bittacomorphinae and the relatively late divergence of the *Ptychoptera lenis* and *Ptychoptera tibialis* groups in the ptychopterine phylogeny.

Although they are merged more homogenously into a plate, *Ptychoptera albimana* also develops parameres extending to the gonocoxal apodeme.

The formation of a parameral bridge is facilitated by the medial orientation of the base of the paramere in all Ptychopterinae. In the *Ptychoptera lenis* and *Ptychoptera tibialis* groups the base of the paramere is directed medially, but the apex takes a sharp bend dorsally, forming a set of parallel apical lobes with both parameres. In taxa exhibiting the bridge configuration, there are often a set of posterodorsal apices, represent the remnants of this apical lobe. In the taxa where these apices are present they show a number of forms, from elongate stylus in *Ptychoptera annandalei* to short clusters of spines as in *Ptychoptera metallica* (a member of the *Ptychoptera contaminata* group). In some taxa there is also an elongate medial filament extending posterior (Fig. 13i&j). This is most notable in the *Ptychoptera contaminata* group, but is also developed to a lesser degree in *Ptychoptera praescutellaris*. A similar, blunter structure is found in *Ptychoptera albimana*, with a bifurcate apex much like the *Ptychoptera contaminata* group (Fig. 9h&i).

Another trend within Ptychopterinae is the shift of the articulation of the parameres posterior along the medial margin of the gonocoxite. This is least developed in the *Ptychoptera lenis* group, where the heavily sclerotized shaft of the paramere extends to the base of the gonocoxal apodeme. The dorsal surface has a thin lateral plate that becomes contiguous with the dorsal surface of the gonocoxite and associates with the modified epandrial apodeme. All other ptychopterine taxa show a shift of the anterior base of the paramere posterior along the medial surface of the gonocoxite. The association with the gonocoxal apodeme is eliminated, and there is often a break in the sclerotization at the base of the paramere; this is particularly pronounced in *Ptychoptera sculleni*, where the sclerotized portion of the paramere floats on the parameral membrane.

In *Parapychoptera* the anterior portion of the parameres (Hakenfortsatz, HF, in Just, 1973) and parameral membrane are closely associated with the ventral margin of the gonocoxite, and base of the paramere is shifted far posterior on the gonocoxite. This forms a dorsal surface to the hypandrium similar to that seen in Bittacomorphinae. The gonocoxal lobe in *Parapychoptera* can be mistaken for the paramere based on its anterior point of origin; however, it emerges from the ventral margin of the gonocoxite. In all ptychopterines the paramere is closely associated with the dorsal margin of the gonocoxite: it is apparent in cleared specimens of *Ptychoptera* (*Parapychoptera*) *lacustris* that the paramere originates posteriorly from the dorsal margin and is directed ventrally along the medial margin of the gonocoxite.

The parameres are not described in any published fossil material, making impossible to draw inferences about polarity of the character states or their potential transformations.

Gonopods

The gonopods in Ptychopteridae have a readily recognizable gonocoxite and gonostylus. The gonopod is completely free of the hypandrium, and is set between the epandrium and hypandrium. Throughout the family the gonopods generally clasp in an opposing manner, but most Bittacomorphinae show a slightly oblique range of motion for the gonostylus. This is most evident as an expanded membranous region on the mediodorsal surface of the joint between the gonocoxite and gonostylus. Most ptychopterines show limited oblique articulation of the gonopods; this may be a result of the dorsal orientation of the terminal division of the hypandrium, which provides another clasping surface for the epandrium to oppose.

Throughout Ptychopteridae the external portion of the gonocoxite is cylindrical, with the medial surface very weakly sclerotized. In most taxa the gonocoxite tapers somewhat anteriorly, though in the *Bittacomorphella sackenii* group the width of the gonocoxite is fairly constant along the length. The

gonocoxites tend to be narrower in Bittacomorphinae compared to Ptychopterinae, though there is considerable overlap in the relative size and shape between the subfamilies. In general the overall form of the gonocoxite is more variable in Ptychopterinae, such as the shield-like gonocoxites of *Ptychoptera sculleni* and the *Ptychoptera takeuchii* group cited above (Figs. 16g, 19f). In all members of the family the lateral surface of the gonocoxite is simple, but many (though not all) ptychopterines show lobes associated with the dorsal or ventral margins.

Gonocoxal Apodeme

The gonocoxal apodeme extends anteriorly beyond the margin of the epandrium/hypandrium into the preceding abdominal segment. In Bittacomorphinae the apodeme is generally triangular, coming to a sub-acute point anteriorly. In Ptychopterinae the gonocoxal apodeme is more variable in configuration. Some taxa share the simple triangular apodeme with Bittacomorphinae, although there is a **dorsal spur of the gonocoxal apodeme** present near the base of the gonocoxite which serves as a point of articulation with the anterolateral epandrium. Taxa with simple gonocoxal apodemes include *Parapteroptera*, and the *Ptychoptera pendula* and *Ptychoptera quadrifasciata* groups, as well as the Afrotropical and Southeast Asian Ptychopterinae. Other taxa, such as the *Ptychoptera contaminata* and *Ptychoptera lenis* groups also exhibit the dorsal spur in a highly modified form to enhance the articulation of the epandrium. This dorsal spur is reduced in *Ptychoptera alexanderi* and absent in the *Ptychoptera japonica* group, suggesting the dorsal spur is not a ground plan feature of Ptychopterinae. However, the dorsal spur is also reduced in *Ptychoptera sculleni*, which is placed in an internal clade within the larger topology of Ptychopterinae.

The Afrotropical and Southeast Asian Ptychopterinae share a simple gonocoxal apodeme with the anterior apex rounded. In some species, such as *Ptychoptera capensis*, the apodeme is quite broad broader. Rounded apodemes are also seen in a group of taxa with enlarged, shield-like gonocoxites.

These include *Ptychoptera sculleni* and the *Ptychoptera takeuchii* group, as well as several mainland east Asian species (ex. *Ptychoptera bellula* Alexander 1937). The relationships between these taxa are unclear, so it is difficult to ascertain whether the character of a rounded gonocoxal apodeme is apomorphic or a homoplasy. There is evidence to suggest that *Ptychoptera sculleni* is sister to the *Ptychoptera pendula* group (in characters such as the structure of the gonocoxal lobes and gonostylus, as well as the larval respiratory siphon), suggesting that this character is homoplastic with regard to that species. The species with broad gonocoxal apodemes also lack the dorsal spur of said lobe, suggesting the epandrium does not articulate with the gonocoxite.

As mentioned previously, the gonocoxal apodeme is linked with the anterolateral apodeme of the epandrium in the *Ptychoptera lenis* group, resulting in a composite articulation linking the movement of both structures. The gonocoxal apodeme of the *Ptychoptera lenis* group is of similar configuration to that found in Bittacomorphinae: a sub-acute triangle, but the dorsal surface forms a broad arc rather than a straight edge. The dorsal spur is massively hypertrophied, and extends posteromedially over the gonocoxite to articulate with the paramere (Fig. 11f). A similar configuration occurs in *Ptychoptera albimana*, though the arcing of the dorsal margin is absent.

In some members of the *Ptychoptera contaminata* group the dorsal spur is not limited to the apodeme, but includes the anterior extremity of the external portion of the gonocoxite as well (Fig. 13g). In this group the external portion of the gonocoxite extends dorsally to the anterior margin of the epandrium, providing a stiffened platform for the support of the epandrial claspers.

Gonocoxal Lobes

While gonocoxal lobes are absent in Bittacomorphinae, many ptychopterines exhibit well developed lobes associated with the gonocoxite, and based on their often ornate structure may serve some purpose in species recognition during mating by the female. There are several different forms of

gonocoxal lobes in Ptychopterinae, each representing a different source of origin and homology. For the standardization of terminology, these lobes will be classified as the ventral gonocoxal lobe, the dorsal gonocoxal lobe, and the medial gonocoxal lobe. The ventral and dorsal gonocoxal lobes are simple, while the medial gonocoxal lobe is often extremely ornate.

The *Ptychoptera lenis* group exhibits the **ventral gonocoxal lobe** (Fig. 11f). This lobe is found on the lateroventral apex of the gonocoxite, and is a simple knob with a rounded apex near the articulation with the gonostylus, which is not found in any other ptychopterine. The ventral gonocoxal lobe is one of several synapomorphies of the *Ptychoptera lenis* group.

Several other taxa develop a triangular lobule on the dorsal surface of the gonocoxite (labelled the **dorsal gonocoxal lobe**) (Figs. 10f, 12f, 13g, 14f, 15f, 16g), including *Parapteroptera*, *Ptychoptera sculleni*, *Ptychoptera alexanderi* and the *Ptychoptera pendula*, *Ptychoptera quadrifasciata*, and *Ptychoptera contaminata* groups. In *Parapteroptera* this lobe is shifted anterior and somewhat medially, becoming more clavate. This lobe is associated with the base of the paramere, although in some taxa (*Ptychoptera sculleni*, the *Ptychoptera pendula* group) the paramere is no longer affixed to the dorsal gonocoxal lobe and instead floats on the supraedeagal membrane.

One of the most distinctive lobes found in Ptychopterinae is a bladelike gonocoxal lobe originating on the medioventral margin and extending dorsally along the medial surface of the gonocoxite, resembling the type of paramere found in Bittacomorphinae. This structure (the **medial gonocoxal lobe**) (Figs. 12g, 14f&g, 15g, 16f) is found in *Parapteroptera*, *Ptychoptera sculleni*, and the *Ptychoptera pendula*, and *Ptychoptera quadrifasciata* groups. In the *Ptychoptera pendula* and the *Ptychoptera quadrifasciata* groups, as well as *Ptychoptera sculleni*, the medial gonocoxal lobe originates posterior to the parameres, and extends dorsally: arcing anteriorly above the paramere in the *Ptychoptera pendula* group and *Ptychoptera sculleni*. In fact, in the *Ptychoptera pendula* group the

medial gonocoxal lobes are fused to the parameral bridge. *Parapterychoptera* is radically different, with the origin of the medial gonocoxal lobe (Hammerfortsatz, HaF in Just, 1973) shifted anterior to the point where the structure can be mistaken for a paramere, as discussed above. Instead of arcing dorsally the medial gonocoxal lobe is directed posterior paralleling the gonocoxite.

Gonostylus

The gonostylus is prominent in all members of Ptychopteridae, although the form is highly variable. The simplest form, exhibited in Bittacomorphinae and some Ptychopterinae, is a simple, weakly tapering stylus, often with a slightly inflated knob or pad at the apex. Bittacomorphines exhibit a cluster of highly sclerotized trichoid sensillae at the apex of the gonostylus, the number and arrangement of which can be used to distinguish species. Members of the *Bittacomorphella sackenii* group have the basal portion of the gonostylus inflated, otherwise the gonostyli within Bittacomorphinae are relatively homogenous with the exception of *Bittacomorphella fenderiana*, which exhibits a finger-like lobe at the base of the gonostylus (Fig. 6f&g).

While the only member of Bittacomorphinae with a lobe associated with the gonostylus is *Bittacomorphella fenderiana*, all members of Ptychopterinae exhibit some form of **basal lobe of the gonostylus**. There are a few species that appear to be exceptions to this, but homologous structures are readily identified. Two such species are *Ptychoptera tibialis* and *Ptychoptera sikkimensis*, but in these taxa the setose ridge along the inner margin of the gonostylus is a modified basal lobe (Fig 17f&g). The third species in the *Ptychoptera tibialis* group (*Ptychoptera garhwalensis*) has a shorter ridge which clearly is a basal lobe, demonstrating the homology. The *Ptychoptera japonica* group also has a reduced basal lobe, but close examination reveals a small nodule which represents the remains of the structure (Fig. 18g).

In the other taxa within Ptychopterinae the basal lobe is prominent, and often highly modified. One of the most common configurations of the lobe is as a small, heavily sclerotized nodule thickly covered in stout trichoid sensillae. The *Ptychoptera lenis* and *Ptychoptera quadrifasciata* groups, *Ptychoptera albimana*, *Ptychoptera annandalei*, *Ptychoptera sculleni* and most Oriental as well as some Afrotropical ptychopterines exhibit this character state (Figs. 8g, 9g, 11f&g, 15f&g, 16f&g). In the *Ptychoptera pendula* group the basal lobe serves as the base, or is modified into, a spine directed medioanteriorly; an exception being an undescribed species near *Ptychoptera townesi* (Fig. 14f&g). Finally, *Ptychoptera alexanderi* has the basal lobe modified into a small, glabrous, sickle directed anterior (Fig. 10f&g).

Other ptychopterines exhibit subdivision of the basal lobe. In *Paraptychoptera* the basal lobe is especially complex, with multiple knob-like, stylate, and scythe-like lobes (Fig. 12f&g). The basal lobe in the *Ptychoptera contaminata* group is enlarged, forming a flag dorsally, and has a secondary scythe-shaped lobe on the medial surface at the base of the gonostylus (Fig. 13g&h). The *Ptychoptera takeuchii* group also have a complex basal lobe, with both paddle-like and stylate portions (Fig. 19f&g). There are some Southeast Asian Ptychopterinae with complex basal lobes, such as *Ptychoptera persimilis* Alexander, 1947.

The **apical stylus of the gonostylus** is highly variable across Ptychopterinae, ranging from a simple cylindrical stylus or blade to dendritic structures with multiple lobes. Based on the character states displayed by Bittacomorphinae it appears that a simple stylus is probably the ground plan character state in Ptychopterinae. Taxa exhibiting this character include the *Ptychoptera japonica* group and *Ptychoptera alexanderi* (Figs. 10f&g, 18f&g). The *Ptychoptera lenis*, *Ptychoptera quadrifasciata*, and *Ptychoptera tibialis* groups also have a simple gonostylus, though it is flattened to the point that in some taxa the gonostylus becomes spatulate (Fig. 15f&g). Most other species Ptychopterinae have a more

heavily modified stylus with multiple accessory lobes. These ptychopterines have an identifiable **secondary lobe of the apical stylus** (Figs. 8f&g, 9f&g, 12f&g, 13g&h, 14f&g, 16f&g, 19f&g), which is highly variable in form. In most species this secondary lobe emerges from the proximal portion of the apical stylus, but in the *Ptychoptera contaminata* group the secondary lobe is developed near the terminal apex, as well as in several Southeast Asian species (Fig. 13 g&h). There also can be tertiary lobes of the apical stylus, though these are not as wide spread and are of limited phylogenetic signal beyond the diagnosis of species.

Another distinctive condition is found in in *Parapteroptera*, the *Ptychoptera pendula* group, and *Ptychoptera sculleni*: a distinctive weakly sclerotized pendulant lobe that emerges ventrally from the gonostylus, as well as a secondary lobe which is weakly sclerotized in *Parapteroptera* and well sclerotized in the *Ptychoptera pendula* group and *Ptychoptera sculleni* (Figs. 12f&g, 14f&g, 16f&g). This appears to be a synapomorphy uniting these taxa.

There are several trends in gonostylus form in the Southeast Asian Ptychopterinae, with the most distinctive being found in *Ptychoptera annandalei*, *Ptychoptera malaisei*, and *Ptychoptera persimilis*. In these taxa the apex of the gonostylus is bifurcate, the secondary lobe and primary lobe of the apical stylus being nearly identical in length. Indeed, in these taxa it can be difficult to ascertain which structure represents the primary lobe. While this distinctive state probably is indicative of the closely allied nature of these species, aspects of the gonostylus and other components of the genitalia show a resemblance to other ptychopterine species of Southeast Asia. Several other Southeast Asian ptychopterines show apical styli similar to the Malagasy species of the subfamily: elongate and fingerlike, with short secondary lobes.

In the *Ptychoptera lenis* and *Ptychoptera tibialis* groups there is a distinctive glabrous ridge on the dorsal surface of the apical stylus, extending to the apex (Figs. 11f, 17f). An apparently homologous

ridge is present on the dorsal margin of the primary apical style and the secondary lobe in *Ptychoptera albimana* (Fig. 9f). The *Ptychoptera quadrifasciata* group has a similar narrow ridge on the dorsal surface of the apical stylus (Fig. 15f), though whether this ridge is homologous is at best questionable, and homoplastic in the current analysis.

Most fossil Ptychopteridae exhibit simple gonopods, though as stated above there is an alternate interpretation of *Crenoptychoptera* where the species is interpreted to have a bilobate gonostylus versus simple gonostylus and epandrial claspers (Lukashevich, 2008). *Proptychopterina* display large, prominent gonocoxites that appear to be fused with the hypandrium (Lukashevich, 1993; Lin & Lukashevich, 2006; Lukashevich, 2008). However, in *Leptychoptera* and *Crenoptychoptera* the gonocoxites are free of the hypandrium and reduced in size, resembling modern members of the family. The evidence for the presence of a basal lobe of the gonostylus in fossil ptychopterids is not conclusive. Both *Proptychopterina* and *Leptychoptera* have structure suggestive of a lobe at the base of the gonostylus. In *Leptychoptera* the lobe at the base of the gonostylus appears to be derived from the gonocoxite. The origin of the structure in *Proptychopterina* is harder to ascertain, as the fossils are impressions rather than amber inclusions (Lukashevich, 1993; Lukashevich & Azar, 2003; Lin & Lukashevich, 2006). However, Lin and Lukashevich (2006) interpret this basal stylus as a component of the gonostylus.

Hypandrium

The most distinctive characteristic of the hypandrium in modern Ptychopteridae is the subdivision of the structure into two distinct parts, observed in the European Ptychopterinae by Peus (1958) and Just (1973). In fact, this characteristic is universal across all extant species, including Bittacomorphinae. The terminology of **basal division** (for the fixed, anterior part of the hypandrium) and **terminal division** (for the posterior or dorsal portion of the hypandrium, which is articulated in some

taxa) will be used here. Just (1973) examined the musculature of the hypandrium and found that the basal and terminal divisions are two divisions serve as attachment points for muscles derived from the 8th and 9th sternites respectively.

The hypogynum of some female Bittacomorphinae superficially replicates the division of the male hypandrium based on a distinct posteromedial subdivision of the structure. The apical portion of the hypogynum consists of the hypogynal valves, which may represent a portion of Sternite IX (Kotrba 2000). This structure being a recapitulation of the hypandrium of the male genitalia seems unlikely: hypogynal valves are found in many lower Diptera, and these structures are reduced in Ptychopterinae.

The basal division of the hypandrium presents three broad forms. The first of these is the **“subhemispherical” basal division** (5a&e, 6a&e, 10a&e, 15a&e, 18a&e) where the basal division extends posterior beyond the bases of the gonocoxite, with the ventral surface expanded out in an arc. This character state is displayed by *Bittacomorpha*, *Bittacomorphella jonesi*, and most of the ptychopterine species lacking spathate lobes of the hypandrium. In these taxa the terminal division is fairly short. In *Bittacomorphella jonesi* and to a lesser extent *Bittacomorpha* shallow sulci are present under the gonopods. In the ptychopterine taxa with an enlarged sperm sac the basal division is similarly subhemispherical.

The Ptychopterinae with a miniaturized sperm sac exhibit a **“band-like” basal division** (Figs. 8a&e, 9a&e, 11a&e, 12a&e, 13a&f, 14a&e, 16a&e, 17a&e, 19a&e) extending as a narrow strip across the underside of the hypopygium. Often the terminal division articulates on a medial extension of the basal division, which is particularly prominent in *Bittacomorphella fenderiana* and the East Asian *Bittacomorphella*. In these taxa the basal division is essentially the subhemispherical configuration, but the ventral profile of the basal division does not arc as prominently, and the ventrolateral surfaces are concave rather than convex. The final configuration of the basal division is distinctive of the

Bittacomorphella sackenii group, where the medial portion of the basal division is extended significantly, forming a prominent triangular profile when combined with the terminal division (Fig. 7a&e).

The **spathate lobes** (Figs. 8a&e, 9a&e, 11a&e, 17a&e) are derived from the lateroposterior margin of the basal division. Spathate lobes are distributed in a number of taxa, including the *Ptychoptera lenis* and *Ptychoptera tibialis* groups, as well as *Ptychoptera albimana*, and the Afrotropical and Southeast Asian Ptychopterinae. These lobes are typically subquadrate or broadly rounded, though they are acutely triangular in some members of the *Ptychoptera lenis* group, and extend posterior or dorsally from the hypandrium. The spathate lobes are associated with the development of the articulated terminal division, with most taxa exhibiting both characters. The *Ptychoptera takeuchii* group is an exception, where the terminal division exhibits some of the characteristics of the articulated form yet lacks spathate lobes.

Parapterychoptera and some of the Southeast Asian Ptychopterinae have a **basal scale** (Zwick & Starý, 2003) developed the ventromedial surface of the basal division. In *Parapterychoptera* this basal scale is a small sclerite associated with the anterior terminus of the eversible sac, projecting lateroposteriorly away from the surface of the basal division. In some species of *Parapterychoptera* the basal scale is almost wholly divided while in others it remains a single sclerite, and is absent completely in *P. (Parapterychoptera) lacustris*. The basal scale found in some Southeast Asian ptychopterines is much larger and fleshier than that seen in *Parapterychoptera*, and is always subdivided into paired triangular lobes. The homology between the structures in *Parapterychoptera* and the Southeast Asian ptychopterinae is unclear, and may be independently derived based on these structural differences.

The shape of the terminal division is highly variable. In Bittacomorphinae many species have a relatively simple, tapering slipper-like structure with the external margins folded dorsally to form a small cupped space often occupied by the external portion of the subapical sclerite of the aedeagus. In

Bittacomorpha, *Bittacomorphella jonei* and *Bittacomorphella fenderiana* there are a pair of lateral lobes associated with the terminal division. In *Bittacomorpha* and *Bittacomorphella jonesi* the entire terminal division is flattened, and takes on a foliform structure. All of Bittacomorphinae have the terminal division directed posterior, on a horizontal plane.

One of the distinguishing features of Ptychopterinae is that the terminal division is redirected from a horizontal plane to a vertical plane, associated with the dorsal rotation of the aedeagus. It is difficult to generalize a ground-plan state for the terminal division in this group. In the taxa mentioned above as having spathate lobes of the hypandrium and a well-articulated terminal division the terminal division is generally trough shaped. In groups with a poorly articulated hypandrium the terminal division often has a suture above the eversible sac and the apex of the terminal division is variably shaped. In some species the apex is shield or plate shaped (*Ptychoptera contaminata* group, *Ptychoptera sculleni*, some of the Southeast Asian Ptychopterinae). The *Ptychoptera pendula* group has a rhomboidal plate, with the apex forming a distinct spur. *Parapteroptera* has the apex of the terminal division (Apikallobus des Ventriums, ApLVe: Just, 1973) narrow and sheath-like. The *Ptychoptera quadrifasciata* group has a unique, spine-like terminal division with a swollen apex; *Ptychoptera alexanderi* and the *Ptychoptera japonica* have a similar spine, though the apex is acute.

In Bittacomorphinae there is a membranous region medially between the basal and terminal divisions. In Ptychopterinae this window is modified, typically becoming more closely associated with one portion of the hypandrium while reducing contact with the other. The membranous structure associated with the basal division of the hypandrium is the **eversible sac** of Zwick and Stary (2003) (Figs. 12h, 13f, 14e, 15e, 16e). Found in a subset of Ptychopterinae (*Parapteroptera*, *Ptychoptera sculleni*, as well as the *Ptychoptera contaminata*, *Ptychoptera pendula*, and *Ptychoptera quadrifasciata* groups), the eversible sac is manifest as a convex membranous lobe bisecting the basal division. The eversible as

appears to be derived from the membranous medial portion of the joint between the basal and terminal divisions as expressed in Bittacomorphinae. In some taxa (i.e. the *Ptychoptera quadrifasciata* group) the eversible sac is not contiguous with the joint between the terminal and basal divisions, and this structure is further developed into a small leaf-like lobe extending posterior. In other taxa the eversible sac reaches the base of the terminal division, and in some taxa (i.e. *Parapteroptera*, the *Ptychoptera pendula* group and *Ptychoptera sculleni*) the base of the terminal division is incised by this structure. The current phylogeny suggests that the eversible sac is a synapomorphy of the clade excluding the *Ptychoptera japonica* group and *Ptychoptera alexanderi*, which was subsequently lost in the clade exhibiting spathate lobes and a well articulated epandrium.

In those taxa with spathate lobes and an articulated epandrium there is a **membranous window** (Figs. 8e, 9e, 11e, 17e) present in the basal portion of the terminal division, which is closed off from the medial apex of the basal division by constriction of the base of the terminal division. This membranous window appears to be derived from the same membranous region at the medial base of the terminal division from which the eversible sac is derived, and in most taxa with eversible sacs the base of the terminal division is heavily incised by that structure. It thus appears that the membranous window is a remnant of the eversible sac that has been closed off by constriction and articulation at the base of the terminal division.

The joint between the basal and terminal divisions has varying degrees of articulation in Ptychopteridae. In Bittacomorphinae the terminal division is well-articulated, particularly in *Bittacomorpha*. Ptychopterines show differing levels of articulation. At one extreme is the *Ptychoptera japonica* group and *Ptychoptera alexanderi*, where the terminal division can only be distinguished from the basal division by a glabrous, lightly depressed remnant of a suture. Many other Ptychopterinae show evidence of a suture between the basal and terminal divisions, but there is extremely limited

articulation present, if any at all. Typically these taxa retain the divided base of the terminal division, where the ventrolateral apices are fused to the posterolateral margins of the basal division.

A highly articulated terminal division has developed in a clade of Ptychopterinae. In these taxa the lateral sutures between the terminal and basal division have been replaced by membrane, allowing a ventroposterior arc of movement; this character state is found in the *Ptychoptera lenis*, *Ptychoptera tibialis*, and *Ptychoptera takeuchii* groups, as well as *Ptychoptera albimana*, the Afrotropical Ptychopterinae, and many Southeast Asian ptychopterines. In some of these taxa the dorsal margin of the membranous area remains sclerotized, forming **lateral extensions of the terminal division** (Figs. 8e, 9e, 11e, 17e). These lateral extensions may be fused to the posterolateral corner of the basal division or detached and floating on the membrane, as seen in the *Ptychoptera lenis* group. The base of the terminal division is constricted in these taxa, giving a degree of flexibility to the hypandrium. In these taxa the terminal division often forms a funnel shaped structure which may facilitate spermatophore transfer by holding the female genital cavity open, especially in those taxa where the subapical sclerite is shortened (i.e. the *Ptychoptera tibialis* group and *Ptychoptera albimana*).

Based on the derived position of the articulated terminal division in Ptychopterinae it appears that this character state was independently derived from the similar condition in Bittacomorphinae. Examination of mating *Bittacomorpha clavipes* has found that the terminal division is folded back during copulation, resting between the female cerci. As the shape of the terminal division is variable between the species of Bittacomorphinae it may be possible that the structure is utilized in species recognition, as ptychopterids are often found in sympatric associations. It appears that the articulated terminal divisions in Ptychopterinae do not function in the same way, as they are much less flexible. Instead, they

may provide additional dorsoventral clasping function against the epandrium, particularly in those species of Ptychopterinae where the gonostyli are shortened and probably are less capable clasping organs.

The early fossil taxa of Ptychopteridae show a configuration of the hypandrium radically different from extant species. In *Proptychopterina* the gonocoxites appear to be fused to the hypandrium (Lukashevich, 1993; Lin & Lukashevich, 2006; Lukashevich, 2008), and there is no evidence of subdivision of the structure. In *Leptychoptera*, however, the hypandrium is distinct from the gonocoxites and forms a broad plate, with a distinct medial lobe at the apex (Lukashevich & Azar, 2003). It is not hard to see how the modern condition could be derived from this structure, if subdivision is not already present. Indeed, there are resemblances between *Leptychoptera* and the terminal division of some *Bittacomorphella* and the *Ptychoptera japonica* group species. The posterior margin of the abdomen of *Crenoptychoptera* also shows a similar medial lobe (Lukashevich, 2008), very reminiscent of the blunt terminal division found in the East Asian *Bittacomorphella*.

Aedeagus

The aedeagus of Ptychopteridae is a complicated structure. The structure of the aedeagus can be broken into several subcomponents for further elaboration: the sperm sac and ejaculatory apodeme (sperm pump), lateral ejaculatory processes, the aedeagal sclerites, and the subapical sclerite. One of the most significant synapomorphies of Ptychopterinae is the dorsal rotation of the aedeagal complex from the typical horizontal orientation found in Bittacomorphinae and most other lower Diptera.

The aedeagus rests in the hypandrium, with the anterior portion often extending into the preceding abdominal segment. The dorsal surface of the aedeagus is covered in a **superaedeagal membrane**, which forms the floor of the male genital chamber. Only the phallotrema and subapical sclerite are exposed, with the internal portion of the aedeagus not functioning as an intermittent organ.

The parameral membrane is often difficult to distinguish from the supraedeagal membrane in most Ptychopterinae, due to the shortened aedeagus.

Sperm Pump

The sperm pump of Ptychopteridae is quite prominent and well developed. In all Ptychopteridae the ejaculatory apodeme appears to compress the sperm sac in a lever like fashion, assisted in this function by the lateral ejaculatory processes. In Bittacomorphinae the structure is sub-globular, with the aedeagus emerging directly posterior. The sperm sac is located in abdominal segment VII, filling much of the internal space. The ejaculatory apodeme is located on the dorsoposterior surface of the sperm sac in this subfamily, contrary to Sinclair *et al* (2007). The ejaculatory apodeme is narrow and tapering in most Bittacomorphinae, though in some taxa it expands weakly towards the apex. The ventral portion of the lateral ejaculatory process of Bittacomorphinae projects anterior into the sperm sac through an ovoid membranous window. In all taxa the sperm sac has a broad opening into the endophallus between the aedeagal sclerites, allowing the transfer of large quantities of seminal fluid.

The enlarged sperm sac is also found in the *Ptychoptera japonica* and *Ptychoptera quadrifasciata* groups, though it does not extend as far into the VIIth abdominal segment. The ejaculatory apodeme in these taxa is similarly spine-like and tapering, but it is placed on the dorsal surface of the sperm sac due to the rotation of the aedeagal complex. These taxa lack a well-developed ventral portion of the lateral ejaculatory process, so the membranous window is absent. In most other Ptychopterinae the relative size of the sperm sac is much smaller, though compared to other lower Diptera the structure is still quite large. In the *Ptychoptera lenis* and *Ptychoptera tibialis* groups the sperm sac is nearly spherical, but in most other Ptychopterinae the sperm sac is weakly narrowed

posteriorly towards the junction with the aedeagal sclerites and flattened dorsally. The ejaculatory apodeme is broad and fanlike, typically larger than the sperm sac, and extends anterior, often into segment VII.

A bizarre exception in Ptychopterinae is *Ptychoptera alexanderi*. While the overall shape of the sperm sac resembles that found in the *Ptychoptera japonica* and *Ptychoptera alexanderi* groups, anterior portion of the structure is inflated, giving it a weak figure-eight shape when viewed dorsally. This is also correlated with a reduction in the lateral ejaculatory processes, described below.

Whether the enlarged ejaculatory apodeme and miniaturized sperm sac represents a single synapomorphic character change, or if this condition evolved more than once is difficult to assess. This is due to the problematic placement of the *Ptychoptera quadrifasciata* group. Based on the presence of the medial gonocoxal lobe, eversible sac, and lateral plates of the subapical sclerite *Ptychoptera quadrifasciata* and associated species should be placed in a clade with *Paraptychoptera*, the *Ptychoptera contaminata* and *Ptychoptera pendula* groups, and *Ptychoptera sculleni*. However, differences in the structure of the terminal division and the Bittacomorphinae like sperm pump suggest that it is an early diverging lineage within Ptychopterinae. Until the position of the *Ptychoptera quadrifasciata* group can be resolved the apomorphic/homoplastic condition of the “higher ptychopterine” sperm pump will be unresolved.

Lateral Ejaculatory Processes and Aedeagal Sclerites

One distinctive morphological feature of all Ptychopteridae are lateral ejaculatory processes emerging from the junction of the sperm pump and aedeagal sclerites which serve as muscle attachment points. Previous authors have not provided consistent homologies of the apodemes, and this has been reflected in the terminology used to label these structures: scheibenförmigen Apodemen (discoid apodeme) (Peus, 1958), Laterales Pumpenapodem (lateral pump apodeme) (LPuAp) (Just,

1973), ventral bridge (Krzeminski and Zwick, 1993), and paramere (Sinclair *et al*, 2007). To understand the homology of these apodemes it is necessary to examine which other structure they are derived from.

Close examination shows that these apodemes emerge from the aedeagal sclerites, extending laterally and posterior. In fact, these structures are contiguous with the aedeagal sclerites, thus some terminology must be rejected: contrary to Sinclair *et al* (2007) these structures do not appear to be derived from the parameres sensu Cumming and Wood (2009). The term ventral bridge (Krzeminski & Zwick, 1993) is also inappropriate, as it implies that the aedeagal sclerites are a ventral extension of the parameres. The structures these apodemes bear closest resemblance to are the lateral ejaculatory processes of lower Brachycera (Sinclair 2000; Cumming & Wood 2009). A recent examination has found lateral ejaculatory processes outside of Brachycera (Sinclair *et al* 2013), and the features and position of the ptychopterid apodemes clearly exhibit homology with these structures.

The orientation of the lateral ejaculatory processes is associated with the size of the sperm pump. In Bittacomorphae and those Ptychopterinae with an enlarged sperm pump the processes are directed transversely lateral, perpendicular to the aedeagal sclerites. In the *Ptychoptera lenis* and *Ptychoptera tibialis* groups the base of the apodeme is directed sublaterally, but the main component of the apodeme is oriented anterior over the sperm sac, parallel to the aedeagal sclerites and ejaculatory apodeme. In the remainder of Ptychopterinae the apodemes are directed anterior at a less severe angle, skirting the margins of the sperm sac. *Ptychoptera alexanderi* shows very weakly developed basal aedeagal apodemes, which are little more than triangular pointed apices on the margin of the aedeagal sclerites and are not as heavily sclerotized as the apodemes found in the remainder of the family.

In those taxa showing transversely oriented lateral ejaculatory processes the base of the apodeme is broad, and tapers towards the apex, where it expands to a disc-like structure. Also

associated with these taxa is a ventral lobe-like portion of the apodeme, most prominently developed in Bittacomorphinae. In some other taxa there reduced structures suggestive of this ventral portion, but further investigation is needed to definitively homologize them. In the taxa with anteriorly directed apodemes the base of the apodeme is narrower and laterally compressed, expanding significantly at the disc-like apex. Finally, in many taxa (the *Ptychoptera contaminata*, *Ptychoptera japonica*, *Ptychoptera pendula* and *Ptychoptera quadrifasciata* groups, as well as *Parapteroptera* and *Ptychoptera alexanderi*) there is a pair of small nodules associated with the base of the basal aedeagal apodemes and aedeagal sclerites.

The actual structure housing the seminal duct has been commonly misidentified in Ptychopteridae (such as Krzeminski & Zwick 1993). The heavily sclerotized, typically conical structure at the apex of the aedeagus (described here as the subapical sclerite) does not carry the sperm internally (Just, 1973; pers. obs.). Rather, the sperm sac opens into a channel formed dorsolaterally by two distinct **aedeagal sclerites** and ventrally by a membrane. There is also a membranous suture dorsally where the aedeagal sclerites meet. The endophallus terminates as a slit at the apex of the aedeagal sclerites, dorsal to the subapical sclerite.

As stated above, the aedeagal sclerites have the lateral ejaculatory processes emerging from their base. In Ptychopterinae the distal portion of the aedeagal sclerites are simple, terminating in a blunt, rounded apex, or sometimes forming a ventral hook-like apical apodeme where it joins with the ventral membrane. Some ptychopterine taxa (the *Ptychoptera pendula* group and *Ptychoptera sculleni*) appear to lack this apical apodeme, which seems to be correlated with a flattening of the aedeagal sclerites. One notable synapomorphy for Ptychopterinae is that the aedeagal sclerites are very short, with a length less than twice that of their width. The subapical sclerite in Ptychopterinae is attached to the ventral membrane at the apex of the aedeagus.

Bittacomorphinae has more elongate aedeagal sclerites, extending posterior at least twice their combined width at the base, especially in *Bittacomorpha*. The apex of the sclerites are rounded like Ptychopterinae, but the apical apodeme is much more prominent and heavily sclerotized, hooking strongly anterior and serving as a point of articulation with the subapical sclerite. In *Bittacomorpha* and *Bittacomorphella jonesi* there is an additional hook-like dorsal apical apodeme projecting posterior above the subapical sclerite, though the function of this dorsal apical apodeme is unknown.

Subapical Sclerite

The final component of the ptychopterid aedeagus is the **subapical sclerite** (Phallusscheide, PhSch in Just, 1973). In a previous study (Krzeminski & Zwick, 1993) this structure has been thought to represent the tubular, intromittent portion of the aedeagus, though as stated above this is not the case. Instead, the subapical sclerite functions as an aedeagal guide or funneling mechanism for the seminal fluid. In particular, the subapical sclerite appears to assist in holding the female genital cavity open during copulation to receive a spermatophore, a function that may be assisted by the parameres. The subapical sclerite takes the form of a heavily sclerotized plate associated with the ventral surface of the apex of the aedeagus, extending posterior to the phallotrema. In Ptychopterinae the subapical sclerite appears to be associated solely with the ventral membrane and the ventral margin of the aedeagal sclerites, while in Bittacomorphinae the subapical sclerite is closely associated and articulates between the apical apodemes of the aedeagal sclerites and the hypandrium.

The subapical sclerite is highly variable in form, and can often be used to distinguish between species. In many species of Bittacomorphinae the subapical sclerite is a tapering cone. The exceptions are an undescribed species of the *Bittacomorphella sackenii* group with a plate-like subapical sclerite, *Bittacomorphella fenderiana* with a reduced, funnel-like subapical sclerite closely associated with the apical apodemes of the aedeagus, and *Bittacomorphella jonesi* in which the subapical sclerite forms a

thin-walled funnel-like structure much more extensively developed than that of *Bittacomorphella fenderiana*. In *Bittacomorpha* the subapical sclerite is massive and triangular, directed dorsoposteriorly.

Ptychopterinae show even greater diversity in the configuration of the subapical sclerite. Aside from the abovementioned forms with lateral lobes, many ptychopterines have an elongate medial spine projecting dorsally from the apex of the subapical sclerite, as seen in the *Ptychoptera japonica* group, *Ptychoptera alexanderi*, and many of the Afrotropical and Southeast Asian ptychopterinae. Other taxa of Ptychopterinae have the subapical sclerite heavily modified.

While Wood (1991) left the homology of the structure unresolved in his diagrams of *Bittacomorpha*, it appears that the subapical sclerite originates from the aedeagus based on the close association with the apex of the aedeagal sclerites. Alternately an argument can be made for a hypandrial origin as in Bittacomorphinae and some Ptychopterinae there are **ventral arms of the subapical sclerite** (Figs. 5d, 6c&d, 7d, 9c&d, 13d&e, 17d) which extend anterolaterally to the junction of the basal and terminal division; this is most pronounced in the aforementioned *Bittacomorphella* sp. near *sackenii*, where the articulation of the subapical sclerite with the apical apodemes of the aedeagus is extremely reduced. However, most members of Ptychopterinae do not show any association between the subapical sclerite and the hypandrium.

In *Parapteroptera* and *Ptychoptera sculleni*, as well as the *Ptychoptera quadrifasciata* and *Ptychoptera pendula* groups, the ventral arms of the subapical sclerite have become detached from the rest of the subapical sclerite, and float between the hypandrium and lateral margin of the subapical sclerite. These **lateral plates** (Figs. 12c&d, 14c&d, 15c&d, 16d) are typically flattened, wide at the ventral margin and tapering dorsally. In *Parapteroptera* and the *Ptychoptera quadrifasciata* group the plates approach the lateral margin of the terminal division, but in the *Ptychoptera pendula* group the plates do not extend as far lateroventrally. In the *Ptychoptera pendula* and *Ptychoptera quadrifasciata*

groups the body of the subapical sclerite is a short, flattened cone extending only slightly beyond the apex of the aedeagal sclerites. *Ptychoptera sculleni* is unique, with the lateral plates remaining at the base of the subapical sclerite and articulating with base of the lateral ejaculatory process. A homologous structure to the lateral plates exists in the *Ptychoptera contaminata* group, where there are two elongate rods fused medially to the subapical sclerite. The configuration seen in the *Ptychoptera contaminata* group probably represents an intermediate state between the attached ventral arm articulating with the hypandrium and the detached lateral plates.

In *Ptychoptera albimana*, *Ptychoptera alina*, and the *Ptychoptera tibialis* group the apical portion of the subapical sclerite is reduced, but the ventral arms are broadened and directed lateroposteriorly to rest against the anterior surface of the terminal division. The lateral wings are broadest in *Ptychoptera albimana* and *Ptychoptera alina*, where they are directly nearly perpendicular to the sagittal axis. In the *Ptychoptera tibialis* group these wings are narrower, shorter, and directed more posterior, and appear to link the movement of the terminal division and the aedeagus. The functional morphology of the wing-like subapical sclerite in *Ptychoptera albimana* and *Ptychoptera alina* is not as clear.

The subapical sclerite of the *Ptychoptera lenis* group is highly distinctive, consisting of a broad base with ventral arms weakly developed and not articulating with the hypandrium, which tapers rapidly to a flattened rod ending in a slightly expanded apex. Furthermore, directly posterior to the phallotrema is a large triangular spur, which largely blocks the opening. The function of this spur is exceedingly difficult to ascertain, as it would appear to hinder spermatophore transmission.

The construction of the aedeagal sclerites and endophallus, the articulated aspect of the subapical sclerite and capability of aedeagal protraction through the lateral ejaculatory processes, suggest a highly modified process of sperm transfer. Ptychopterids have a complex, multichambered

accessory gland complex associated with their soft tissue genital tract (Sinclair *et al* 2007), a feature associated with the production of spermatophores in other taxa and resulting in hypothesized spermatophore production in Ptychopteridae (Sinclair *et al* 2007; Sinclair *et al* 2013). This has been confirmed in *Bittacomorpha clavipes*, as female specimens reared by the authors and allowed to mate have plugs of dried white spermatophores in their genital chamber.

The hypertrophied sperm pump and lateral ejaculatory processes appear to be correlated with the production of spermatophores, as they would allow the transfer of large amounts of seminal fluid of high viscosity. The construction of the aedeagal sclerites also facilitates this transfer, because while the aedeagal sclerites themselves are inflexible the medial membranous suture between them and the flexible ventral membrane allow expansion of the endophallus. Finally, the subapical sclerite serves to hold open the female genital chamber and guide the spermatophore internally.

There is currently no information from the fossil record on the aedeagal complex of extinct ptychopterids.

Intrafamilial Considerations

The placement of Ptychopteridae in lower Diptera has varied across published phylogenies (Henning, 1973; Wood & Borkent, 1989; Oosterbroek & Courtney, 1995; Wiegmann *et al*, 2011). Based on the most recent combined molecular and morphological analysis (Wiegmann *et al*, 2011) Ptychopteridae is sister to Psychodomorpha (including Tanyderidae) + Culicomorpha, though this position is not strongly supported. Previous analyses have placed Ptychopteridae as an ingroup within Psychodomorpha (Henning, 1973) or Ptychopteromorpha (including Tanyderidae) as sister to Culicomorpha (Oosterbroek & Courtney, 1995). Some of the structural interpretations in Ptychopteridae may have wider implications on the assessment of structures in other groups of lower Diptera.

One of the most striking similarities in structure with another group is the presence of epandrial clasping lobes in both Ptychopteridae and Psychodidae. However it seems unlikely based on other characters that these families are sister groups; instead this likely represents convergent evolution of structures. In particular, many surveys of the morphology of Psychodidae have used exemplars from Psychodinae, which is a highly apomorphic subfamily (Curler & Moulton, 2012). The structure of the epandrial claspers in the early diverging groups of Psychodidae differs markedly from those found in Psychodinae (G.R. Curler, pers. comm.). Similarly, as examined above, structure of the epandrial claspers in Ptychopteridae, and particularly Ptychopterinae, is highly variable thus well-articulated character state is probably apomorphic within Ptychopterinae. Furthermore, ptychopterids exhibit a folding clasping action of the epandrium facilitated by the bilobate nature of the structure that is absent in Psychodidae. This supports the assumption that both families evolved epandrial claspers independently.

Lateral ejaculatory processes have been described in Bibionomorpha, throwing into doubt the hypothesis that they represent a synapomorphy of Brachycera (Sinclair *et al*, 2013). The presence of lateral ejaculatory processes of Ptychopteridae expands the phylogenetic distribution of this structure considerably. Examination of this character in other lower Dipteran taxa is merited, to determine if there are other modified forms of the lateral ejaculatory process present. In fact, some taxa in Psychodomorpha *sensu* Wiegmann *et al* (2011) have distinct lateral ejaculatory processes. For example, the paired lobes associated with the sperm sac in the subfamily Blepharicerinae of Blephariceridae probably represent lateral ejaculatory processes (i.e. Courtney, 2000 – Figs. 22, 27, 32, 37, 42, 52, 59-64, 66, 68). Whether lateral ejaculatory processes are present in Tanyderidae is debateable. Anterolateral extensions of the intromittent organ of the aedeagus are present in *Araucoderus*, with a ventral extension of the paramere articulating on the dorsoanterior apex. At this point it is difficult to ascertain whether these represent reduced lateral ejaculatory processes, or are a novel structure derived from the base of the distal portion of the aedeagus. In *Protoplasa* the ventral extension of the paramere is

fused to the anterodorsal portion of the aedeagus. Assessing the presence of lateral ejaculatory processes in Psychodidae is problematic, but there is an association of the ventral portion of the paramere and the base of the aedeagus similar to that seen in Tanyderidae, and there are other possible homologous structures in some of the early diverging subfamilies (G.R. Curler, pers. comm.). Lateral ejaculatory processes are absent in Culicomorpha, Deuterophlebiidae, and Nymphomyiidae due to the membranous aedeagus, while their development in Tipulomorpha needs further examination.

One of the most interesting structures in Ptychopteridae is the subapical sclerite of the aedeagus. This structure resembles the ventral plate found in most Culicomorpha (Wood & Borkent, 1982; Wood, 1991; Sinclair *et al*, 2007). In Culicomorpha the membranous aedeagus is supported by a sclerotized “ventral plate” (Wood & Borkent, 1982), which also serves to open the female genital chamber (Wood, 1978). The subapical sclerite in Ptychopteridae may have a similar function: this is particularly apparent in Bittacomorphinae where the ventral arms of the subapical sclerite articulate off the hypandrium and can be protracted posteroventrally. In many culicomorph taxa the ventral plate is associated with the gonocoxite (Wood & Borkent, 1982; Sinclair *et al* 2007). This is not the case in Ptychopteridae, but there are differences in the configuration of the gonopods and aedeagus which may explain these features. In Culicomorpha the aedeagus is membranous and gonocoxites are often in fairly close contact ventrally, particularly in Chironomoidea; in contrast ptychopterids have well separated gonocoxites and a sclerotized aedeagal complex. It is possible that Culicomorpha utilizes the gonocoxites to articulate the ventral plate because the aedeagus is not rigid, while ptychopterids can articulate the subapical sclerite with the protraction of their well-sclerotized aedeagus. This potential homology merits further investigation.

Sinclair *et al* (2007) examined the soft-tissue genital tract of several species of Ptychopteridae, and found them to possess a complex, multichambered accessory gland complex. Similar

multichambered accessory glands are found in Culicomorpha and Bibionomorpha *sensu stricto* (Sinclair *et al* 2007; Sinclair *et al* 2013), which both produce spermatophores. Based on examination of mated female specimens ptychopterids produce spermatophores as well, and the remainder of the aedeagal morphology reflects this. Though the homology between these taxa is still unresolved (Sinclair *et al* 2013), the similarity of position and function of the subapical sclerite and ventral plate suggests that spermatophore production in Ptychopteridae and Culicomorpha may have evolved in a common ancestor. Unlike Culicomorpha and Bibionomorpha *sensu stricto*, Ptychopteridae retains a sclerotized sperm pump apparatus. However, this may be the result of alternate methods of spermatophore transfer between these taxa. The hypertrophied sperm pump and lateral ejaculatory processes appears have evolved to facilitate the transfer of large quantities of potentially viscous seminal fluids through the comparatively narrow endophallus.

Summary

The morphology of the male genitalia of Ptychopteridae is complex, but structures can be homologized within the family and the larger context of Diptera. The epandrium is a fundamentally bilobate structure which becomes undivided in some species of Bittacomorphinae. In a number of taxa the epandrial lobes have developed an opposing clasping function through epandrial claspers, sometimes with discrete articulation from the remainder of the epandrial lobe; based on preliminary phylogenies opposed clasping structures on the epandrium probably evolved multiple times. These clasping structures do not appear represent cerci, which are undeveloped in the family.

There has been confusion over the structures representing parameres in Ptychopteridae (Wood, 1991 vs. Sinclair *et al*, 2007). Based on the interpretation of the paramere as a structure associated with the gonocoxal lobe (Cumming & Wood, 2009) the paired stylus or plate associated with the gonocoxite represents the true parameres. In Bittacomorphinae the parameres are separate, though in

Bittacomorpha there is an extensive membrane between the parameres extending nearly to their apex. Some taxa in Ptychopterinae also have separate parameres, but there is a trend toward fusion of the parameres into a bridge over the aedeagus, as well as a shift in the point of articulation with the gonocoxite from the gonocoxal apodeme posterior along the mediodorsal margin of the gonocoxite.

The gonopods in Ptychopteridae can be simple or complex. In Bittacomorphinae they tend to be simple tapering stylus with a cluster of stout trichoid sensillae at the apex, while ptychopterines tend toward more complex gonopods with gonocoxal lobes and subdivisions of the gonostylus.

The hypandrium is subdivided into a basal and terminal division in all members of the subfamily. The terminal division can be relatively fixed or well-articulated. The basal division of the hypandrium can take several broad forms: subhemispherical, band-like, or triangular. In Ptychopterinae the terminal division is reoriented dorsally (as well as the aedeagus), while it projects directly posterior in Bittacomorphinae. In some members of Ptychopterinae there are accessory structures associated with the hypandrium such as spathate lobes or an eversible sac which may be useful as phylogenetic characters.

The aedeagus has been modified to pass a spermatophore. The structure is dominated by large sperm pump, filling most of the VIIth abdominal segment in Bittacomorphinae. There is a distinct ejaculatory apodeme, small and spine-like in Bittacomorphinae and ptychopterine taxa with enlarged sperm sacs, massive and fan-like in the remaining Ptychopterinae. The ejaculatory apodeme acts as a lever to compress the sperm sac. The epiphallus is composed of paired aedeagal sclerites, from which a set of lateral ejaculatory processes are derived. These lateral ejaculatory processes function to compress the sperm sac and assist in protracting the aedeagus. At the posterior apex of the aedeagal sclerites there are apical apodemes in Bittacomorphinae and some Ptychopterinae. The subapical sclerite

associated with the ventral apex of the aedeagus and assists in opening the female genital chamber to accept a spermatophore, and is possibly homologous to the ventral plate of Culicomorpha.

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Appendix I: Species groups of *Ptychoptera*

Unfortunately the authors have not had access to material of all the described species of *Ptychoptera* in this study, so some species were placed based on published illustrations of the male genitalia. Putative synapomorphies of each species group *highlighted in italics*.

Parapteroptera (Europe, West Asia, North Africa)

- Ptychoptera (Parapteroptera) agnes* Krzeminski & Zwick, 1993*
- Ptychoptera (Parapteroptera) delmastroi* Zwick & Stary, 2003*
- Ptychoptera (Parapteroptera) handlirschi* Cizek, 1919
- Ptychoptera (Parapteroptera) helena* Peus, 1958
- Ptychoptera (Parapteroptera) lacustris* Meigen, 1930 +
- Ptychoptera (Parapteroptera) longicauda* Tonnoir, 1919
- Ptychoptera (Parapteroptera) paludosa*, Meigen 1804
- Ptychoptera (Parapteroptera) resseli* Theischinger, 1978 **New Combination**
- Ptychoptera (Parapteroptera) silvicola*, Zwyrtsek & Rozkosny, 1967
- Ptychoptera (Parapteroptera) surcoufi* Seguy, 1925*

Diagnosis: Epandrium with *flattened triangular epandrial lobes, well-articulated but poorly sclerotized epandrial claspers without internal musculature*, epiproct does not reach posterior margin of

epandrium. Gonocoxal apodeme with weak dorsal spur, dorsal and medial gonocoxal lobes present, gonostylus complex, apical stylus of gonostylus desclerotized, secondary lobe present. Basal division of hypandrium subhemispherical, eversible sac present, terminal division emarginate ventrally *parameres and gonocoxal lobes fused to supraedeagal membrane. Aedeagus with elliptical ejaculatory apodeme, floating lateral plates of subapical sclerite present.*

***Ptychoptera contaminata* group** (Holarctic)

Ptychoptera contaminata Linnaeus, 1758

Ptychoptera hugoi Tjeder, 1968

Ptychoptera metallica Walker, 1848 +

Ptychoptera minuta Tonnoir, 1919

Ptychoptera scutellaris Wiedemann, 1818

Ptychoptera subscutellaris Alexander, 1921

Diagnosis: *Epandrial lobes dome-like and triangular, epandrial claspers well-articulated with distinctive ventral basal lobe, epiproct does not reach posterior margin of epandrium, quadrate paired subepandrial sclerites present. Gonocoxite sweeping upward to articulate epandrial lobe, dorsal gonocoxal apodeme present; gonostylus with basal lobe forming sickle shaped structure directed anteromedially, often with stout spines, apical stylus with flattened secondary lobe apically. Basal division of hypandrium sub-hemispherical, eversible sac present, terminal division emarginate ventrally, apex forming broad ovoid plate. Aedeagus: subapical sclerite with bar-like lateral lobes attached.*

***Ptychoptera japonica* group** (Japan)

Ptychoptera ichitai Nakamura & Saigusa, 2009*

Ptychoptera japonica Alexander, 1913

Ptychoptera kyushuensis Nakamura & Saigusa, 2009*

Ptychoptera yamato Nakamura & Saigusa, 2009 +

Diagnosis: Nematiform epandrium, epiproct reaching posterior margin of epandrium. Dorsal spur of gonocoxal apodeme present, all gonocoxal lobes absent, *gonostylus with highly reduced basal lobe*, simple apical stylus without secondary lobe. Basal division of hypandrium subhemispherical, *division between basal and terminal divisions of hypandrium weakly developed*, terminal division forming acute spine. Aedeagus with bittacomorphine-like sperm pump, *lateral ejaculatory processes ending in scythe-like apodemes*, subapical sclerite formed to spine.

***Ptychoptera lenis* group** (Western North America, Eastern Asia)

Ptychoptera byersi Alexander, 1916

Ptychoptera daimio, Alexander, 1921

Ptychoptera lenis lenis Osten Sacken, 1877

Ptychoptera lenis coloradensis Alexander, 1937 +

Ptychoptera minor Alexander, 1920

Ptychoptera obscura Peus, 1958

Ptychoptera uta Alexander, 1947

Diagnosis: *Epandrial lobes merged with massive tapering composite epandrial claspers*, ventromesal lobe present on medial surface of epandrial claspers, epiproct reaching posterior margin of epandrium. Paramere broadly attached to dorsal surface of gonocoxite, at most weakly joined medially. Dorsal spur of gonocoxal apodeme extremely well developed, directed anterior, *ventral gonocoxal lobe present*, gonostylus with simple knob-like basal lobe, apical stylus simple with glabrous dorsal ridge, lacking secondary lobe. Basal division of hypandrium band-like, spathate lobes present and often acutely

triangular, terminal division well-articulated, constricted basally, membranous window present.

Aedeagus with *lateral ejaculatory processes bent at a right angle anteriorly, subapical sclerite rod-like and extremely elongate.*

***Ptychoptera quadrifasciata* group** (Eastern North America)

Ptychoptera osceola Alexander, 1959

Ptychoptera quadrifasciata Say, 1824 +

Diagnosis: Epandrium with short triangular epandrial lobes lacking, epiproct reaching posterior margin of epandrium. Dorsal spur of gonocoxal apodeme present, dorsal and medial gonocoxal lobes present, *dorsal surface of gonocoxite detached anteriorly to support paramere*, gonostylus with knob-like basal lobe, apical stylus simple without secondary lobe. Hypandrium with basal division subhemispherical, eversible sac present, terminal division not emarginate ventrally, poorly articulated, spine-like and often with inflated apex. Aedeagus with bittacomorphinae-like sperm pump, subapical sclerite with floating lateral plates present.

***Ptychoptera pendula* group** (Western North America)

Ptychoptera monoensis Alexander, 1947

Ptychoptera pendula Alexander, 1937 +

Ptychoptera townesi Alexander, 1943

Diagnosis: Epandrium with *short triangular epandrial lobes with ventral spine*, epiproct does not reach posterior margin of epandrium, *hypoproct small and ovoid, subepandrial membrane sclerotized into paired subepandrial sclerites covering nearly the entire ventral surface*. Dorsal spur of gonocoxal apodeme present, dorsal and medial gonocoxal lobes present; gonostylus with variable basal lobe, apical stylus of gonostylus desclerotized, pendulant, secondary lobe present. Basal division of

hypandrium subhemispherical, eversible sac present, terminal division of hypandrium emarginate ventrally, poorly articulated, with lateral lobes present subapically. Aedeagus with floating lateral plates present.

***Ptychoptera takeuchii* group** (East Asia, Western North America)

Ptychoptera pallidicostalis Nakamura & Saigusa, 2009*

Ptychoptera takeuchii Tokunaga, 1938*

Ptychoptera yasumatsui Tokunaga, 1939 +

Diagnosis: Nematiform epandrium, epiproct reaching posterior margin of epandrium, *hypoproct small and ovoid*. Dorsal spur of gonocoxal apodeme absent, gonocoxal apodeme rounded, gonocoxite ovoid and enlarged, lacking gonocoxal lobes; gonostylus with complex basal lobe, apical stylus divided, secondary lobe paddle-like. Basal division of hypandrium bandlike, *dorsal apices less the ½ height of terminal division*, spathate lobes absent, terminal division weakly articulated, base constricted, apex quadrate.

***Ptychoptera tibialis* group** (Indian Subcontinent)

Ptychoptera garhwalensis Alexander, 1959

Ptychoptera sikkimensis Alexander, 1965

Ptychoptera tibialis Brunetti, 1911 +

Diagnosis: Epandrial lobes merged with massive blunt composite epandrial claspers, ventromesal lobe present, with *roughened knob dorsally*, epiproct does not reach posterior margin of epandrium. *Dorsal spur of gonocoxal apodeme absent*, gonocoxal lobes absent. Gonostylus simple, basal lobe reduced or simple triangular lobe, dorsal glabrous ridge present. Hypandrium with basal division

band-like, hypandrial spathate lobes small and leaf-like, terminal division constricted basally, well-articulated, membranous window present, apex forming rounded plate. Aedeagus with subapical sclerite with distinct lateral wings.

Afrotropical Ptychopterinae (Sub-Saharan Africa)

Ptychoptera africana Alexander, 1920 +

Ptychoptera camerounensis Alexander, 1921

Ptychoptera capensis Alexander, 1917

*Ptychoptera kosiensis** Stuckenberg, 1983

*Ptychoptera uelensis** Alexander, 1928

Diagnosis: Nematofem epandrium, epiproct reaching posterior margin. Dorsal spur of gonocoxal apodeme present, gonocoxal apodeme rounded, gonocoxal lobes absent, gonostylus typically short. Basal division of hypandrium band-like, spathate lobes present, terminal division constricted basally, well-articulated, membranous window present. *Aedeagus with apex of lateral ejaculatory processes extremely broad, extending dorsally from remainder of structure*, apex of subapical sclerite spine-like. Possibly non-monophyletic.

Malagasy Ptychopterinae (Madagascar)

Ptychoptera madagascariensis Alexander, 1937

Ptychoptera pauliani Alexander, 1957

Ptychoptera robinsoni Alexander, 1957*

Diagnosis: Nematofem epandrium, epiproct reaching posterior margin. Dorsal spur of gonocoxal apodeme present, gonocoxal apodeme rounded, gonocoxal lobes absent; gonostylus with divided basal lobe, apical stylus elongate and fingerlike, secondary lobe present. Hypandrium band-like,

spathate lobe present, terminal division with constricted base, well-articulated, membranous window present. Possibly non-monophyletic.

Southeast Asian Ptychopterinae (Southeast Asia)

Ptychoptera annandalei Brunetti, 1918

Ptychoptera bannaensis Kang, Yao & Wang, 2013*

Ptychoptera bellula Alexander, 1937

Ptychoptera chalybeata Alexander, 1956

Ptychoptera formosensis Alexander, 1924

Ptychoptera gutianshana Yang & Chen, 1995 *

Ptychoptera javensis Alexander, 1937

Ptychoptera lii Kang, Yao & Wang 2013*

Ptychoptera longwangshana Yang & Chen 1998*

Ptychoptera lushuiensis Kang, Yao & Wang 2013*

Ptychoptera malaisei Alexander, 1946

Ptychoptera noonandani Paramonov, 2013*

Ptychoptera praescutellaris Alexander, 1946

Ptychoptera persimilis Alexander, 1947

Ptychoptera qinggouensis Kang, Yao & Wang, 2013*

Ptychoptera sumatrensis Alexander, 1936

Ptychoptera wangae Kang, Yao & Wang, 2013*

Diagnosis: Nematiform epandrium (except *Ptychoptera malaisei*), hypandrium with spathate processes present, terminal division well-articulated. Other characters highly variable.

Notes: This is a non-monophyletic assemblage containing species displaying a diversity of character states which are problematic to assign to other species groups. Some species in this group show affinities to the Afrotropical and Malgasy Ptychopterinae, the *Ptychoptera takeuchii* group, and some are difficult to associate with other species at all. This is further complicated by the fact that the existing material of many of these species is fragmentary. There are several morphotypes that can be identified, but many of the characters which distinguish these morphotypes are known to plesiomorphic or homoplastic in other taxa.

Species near other species groups, though not readily assigned to them

Ptychoptera albimana Fabricius, 1787 + (Europe)

Near the *Ptychoptera lenis* and *Ptychoptera tibialis* groups. Differs in that the epandrium resembles an intermediate between the nematoform and composite types, subapical sclerite short, with lateral processes.

Ptychoptera alina Krzeminski & Zwick, 1993 (Caucasus)

Near the *Ptychoptera lenis* group. Differs in the configuration of the leaf-like hypandrial spatulate lobes and the subapical sclerite short, with lateral processes.

Ptychoptera alexanderi Hancock, 2006 + (Central America)

Near the *Ptychoptera japonica* group. Differs in retaining a sickle-like basal lobe of the gonostylus, otherwise very similar.

Ptychoptera perbona Alexander, 1946 (Southeast Asia)

Southeast Asian ptychopterine. Differs in lacking spatulate lobes of hypandrium. Available material in the study was fragmentary.

Ptychoptera sculleni Alexander, 1943 + (Western North America)

Near the *Ptychoptera pendula* group. Differs in a nematoform epandrium, enlarged gonocoxites with rounded gonocoxal lobes, and the structure of the subapical sclerite.

Species with insufficient material or illustrations for placement

Ptychoptera clitellaria Alexander 1935^

Ptychoptera distincta Brunetti, 1911^

Ptychoptera ichneumonoidea Alexander, 1946^*

Ptychoptera matongoensis Alexander, 1958^

Ptychoptera peusi Joost, 1974*

Ptychoptera xinglongshana Yang, (1996)*

*Specimens not examined by the authors

+ Figured in this publication

^ Known only from female specimens

Appendix II: Morphological Characters of the Male Genitalia of Ptychopterinae

Epandrium

1. Epandrial collar: (0), absent; (1), partial; (2), complete
2. Lateral margin of epandrial collar (epandrial apodeme): (0), simple angle; (1), extended ventrally to articulate with hypandrium
3. Epandrial Apodeme: (0), No joint; (1), Joint near epandrium
4. Epandrium: (0), simple plate; (1), bilobate
5. Epandrial claspers: (0), absent or reduced; (1), present
6. Epandrial clasper articulation: (0), well-articulated; (1), contiguous
7. Epandrial clasper apex: (0), rounded; (1), pad; (2), point; (3), blunt
8. Epandrial clasper sclerotized: (0), well sclerotized; (1), poorly sclerotized

- 9. Epandrial clasper configuration: (0), nematoform; (1), simple curving cylindrical stylus; (2), flattened cylindrical stylus with basal lobes; (3) composite structure articulating on the epiproct
- 10. Ventromesal lobe present on epandrial clasper: (0), absent; (1), present
- 11. Subapical spine: (0), absent; (1), present

Proctiger

- 12. Male cerci: (0), present; (1), absent
- 13. Cercus/Posteromedial stylus form: (0), fleshy lobe (1), triangular acute stylus; (2), low knob; (3), elongate strip bordering epiproct; (4), plate with finger-like extension
- 14. Epiproct: (0), not readily apparent, membranous; (1), easily distinguishable
- 15. Epiproct reaching epandrial collar: (0), present; (1), absent
- 16. Hypoproct: (0), completely membranous; (1), ovoid sclerite suspended in membrane; (2), tongue-like; (3), plate
- 17. Subepandrial sclerite: (0), absent; (1), sclerotized, single sclerite associated with hypoproct; (2), sclerotised, divided into pair sclerites

Gonopod

- 18. Gonocoxal apodeme extent: (0), confined to anterior margin of hypandrium, not extended as narrow process; (1), elongate, extending well beyond anterior margin of hypandrium
- 19. Dorsal spur of gonocoxal apodeme: (0), absent; (1), present
- 20. Dorsal spur of gonocoxal apodeme directed posterior: (0), absent; (1), present
- 21. Apex of gonocoxal apodeme rounded: (0), absent; (1), present
- 22. External portion of gonocoxite curved dorsally to articulate with epandrium: (0), absent; (1), present
- 23. Gonocoxite shape: (0), tapering to gonostylus; (1), expanding to gonostylus; (2), ovoid; (3), cylindrical
- 24. Dorsal gonocoxal lobe: (0), present; (1), absent
- 25. Medial gonocoxal lobe: (0), absent; (1), present
- 26. Ventral gonocoxal lobe: (0), absent; (1), present
- 27. Dorsal surface of gonocoxite: (0), simple; (1), divided, with medial arm supporting paramere

- 28. Basal lobe of gonostylus: (0), absent; (1), present
- 29. Structure of basal lobe of gonostylus: (0), simple, peg-like; (1), simple, knob-like; (2), scythe-like; (3), complex, multiple lobes; (4), ridge
- 30. Apical stylus of gonostylus: (0), simple; (1), secondary lobe present; (2), complex
- 31. Apical stylus of gonostylus: (0), well sclerotized; (1), poorly sclerotized
- 32. Apical stylus of gonostylus pendulant: (0), absent; (1), present
- 33. Secondary lobe of apical stylus of gonostylus (0), absent; (1), present
- 34. Dorsal glabrous ridge of gonostylus: (0), absent; (1), present
- 35. Gonostylus with stout sensillae on medial apex: (0), absent; (1), present, forming ordered lines; (2) present, scattered

Paramere

- 36. Parameres: (0), fused; (1), paired and separate
- 37. Basal portion of paramere directed medially: (0), present; (1), absent
- 38. Base of paramere shifted anterior on dorsal surface of gonocoxite: (0), absent; (1), present
- 39. Paramere attachment with dorsal surface of gonocoxite: (0), broad; (1), narrow; (2), floating on membrane
- 40. Medioposterior extension of paramere: (0), absent; (1) present
- 41. Apices of Paramere: (0), inevident; (1), distinguishable
- 42. Distal portion of paramere angle: (0), directed posterior; (1), directed dorsally; (2), directed ventrally, (3), directed medially

Hypandrium

- 43. Shape of hypandrium: (0), indistinct; (1) roughly triangular; (2), sub-hemispherical band; (3), ringlike band
- 44. Parameres and gonocoxal lobes fused to dorsal hypandrial membrane, forming floor of genital chamber: (0), absent; (1), present
- 45. Eversible sac of hypandrium: (0), absent; (1), present
- 46. Eversible sac extent: (0), extending to base of terminal division; (1), well separated from base of terminal division

- 47. Hypandrial spathate lobes: (0), absent; (1), present
- 48. Terminal division of hypandrium: (0), absent; (1), present
- 49. Terminal division articulation: (0), poorly articulated; (1), well-articulated; (2), almost inevident
- 50. Terminal division shape: (0), divided basally (1), undivided basally
- 51. Base of terminal division constricted: (0), absent; (1), present
- 52. Apex of terminal division: (0), convex plate; (1), triangular; (2), spine-like (3), circular plate; (4), quadrate; (5), with lateral processes
- 53. Dorsolateral extensions of terminal division: (0), absent; (1), present
- 54. Membranous window of terminal division: (0), absent; (1), present
- 55. Membranous window extent: (0), does not extend to terminal division margin; (1), extends to terminal division margin
- 56. Lateral lobules of terminal division: (0), absent; (1), present

Aedeagus

- 57. Terminal division and aedeagus rotated: (0), unrotated; (1), rotated
- 58. Shape of ejaculatory apodeme: (0), narrow, tapering; (1), fanlike; (2), reduced
- 59. Ejaculatory apodeme size: (0), larger than sperm sac; (1), smaller than sperm sac
- 60. Lateral ejaculatory processes: (0), absent; (1), present
- 61. Lateral ejaculatory process orientation: (0), directed laterally; (1), directed anterior at nearly right angle
- 62. Dorsal Margin of Lateral Ejaculatory Process: (0), straight; (1), convex
- 63. Apex of lateral ejaculatory process: (0), rounded apodeme directed anteroventrally; (1), large rounded apodeme directed anterodorsally; (2), scythe-like
- 64. Ventral portion of lateral ejaculatory process: (0), absent; (1), present
- 65. Ventral portion of lateral ejaculatory process: (0), does not extend into sperm sac; (1), extends into sperm sac
- 66. Tubercles associated with base of lateral ejaculatory process: (0), absent; (1), present
- 67. Aedeagal sclerites shortened: (0), more than 2x as long as combined width at base; (1), less than 2x as long as combined width at base

- 68.** Aedeagal Sclerites Flattened: (0), absent; (1), present
- 69.** Aedeagal sclerites medial membrane: (0), aedeagus uniformly sclerotized; (1) aedeagus composed of lateral sclerotized regions joined by medial membrane
- 70.** Ventral apical apodemes of aedeagus: (0), absent; (1), present
- 71.** Ventral plate/Subapical Sclerite: (0), absent; (1), present
- 72.** Subapical sclerite shape: (0) conical; (1), platelike, (2), spine-like; (3), rod-like; (4), reduced; (5), winglike
- 73.** Ventral extension of subapical sclerite: (0), absent; (1), present, attached; (2), present, detached
- 74.** Ventral extension of subapical sclerite forming bar-like structures.
- 75.** Ventral Surface of subapical sclerite: (0), smooth; (1), serrated

Appendix III:

Morphological Matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	
Appendix III:																																			
Morphological Matrix																																			
<i>Tricyphona inconstans</i>	0	-	-	0	0	-	-	-	-	0	1	-	0	-	0	0	0	0	0	-	-	0	0	0	1	0	0	1	0	2	0	0	0	0	0
<i>Araucoderus gloriosus</i>	0	-	-	0	0	-	-	-	-	0	0	0	0	-	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	-	0	0	0	0	0
<i>Protoplasia fitchii</i>	0	-	-	0	0	-	-	-	-	0	0	0	0	-	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	-	0	0	0	1	0
<i>Edwardsina gigantea</i>	0	-	-	0	0	-	-	-	-	0	0	0	0	-	0	0	0	0	0	-	-	0	2	0	0	0	0	0	0	-	1	0	0	0	0
<i>Culicoides crepuscularis</i>	0	-	-	0	0	-	-	-	-	1	0	0	0	-	0	0	0	0	0	-	-	0	0	1	0	0	0	0	0	-	0	0	0	0	0
<i>Dixa modesta</i>	0	-	-	0	0	-	-	-	-	0	0	0	0	-	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	-	0	0	0	0	0
<i>Bittacomorpha clavipes</i>	0	-	-	0	1	0	1	0	0	0	0	0	3	0	-	1	2	1	0	-	0	0	1	1	0	0	0	0	0	-	0	0	0	0	0
<i>Bittacomorphella fenderiana</i>	0	-	-	1	1	0	2	0	1	0	0	1	1	1	1	2	1	0	-	0	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0
<i>Bittacomorphella pacifica</i>	0	0	-	0	1	0	2	0	1	0	0	0	3	0	-	1	1	1	0	-	0	0	3	1	0	0	0	0	0	-	0	0	0	0	0
<i>Ptychoptera africana</i>	1	1	0	1	1	1	2	0	0	0	1	-	1	0	2	2	1	1	0	1	0	1	0	0	1	0	0	0	1	4	1	0	0	1	0
<i>Ptychoptera albimana</i>	1	1	0	1	1	1	0	0	1	1	0	1	1	0	2	1	1	1	0	0	0	0	0	0	1	0	0	0	1	4	1	0	0	1	1
<i>Ptychoptera alexanderi</i>	1	1	1	1	1	0	0	0	0	0	1	-	1	0	2	1	1	0	0	0	0	0	0	1	0	0	0	0	1	2	0	0	0	0	0
<i>Ptychoptera annandalei</i>	2	1	?	1	1	1	0	0	0	0	1	-	1	0	2	?	1	1	0	0	0	0	2	1	0	0	0	0	1	3	1	0	0	1	0
<i>Ptychoptera bellula</i>	2	?	?	1	1	0	0	0	0	1	1	-	1	0	1	2	1	1	0	1	0	1	0	2	0	1	0	0	1	2	0	0	0	0	0
<i>Ptychoptera capensis</i>	2	1	0	1	1	1	0	0	0	0	1	-	1	0	?	?	1	1	0	1	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0
<i>Ptychoptera lenis coloradensis</i>	2	1	0	1	1	1	0	0	3	1	1	0	3	1	0	2	0	1	1	1	0	0	1	0	0	1	0	1	1	0	0	0	0	0	1
<i>P. (Parapterychoptera) lacustris</i>	2	0	-	1	1	0	0	1	2	0	0	1	-	1	1	2	1	1	1	0	0	0	0	1	0	1	0	0	1	3	1	1	0	1	0
<i>Ptychoptera madagascariensis</i>	2	1	0	1	1	1	0	0	0	0	1	1	-	1	0	?	?	1	1	0	1	0	1	0	0	1	0	0	1	1	1	0	0	0	0
<i>Ptychoptera metallica</i>	2	0	-	1	1	0	0	2	0	1	0	2	1	1	0	2	1	1	0	0	1	0	0	1	0	0	0	0	1	3	1	0	0	0	0
<i>Ptychoptera pendula</i>	2	0	-	1	0	-	-	-	-	1	0	1	1	1	1	1	2	1	1	0	0	0	1	0	1	0	0	1	2	1	1	1	1	0	0
<i>Ptychoptera perbona</i>	2	?	?	1	1	1	0	0	0	0	1	-	1	0	?	?	1	1	0	1	0	1	1	1	0	0	0	1	1	1	0	0	0	0	0
<i>Ptychoptera persimilis</i>	2	1	1	1	1	1	0	0	0	0	1	-	1	0	3	0	1	1	0	1	0	1	0	0	1	0	0	0	1	2	1	0	0	1	0
<i>Ptychoptera praescutellaris</i>	2	1	1	1	1	1	0	0	0	0	1	-	1	0	1	1	1	1	0	1	0	1	0	1	0	1	0	0	1	3	1	0	0	0	0
<i>Ptychoptera quadrifasciata</i>	2	0	-	1	0	-	-	-	-	0	1	-	1	0	2	2	1	1	0	0	0	0	1	0	1	0	1	1	1	0	0	0	0	1	1
<i>Ptychoptera sculleni</i>	2	1	0	1	1	1	0	0	0	1	1	-	1	1	2	1	1	0	0	1	0	0	1	0	0	1	0	0	1	1	1	1	1	1	0
<i>Ptychoptera tibialis</i>	1	1	0	1	1	1	3	0	3	1	1	0	4	1	1	2	2	1	0	0	0	0	1	1	0	0	0	0	1	4	0	0	0	0	1
<i>Ptychoptera yamato</i>	2	1	1	1	1	1	0	0	0	0	1	-	1	0	2	1	1	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0
<i>Ptychoptera yasumatsui</i>	2	1	1	1	1	1	0	0	0	0	1	-	1	1	1	1	2	1	0	0	1	0	2	1	0	0	0	0	1	3	1	0	0	1	0

Appendix III:

Morphological Matrix

	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65
<i>Tricyphona inconstans</i>	0	0	0	0	-	0	0	-	4	0	0	-	0	0	-	-	-	-	-	-	-	-	0	0	1	0	-	-	-	-	-
<i>Araucoderus gloriosus</i>	0	0	0	0	-	0	1	0	0	0	0	-	0	0	-	-	-	-	-	-	-	-	0	0	0	0	-	-	-	-	-
<i>Protoplasia fitchii</i>	0	0	0	0	-	0	1	0	0	0	0	-	0	0	-	-	-	-	-	-	-	-	0	0	0	0	-	-	-	-	-
<i>Edwardsina gigantea</i>	0	0	0	0	-	0	0	-	0	0	0	-	0	0	-	-	-	-	-	-	-	-	0	0	0	0	-	-	-	-	-
<i>Culicoides crepuscularis</i>	0	1	1	0	-	0	1	0	4	0	0	-	0	0	-	-	-	-	-	-	-	-	0	2	-	0	-	-	-	-	-
<i>Dixa modesta</i>	0	0	0	0	-	0	0	-	4	0	0	-	0	0	-	-	-	-	-	-	-	-	0	2	-	0	-	-	-	-	-
<i>Bittacomorpha clavipes</i>	2	1	1	0	-	0	1	0	2	0	0	-	0	1	1	0	1	0	0	0	-	1	0	0	1	1	0	0	0	1	1
<i>Bittacomorphella fenderiana</i>	1	1	1	0	-	0	1	1	2	0	0	-	0	1	1	0	0	0	0	0	-	1	0	0	1	1	0	0	0	1	1
<i>Bittacomorphella pacifica</i>	1	1	1	0	-	0	1	0	1	0	0	-	0	1	0	1	0	1	0	0	-	0	0	0	1	1	0	0	0	1	0
<i>Ptychoptera africana</i>	0	0	0	1	1	0	1	1	3	0	0	-	1	1	1	1	1	5	1	1	0	1	1	1	0	1	1	0	1	0	1
<i>Ptychoptera albimana</i>	0	0	0	1	0	0	1	0	3	0	0	-	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1	1
<i>Ptychoptera alexanderi</i>	2	0	0	1	2	0	1	1	2	0	0	-	0	1	0	1	0	2	0	0	-	0	1	0	1	1	0	0	0	0	0
<i>Ptychoptera annandalei</i>	2	0	0	1	1	0	1	1	3	0	0	-	1	1	1	1	1	5	1	1	1	1	0	1	1	0	1	?	?	?	0
<i>Ptychoptera bellula</i>	0	1	0	1	1	0	1	3	3	0	0	-	1	1	1	0	1	1	0	0	-	0	1	1	0	1	1	0	0	0	0
<i>Ptychoptera capensis</i>	0	0	0	1	1	0	1	3	3	0	0	-	1	1	1	1	1	1	?	1	1	0	1	1	0	1	1	0	1	0	-
<i>Ptychoptera lenis coloradensis</i>	0	1	0	1	0	0	1	1	3	0	0	-	1	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	0	0	0
<i>P. (Parapteroptera) lacustris</i>	0	0	0	1	1	0	1	1	2	1	1	0	0	1	0	0	0	2	0	0	-	0	1	1	0	1	1	0	0	0	-
<i>Ptychoptera madagascariensis</i>	0	0	0	1	1	1	1	2	2	0	1	0	0	1	0	0	0	3	0	0	-	0	1	1	0	1	1	0	0	0	-
<i>Ptychoptera metallica</i>	0	0	0	1	2	0	0	-	2	0	1	0	0	1	0	0	0	1	0	0	-	1	1	1	0	1	1	0	0	0	-
<i>Ptychoptera pendula</i>	0	0	0	1	1	0	0	-	2	0	0	-	0	1	0	0	0	5	0	0	-	1	1	1	0	1	?	0	?	?	?
<i>Ptychoptera perbona</i>	2	0	0	1	1	0	1	0	3	0	0	-	1	1	1	1	1	1	1	?	?	1	1	1	0	1	1	?	?	?	0
<i>Ptychoptera persimilis</i>	0	0	0	1	1	1	1	1	0	3	0	0	-	1	1	1	1	1	1	1	?	0	1	1	0	1	0	0	1	?	?
<i>Ptychoptera praescutellaris</i>	0	0	0	1	1	0	1	1	2	0	1	1	0	1	0	1	0	2	0	0	-	0	1	0	1	1	0	0	0	1	0
<i>Ptychoptera quadrifasciata</i>	0	0	0	1	1	0	1	1	2	0	1	1	0	1	0	1	0	2	0	0	-	0	1	0	1	1	0	0	0	1	0
<i>Ptychoptera sculleni</i>	0	0	0	1	2	0	0	-	2	0	1	0	0	1	0	0	0	4	0	0	-	0	1	1	0	1	1	0	0	1	0
<i>Ptychoptera tibialis</i>	0	0	0	1	0	0	1	0	3	0	0	-	1	1	1	1	1	3	1	1	1	0	1	1	0	1	1	1	0	0	-
<i>Ptychoptera yamato</i>	0	0	0	1	1	0	1	0	2	0	0	-	0	1	0	1	0	2	0	0	-	0	1	0	1	1	0	0	2	1	0
<i>Ptychoptera yasumatsui</i>	0	0	0	1	1	0	1	0	2	0	0	-	0	1	0	1	1	4	0	0	-	1	1	1	0	1	1	1	0	0	-

Appendix III:

Morphological Matrix

	66	67	68	69	70	71	72	73	74	75
<i>Tricyphona inconstans</i>	-	0	0	0	0	0	0	-	-	-
<i>Araucoderus gloriosus</i>	-	0	0	0	0	0	-	-	-	-
<i>Protoplasia fitchii</i>	-	0	0	0	0	0	-	-	-	-
<i>Edwardsina gigantea</i>	-	0	0	0	0	0	-	-	-	-
<i>Culicoides crepuscularis</i>	-	-	-	-	-	1	1	0	0	0
<i>Dixa modesta</i>	-	-	-	-	-	1	1	0	0	0
<i>Bittacomorpha clavipes</i>	0	0	0	1	1	1	0	1	0	0
<i>Bittacomorphella fenderiana</i>	0	0	0	1	1	1	1	1	0	0
<i>Bittacomorphella pacifica</i>	0	0	0	1	1	1	0	1	0	0
<i>Ptychoptera africana</i>	0	1	0	1	1	1	2	0	-	0
<i>Ptychoptera albimana</i>	1	1	0	1	1	1	5	1	0	0
<i>Ptychoptera alexanderi</i>	1	1	1	1	1	1	2	1	0	1
<i>Ptychoptera annandalei</i>	?	1	0	1	0	1	2	0	-	0
<i>Ptychoptera bellula</i>	0	1	0	1	0	1	0	0	-	0
<i>Ptychoptera capensis</i>	1	1	0	1	1	1	2	0	-	0
<i>Ptychoptera lenis coloradensis</i>	1	1	0	1	1	1	3	1	0	0
<i>P. (Parapterychoptera) lacustris</i>	1	1	1	1	0	1	2	2	0	0
<i>Ptychoptera madagascariensis</i>	1	1	0	1	0	1	2	1	0	0
<i>Ptychoptera metallica</i>	1	1	1	1	0	1	5	1	1	0
<i>Ptychoptera pendula</i>	1	1	1	1	0	1	1	2	0	0
<i>Ptychoptera perbona</i>	1	1	?	1	?	1	2	0	-	0
<i>Ptychoptera persimilis</i>	1	1	?	1	0	1	0	0	-	0
<i>Ptychoptera praescutellaris</i>	?	1	0	1	0	1	0	0	-	0
<i>Ptychoptera quadrifasciata</i>	1	1	0	1	1	1	0	2	0	0
<i>Ptychoptera sculleni</i>	1	1	1	1	0	1	0	2	0	0
<i>Ptychoptera tibialis</i>	1	1	0	1	1	1	5	1	0	0
<i>Ptychoptera yamato</i>	1	1	0	1	1	1	2	1	0	1
<i>Ptychoptera yasumatsui</i>	1	1	1	1	0	1	0	0	-	0

Table 1: Historical terminology used by workers on Ptychopteridae.

Table 1: Historical terminology used by workers on Ptychopteridae.					
Author	Epandrium			Proctiger	
Fasbender & Courtney	Epandrium	Epandrial Clasper	Subepandrial Sclerite	Epiproct	Hypoproct
Alexander 1927, 1981	9th Tergite	Surstyle/ Tergal Horn	-	-	Proctiger
Just, 1983	Dorsumkomplex	Surstyle	-	-	Afterschuppe
Krzeminski & Zwick, 1993	Fused Tergites VIII/IX	Surstyle	Tegmen	-	Proctiger
Lukashevich, 2008 & 2012	Epandrium	Surstyle	-	-	-
Peus, 1958	Dorsum	Surstyle	-	-	Proctiger
Zwick & Sary, 2003	Last Tergite	Surstyle	-	-	Proctiger
Nakamura & Saigusa, 2009	Epandrium	Lateral Process of Epandrium	-	Posteromedial Triangular-Area	
Author	Paramere	Gonopod			
Fasbender & Courtney	Paramere	Gonopod	Gonocoxite	Gonostylus	
Alexander 1927, 1981	Gonapophysis	-	Basistyle	Dististyle	
Just, 1983	Hakenfortsatz	-	Gonocoxopodit	Stylus	
Krzeminski & Zwick, 1993	Tegmen	Gonopod	Gonocoxite	Gonostylus	
Lukashevich, 2008 & 2012	-	Gonopod	Gonocoxite	Gonostylus	
Peus, 1958	Parameren	-	Coxit	Stylus	
Zwick & Sary, 2003	Tegmen	Gonopod	Gonocoxite	Gonostylus	
Nakamura & Saigusa, 2009	Gonocoxal Bridge	Gonopod	Gonocoxite	Gonostylus	
Author	Hypandrium				
Fasbender & Courtney	Hypandrium	Basal Division	Terminal Division	Eversible Sac	Spathate Lobes
Alexander 1927, 1981	9th Sternite	-	-	-	Accessory Apical-Appendage
Just, 1983	Ventrumkomplex	Ventrum 1/ Sternum 8	Ventrum 2/ Sternum 9	Schwellkörper	-
Krzeminski & Zwick, 1993	Hypandrium	Base of Hypandrium/ Basolateral Sclerites	Apex of Hypandrium/ Medial Sclerite	Membranous Area	Paramedian Lobes
Lukashevich, 2008 & 2012	Hypandrium	-	-	-	-
Peus, 1958	Ventrum	Sternum 8/ Basale Teil	-	Schwellkörper	-
Zwick & Sary, 2003	Hypoproct	-	-	Eversible Sac	-
Nakamura & Saigusa, 2009	Hypandrium	Main part	Median Region/ Cone-like part	Membranous Area	Flap-like Lobes
Author	Aedeagus				
Fasbender & Courtney	Aedeagus	Lateral Ejaculatory Process	Aedeagal Sclerite	Subapical Sclerite	
Alexander 1927, 1981	Aedeagus	Chitinized Arm of Aedeagus	-	-	
Just, 1983	Aedoeagus	Laterales Pumpenapodem	-	Phallusscheide	
Krzeminski & Zwick, 1993	Aedeagus	Paramere	Parameral Bridge	Penis	
Lukashevich, 2008 & 2012	-	-	-	-	
Peus, 1958	Aedoeagus	Scheibenförmigen Apodem	-	-	
Zwick & Sary, 2003	-	-	-	-	
Nakamura & Saigusa, 2009	Aedeagus	-	-	-	

Figure Notes:

All scale bars are 0.5mm unless otherwise noted. The morphological structures figured here are colorized to facilitate the recognition of homologous structures. The color scheme is largely based on Wood (1991), Sinclair *et al* (1994), and Cumming *et al* (1995), modified to better differentiate between structures of Ptychopteridae. Color key:

Grey-brown: Epandrium (♀ Epigynium)
 Light Grey: Epandrial Collar (♀ Epigynial Collar)
 Dark Brown: Cercus/ Posteromedial Stylus
 Tan: Ventromesal Lobe of Epandrium
 Dark Green: Epiproct
 Light Green: Hypoproct
 Light Purple: Base of Paramere
 Dark Purple: Apex of Paramere
 Light Orange: Gonocoxal Apodeme
 Dark Orange: Gonocoxite
 Yellow: Apical Stylus of Gonostylus
 Greenish Yellow: Basal Lobe of Gonostylus
 Light Blue: Terminal Division of Hypandrium (♀ Genital Fork)
 Dark Blue: Basal Division of Hypandrium (♀ Hypogynium)
 Midnight Blue: Eversible Sac/ Membranous Window of Paramere
 Dark Red: Sperm Pump of Aedeagus
 Light Red: Lateral Ejaculatory Processes and Aedeagal Sclerites
 Pink: Subapical Sclerite

Figure Abbreviations:

AEA: Ejaculatory Apodeme, AES: Aedeagal Sclerite, AEV: Ventral Apical Apodeme of Aedeagus, ALP: Lateral Ejaculatory Process AS: Sperm Sac, ASA, Subapical Sclerite of Aedeagus, ASP: Lateral Plate of Subapical Sclerite, AVA: Ventral Arm of Subapical Sclerite, CRC: Cercus, ECA: Epandrial Apodeme, ECL: Epandrial Collar, ECP: Epandrial Clasper, EL: Epandrial Lobe, EPI: Epiproct, EPG: Epigynium, EPP: Epandrial Plate, EPS: Posteromedial Stylus of Epandrium, ESS, Subapical Spine of Epandrium, EVL: Ventromesal Lobe of Epandrium, GAS: Apical stylus of gonostylus, GBL: Basal lobe of gonostylus, GCT: Gonocoxite, GCA: Gonocoxal Apodeme, GDS: Dorsal spur of gonocoxal apodeme, GLD: Dorsal Gonocoxal Lobe, GLM: Medial Gonocoxal Lobe, GLV: Ventral Gonocoxal Lobe, GSL: Secondary lobe of Apical Stylus of Gonostylus, GFK: Genital Fork, GST: Gonostylus, HBD: Basal Division of Hypandrium, HES: Eversible sac of Hypandrium, HLT: Lateral lobule of terminal division, HMW: Membranous Window of Terminal Division, HPG: Hypogynium, HSL: Spathate Lobe of Hypandrium, HTD: Terminal Division of Hypandrium, HTE: Lateral Extension of Terminal Division, HVL: Hypogynial Valves, HYP: Hypoproct, PMB: Paramere Base, PME: Posteromedial Extension of Paramere, PPA: Apical Process of Paramere

Figure Captions

Figure 1. Maximum Parsimony phylogeny based on male genitalia characters. Bremer support values are shown above the branch, Bootstrap support values below. Bootstrap support under 50 is not shown.

Figure 2. Maximum Parsimony phylogeny tracing character state changes of the male genitalia within Ptychopteridae.

Figure 3. Bayesian Inference phylogeny based on male genitalia characters. Posterior probabilities are shown below the branch.

Figure 4. Bayesian Inference phylogeny tracing character state changes of the male genitalia within Ptychopteridae.

Figure 5. *Bittacomorpha clavipes* Fabricius, 1781, male. a. Male genitalia, lateral view; b. Epandrium, dorsal view; c. Aedeagus, dorsal view; d. Aedeagus, lateral view; e. Hypandrium, ventral view; f. Gonopod, lateral view; g. Gonopod, dorsal view; h. Paramere, lateral view. Scale bars 0.5mm.

Figure 6. *Bittacomorphella fenderiana* Alexander, 1947, male. a. Male genitalia, lateral view; b. Epandrium, dorsal view; c. Aedeagus, dorsal view; d. Aedeagus, lateral view; e. Hypandrium, ventral view; f. Gonopod, lateral view; g. Gonopod, dorsal view; h. Paramere, lateral view; i. Paramere, dorsal view. Scale bars 0.5mm.

Figure 7. *Bittacomorphella pacifica* Alexander, 1958, male (*Bittacomorphella sackenii* group). a. Male genitalia, lateral view; b. Epandrium, dorsal view; c. Aedeagus, dorsal view; d. Aedeagus, lateral view; e. Hypandrium, ventral view; f. Gonopod, lateral view; g. Gonopod, dorsal view; h. Paramere, lateral view. Scale bars 0.5mm.

Figure 8. *Ptychoptera africana* Alexander, 1920, male. a. Male genitalia, lateral view; b. Epandrium, dorsal view; c. Aedeagus, anterior view; d. Aedeagus, lateral view; e. Hypandrium, posterior view; f. Gonopod, lateral view; g. Gonopod, dorsal view; h. Paramere, dorsal view; i. Paramere, anterior view. Scale bars 0.5mm.

Figure 9. *Ptychoptera albimana* Fabricius, 1787, male. a. Male genitalia, lateral view; b. Epandrium, dorsal view; c. Aedeagus, anterior view; d. Aedeagus, lateral view; e. Hypandrium, posterior view; f. Gonopod, lateral view; g. Gonopod, dorsal view; h. Paramere, dorsal view; i. Paramere, anterior view. Scale bars 0.5mm.

Figure 10. *Ptychoptera alexanderi* Hancock, 2006, male. a. Male genitalia, lateral view; b. Epandrium, dorsal view; c. Aedeagus, anterior view; d. Aedeagus, lateral view; e. Hypandrium, posterior view; f. Gonopod, lateral view; g. Gonopod, dorsal view; h. Paramere, dorsal view; i. Paramere, anterior view. Scale bars 0.5mm, except h & i 0.25mm.

Figure 11. *Ptychoptera lenis coloradensis* Alexander, 1937, male (*Ptychoptera lenis* group). a. Male genitalia, lateral view; b. Epandrium, dorsal view; c. Aedeagus, anterior view; d. Aedeagus, lateral view;

e. Hypandrium, posterior view; f. Gonopod, lateral view; g. Gonopod, dorsal view; h. Paramere, dorsal view. Scale bars 0.5mm.

Figure 12. *Ptychoptera (Parptychoptera) lacustris* Meigen, 1830, male. a. Male genitalia, lateral view; b. Epandrium, dorsal view; c. Aedeagus, anterior view; d. Aedeagus, lateral view; e. Hypandrium, posterior view; f. Gonopod, lateral view; g. Gonopod, dorsal view; h. Paramere, dorsal view. Scale bars 0.5mm.

Figure 13. *Ptychoptera metallica* Walker, 1848, male (*Ptychoptera contaminata* group). a. Male genitalia, lateral view; b. Epandrium, lateral view; c. Epandrium, dorsal view; d. Aedeagus, anterior view; e. Aedeagus, lateral view; f. Hypandrium, posterior view; g. Gonopod, lateral view; h. Gonopod, dorsal view; i. Paramere, dorsal view; j. Paramere, anterior view. Scale bars 0.5mm.

Figure 14. *Ptychoptera pendula* Alexander, 1937, male (*Ptychoptera pendula* group). a. Male genitalia, lateral view; b. Epandrium, dorsal view; c. Aedeagus, anterior view; d. Aedeagus, lateral view; e. Hypandrium, posterior view; f. Gonopod, lateral view; g. Gonopod, dorsal view; h. Paramere, dorsal view. Scale bars 0.5mm.

Figure 15. *Ptychoptera quadrifasciata* Say, 1824, male (*Ptychoptera quadrifasciata* group). a. Male genitalia, lateral view; b. Epandrium, dorsal view; c. Aedeagus, anterior view; d. Aedeagus, lateral view; e. Hypandrium, posterior view; f. Gonopod, lateral view; g. Gonopod, dorsal view; h. Paramere, dorsal view; i. Paramere, anterior view. Scale bars 0.5mm.

Figure 16. *Ptychoptera sculleni* Alexander, 1943, male. a. Male genitalia, lateral view; b. Epandrium, dorsal view; c. Aedeagus, anterior view; d. Aedeagus, lateral view; e. Hypandrium, posterior view; f. Gonopod, lateral view; g. Gonopod, dorsal view; h. Paramere, dorsal view. Scale bars 0.5mm.

Figure 17. *Ptychoptera tibialis* Brunetti, 1911, male (*Ptychoptera tibialis* group). a. Male genitalia, lateral view; b. Epandrium, dorsal view; c. Aedeagus, anterior view; d. Aedeagus, lateral view; e. Hypandrium, posterior view; f. Gonopod, lateral view; g. Gonopod, dorsal view; h. Paramere, dorsal view. Scale bars 0.5mm.

Figure 18. *Ptychoptera yamato* Nakamura & Saigusa, 2009, male (*Ptychoptera japonica* group). a. Male genitalia, lateral view; b. Epandrium, dorsal view; c. Aedeagus, anterior view; d. Aedeagus, lateral view; e. Hypandrium, posterior view; f. Gonopod, lateral view; g. Gonopod, dorsal view; h. Paramere, dorsal view. Scale bars 0.5mm.

Figure 19. *Ptychoptera yasumatsui* Tokunaga, 1939, male (*Ptychoptera takeuchii* group). a. Male genitalia, lateral view; b. Epandrium, dorsal view; c. Aedeagus, anterior view; d. Aedeagus, lateral view; e. Hypandrium, posterior view; f. Gonopod, lateral view; g. Gonopod, dorsal view; h. Paramere, dorsal view.

Figure 20. *Bittacomorpha clavipes* Fabricius, 1781, female. a. Female genitalia, lateral view; b. Epigynium, dorsal view; c. Hypogynium, ventral view. *Bittacomorphella fenderiana* Alexander, 1947, female. d. Female genitalia, lateral view; e. Epigynium, dorsal view; f. Hypogynium, ventral view.

Figure 21. *Ptychoptera metallica* Walker, 1848, female (*Ptychoptera contaminata* group). a. Female genitalia, lateral view; b. Epigynium, dorsal view; c. Hypogynium, ventral view. *Ptychoptera lenis coloradensis* Alexander, 1947, female (*Ptychoptera lenis* group). d. Female genitalia, lateral view; e. Epigynium, dorsal view; f. Hypogynium, ventral view.

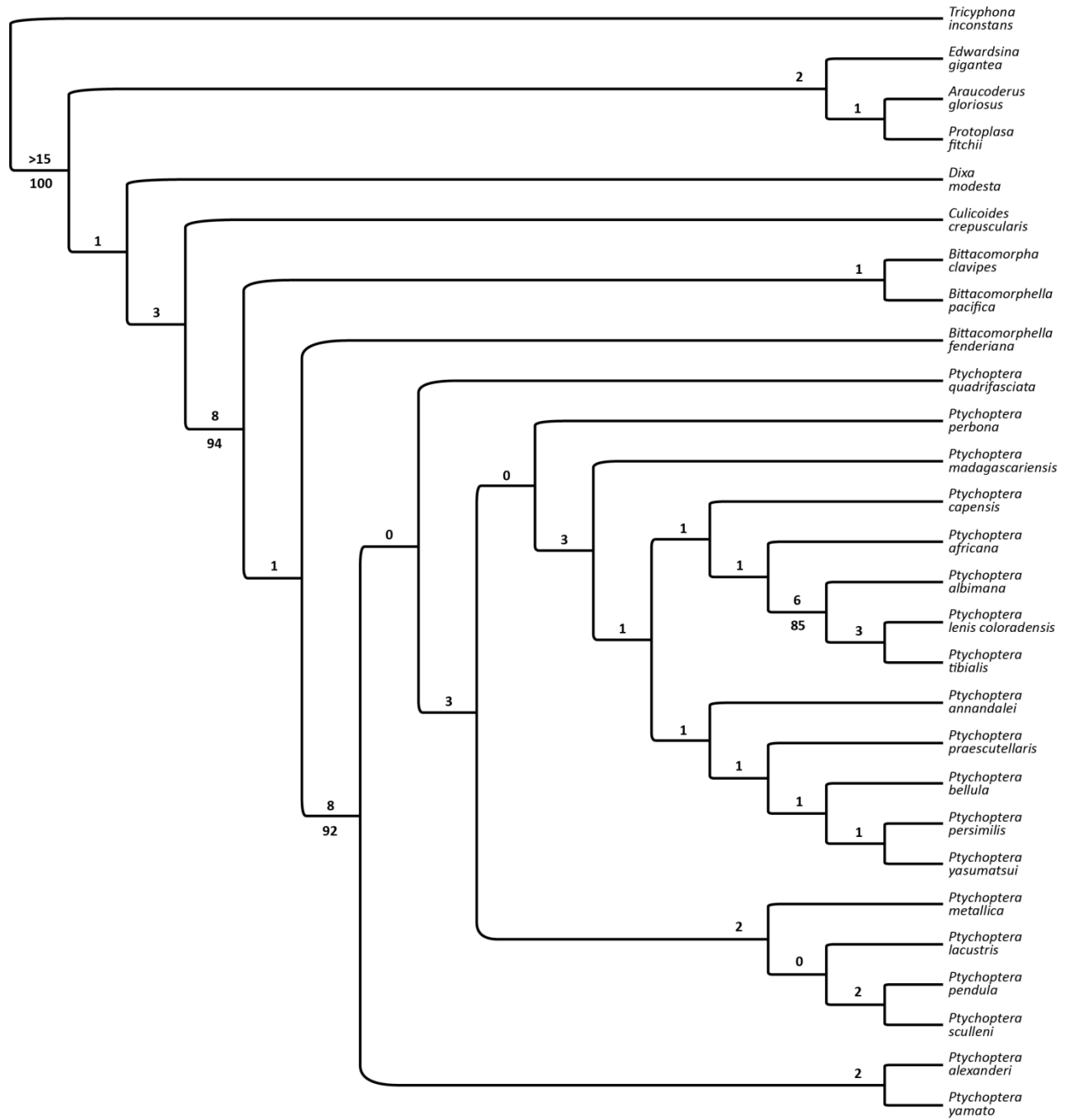


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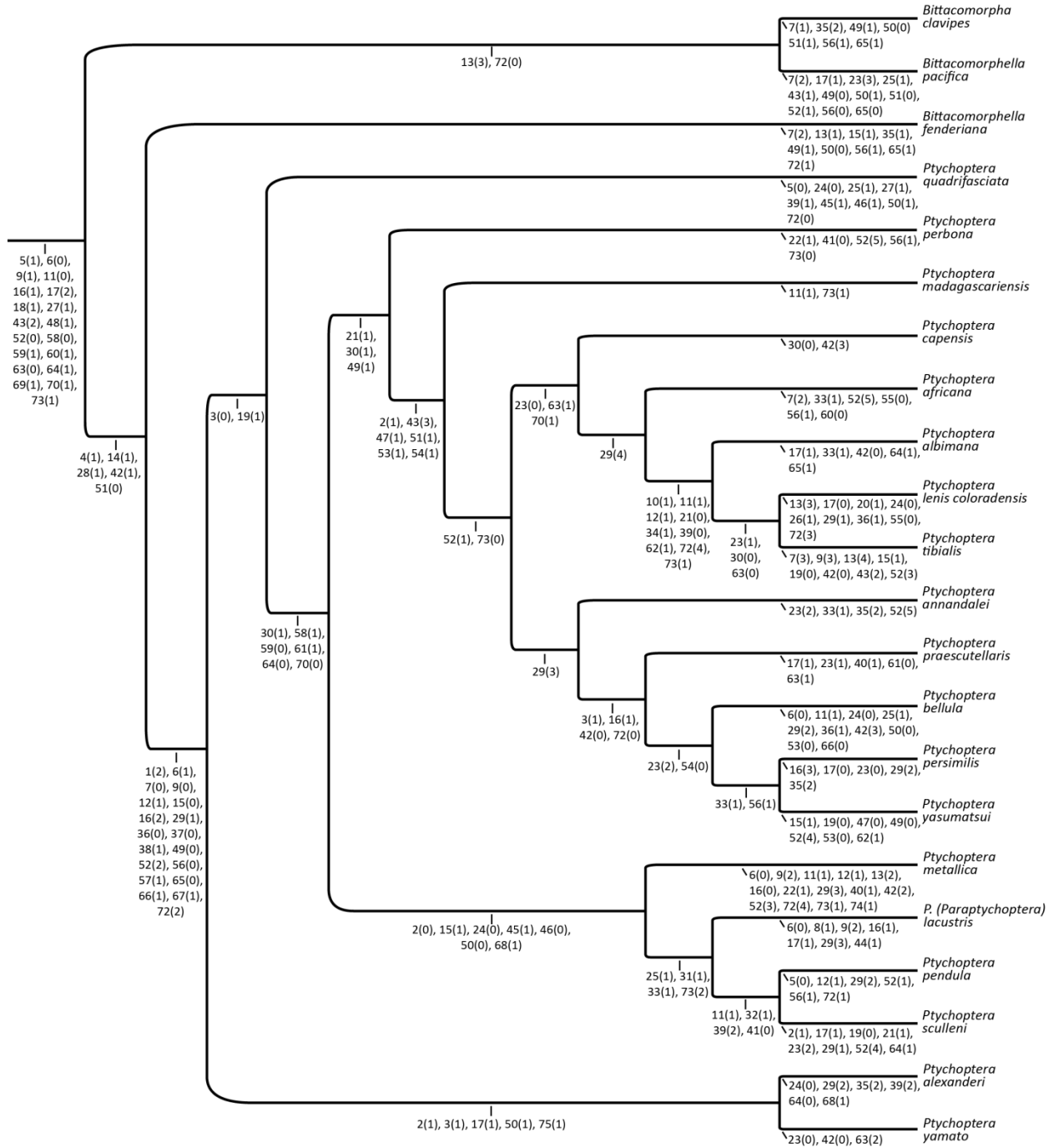


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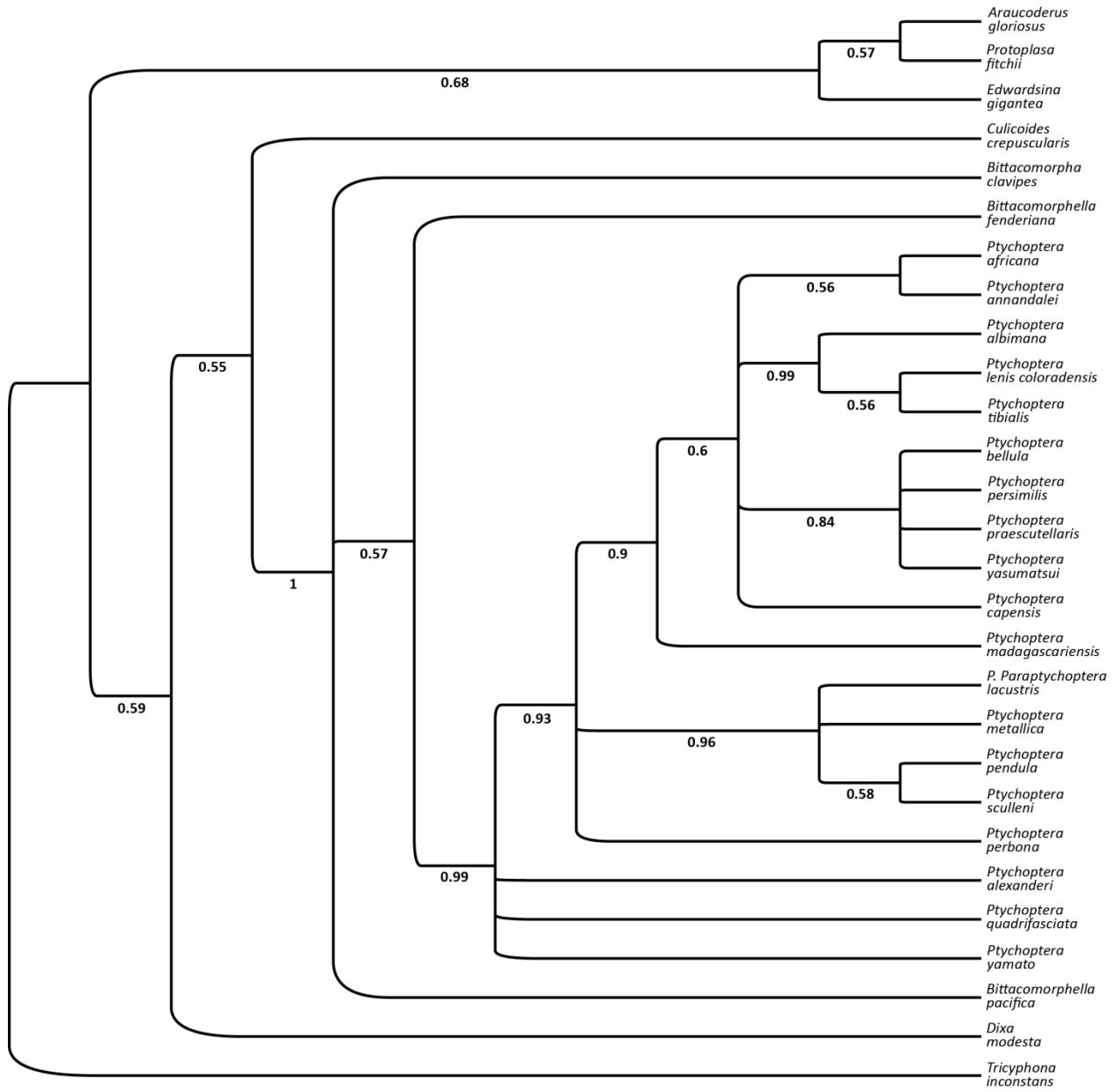


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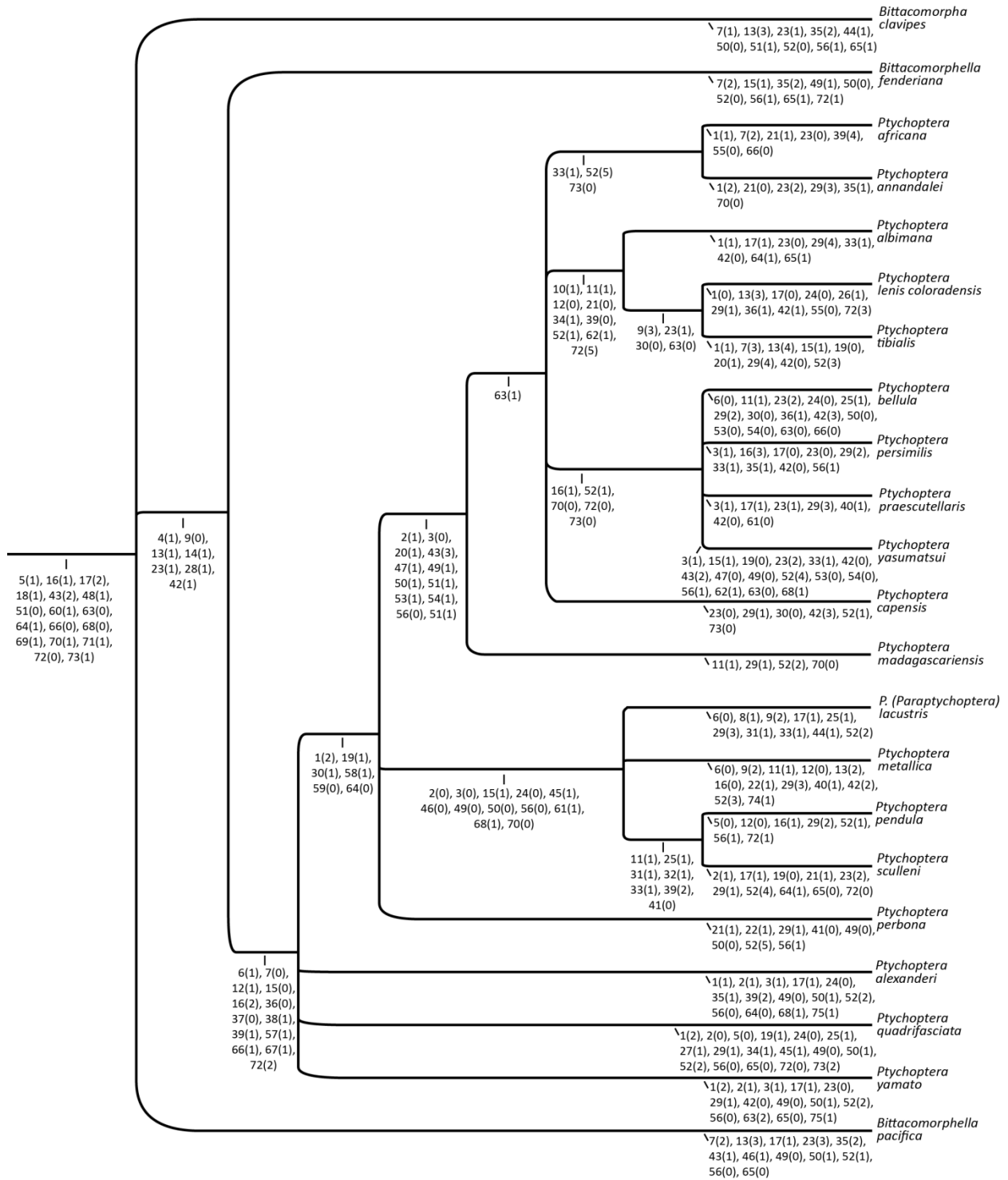


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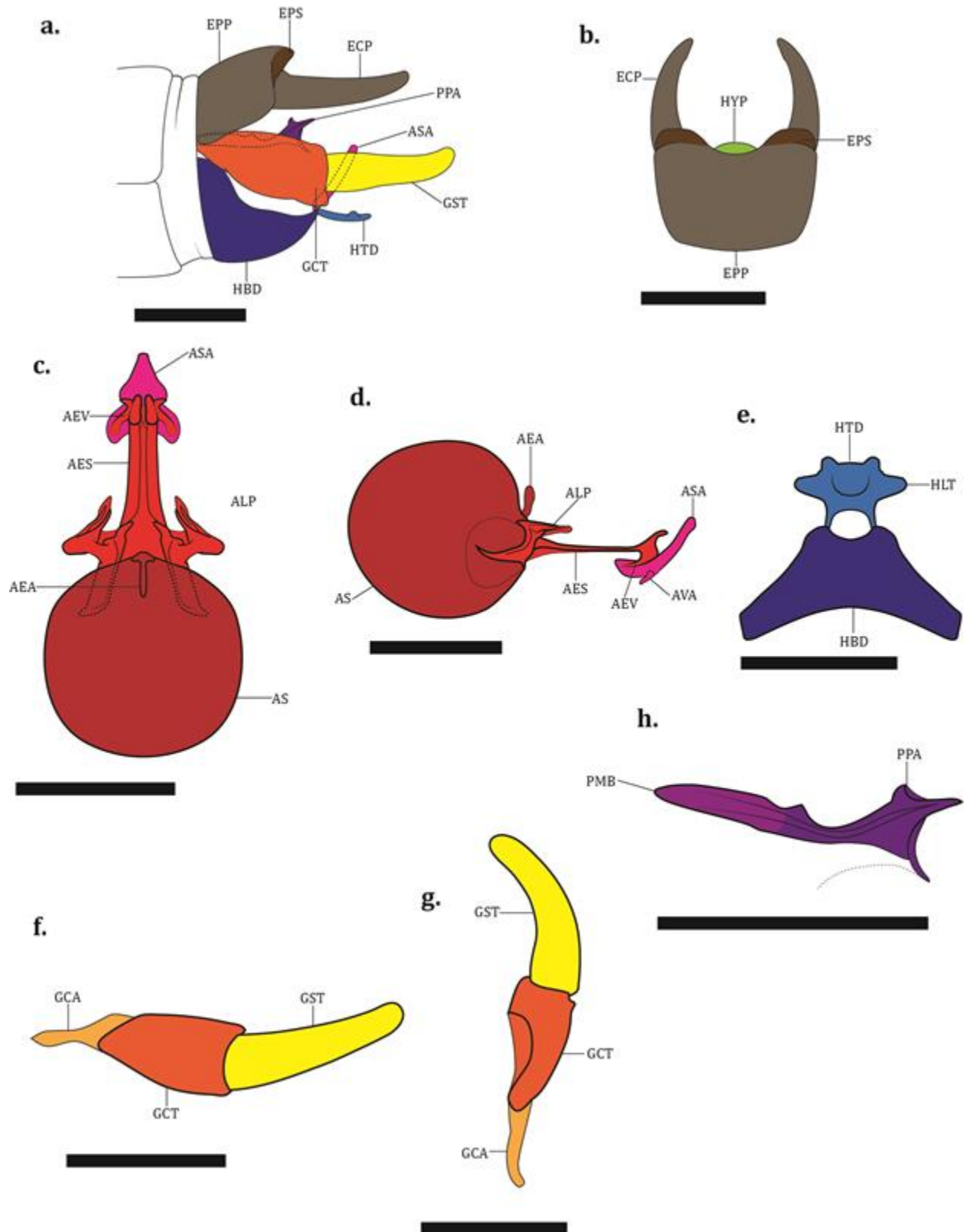


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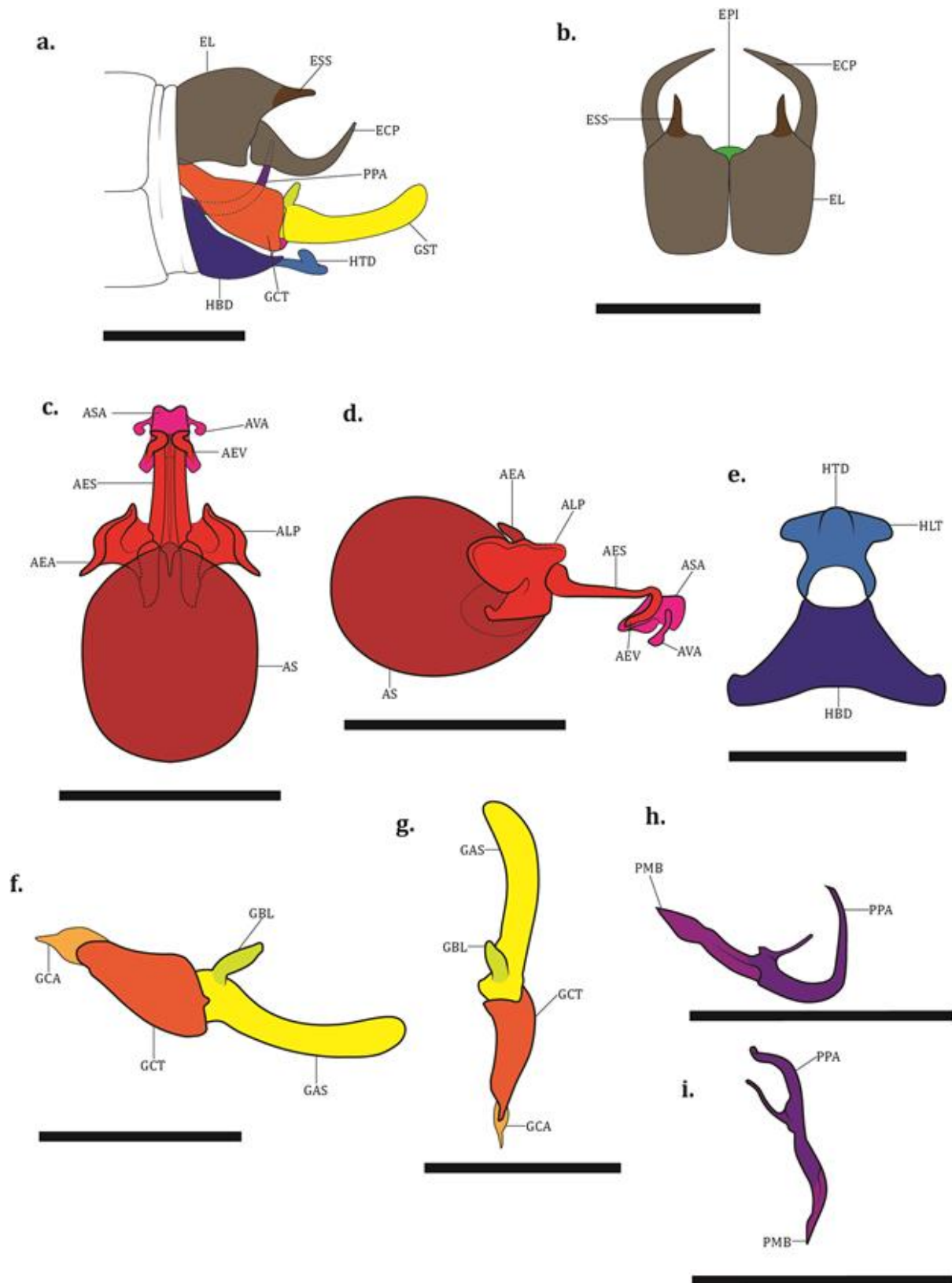


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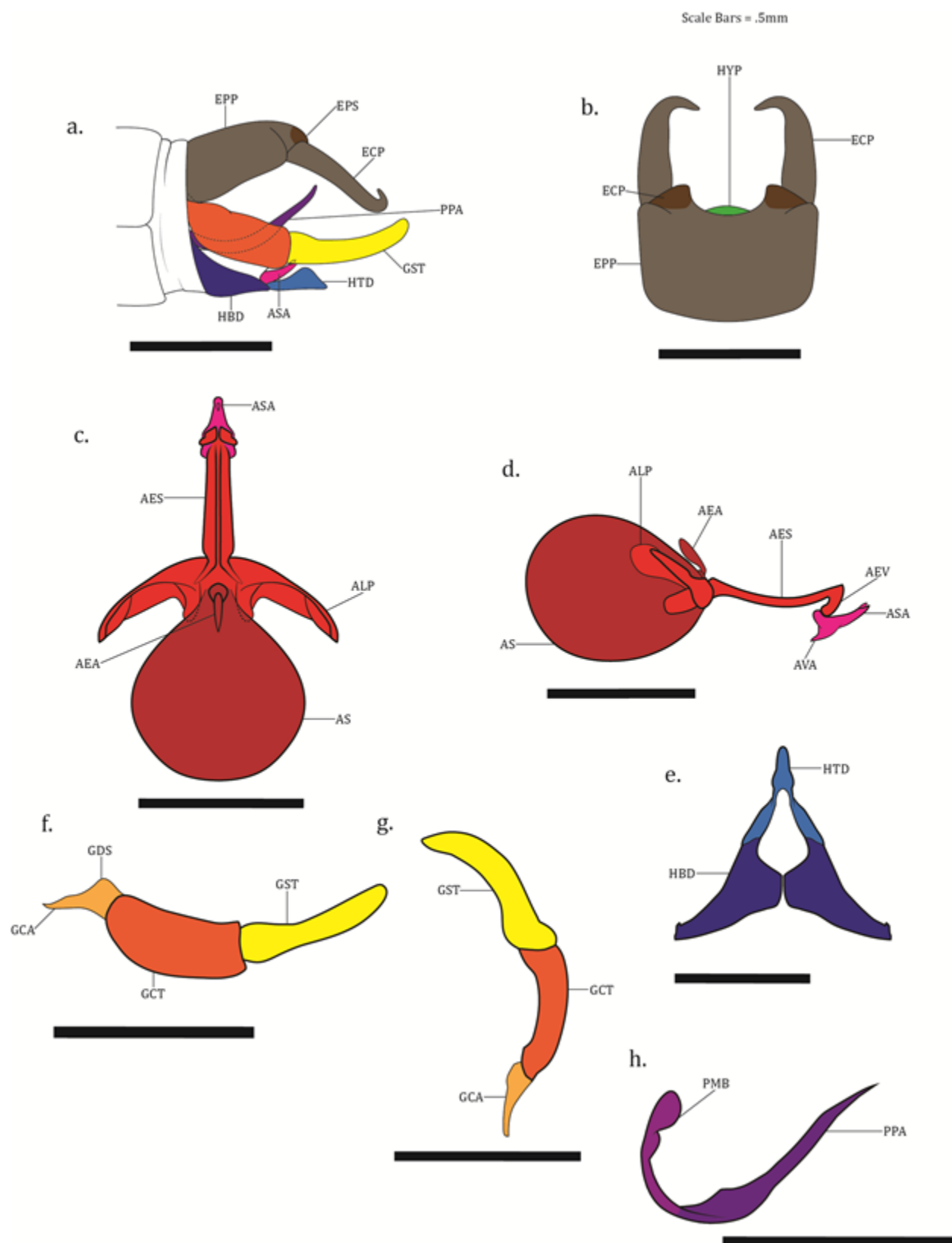


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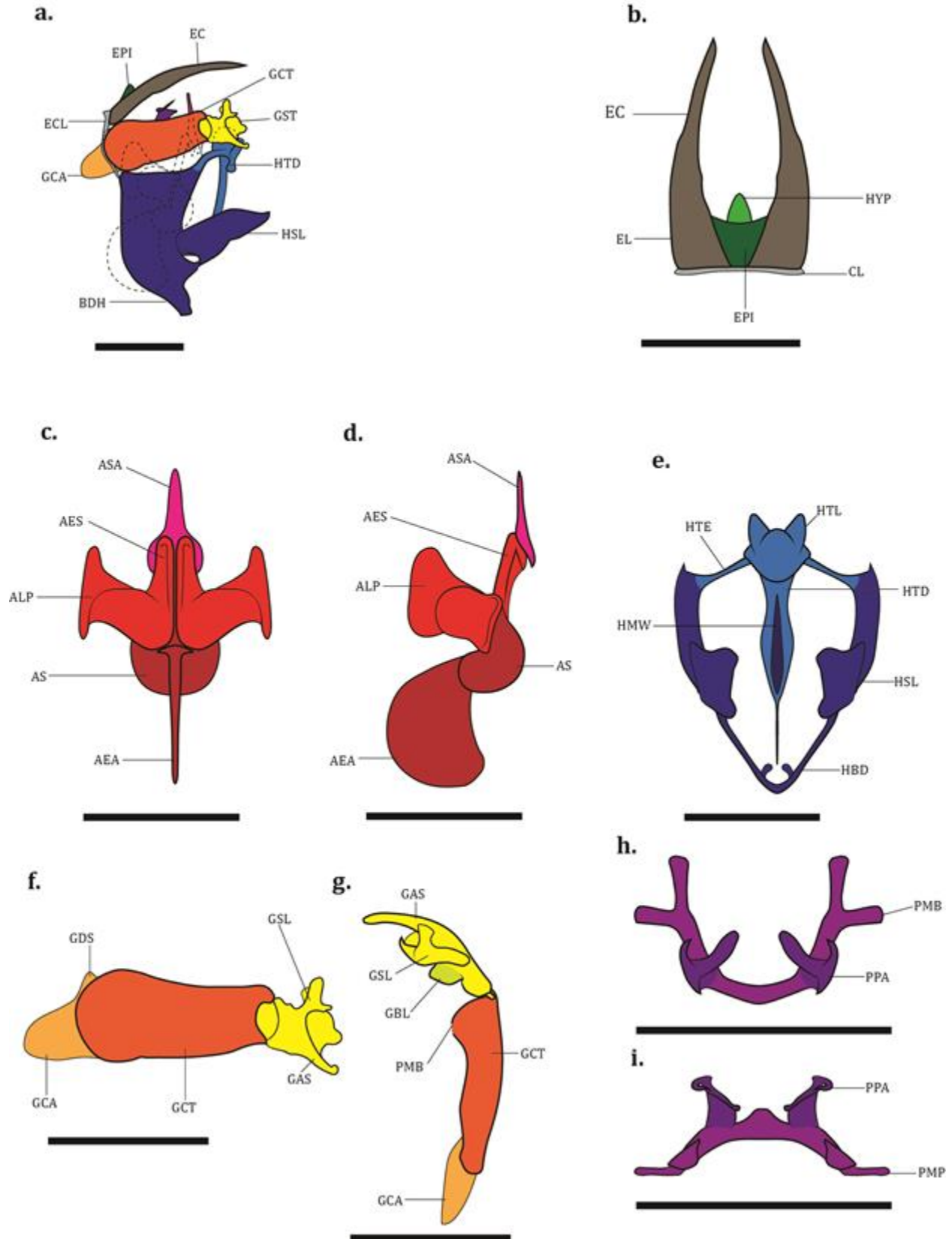


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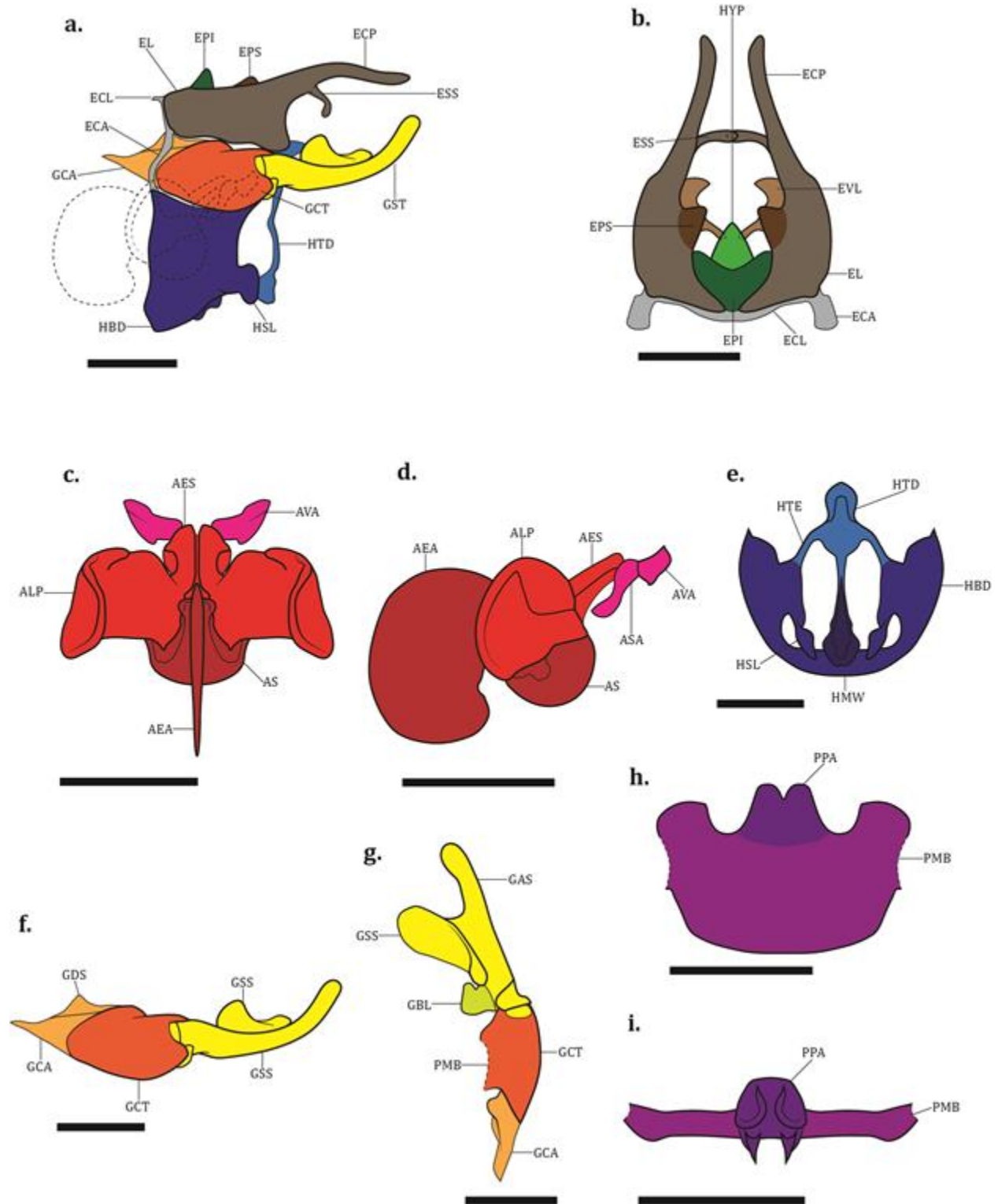


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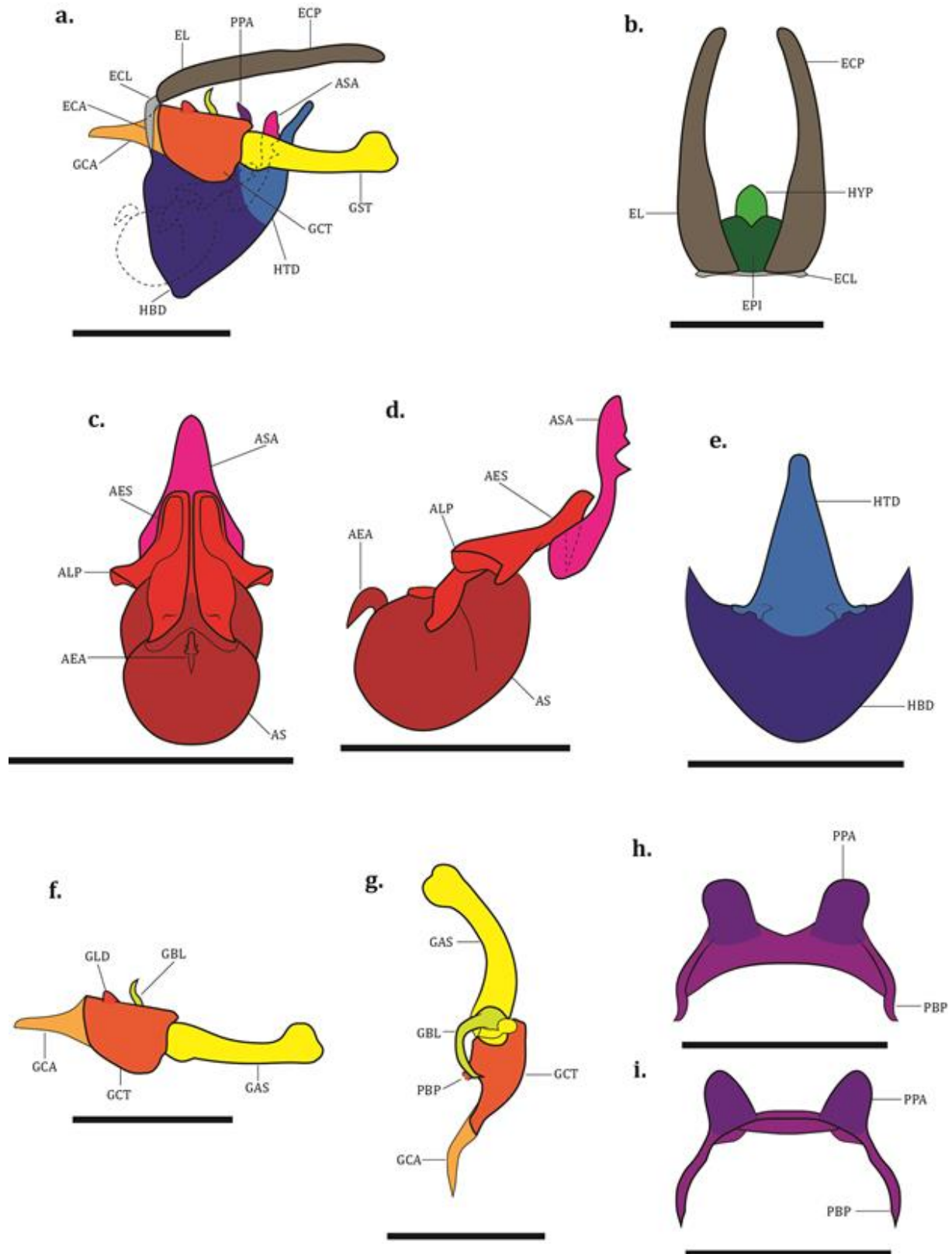


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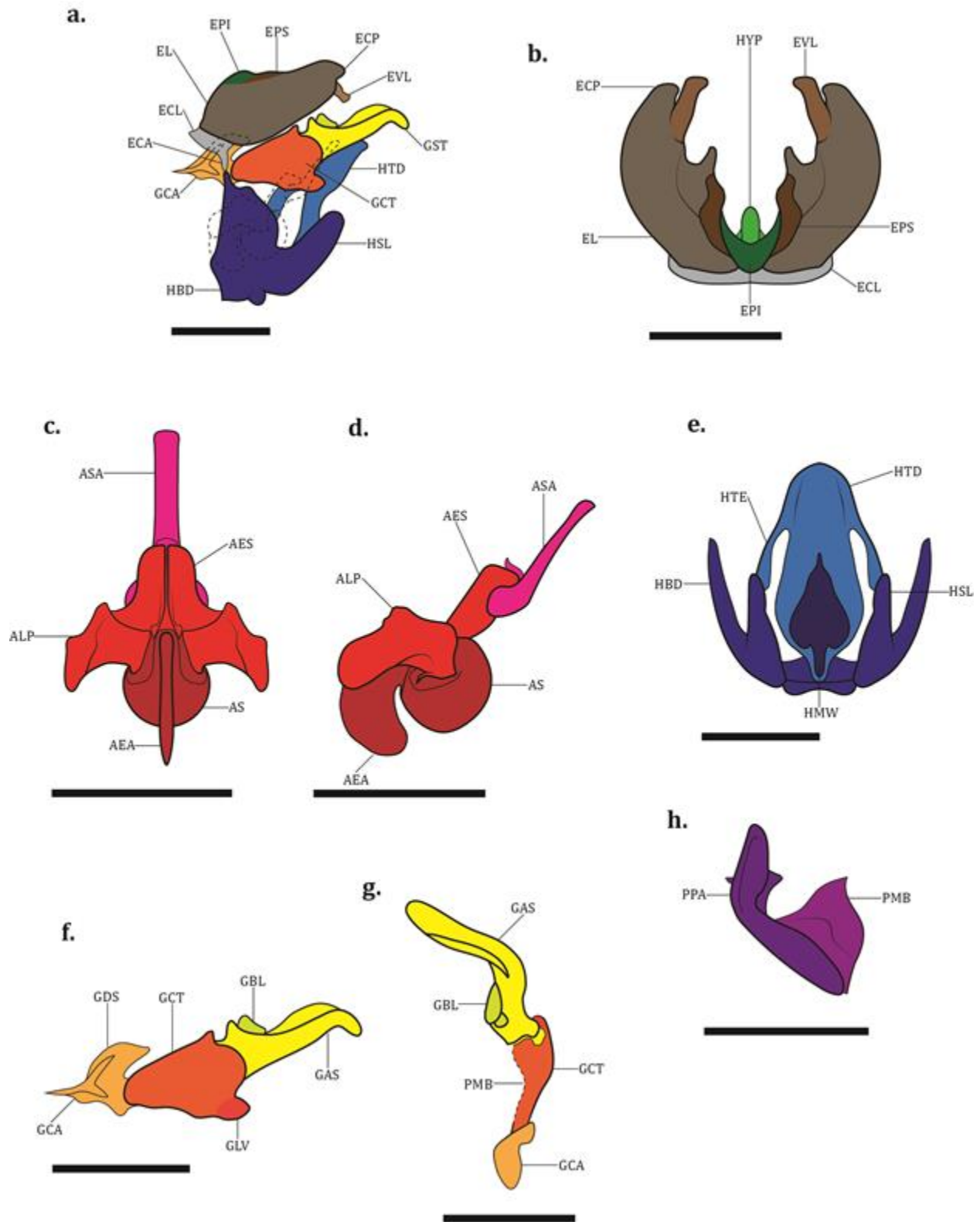


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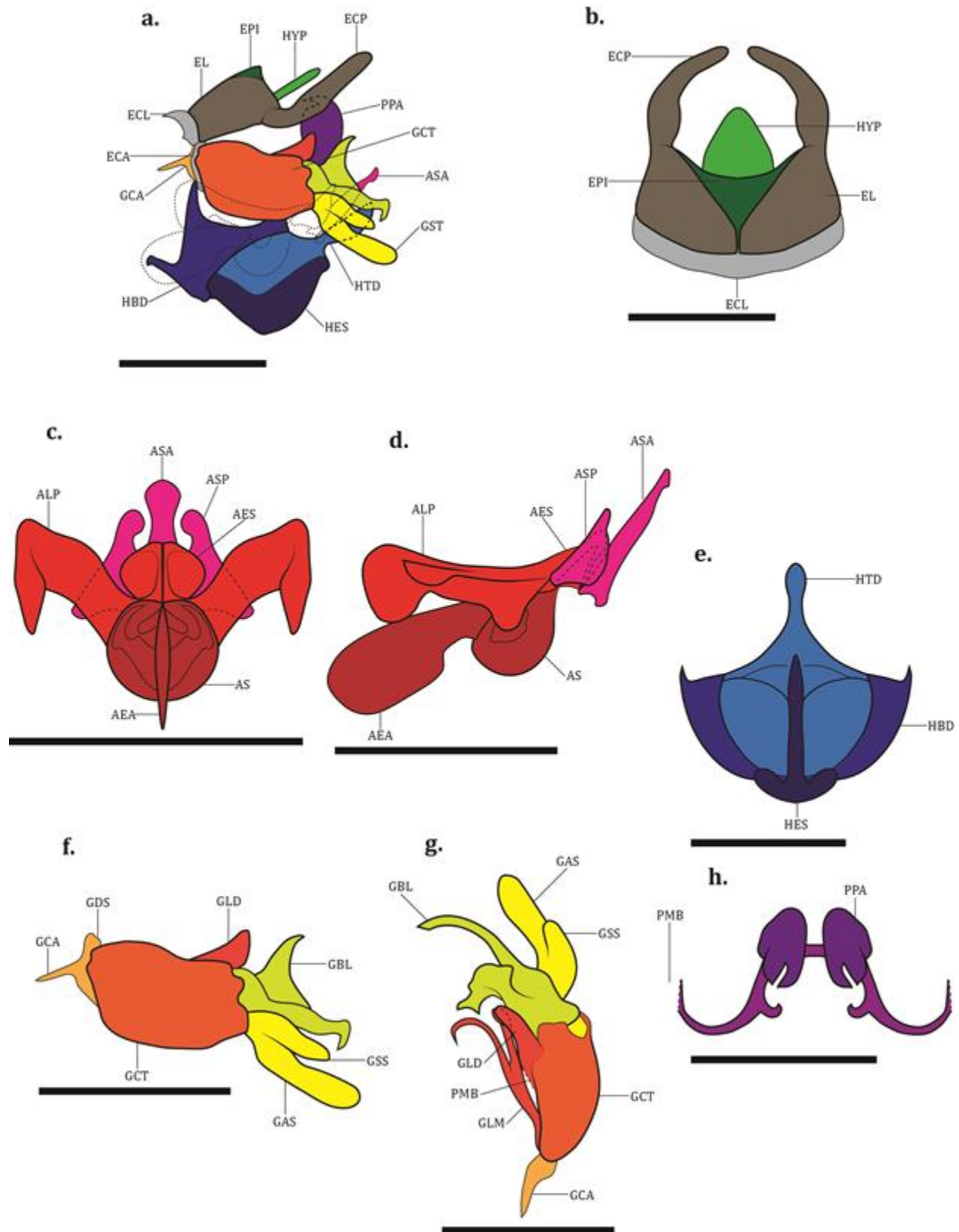


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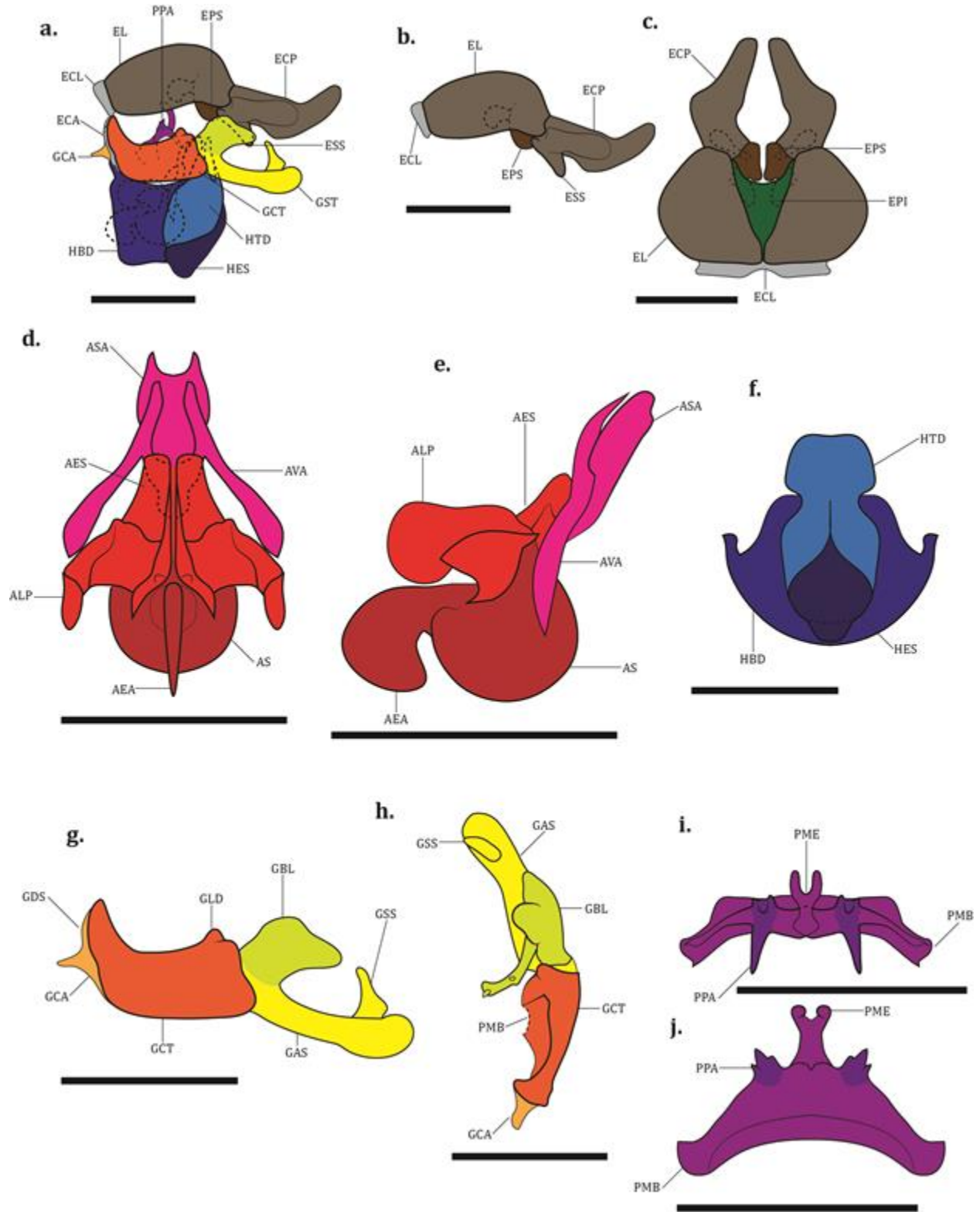


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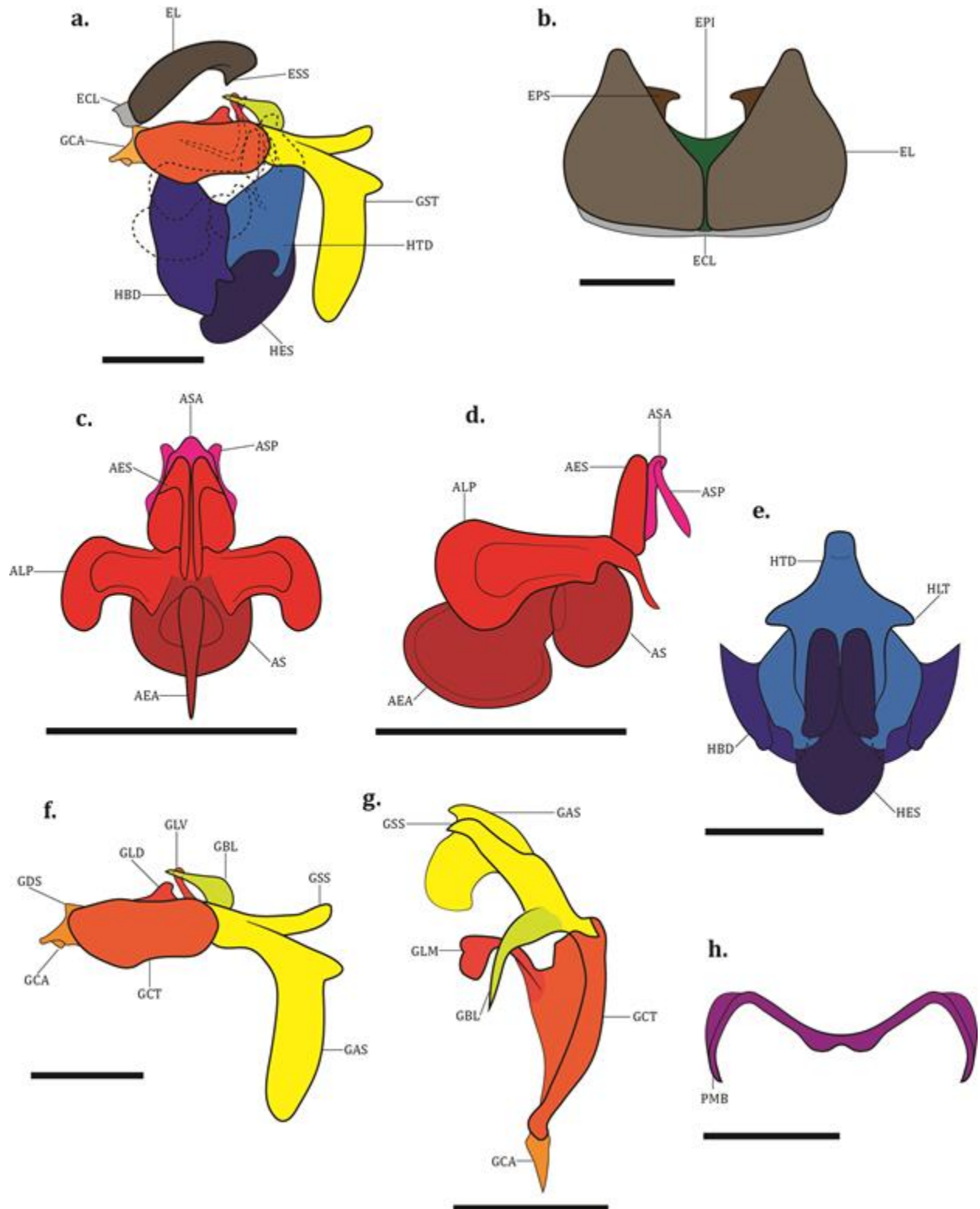


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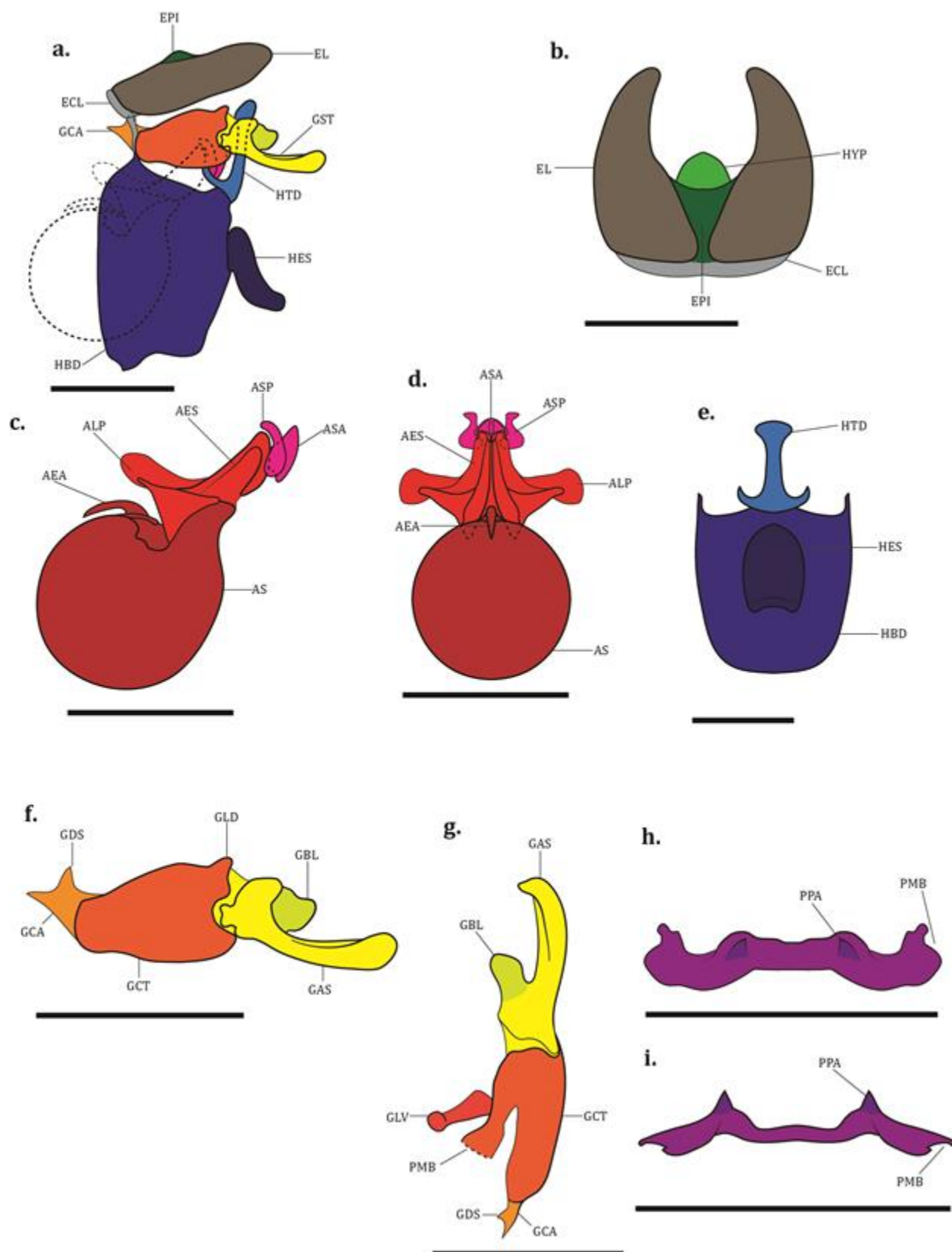


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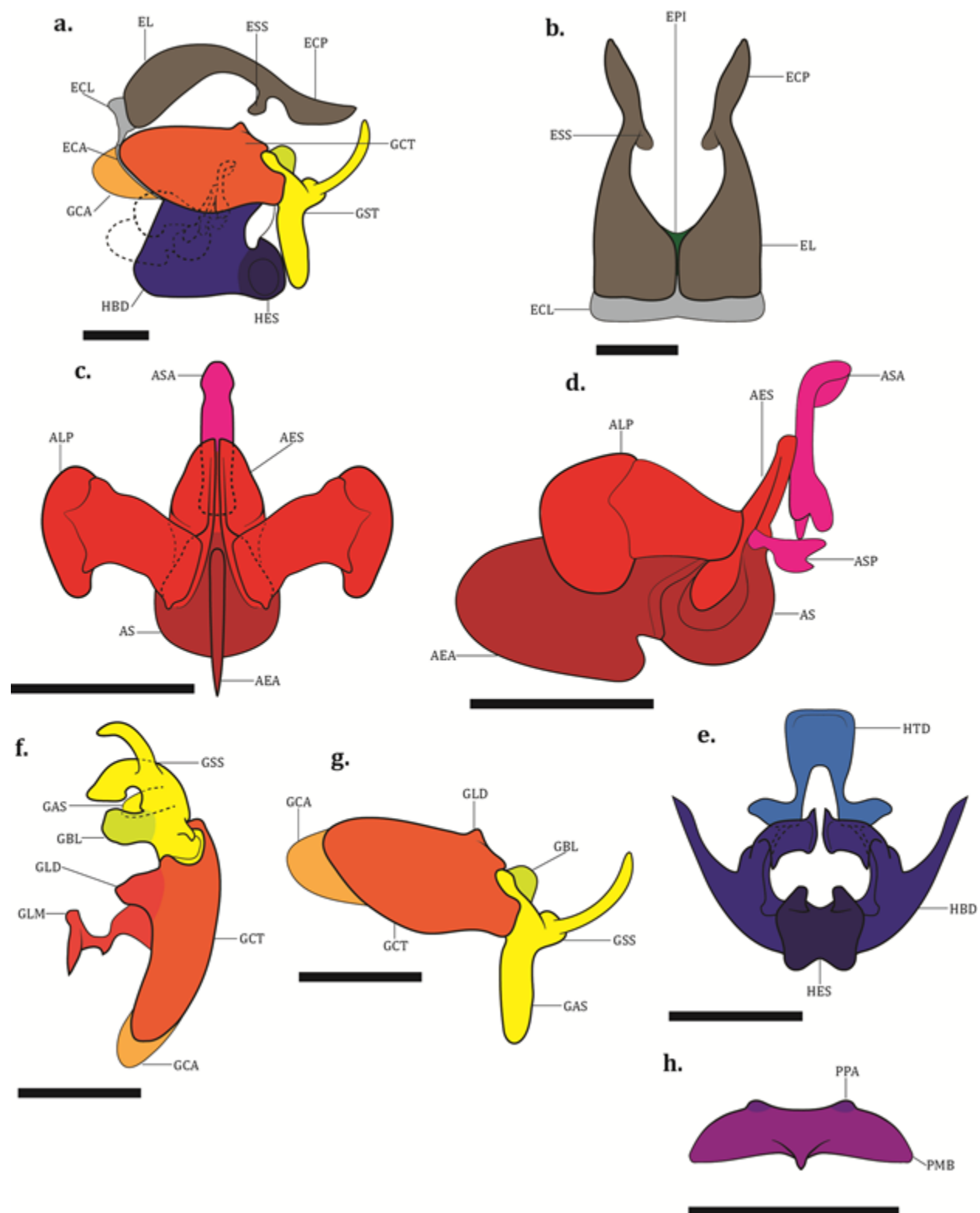


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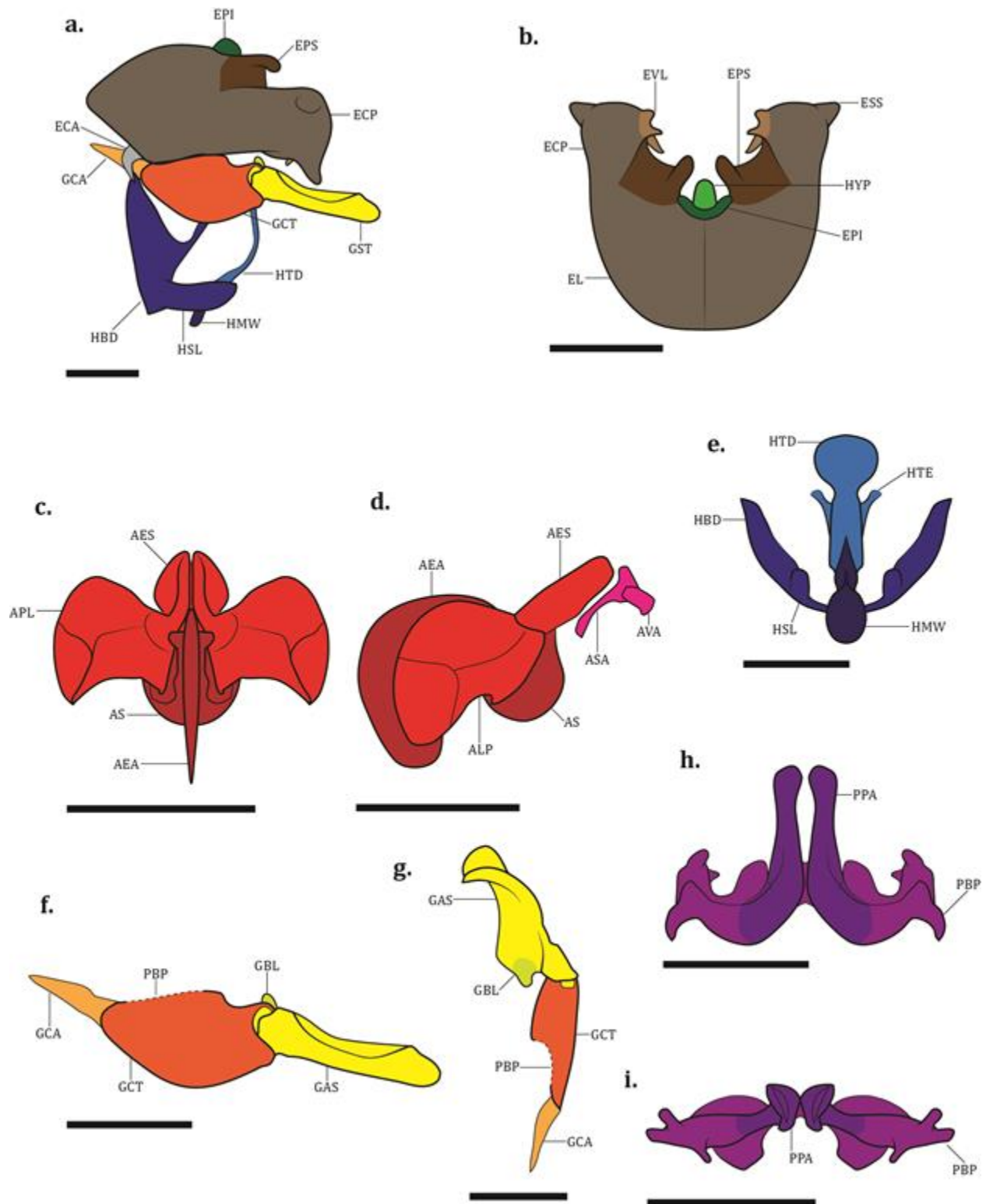


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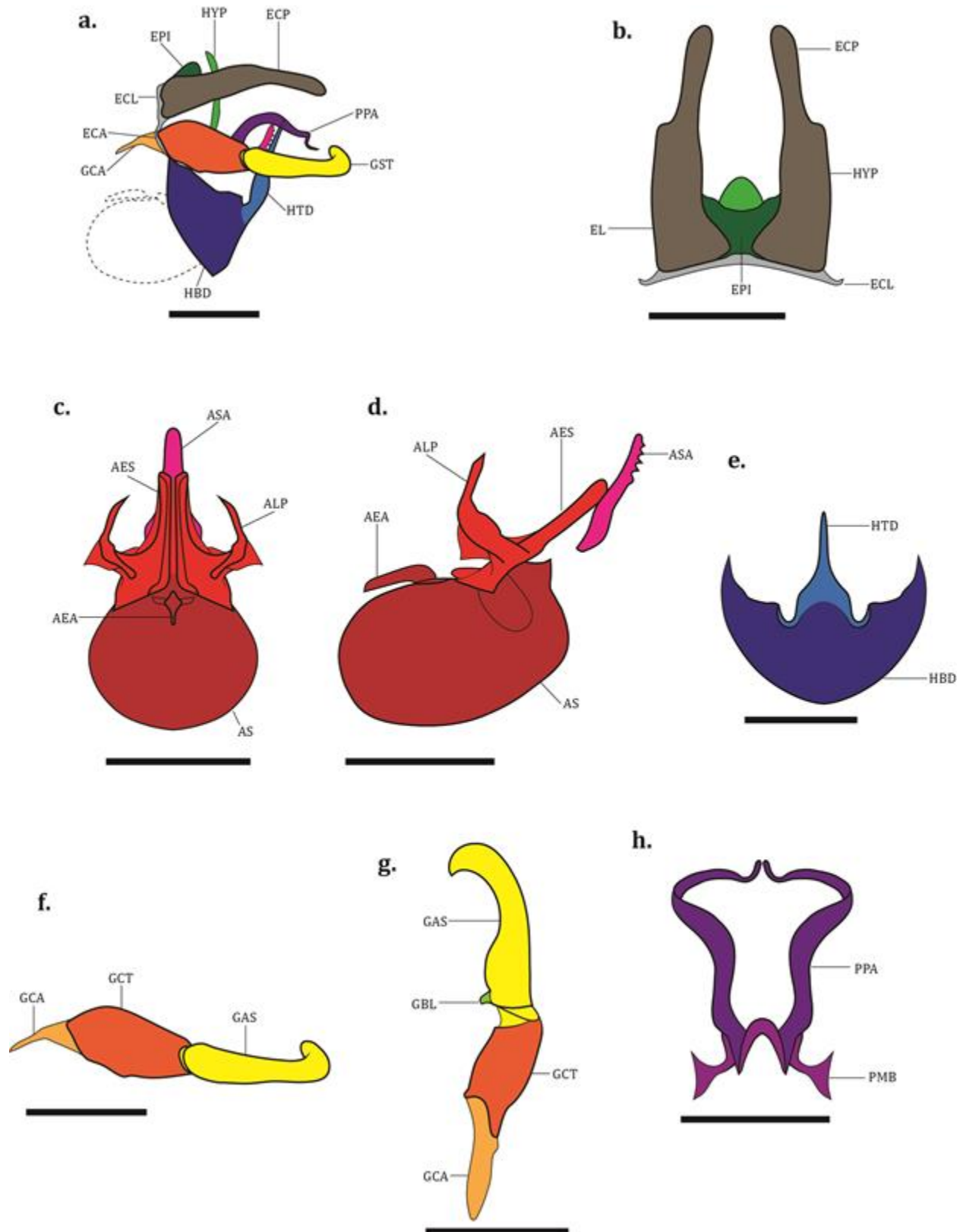


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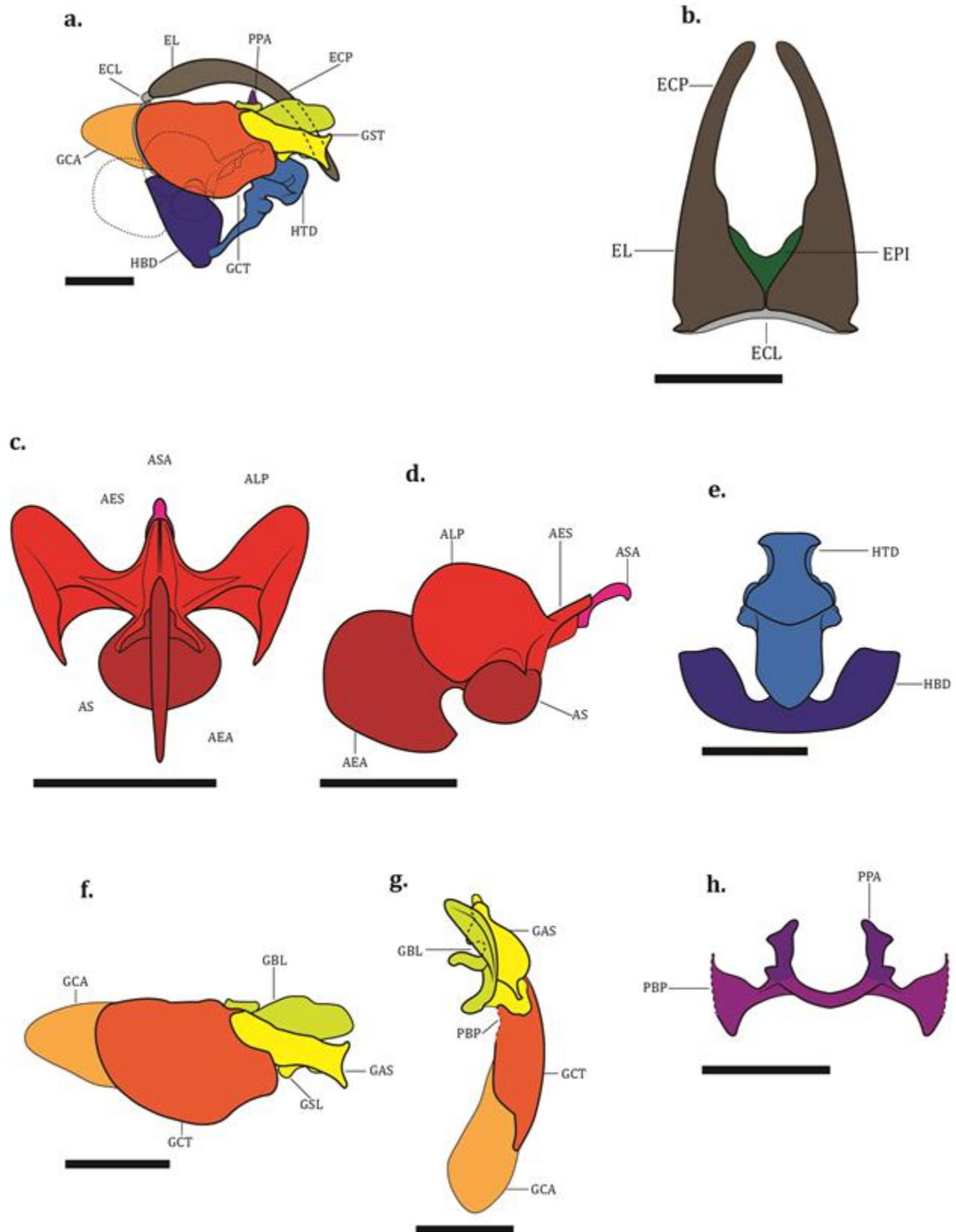


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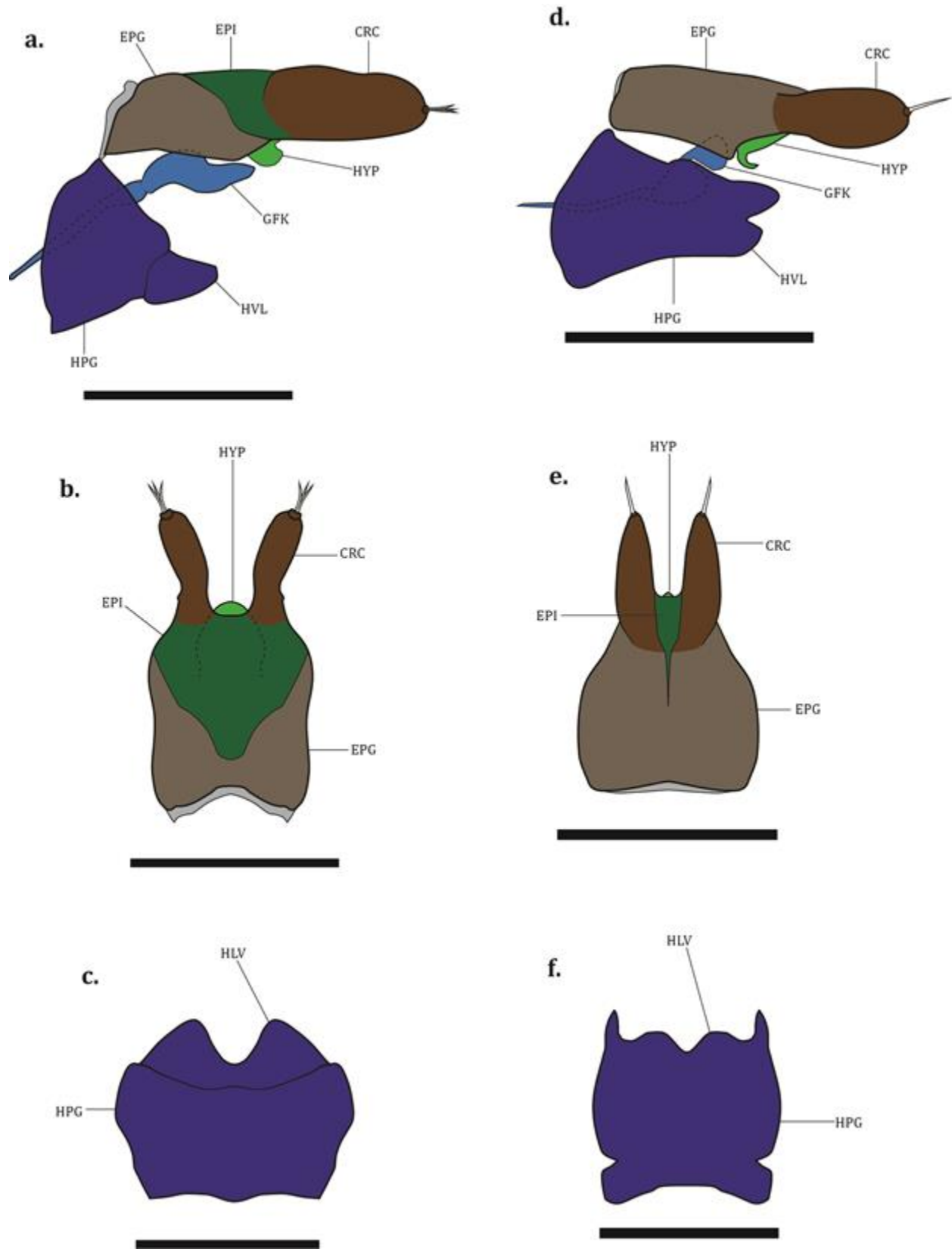


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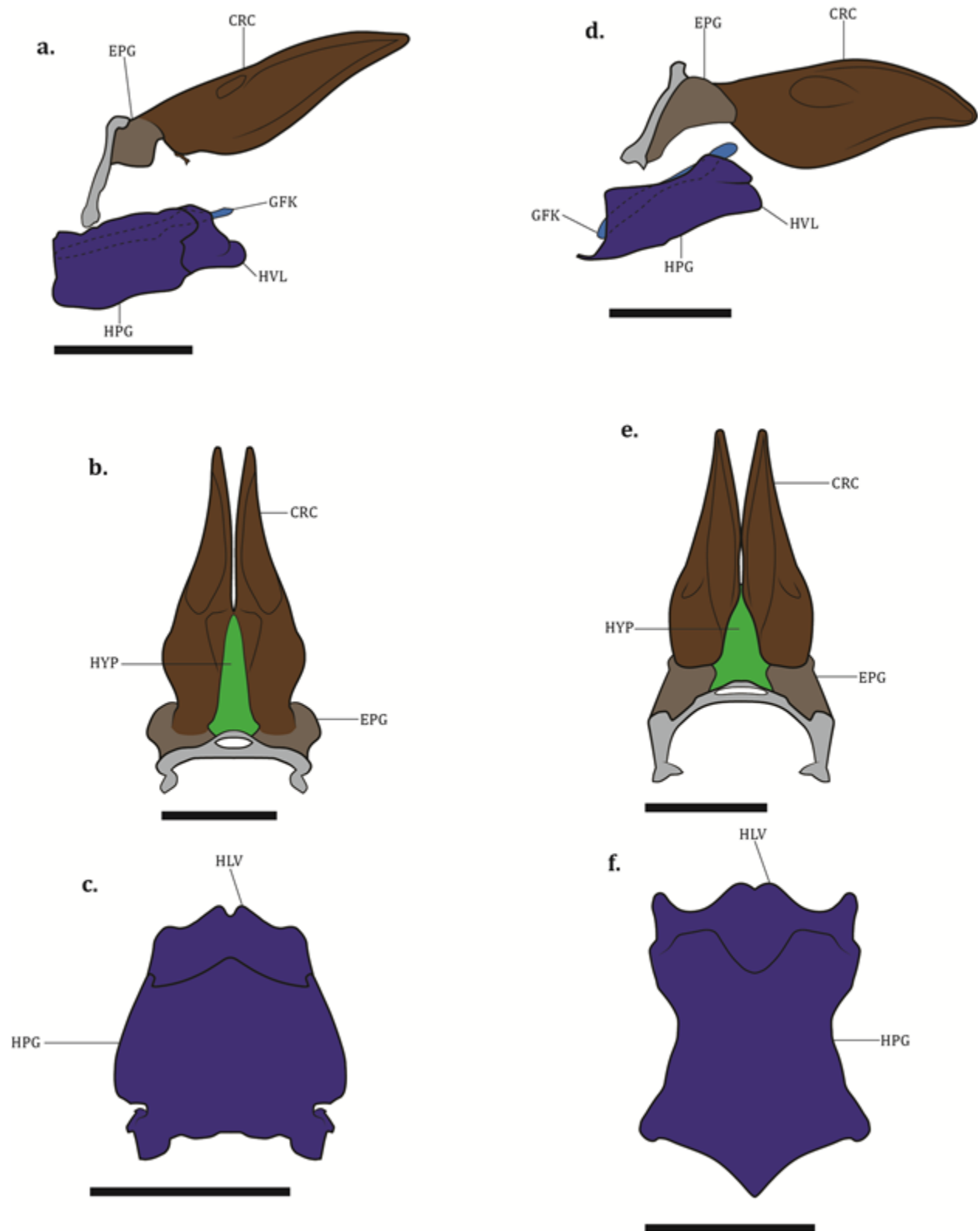


Figure 21.

CHAPTER FIVE: AN ILLUSTRATED KEY TO THE PHANTOM CRANE FLIES OF NORTH AMERICA (DIPTERA: PTYCHOPTERIDAE)

To be submitted to *The Canadian Journal of Arthropod Identification*

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Abstract

Members of the family Ptychopteridae are flies closely associated with saturated organic sediments, and are found through the Holarctic as well as the Afrotropical region. Adults resemble true crane flies (Tipulidae) or large fungus gnats (Mycetophilidae *sensu lato*), while the immature stages are quite distinctive, with the larvae with an anal respiratory siphon, and the pupa with one thoracic respiratory organ hypertrophied. The key provided here is a comprehensive guide allowing the determination of the adults of all described species of Ptychopteridae in the New World. Higher taxonomic groups and some species are diagnosable by photomicrographs, while certain species groups are illustrated with line drawings to highlight distinctive internal structures. Incorrect usage of names in the literature is noted and a diagram of common misapplication of species names is provided. Four new species of Nearctic *Ptychoptera* are described within: *Ptychoptera abbreviata*, *Ptychoptera bilobata*, *Ptychoptera espica*, and *Ptychoptera lacrimiformis*. *Ptychoptera coloradensis* is elevated from subspecies to full specific rank and a neotype of *Ptychoptera quadrifasciata* is designated and the species redescribed.

Introduction

Ptychopteridae Osten Sacken, 1862 is the sole extant family in the Dipteran infraorder Ptychopteromorpha (Lukashevich, 2008; Lukashevich, 2012), a group of uncertain affinity in lower Diptera suggested to be close to Culicomorpha and Psychodomorpha (Wood & Borkent, 1989; Oosterbroek & Courtney, 1995; Wiegmann *et al*, 2011). Ptychopteridae is divided into two subfamilies:

Bittacomorphinae Alexander, 1919 and Ptychopterinae Osten Sacken, 1862. Ptychopterinae is the more diverse of these taxa, consisting of a single genus *Ptychoptera* Meigen, 1803 with subgenera *Ptychoptera* (*Ptychoptera*) in the Holarctic and Afrotropical regions and *Ptychoptera* (*Parapteroptera*) in Europe and North Africa). Globally the genus contains 77 described species. *Ptychoptera* is found throughout the Nearctic, although individual species groups have more limited distributions. Bittacomorphinae is divided into the genera *Bittacomorpha* Westwood, 1835 and *Bittacomorphella* Alexander, 1916. *Bittacomorphella* has been collected in eastern Asia (including Japan and Taiwan; see Nakamura & Saigusa, 2009; Young & Fang, 2011; Kang *et al*, 2012), while in North America species of *Bittacomorphella* are resident in the Appalachian Mountains and Northeast mixed forest flatlands, as well as the Coast, Cascade, and Sierra Nevada Ranges of the west. *Bittacomorpha* is recorded only from the Nearctic and Central America (Fasbender, unpublished data), represented by two species, one widespread east of the Rocky Mountains and one restricted to areas west of and including the Cascade and Sierra Nevada ranges.

As larvae ptychopterids are closely associated with saturated sediments, including seepages (Alexander, 1920), lacustrine margins (Hodkinson, 1973), and depositional zones in streams (Harris & Carlson, 1978; Mattingly, 1987; Wolf & Zwick, 1997). Larval ptychopterids play an important role in nutrient cycling, and can be found in high densities in suitable habitats (Mattingly, 1987; Wolf & Zwick, 2001). They are specialist consumers of fine particulate organic matter (FPOM) (Mattingly, 1987; Wolf *et al*, 1997), which they collect by burrowing into anoxic sediments (Hodkinson, 1973; Mattingly, 1987; Wolf & Zwick, 2001). The larval bodyplan is eucephalous, the thoracic segments short and inflated, abdominal segments cylindrical with VII-IX modified into a conical anal division housing an elongate respiratory siphon. The tracheal system is metapneustic. Pupae reside in the same habitats as larvae,

moving to the surface for eclosion. Pupae are readily distinguished from other lower Dipteran taxa by the unequal development of the respiratory horns, with one hypertrophied to the point of exceeding the length of the remainder of the body.

Adult ptychopterids exhibit a plesiomorphic lower Dipteran bodyplan, with an elongate abdomen and legs. Unlike Tipulidae and other crane fly-like taxa, ptychopterids have a finger-like lobe at the base of the halter called the prehalter, unique in Dipera. Members of Ptychopterinae resemble large fungus gnats (Alexander, 1943), while the thread-like abdomen and extremely elongate, striped legs make bittacomorphines immediately recognizable.

While the ptychopterid faunas of Europe (Audcent, 1934; Peus, 1958; Zitek-Zwyrtek, 1971; Draskovits, 1983; Krzeminski, 1986; Krzeminski & Zwick, 1993; Stubbs, 1993; Ujvárosi *et al*, 2011) and Japan (Nakamura & Saigusa, 2009) have been extensively surveyed, the Nearctic has seen limited work outside of species descriptions, which have typically been unillustrated. The most comprehensive works concerning the Nearctic fauna are Alexander, 1920 and Alexander, 1967 for the eastern and western species respectively, but both publications are limited in their area of coverage. Alexander, 1943 and Alexander 1981 also contain keys to the genera of Ptychopteridae, but these are essentially adapted from previous publications.

The keys presented here represent the first comprehensive adult key for the Nearctic Ptychopteridae and the first larval key distinguishing between species groups in the region. The scope of this key is inclusive of all of North America. Also included are the known Central American species of Ptychopteridae: *Ptychoptera alexanderi* Hancock, 2006 and *Bittacomorpha clavipes* Fabricius, 1781. Emphasis was made on using non-genitalic characters in as many couplets as possible, but many species are distinguishable only through examination of male genitalia.

Materials and Methods

The material examined in this study was collected by the authors or obtained on loan from the following institutions: Clemson University Arthropod Collection (CUAC), Natural History Museum of Denmark (ZMUC), the Field Museum of Chicago (FMNH), Harvard Museum of Comparative Zoology (MCZ), Hunterian Museum of Glasgow (HMG), Illinois Natural History Survey (INHS), Iowa State Insect Collection (ISIC), University of Kansas Snow Entomological Museum (KU), Michigan State University Arthropod Research Collection (ARC), University of Michigan Museum of Zoology (UMMZ), University of Minnesota Museum of Arthropods (UMSP), Oregon State University (ORSU), Pacific Northwest Diptera Research Lab (PNDL), Purdue University Entomology Research Collection (PERC), Smithsonian National Museum of Natural History (USNM), Washington State University James Entomological Collection (WSU). Line breaks in label data of the specimens examined are denoted by a “,”, and separate labels are designated using a “/”.

Specimens were examined using Olympus SZX12 and SZX9 stereomicroscopes and a Nikon E800 compound microscope. A Nikon DS-Fi1 camera on a detachable mount was used to capture photomicrographs from the SZX12 and E800 microscopes; these microscopes were additionally fitted with camera lucida devices for rendering illustrations.

Male genitalia were dissected and cleared for observation using the following technique. The posterior abdominal segments were cut from the specimen using a set of dissecting scissors. The genitalia of dried specimens was hydrated for 18-24 hours prior to clearing to assure complete and even action of the clearing agent. Specimens preserved in alcohol were similarly hydrated for 20 minutes to ensure even clearing. Shell vials were prepared by adding a dry KOH pellet to a measured amount of deionized water. The vials were capped and the KOH allowed to dissolve, at which time the vials were shaken vigorously to ensure a uniform concentration within the vial. The hydrated specimens were then

individually placed in a marked vial and recapped and set on a warming plate, with the solution heated to approximately 60C. Specimens were observed individually at five minute intervals until sufficient clearing had occurred, at which time the specimen was transferred twice to a fresh container of deionized water for ten minutes to dilute any remaining KOH. Specimens were then be taken through a series of ethanol solutions from 30-50-70-95%, further rinsing the specimen and preparing it for transfer to glycerin. Glycerin transfer was accomplished by placing a small amount of pure glycerin into a well of a spot plate for each sample and filling the remainder of the well with 95% ethanol and vigorously stirring the well to bring the glycerin into solution. The genitalia were then transferred to the wells and the plate was placed under an incandescent lamp to evaporate ethanol from the solution. The genitalia were then transferred to a glycerin filled watch glass for observation and finally to microvials associated with the originating specimen.

Terminology used in descriptions is based on Cumming & Wood, 2009, with certain terms modified based on ingroup homologies of Ptychopteridae (see Fasbender & Courtney, in review). Illustrations were produced by either sketching a specimen using the camera lucida and scanning them for tracing in Adobe Illustrator CS5, or taking a series of photomicrographs and tracing them in Adobe Illustrator. Photomicrographs were produced by taking a stack on images in varying focal planes using the Nikon DS-Fi1. These images were then aligned and stacked in Adobe Photoshop CS5 12.0.4.

Results and Discussion

The nomenclature of the Nearctic Ptychopteridae was last cataloged in Alexander, 1965 and there has never been a comprehensive descriptive treatment of the Nearctic taxa. Alexander, 1920 and Alexander, 1967 respectively represent the best coverage of the eastern and western taxa, but both are incomplete with regard to the taxa of each region, and Alexander 1967 contains taxonomic errors.

Because of the limited attention paid to the classification in the region there are several nomenclatural issues that require resolution to create an accurate key to Nearctic ptychopterids.

Most of the species found in the Nearctic region can be placed into one of several species groups based on adult morphology. The composition of these groups is presented in Table 1. It must be noted that larval taxonomy for Ptychopteridae is far less developed than adult taxonomy, and many larvae are unknown. At this stage there is not sufficient comparative study of larval characters to differentiate between species.

Due to the paucity of keys and other literature for the Nearctic Ptychopteridae, there are numerous incorrectly determined specimens in collections. This is even more problematic in light of the misidentification of several species in the *Ptychoptera lenis* group in one of the few publications to illustrate these taxa: Alexander, 1967. Based on examination of the holotypes of these species, the species identified as *Ptychoptera minor* Alexander, 1920 is actually *Ptychoptera lenis* Osten Sacken 1877. The species illustrated as *P. lenis* was actually undescribed, here named *Ptychoptera lacrimiformis* sp. n. *P. minor* was not illustrated in Alexander, 1957. These and other common misidentifications are presented in Table II.

The taxonomy of *Ptychoptera coloradensis* Alexander, 1937 has been problematic. The species was described as a subspecies of *P. lenis*, but the taxon is clearly distinct from either of the species which have been treated as *P. lenis* so it is elevated to a full species here. There have been online nomenclatural indices (EoL, 2013) that have presented *P. coloradensis* as a distinct species previous to this publication, but these are not the results of a published nomenclatural act. The description of *P. coloradensis* is very brief, and the diagnostic characters cited (small size, presence of a subapical spine in the axil of the ventromesal lobe of the epandrial lobe (Alexander, 1937)) are not useful in separating species within the *P. lenis* group.

This issue is further compounded because, although morphologically distinctive from other *P. lenis* Group species, *P. coloradensis* shows morphological variability across its range, and likely represents a cryptic species complex. *Ptychoptera obscura* Peus, 1958 and *Ptychoptera uta* Alexander, 1947 may in fact represent ingroups within the current concept of *P. coloradensis*, but available morphological evidence and limited molecular sampling is not sufficient to draw any firm conclusions. These issues mean that *P. coloradensis* as treated in this key should be viewed circumspectly: with wider molecular sampling and morphological data from immature life stages this “species” will probably be broken up.

Ptychoptera obscura was described by Peus based on specimens he examined from the Museum für Naturkunde, Berlin. In his description he cites the label data as follows (translated from German):

‘In the collection of the Zoological Museum *there were* 4 undetermined specimens of this species in a row next to each other, but only the first individual had a piece of paper with Enderlein’s handwriting “Berlin Prof. F. Karsch S.” (“S” means: collector). I have provided the other 3 individuals with identical labels, with the suffix “(teste Enderlein) (F. Peus)”...

...I have called this species “obscura”, not only because of their unadorned appearance, but mainly for their “obscure” origin: it is remarkable that this so very peculiar species has not been found anywhere else from the state of Brandenburg or anywhere in Germany, *but* I have to accept the word “Berlin” on the original label, because I could not cast doubt on its accuracy.’

No specimens of *P. obscura* have been collected in Europe since Peus’s work. However, comparison with the Nearctic ptychopterid fauna shows that this species is a member of the *P. lenis* Group, very close to *P. coloradensis*. Specimens in the University of Kansas Snow Entomological Collection collected in southern Colorado and northern New Mexico are morphologically conspecific with *P. obscura*. It appears that the label present on the specimens examined by Peus was either incorrect or misleading. Thus

P. obscura is not a European species as originally described, but rather a member of the *P. lenis* Group native to the southern Rocky Mountains.

The original holotype of *Ptychoptera quadrifasciata* Say, 1824 has been lost (Alexander, 1959; J. Gelhaus, pers. comm.). *Ptychoptera rufocincta* Osten Sacken, 1860 was regulated to synonymy by Alexander (1965). The authors have found that the previous concept of *Ptychoptera quadrifasciata* actually represents two species, one eastern (*P. quadrifasciata*) and one western (*Ptychoptera abbreviata* sp. n.). Because of this situation it has become necessary to designate a neotype according to Article 75.3 (ICZN 1999).

Descriptions

Ptychoptera lenis Group

Ptychoptera bilobata Copley & Cannings sp. n.

Diagnosis

Adult. Fore- and midcoxae with brown dot on anterodorsal surface, hindcoxae with upper portion of lateral surface brown. Male genitalia with hypandrial spathate lobes extending beyond ventral margin of gonopods, epandrial lobe with accessory subapical spine laterally at apex.

Female and immature stages unknown.

Description

Adult. Measurements (n=1). Overall length 9.58mm. **Head.** Width: 1.13mm, Height: 1.00mm, Length: 0.58mm; Antenna flagellum length: 4.75mm. **Thorax.** Length: 2.6mm, Height: 1.6mm; Wing length: 10.2mm, Width: 2.1. **Abdomen.** Length: 6.4mm.

Head. Vertex shining black, evenly provided with elongate trichoid sensilla posteriorly; frons extremely narrow strip, black. Occiput and genae with dense elongate yellow trichoid sensilla. Antennae: scape bright yellow, oblong cylinder with ring of long black trichoid sensilla well separated from dorsal apex; pedicel yellow basally, brown dorsally, globular, ring of trichoid sensilla on lateral margin. Flagellomeres brown, fusiform. Facial sclerite black, indistinct from clypeus, weakly inflated. Clypeus rhomboidal, inflated, generally covered in yellow sensilla, dark yellow at margins, with broad brown stripe medially, expanding dorsally. Maxillary palpus with segments 1&2 yellow, segment three fading to brown, distal segments brown. Labrum thimble-shaped, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae bright yellow.

Thorax. Antepronotum with transverse fold broader than height of anterior ridge, yellow medially, brown at lateroventral extremity, with elongate yellow trichoid sensilla at lateroventral apex, medial lobe approximately one third width of remainder of antepronotum, highly tapered trapezoid, dorsal surface with medial notch. Prescutum and scutum greasy black, with numerous microscopic punctures with broad yellow stripe from posterior apex of prescutum to scutellum; medial and prescutal suture with row of minute clear trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum as longer yellow sensilla; long clear prealar sensilla present. Scutellum yellow. Mediotergite of metanotum greasy black, with light pollinosity, medially with elongate tapering yellow stripe extending less than $\frac{1}{2}$ length, lateral corners with short yellow triangular patches. Laterotergite of metanotum pollinose black, except for yellow patch near wing base, dorsal patch of very elongate yellow trichoid sensilla. Pleural sclerites all black, with heavy pollinosity. Anepisternal cleft narrow, membrane yellow. Suture between epimeron and metapleurite incomplete, weak. **Wing.** Hyaline, weak infuscation extending from base of R_{1+2} to CuA_1+CuA_2 fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 4.82mm, Apex of Sc to Apex of R_1 1.04mm, R_{3+4+5} stem 0.81mm, slight posterior turn at fork from R_{1+2} ; R_{4+5} stem 1.68mm; R_4 after fork 1.60mm, R_5 after fork

1.67mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 2.07 : 1.97$. r-m 0.35mm; M distal to r-m 2.28mm; M_1 0.75mm, arcuate, M_2 0.50mm; $M\text{distal}:M_1 = 1.00:0.32$, $R_{3+4+5}:M\text{distal} = 1.00:2.81$, $R_4:M_1 = 1.00:0.46$. CuA_1 proximal 0.28mm, distal 2.22mm; CuA_2 1.19mm sinuous. A_1 straight for 3.08mm. m-cu joins R_{3+4+5} before r-m. Halter yellow. Prehalter yellow. **Legs.** Forecoxae yellow, dorsal margin with dark brown spot, midcoxae yellow with dark brown spot on dorsoanterior apex, hindcoxae with upper half of lateral surface dark brown. Femur and tibia yellow, darkening slightly at shared joint, joint of tibia and first tarsomere brown. First tarsomere light brown proximally, darkening distally. All other tarsi brown. 5th tarsomere can fold back on penultimate tarsomere. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae on distal half.

Abdomen. Tergites and sternites dark brown, posterior and lateral margins yellow except segment I which is uniform color, evenly covered in elongate yellow sensilla. Sternite VII forming plate under genitalia, posterolateral margins semicircularly expanded, medial triangular lobe absent. **Male Genitalia.** Epandrial collar complete, narrow, epandrial apodemes broad and triangular, extending flat across gonocoxal apodeme to hypandrium, break at epandrium absent. Epandrial lobes fused to composite claspers: massive, clawlike, medial curve moderately-developed fingerlike to apex; subapical spine placed subapically, finger-like with rounded apex, secondary fingerlike spine placed on lateral surface of epandrial apex; ventromesal lobe located $\frac{3}{4}$ length of epandrial lobe, ovoid in cross section basally, not petiolate, directed ventromedially, tapering acutely to rounded point, nodulated on dorsoanterior surface near apex, nodules spaced less than individual width apart; medial stylus rounded and flattened, weakly curved medially. Epiproct prominent, posterior with U-shaped notch medially; posteromedial stylus poorly distinguished; hypoproct as per genus.

Parameres paired, sclerotized portion separate and held together anterior with parameral membrane, medial spur present; lateral spur present, directed straight lateral, less than 1/4th length of

apical lobe, apex rounded; apex of paramere blade-like, laterally compressed, dorsal margin convex, ventral margin straight. Apex of paramere nearly vertical.

Gonocoxite tapers anteriorly to gonocoxal apodeme; apodeme rounded in dorsal view, acutely triangular laterally, posterior portion directed to articulate with paramere. Anterior part of gonocoxite bulbous, ventral gonocoxal lobe present. Dorsomedial margin of gonocoxite forming flat plate extending over basal portion of paramere, medial anterior margin with small lobule provided with small cluster of elongate trichoid sensilla. Gonostylus with basal lobe knoblike and heavily provided with stout trichoid sensilla, apical stylus simple, round in cross section with rounded apex, dorsal glabrous ridge present; curved medially.

Hypandrium with basal division bandlike. Spathate lobes present, acutely triangular, extending dorsally towards epandrium, tip rounded extending dorsally beyond gonopods, medial margin rounded at base, contact along medial margin. Terminal division base with two knoblike structures, narrowing to a narrow sclerotized septum flanked by circular openings to the lateral canals of the terminal division. Lateral margins largely concealed by the hypandrial spathae. Above the septum heavily sclerotized pendant; lacrimiform membranous window set dorsal to pendant. Apex of terminal division triangular, arrow-like, forming subobtuse angle in dorsal view. External surface of apex densely set with stout trichoid sensilla. Lower 2/3rds of terminal division laterally attached to remaining hypopygium with membranous tissue, lateral extensions of terminal division floating.

Aedeagus rotated 20 degrees from vertical. Aedeagal sclerites blunt, approximately 2/3rds length of sperm sac, lateral sclerites expanding ventro-basally; apical apodemes absent, apex rounded; lateral ejaculatory processes similar in shape to ejaculatory apodeme but approximately quarter size, extending anteroventrally, paralleling ejaculatory apodeme. Sperm sac nearly spherical, smaller than ejaculatory apodeme. Ejaculatory apodeme attached dorsoanteriorly to sperm sac, not closely

associated with aedeagus, larger than sperm sac, extending anteriorly into segment VII, arcing ventrally to enlarged rounded terminus; curling around anterior margin of sperm sac. Subapical sclerite well developed, narrow flat rod extending over twice the length of the aedeagus proper, divided basally with medial membranous portion and sclerotized prongs extending to lateral base of aedeagus, narrowing to parallel sided rod apically, apex obtusely flattened like a knife's edge, weakly rounded, dorso-medial spine present at phallotreme.

Figures. Male genitalia 25, Wing 26, Distribution 27.

Material Examined. Paratype. Seattle, WASH. U.W. Campus, IV-28 1956, RW Sleeper (Pinned: 1 m#) (ORSU).

Taxonomic Notes. This species is similar to *Ptychoptera byersi*, but differs in the presence of a lateral lobe at the apex of the epandrial clasper. These species are allopatric, with *P. bilobata* known only from the Fraser Valley of British Columbia and Seattle, while *P. byersi* occurs in the Great Basin of California, Nevada, Oregon, and Utah.

***Ptychoptera lacrimiformis* Fasnider & Courtney (sp. nov.)**

Ptychoptera lenis Osten Sacken, Alexander 1967: 10-11, 171 (misidentification, illustration)

Diagnosis.

Larva. Labral brushes short, not extending dorsoposteriorly over labrum; incisor lobe of mandible with poorly defined denticulations; postmentum with broad rounded denticulations (applies to all *Ptychoptera lenis* group).

Pupa. Four anteromedial setae present in quadrate formation, not raised on lobe; male genital lobule with obvious blunt pseudoclasper lobes not convergent, female genital lobule with apex of hypogynum with short apical suture.

Adult. Male. Epandrium divided into two massive pseudoclaspers, ventromesal lobule of epandrium forms a pendulant inverse teardrop-shaped blade tapering ventrally, parameres without lateral process, directed dorsally. **Female.** Subgenital plate with small triangular lobes ventrolateral to cerci (applies to all *Ptychoptera lenis* group).

Description.

Larva (4th instar). Measurements (n=5). Length (measured from frontoclypeal apotome to abdominal segment VIII): 31.8mm (27.3-37.8mm); Cranial width (measured a lateral extremities of genae): 1.05mm (1.00-1.15mm); Frontoclypeal apotome length: 0.73mm (0.65-0.82mm) Body translucent white, lightly sclerotized except for head capsule and respiratory siphon.

Head. Cranium dull orange in color, heavily sclerotized, frontoclypeal apotome with anterior margin blunt straight edge, having branching like setiform at apicolateral margin; occipital margins taper outward, giving cranium a trapezoidal appearance, occipital margin forms broad M-shape from posterior emargination on each gena. Frontoclypeal apotome square anteriorly, obscuring clypeus in dorsal view, tapering to rounded tip beyond the epicondyle; posterior margin of frontoclypeal apotome does not reach posterior cranial margin. Anterior terminus of gena well posterior of anterior margin of frontoclypeal apotome; posterior margin of gena with rounded lateral margin, dorsally emarginate forming narrow posterior band, with band widening at ecdysial stem line. Subgenal sclerite present, rectangular in shape, wider than long. Single stemmata prominent on each gena immediately posterior to base of mandible. Antennae inserted at anterior terminus of ecdysial lines, consisting of basal ring and two cylindrical segments, terminating in a cluster of setae; dorsomedially dorsal elongate sensillum with notch-like opening at tip, ventromedial massive conical sensillum, dorsally short, thread-like sensillum lateromedially, bisegmented sensillum with barrel-like base and conical apex, and lateroventrally rod-like elongate sensillum. Labrum triangular, anterior margin with heavily sclerotized

band; ventrolateral margins with prominent setal brushes of bacilliform shape, divided midway along length with prominent curved sensilla; epipharynx well-developed each side of median with dorsal hook-like sensilla and ventral pit, stout, curved sensilla set at lateral edge along lower portion of incision. Setae of labral brush short, not extending dorsomedially over labrum, individual macrotrichia with serrations along posterior edge apically. Mandibles immediately below antennae, flanking labrum, directed posteromedially molar lobe broadly elliptical, narrowest at base, anterior margin with abrupt downward angle to terminal section, two prominent branching trichoid sensilla on anterior margin; ventroproximal concavity roughly semi-circular, lightly sclerotized, extending approximately halfway to medial margin and 3/4s of the way to anterior margin; prostheca prominent on posterior margin, composed of long macrotrichia proximally and shorter macrotrichia distally; mandibular comb largely concealed behind incisor lobe, relatively straight with short macrotrichia; incisor lobe of mandible semicircular, with small denticulations on posterior margin. Maxillae: Cardo heavily sclerotized on outer surface, squared dorsally, narrowing ventrally, with long fringe of macrotrichia at margin with endite lobes; lacinia and stipes closely associated; stipes well developed with peg-like palpus near anteriomedial margin, medial margin with comb of tapering sensilla, moderate length; lacinia broadly padlike, posteriomedial surface with hemispherical brush provided with numerous long macrotrichia, lower posterior margin of brush with several large sensilla, anterodorsal margin with line of moderately sized macrotrichia, small thumb-like lobe anteromedial to lacinial brush, possibly the remnant of galea, base with anterior sensillum with stout base and branching to sub-sensilla. Prementum oval in shape, tapering slightly to disk-like apex, lateral margins of apical disk with dark nodulations. Postmentum broad, forming posteriorly directed arc slightly narrowing to lateral margins, glabrous, anterior margin with rounded well-defined denticulations, denticulations width decreased compared with posterior postmentum.

Postcranial Body. Prothoracic segment cone-like, short, set with microtrichia near anterior margin. Thoracic segments 2 + 3 much wider, bulging and rounded. Thoracic segments each with two paired patches of three long setae (~.16mm), arranged in a transverse line on posteroventral margin. Abdominal segments each with many shallow transverse folds, and sparsely arranged sensilla (~.12mm length). Abdominal segments I-III each with pair of extremely short ventral prolegs, prolegs apically with a single, sickle-shaped claw. Abdominal segments I-V posteriorly with swollen annular creeping welt. Segment VI conical. Segments VII and VIII with ring of setae near posterior margin and pair of somewhat larger setae anterolaterally. Anal papillae and siphon glabrous, siphon with shallow transverse ridges at base.

Pupa. Measurements (estimated from exuviae): Length (Apex of cephalothorax to tip of genital lobe) 20-25mm; Width (across base of cephalothorax) 2.5-3mm

Overall cephalothoracic structures, abdominal tubercles, posterior bands of abdominal segments, and genitalia dark brown, well sclerotized. Remainder of abdomen lightly sclerotized, pale, excepting tubercles.

Head. Dorsolateral cephalic sensilla on large nodule near ocular margin, three trichoid setae present: stout central sensilla and two flagellar marginal sensilla; dorsoapical trichoid sensilla well developed; clypeolabrum rhomboid in shape, clypeal-labral 1 developed as large campaniform sensilla near center of dorsolateral margins; other clypeal-labral invident. Ocular sensilla 1 and 2 trichoid, on raised node near clypeal-labral margin, ocular 2 dorsolateral to ocular 1. Ocular sensilla 3 and 4 trichoid, placed on smaller nodes, ocular 3 midway above ventral margin of eye, ocular 4 dorsolateral to ocular 3, not placed on ventral margin of eye.

Thorax. Scutum with 4 stout anteromedial sensilla in quadrate formation near right respiratory horn, not produced on lobe; anterolateral sensilla absent; dorsal sensilla minute, present primarily as black nodes in irregular pattern; supraalar trichoid sensilla of variable pattern. Scutellum with transverse

row of 3-5 nodules each with single trichoid sensilla. Mediotergite with four sagittal rows of muscle plaques, medial rows more prominent. Two nodules present at anteriolateral margin near laterotergite suture, distal nodule with trichoid sensilla. In some specimens posterior marginal region on either side of median with sparsely scattered nodules each with three minute trichoid sensilla in transverse row, not present in others. Metanotum with single row of nodules, discontinuous across median; larger nodules with single prominent trichoid sensilla emergent, interspersed with irregular number smaller nodules, some with smaller trichoid sensilla, others bare.

Abdomen. Densely set with rows of tubercles . Tubercles in transverse rows on dorsal and ventral surface, with sagittal rows on lateral surface. Each tubercle consisting of a cylindrical base topped with a crenelate cap of 3-7 denticles, the posterior denticles larger, 1-2 trichoid sensilla emerging from center of tubercle. Penultimate abdominal segment without tubercles. All abdominal segments posteriorly with sclerotized band broken into transverse dorsal and ventral sections, quadrate lateral sections; anterior bands poorly sclerotized, posterior bands increasingly well sclerotized; larger tubercles with irregular number of denticles arranged in transverse row along posterior margin of sclerotized bands. **Male Primordial Genitalia.** With prominent medial genital lobule similar to female, epandrium readily apparent with prominent medial suture and pseudoclasper apices descending ventroposteriorly from anteriolateral apex; anteriolateral apex with medial margins of epandrial clasper lobe rising to ascendant proctiger; epandrial clasper apices blunt, well separated. Gonopod sheath well developed, gonocoxite/gonostylus joint obscure, gonostyli apices meet medially; acute terminal lobes protruding laterally from midpoint of gonostylus. Hypandrial sheath with terminal division readily seperable from basal division, apex of terminal division slightly divergent posteriorly from remainder of genitalia, hypandrial spathae apparent as basal lobules flanking terminal division. **Female Primordial Genitalia.** Prominent medial genital lobule arching posteriorly over genitalia, cerci readily evident with terminal lobes emergent from basal-lateral portion. Hypogynium easily distinguishable, hypogynal lobes

distinct, located at posteriolateral corners, apex of hypogynium subtrapezoidal with medial suture initiated along posterior margin fading midway across apex.

Adult. Measurements (n=5). Overall length 10.82mm (10-51-11.16mm). **Head.** Width: 1.08mm (0.95-1.25mm), Height: 1.08mm (1.00-1.15mm), Length: 0.64mm (0.53-0.73mm); Flagellomere Proportions: Flagellomere Proportions: 1 : 0.53 : 0.49 : 0.49 : 0.46 : 0.46 : 0.43 : 0.39 : 0.38 : 0.38 : 0.38 : 0.38 : 0.35. **Thorax.** Length: 2.88mm (2.86-3.00mm), Height: 2.15mm (2.05-2.25mm); Wing length: 11.22mm (10.14-12.86mm), Width: 2.66mm (2.50-2.81mm); Leg Proportions Femur: 1.0, 1.13, 1.25mm; Tibia: 1.1, 1.14, 1.53; Tarsomeres: Foreleg 0.77-0.19-0.1-0.1-0.07, Midleg 0.66-0.16-0.1-0.07-0.06mm, Hindleg 0.75-0.14-0.1-0.09-0.05. **Abdomen.** Length: 7.27mm (7.00-7.57mm); Male Genitalia Width: 1.16mm (1.12-1.20mm), Height: 1.55mm (1.32-1.65mm)

Head. Vertex wide, shining black, tapering posteriorly, moderately set with setae; frons somewhat concave, forming V-shaped transverse ridge above antennae. Prominent cluster of trichoid sensilla on medial ventral margin of eye near facial sclerite. Occiput with dense long yellow setae projecting posteriorly. Antennae: scape yellow, cylindrical with long brown setae projecting dorsally from anterior surface; pedicel cylindrical, narrowing slightly at base, with short black setae; flagellomeres brown bacilliform. Facial sclerite indistinct, heavily incised by clypeus. Clypeus large, rhomboidal, bulbous, covered in microtrichia, reddish brown fading to yellow laterally; fine setae along lateral margins. Maxillary palpi emerge from under clypeus, 5-segmented, brown. Labrum small, bluntly triangular, mostly concealed by clypeus, hypopharynx concealed. Labellum semi-circular, anterior margin straight, orange.

Thorax. Antepronotum band-like, with transverse fold, light yellow; anterior portion of fold ending halfway down width of head in a terminal knob ringed with setae, small trail of setae extending dorsally; posterior section of fold forming obtuse dorsal angle medially, extending ventrally beyond

anterior terminus to propleuron/coxa, darkening to velvet black. Prescutum well developed, broadly dividing the rest of scutum; surface glabrous black, heavily stippled; prescutal suture fringed with sparse yellow setae; . Scutum heavily incised by prescutum, transverse suture extends approximately midway across scutum, merging with prescutal suture. Surface of scutum glabrous black, heavily stippled, except for glabrous yellow band between prescutum and scutellum. Scutellum yellow, ovoid, dorsal surface with long, yellow setae. Mediotergite well developed, rounded, largely stippled glabrous black except for anterolateral margins and small anterior medial acute triangle of stippled glabrous yellow; dorsal portion covered with sparse yellow setae. Episternum narrowly trapezoidal, velvety black, slightly pollinose, covered in fine microtrichia; anepisternal suture indistinct; narrow sclerotized glabrous posterodorsal extension extending toward scutum, posterior margin with setae, membranous region surrounding lobe yellow. Anterior basalare velvety black, with triangular yellow orange coloration, posterior basalare velvety black ventrally, yellow dorsally. Epimeron velvety black, slightly pollinose, line of fine setae 1/3 of length above ventral margin; dorsal apex orange-yellow, glabrous, densely set with setae on lower margin. Epimeron-metapleuron suture not well defined. Laterotergite trapezoidal, narrowing anteriorly, with anterior prominence above halter, glabrous, black, with moderate number of macrotrichia. Metapleurite sub-trapezoidal, velvety black, pollinose, covered in fine microtrichia and sparse macrotrichia of moderate length. **Wing.** Localized faint infuscation at sc-r, r-m, m-cu, base of R_{4+5} fork, base of M_{1+2} fork in some specimens; membrane without macrotrichia but with dense covering of microtrichia. All veins covered in short stout macrotrichia. Sc: 7.30mm, apex of Sc to apex of R_1 1.20mm, R_{3+4+5} stem 1.07mm, slight anterior turn at fork from R_{1+2} ; R_{4+5} stem 2.12mm; R_4 after fork 2.65mm, R_5 after fork 2.50mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 1.98 : 2.47$. r-m 0.46mm; M distal to r-m 3.07mm; M_1 1.25mm, curved proximally, M_2 0.84; Mdistal: M_1 , 2.45:2.00, R_{3+4+5} :Mdistal, 2.87:1:00, $R_4:M_1$, 2.12:1.00. CuA_1 proximal 0.37, distal 2.50; CuA_2 1.62mm with anterior angle well developed, posterior angle absent. A_1 straight for 2.88. r-m joins R_{3+4+5} well before R_3 divergence. Halter yellow. Prehalter yellow.

Legs. Coxa robust, primarily yellow with chocolate brown markings. Forecoxa with brown markings anterodorsally, setae on anterior surface; midcoxa with small brown splotch anterodorsally, and brown stripe from posterodorsal to anteroventral margins, setae on anterior surface; hindcoxa brown except on posteroventral margin, setae on posterior surface. Femur and tibia light brown proximally and dark brown near distal margin giving a slight banding effect; femur proximally yellow, tibia proximally light brown. Tarsi uniformly brown, with double row of minute stout spines.

Abdomen. Tergites and sternites mostly stippled deep brown, with well-defined yellow borders along lateral and posterior margins, except segments I and VII uniform brown, moderately set with fine yellow setae. **Male Genitalia.** Epandrium markedly bifurcate, medially opposed clawlike epandrial claspers dominant structure, epandrium rising well above surface of tergite VII, dark reddish brown; lateral surface with uniformly scattered setae, forming sparse apical fringe along medial margin; apex conical, with elongate subapical spine closely associated with ventral surface of terminus. Medial margin with pendulous ventromesal lobe projecting ventrally, divided into discous base with inverse lacrimiform blade narrowing ventrally, slightly emarginate anteriorly. Medial surface of blade nodulated, with sparse setae, anterior margin concave, posterior margin convex. Posteromedial stylus ventromedially positioned near lateral margin of epiproct, pendulant bladelike, tip obtusely rounded, lateral edge slightly concave, glabrous. Epiproct with U-shaped medial notch; tapering toward anterior margin of epandrial complex. Hypoproct tonguelike, tapering to slightly flattened. Subepandrial sclerite evident only as lightly sclerotized strips in sub-epandrial membrane anterolaterally to hypoproct.

Parameres not fused, basal portion extending medially to dorsally ascendant blade. Basal portion glabrous, poorly sclerotized except for longitudinal ridge. Ascendant blade highly sclerotized, foliform claw, posterior margin concave, anterior margin convex. Anterodorsal edge of blade and apex slightly divergent laterally, coming to obtuse point. Lateral ridge of blade absent.

Gonocoxite tapers anteriorly to gonocoxal apodeme; apodeme rounded in dorsal view, acutely triangular laterally, posterior portion arced dorsally to articulate with paramere. Anterior part of gonocoxite bulbous, ventral gonocoxal lobe present. Dorsomedial margin of gonocoxite forming flat plate extending over basal portion of paramere, medial anterior margin with small lobule provided with small cluster of elongate trichoid sensilla. Gonostylus with basal lobe knoblike, with stout trichoid sensilla dense, apical stylus simple, round in cross section with rounded apex, dorsal glabrous ridge present; curved medially.

Hyandrium with basal division bandlike. Spathate lobes present, acutely triangular, extending dorsally towards epandrium, tip rounded and not extending dorsally beyond gonopods, medial margin rounded at base, not in contact. Terminal division base with two knoblike structures, narrowing to a narrow sclerotized septum flanked by circular openings to the lateral canals of the terminal division. Lateral margins largely concealed by the hypandrial spathae. Above the septum heavily sclerotized pendant; lacrimiform membranous window set dorsal to pendant. Apex of terminal division triangular, arrow-like, forming subobtuse angle in dorsal view. External surface of apex densely set with stout trichoid sensilla. Lower 2/3rds of terminal division laterally attached to remaining hypopygium with membranous tissue, lateral extensions of terminal division floating.

Aedeagus rotated 20 degrees from vertical. Aedeagal sclerites blunt, approximately 2/3rds length of sperm sac, lateral sclerites expanding ventrobasally; apical apodemes absent, apex rounded; lateral ejaculatory processes similar in shape to ejaculatory apodeme but approximately quarter size, extending anteroventrally, paralleling ejaculatory apodeme. Sperm sac nearly spherical, smaller than ejaculatory apodeme. Ejaculatory apodeme attached dorsoanteriorly to sperm sac, not closely associated with aedeagus, larger than sperm sac, extending anteriorly into segment VII, arcing ventrally to enlarged rounded terminus; curling around anterior margin of sperm sac. Subapical sclerite well

developed, narrow flat rod extending over twice the length of the aedeagus proper, divided basally with medial membranous portion and sclerotized prongs extending to lateral base of aedeagus, narrowing to parallel sided rod apically, apex obtusely lunate ovoid, blunt, dorso-medial spine present at phallotrema.

Female Genitalia. Tergite VII brown, lightening posteromedially. Cerci brown at base, orange apically, lateral ridge well defined, dorsal furrow well developed, dark orange. Cercus length:width, 2.5:1. Hypogynium orange, rotated dorsally approximately 30 degrees from vertical; somewhat bulbous, prow-like, widening ventrally, dorsal apex slightly widening to form near equilateral triangle. Apex marginally with small triangular, tongue-like lobes nestled laterally under cerci.

Figures. Male genitalia 28, Wing 29, Distribution 30.

Taxonomic Notes

The taxonomy of the *Ptychoptera lenis* group has been problematic, with many descriptions relying on variable characters such as the configuration of the subapical spine of the epandrial clasper. Examination of the type material of various species has shown that configuration of the parameres and ventromesal lobe of the epiandrium represent the best diagnostic characters of the group. Upon examination of the male syntype of *Ptychoptera lenis* (which is conspecific with the morphospecies distributed in the Sierra Nevada range), it has become apparent that the majority of specimens historically assigned to that name actually represent *Ptychoptera coloradensis* or *Ptychoptera lacrimiformis*.

Etymology:

Lacrimiformis refers to the inverse teardrop shape of the ventromesal lobe.

Bionomics:

Comprehensive phenological data is available from one site near Robson, British Columbia, collected from 1937 to 1940. The earliest record of adults in the area is mid-April, while the latest record is late August. May and July seem to be peaks of emergence, with no records in June. It is unknown whether this represents a bivoltine lifecycle, or if no collections occurred in June. June collections have occurred at other localities.

Material Examined. Holotype. USA, Washington, Skagit Co., seeps along Hwy 530, Sauk Riv, 48°20.06'N 121°32.99'W, 30.VI.2010 coll. GW Courtney, on vegetation / flying over seep (GWC) (USNM). **Other Material.** Hagensborg, B.C. 12-VII-1992 A. Borkent CD1428 (GLAHM). Salmon Arm B.C. 8-VI-1990 A. Borkent CD 1210 (GLAHM). Brit.Columbia, Robson, V.2.1937, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, V.17.1937, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, V.23.1937, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, V.15.1938, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, V.3.1939, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, VII.16.1939, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, VII.23.1939, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, VII.30.1939, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, VIII.6.1939, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, VIII.23.1939, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, IV.13.1940, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, IV.24.1940, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, V.12.1940, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, VII.16.1940, H.H. Foxlee (UMMZ). British Columbia, Vancouver Island, April 30, 1951, R. Guppy #2 (UMMZ). British Columbia, Vancouver Island, April 26, 1951, R. Guppy #2 (UMMZ). British Columbia, Vancouver Island, May 3, 1951, R. Guppy #1 (UMMZ). British Columbia, Vancouver Island, May 5, 1951, R. Guppy #1 (UMMZ). British Columbia, Vancouver Island, May 9, 1951, R. Guppy #1 (UMMZ). British Columbia, Vancouver Island, May 12, 1951, R. Guppy #2 (UMMZ). British Columbia, Vancouver Island, V-13, 1951, R. Guppy # (UMMZ). British Columbia, Vancouver Island, V-14, 1951 2, Richard Guppy

(UMMZ). British Columbia, Vancouver Island, May 16, 1951, R. Guppy #2 (UMMZ). British Columbia, Vancouver Island, May 24, 1951, R. Guppy #4 (UMMZ). British Columbia, Vancouver Island, Hennedy Lake, 1951 R. Guppy #11 VI-15 (UMMZ). OREGON: Benton Co., Corvallis, Sulphur Springs, 44°36'N 123°24'W 100M, 15 May 1999 sweeping, ieg. AVZ Brower (ORSU). MALTBY, WASH, 18-IV-64, D. MILNE (ORSU). Olympia, Wash, 4 10 94 (WSU). Seattle, Wash. (ORSU). WASHINGTON: Bear Crk., nr. Rimrock Lk., 8mi, SW Tieton R5, 3000ft, 27-30 May 1986, W. J. Turner Sweep (WSU). Washington, Mt. Rainier, 2700'-VIII-13.'40, (H.+M. Townes) (USNM). WASHINGTON, Olympic Nat. Pk., Olympic HtSpgs., July 20, 1953, K. M. Fender (UMMZ). WASHINGTON, Olympic Nat. Pk., Dosewallips R., July 24, 1953, K. M. Fender (UMMZ). WASHINGTON: Whatcom Co., Silver Fir Cmpgr., 14 mi. E Glacier RS, No. Frk. Nooksack R., 2000ft., VIII-(8-11)-74 W. J. Turner Collector (WSU). USA, Washington, Jefferson Co., Olympic National Park, Queets River Valley, mile 3.2, 47°33.52'N 124°10.97'W 35m, 20.vii. 2012 coll. GW Courtney, from roadside seepage (ISIC). USA, Washington, Jefferson Co., Olympic National Park, Queets River Valley, mile 3.2, 47°33.52'N 124°10.97'W 35m, 28 May 2012 coll. GW Courtney, from roadside seepage (ISIC).

***Ptychoptera pendula* Group**

***Ptychoptera espica* Fasbender, sp. n.**

Diagnosis.

Adult. Scutum shining, glabrous; posterior margins of abdominal segments black with narrow yellow margin. Male genitalia with epandrial clasper undeveloped, subepandrial sclerite divided, heavily sclerotized across ventral surface of epandrium; gonopod with gonostylus basal lobe lacking spine, apical stylus poorly sclerotized and pendulant with secondary lobe rounded semicircular.

Description

Adult. Measurements (n=1). Overall length 8.28mm. **Head.** Width: 0.75mm, Height: 0.91mm, Length: 0.58mm; Antenna flagellum length: 4.2mm. **Thorax.** Length: 2.1mm, Height: 2.1mm; Wing length: 9.5mm, Width: 2.2mm. **Abdomen.** Length: 5.6mm

Head. Vertex shining black, sparsely set with trichoid sensilla; frons extremely narrow strip, black. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: scape dark yellow, oblong cylinder with long black setae, projecting dorsally from anterior surface; base of pedicel light brown, distal portion yellow, globular, line of trichoid sensilla on lateral margin. Flagellomeres brown, fusiform. Facial sclerite black, distinct from clypeus, forming bent square sclerite above clypeus. Clypeus ventrally tapering subtriangular, bulbous, generally covered in yellow sensilla, dark brown. Maxillary palpus with proximal segments yellow, 5th segment brown. Labrum leaf shaped, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae yellow.

Thorax. Antepronotum with central crease broad, yellow medially, brown at lateroventral extremity, medial lobe approximately half width of remainder of antepronotum, highly tapered trapezoid, dorsal surface with medial notch. Prescutum and scutum shining, glabrous black, with narrow yellow stripe from posterior apex of prescutum to scutellum; medial and prescutal suture with row of minute clear trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum as longer yellow sensilla; long clear prealar sensilla present. Scutellum yellow. Mediotergite of metanotum lightly pollinose black, patch of short yellow trichoid sensilla medially. Laterotergite of metanotum pollinose black, except for yellow patch near wing base, dorsal patch of very elongate yellow trichoid sensilla. Pleural sclerites all black, with medium pollinosity. Anepisternal cleft narrow, membrane yellow. Suture between epimeron and metapleurite incomplete, weak. **Wing.** Hyaline, weak infuscation

extending from base of R_{1+2} to CuA_1+CuA_2 fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 6.8mm, Apex of Sc to Apex of R_1 1.48mm, R_{3+4+5} stem 1.16mm, weakly bowed along length, nearly traverse angle at base; R_{4+5} stem 1.85mm; R_4 after fork 2.0mm, R_5 after fork 1.85mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.0 : 1.72 : 1.59$. r-m 0.35mm; M distal to r-m 2.65mm; M_1 0.95mm, arcuate, M_2 0.6mm; Mdistal: $M_1 = 1.0 : 0.95$, $R_{3+4+5}:M\text{distal} = 1.0 : 0.81$, $R_4:M_1 = 1.0 : 0.47$. CuA_1 proximal 0.27mm, distal 2.4mm; CuA_2 1.45mm with anterior angle well developed, posterior angle absent. CuA_2 to A_1 straight for 2.2mm. r-m joins R_{3+4+5} at well before R_3 divergence. Halter yellow. Prehalter yellow. **Legs.** Forecoxae yellow, midcoxae yellow with dark spot on dorsoanterior apex, hindcoxae black. Femur and tibia yellow. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensillae.

Abdomen. Tergites and sternites black, posterior and posterior portion of lateral margins yellow except segment I which is uniform color, moderately covered in elongate yellow sensilla. **Male Genitalia.** Epandrial collar incomplete, developed laterally, epandrial apodemes well developed, extending to lateroanterior apex of hypandrium, extending threadlike across gonocoxal apodeme, prominent break between epandrial collar and epandrial apodeme. Epandrial lobes triangular, posterior portion curving ventrally, anterior margin largely straight, curved posterior near lateral margins; lateral margin straight, rounded angle anterior, convergent; medial margin parallel at contact of epandrial lobes, curving laterally, straightening to nearly parallel posterior; anterior apex triangular, forming nearly right angle. Epiproct prominent, posterior margin weakly emarginate with low lateral lobes, epandrial lobes in contact for over $\frac{1}{2}$ of length anteriorly. Posteromedial stylus knob-like, directed medially, placed nearly at apex of epandrial lobe. Ventral surface of epandrial lobe apex flat. Hypoproct small ovoid sclerite tucked under epiproct. Subepandrial membrane heavily sclerotized over nearly the entire surface, divided into paired baciliform sclerites roughly corresponding to ventral surface of each epandrial lobe.

Parameral bridge floating on medial membrane of gonocoxite. Lateral apices spine-like, bridge directed posteromedially, then dorsomedially, forming trapezoidal arc.

Lateral margins of paramere with subrectangular lobe. Gonocoxal apodeme as per genus. General shape of gonocoxite as per genus. Dorsal gonocoxal lobe high, triangular, nearly touching epandrium. Medial gonocoxal lobe narrow and straplike, directed at right angle medially from gonocoxite before turning dorsally at a right angle, expanding to bean-shaped apex with numerous stout cylindrical sensilla on anterior surface. Gonostylus with basal lobe with broad rounded base, forming medially directed rounded lobe, secondary lobule on base directed posterior. Apical stylus pendulant directed at approximately 45 degree ventral angle, forming broad laterally compressed paddle-like lobe, apex poorly sclerotized, secondary lobe forming semicircular lobule on dorsal surface, with tertiary lobule located directly posterior, both moderately sclerotized and with patches of elongate trichoid sensilla on the medial surface.

Basal division of hypandrium with paired triangular lobes on posteromedial margin. eversible sac rectangular in posterior view, swollen ventrally, to dorsal margin of terminal division. Terminal division broadly attached to basal division, pentagonal, inflated, lateral apices forming acute points with patches of heavily sclerotized sensilla at base, dorsal apex broadly triangular.

Aedeagus oriented vertical, ejaculatory apodeme with base narrow; dorsal margin of lateral ejaculatory process straight; apex of aedeagal sclerites blunt, flattened, subapical sclerite having medial portion trowel-shaped with ventral keel. Lateral plates small, not extending beyond apex of subapical sclerite, triangular, nearly equilateral.

Aedeagus oriented vertical. Aedeagal sclerites obtusely pointed, approximately subequal to length of sperm sac, lateral sclerites convergent; apical apodemes absent, apex angled; lateral ejaculatory processes directed anterolaterally, discoid apodeme ovoid, directed ventrally. Sperm sac

nearly spherical, smaller than ejaculatory apodeme. Ejaculatory apodeme attached dorsoanteriorly to sperm sac, closely associated with aedeagus, larger than sperm sac, extending anteriorly into segment VII, arcing ventrally to enlarged rounded terminus; fan-like curling around anterior margin of sperm sac. Subapical sclerite well developed, conical triangle not extending beyond apex of aedeagal sclerites; lateral plates small, not extending beyond apex of subapical sclerite, triangular, nearly equilateral.

Female Genitalia. Tergite dark brown with light yellow margin. Cerci brown on basal margin, remainder orange, lateral ridge poorly defined, dorsal furrow well developed, brown. Cercal length:width, 4:1. Hypogynium brown laterally, orange ventromedially, moderately set with setae, rotated dorsally approximately 30 degrees from vertical; lateral margins swollen in a broadly subquadrate shape, overall structure tapering ventrally, dorsal apex slightly widening to form triangle, hypogynial valves inevident. Apex triangular slightly extended medially, lateral corner narrowly triangular. Lateral margin partially exposed, straight.

Figures. Male genitalia 31, Wing 32, Distribution 33.

Taxonomic Notes. *Ptychoptera espica* is extremely similar to *Ptychoptera townesi*, differing in the absence of an elongate spine on the basal lobe of the gonostylus, and female hypogynium with lateral surfaces not as bulbously expanded. This species appears to be confined to the Olympic Peninsula of Washington state.

Etymology. *Espica* refers to the absence of the elongate articulated spine on the basal lobe of the gonostylus.

Material Examined. Holotype. USA, Washington, Jefferson Co. Olympic National Park, Queets River Valley, 47°34.30'N, 124°08.40'W 50m, 28 May 2012 coll. GW Courtney, from "Skunk cabbage" seep (Alcohol: 1 m#, 6 f#) (USNM) **Paratype.** Same as holotype specimen (Alcohol 2 f#) (ISIC).

WASHINGTON Lewis & Clark, St. Pk. Lewis Co. July 12, 1953, K.M Fender (Pinned: 1 m#) (UMMZ).

WASHINGTON Olympic N.P. Hoh River, July 19, 1953, K.M. Fender (Pinned: 2 m#, 2 f#) (UMMZ).

***Ptychoptera quadrifasciata* Group**

***Ptychoptera abbreviata* Fasbender & Courtney, sp. n.**

Diagnosis

Adult. Wing with four bands, abdomen striped black and orange. Male genitalia with epandrial lobes not developed into epandrial claspers, apices not convergent; gonostylus with knob-like basal lobe and simple laterally compressed apical stylus; hypandrium with leaf-like eversible sac not extending to ventral margin; aedeagus with sperm sac larger than remainder of aedeagus, apices of lateral plates of subapical sclerite convergent.

Description

Adult. Measurements (n=1). Overall length 6.25mm. **Head.** Width: 0.85mm, Height: 0.73mm, Length: 0.55mm; Antenna flagellum length: 3.25mm. **Thorax.** Length: 1.9mm, Height: 1.9mm; Wing length: 6.3mm, Width: 1.6mm **Abdomen.** Length: 3.8mm

Head. Vertex shining black, sparsely set with trichoid sensilla; frons extremely narrow strip, black. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: scape yellow, oblong cylinder with long black setae, projecting dorsally from anterior surface; pedicel yellow, globular, line of trichoid sensilla on lateral margin. Flagellomeres brown, fusiform. Facial sclerite black, divided by clypeus, forming paired triangular sclerites laterally and above clypeus. Clypeus subtriangular, bulbous, generally covered in yellow sensilla, yellow. Maxillary palpus yellow, majority of 5th segment brown. Labrum leaf shaped, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae yellow.

Thorax. Anteprenotum with central crease narrow, anterior corners yellow, remainder fading to brown, medial lobe approximately half width of remainder of anteprenotum, highly tapered trapezoid, dorsal surface with medial notch. Prescutum and scutum greasy black, surface with numerous minute punctures;; medial and prescutal suture with row of minute clear trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum as longer yellow sensilla; long clear prealar sensilla present as line extending nearly to anterior margin. Scutellum brown. Mediotergite of metanotum greasy black, covered in minute punctures, patch of short yellow trichoid sensilla medially poorly developed. Laterotergite of metanotum greasy black, with minute punctures, dorsal patch of very elongate yellow trichoid sensilla. Pleural sclerites orange medially, fading to brown at margins, glabrous. Anepisternal cleft broad, membrane yellow. Suture between epimeron and metapleurite complete.

Wing. With four distinct dark bands, first extending in br & bm distal of crossvein h to approximately $1/5^{\text{th}}$ of length of cells, second band in br & bm starting $1/3^{\text{rd}}$ length and terminating at half length of cells, third band extending from base of R_{1+2} to angle of CuA_2 , fourth and distal band extending from apex of R_1 to M_2 ; membrane with macrotrichia in all cells, densest towards wing margin. All veins covered in short stout macrotrichia. Sc: 4.6mm, Apex of Sc to Apex of R_1 0.8mm, R_{3+4+5} stem 0.49mm, weakly bowed along length, nearly traverse; R_{4+5} stem 1.21mm; R_4 after fork 1.41mm, R_5 after fork 1.46mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.0 : 2.46 : 2.87$. r-m 0.27mm; M distal to r-m 1.73mm; M_1 0.84mm, arcuate, M_2 0.67mm; $M_{\text{distal}}:M_1 = 1.0:0.48$, $R_{3+4+5}:M_{\text{distal}} = 1.0:3.53$, $R_4:M_1 = 1.0:0.59$. CuA_1 proximal 0.25mm, distal 1.75mm; CuA_2 1.0mm with anterior angle well developed, posterior angle absent. CuA_2 to A_1 straight for 1.73mm. r-m joins R_{3+4+5} at well before R_3 divergence. Halter yellow. Prehalter yellow.

Legs. Coxae yellow. Femur and tibia yellow. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5^{th} tarsomere can fold back on pentultimate tarsomere. Mid and hind 1^{st} tarsomere with widely spaced row of minute, spine-like trichoid sensillae.

Abdomen. Base of segments I-V orange, posterior portion brown, posterior segments brown, moderately covered in elongate brown sensilla. **Male Genitalia.** Epandrial collar complete, epandrial apodemes well developed, extending to lateroanterior apex of hypandrium, extending threadlike across gonocoxal apodeme, prominent break between epandrial collar and epandrial apodeme. Epandrial lobes tapering subtrapezoidal, anterior margin largely straight, only weak curve near lateral apex; lateral margin weakly convex, convergent apically; medial margin concave, straight and parallel basally, beyond epiproct curving laterally; anterior apex blunt, squared off; epandrial lobe apices extend to apex of terminal division. Epiproct prominent, posterior margin weakly emarginate, epandrial lobes with in contact for 1/4th of length. Posteromedial stylus absent. Ventral surface of epandrial lobe flat. Hypoproct with external portion tongue-like, internal portion plate-like, extended laterally beyond base of external portion; subepandrial membrane otherwise membranous.

Parameral bridge nearly straight, narrow. Apices of paramere directed dorsally, cylindrical with rounded apex.

Gonocoxal apodeme as per genus. General shape of gonocoxite as per genus. Dorsal gonocoxal lobe located near base of gonostylus, short, recumbent triangular. Medial gonocoxal lobe narrow and straplike, forming broad arc at base, directed dorsomedially, the directed straight dorsally flattening and expanding at apex, medial margin very thin and slightly convex. Gonostylus with basal lobe low knob tilted slightly posterior from vertical, cylindrically petiolate at base, rounded apex with stout trichoid sensilla. Apical stylus subspatulate, flattened, expanding to rounded apex, secondary lobe absent.

Basal division of hypandrium subhemispherical, greater than two times as tall as wide, eversible sac ovoid leaf-like, adhered at dorsal margin, extended ventroposterior, not approaching either dorsal or ventral margin of basal division. Terminal division narrow, broadly attached to basal division as

dorsally directed C-shape with lateral apices acute, medially with elongate medial stylus, extending nearly to epandrial lobes, apex inflated triangle.

Aedeagus oriented 45 degrees from vertical. Aedeagal sclerites obtusely pointed, approximately third length of sperm sac, lateral sclerites expanding convergent; apical apodemes present, apex angled; lateral ejaculatory processes directed laterally, discoid apodeme ovoid, directed ventrally. Sperm sac oblong, much larger than ejaculatory apodeme, extending into segment VII. Ejaculatory apodeme attached dorsally to sperm sac, closely associated with aedeagus, larger than sperm sac, scythe-like paralleling dorsal surface of sperm sac. Subapical sclerite trowel-shaped with medial internal keel, not extending beyond apex of aedeagal sclerites; lateral plates prominent, extending beyond apex of medial portion, base rounded, extended laterally, dorsomedial apex directed dorsomedially and convergent, spinelike.

Female Genitalia. Tergite VII orange medially, brown at lateral margins. Cerci uniformly orange, lateral ridge poorly defined, dorsal furrow well developed, dark orange. Cercal length:width, 4:1. Hypogynium uniformly orange, moderately set with setae, rotated dorsally approximately 45 degrees from vertical; lateral margins flat, dorsal apex not expanded, rounded, hypogynial valves inevident. Apex round slightly extended medially, lateral corner rounded. Lateral margin hidden by Sternite VII.

Figures. Male genitalia 34, Wing 35, Distribution 36.

Taxonomic Notes. *Ptychoptera abbreviata* is similar to *P. quadrifasciata*, differing in the abbreviate epandrial lobes and the structure of the lateral plates of the subapical sclerite. This species is found through the Midwestern US east of the Rocky Mountains, though the eastern border of the range is currently poorly delimited, but probably lies between the Mississippi River and Illinois/Indiana border.

Material Examined. Holotype. Valentine, Nebraska, June 9 1950, Hicks, Slater, Laffoon (Pinned: 1m#) (USNM) **Paratypes.** Valentine, Nebraska, June 9 1950, Hicks, Slater, Laffoon (Pinned: 11 m#, 3 f#) (ISIC). **Other Material.** Boulder Co., CO, 16 Aug 2010, B. Kondratieff & D. Rees, Stazio Ball Fields, Boulder (Pinned: 2 m#, 2 f#) (CSU). Larimer Co., CO, 6 June 2010, R. Stoak & A. Blevins, B. Kondratieff, Soapstone Prairie Natural Area, Graves Creek (Pinned: 1 m#, 1 f#) (CSU). Larimer Co., CO, 6 June 2010, R. Stoak & A. Blevins, B. Kondratieff, Soapstone Prairie Natural Area, Spottlewood Cr. Area (Pinned: 1 m#, 3 f#) (CSU). Larimer Co., CO, 3 July 2006, D. Leatherman, Fort Collins, Running Deer NA, Poudre R, S. Prospect (Pinned: 1 f#) (CSU). Weld Co., CO, 6 June 2010, R.S. & K. Stoaks, Meadow Springs, Sweep Net (Pinned: 1 m#, 1f#) (CSU). Iowa Lakeside Lab., Dickinson Co., Iowa, July 18, 1959, Jean L. Laffoon (pinned: 1 m#) (ISIC). USA Iowa, Dickinson Co. Iowa Lakeside Lab, sampling in Seep May-17-10, 43.383374N, 95.179974W, GW Courtney + A Fasbender (Pinned: 1 m#) (ISIC). USA Iowa, Dickinson Co. Silver Lake Fen May-17-2010, Hillside Seep nr. Marsh, 43.437472N, 95.365009W, GW Courtney + A Fasbender (Pinned: 1 f#) (ISIC). Sioux City, IOWA, June 11, 1949, Slater & Laffoon (Pinned: 8 m#, 3 f#) (ISIC). 3 m S Afton, Minn. May 19 1956 (Pinned: 1 m#) (ISIC). Itasca State, Park, Minn. IX-2 1950, Jean Laffoon (Pinned: 1 m#) (ISIC). Itasca Park, Minn. Aug 11 1951 (Pinned: 1 f#) (ISIC). Minnehaha Park, Hennepin Co., Minn. June 23 1956 (Pinned: 1 m#, 1 f#) (ISIC). Mora, Minnesota, June24-30, 1934, C.R. Yeager (Pinned: 2 f#) (ISIC). Mississippi Bluff, 1-2 m N State Line, Houston Co. Minn. June 19_ (Pinned: 1 m#) (ISIC). John Latsch St. Pk., S Minneiska, Minn. May 25 1956 (Pinned: 8 m#, 1 f#) (ISIC). MINNESOTA: WASHINGTON CO. Falls Creek State Natural Area, 10 miles N. of Stillwater, 6.vii.1994, col. Daniel E. Hansen (Pinned: 1 m#) (ISIC). Winona Co., Minn. May 25 1940 (Pinned: 1 m#) (ISIC). Extreme nw. corner, Brown Co., Nebraska, June 10, 1950, Hicks, Slater, Laffoon (Pinned: 5 m#) (ISIC). Garden Co., NE, 22 May 1998, B. Kondratieff, N. Platte R. Rd. 199 (Pinned: 1 m#) (CSU).

***Ptychoptera quadrifasciata* Say, 1824**

Ptychoptera quadrifasciata Say, 1824: 359 (original description)

Ptychoptera rufocincta Osten Sacken 1860: 252 (description)

Ptychoptera rufocincta Osten Sacken, Alexander 1920: 775-779 (description of larva and pupa)

Ptychoptera quadrifasciata Say, Alexander 1927: 7 (catalog)

Ptychoptera rufocincta Osten Sacken, Alexander 1927: 7 (catalog)

Ptychoptera quadrifasciata Say, Alexander 1965: 97 (catalog)

Ptychoptera rufocincta Osten Sacken, Alexander 1965: 97 (catalog, synonymy)

Diagnosis

Adult. Wing with four bands, abdomen striped black and orange. Male genitalia with epandrial lobes not developed into epandrial claspers, apices convergent; gonostylus with knob-like basal lobe and simple laterally compressed apical stylus; hypandrium with leaf-like eversible sac not extending to ventral margin; aedeagus with sperm sac larger than remainder of aedeagus, apices of lateral plates of subapical sclerite divergent.

Description

Adult. Measurements (n=1). Overall length 5.83mm. **Head.** Width: 0.98mm, Height: 0.78mm, Length: 0.53mm; Antenna flagellum length: 3.83mm. **Thorax.** Length: 1.9mm, Height: 1.9mm; Wing length: 5.5mm, Width: 1.2mm. **Abdomen.** Length: 3.4mm

Head. Vertex shining black, sparsely set with trichoid sensilla; frons extremely narrow strip, black. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: scape yellow, oblong cylinder with long black setae, projecting dorsally from anterior surface; pedicel yellow, globular, line of trichoid sensilla on lateral margin. Flagellomeres brown, fusiform. Facial sclerite black, divided by clypeus, forming paired triangular sclerites laterally and

above clypeus. Clypeus rhomboidal, bulbous, generally covered in yellow sensilla, dorsal quarter black, remainder yellow. Maxillary palpus yellow, apex of 5th segment brown. Labrum leaf shaped, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae yellow.

Thorax. Antepronotum with central crease narrow, anterior corners yellow, remainder fading to brown, medial lobe approximately half width of remainder of antepronotum, highly tapered trapezoid, dorsal surface with medial notch. Prescutum and scutum greasy black, surface with numerous minute punctures; medial and prescutal suture with row of minute clear trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum as longer yellow sensilla; long clear prealar sensilla present as line extending nearly to anterior margin. Scutellum brown. Mediotergite of metanotum greasy black, covered in minute punctures, patch of short yellow trichoid sensilla medially poorly developed. Laterotergite of metanotum greasy black, with minute punctures, dorsal patch of very elongate yellow trichoid sensilla. Pleural sclerites orange medially, fading to brown at margins, glabrous. Anepisternal cleft broad, membrane yellow. Suture between epimeron and metapleurite complete.

Wing. With four distinct dark bands, first extending in br & bm distal of crossvein h to approximately 1/5th of length of cells, second band in br & bm starting 1/3rd length and terminating at half length of cells, third band extending from base of R_{1+2} to angle of CuA_2 , fourth and distal band extending from apex of R_1 to M_2 ; membrane with macrotrichia in all cells, densest towards wing margin. All veins covered in short stout macrotrichia. Sc: 4.9mm, Apex of Sc to Apex of R_1 1.11mm, R_{3+4+5} stem 0.49mm, weakly bowed along length, nearly traverse; R_{4+5} stem 1.43mm; R_4 after fork 1.6mm, R_5 after fork 1.71mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.0 : 2.91 : 3.26$. r-m 0.27mm; M distal to r-m 1.93mm; M_1 1.09mm, arcuate, M_2 0.74mm; $M\text{distal}:M_1 = 1.0:0.56$, $R_{3+4+5}:M\text{distal} = 1.0:3.93\text{mm}$, $R_4:M_1 = 1.0:0.68$. CuA_1 proximal 0.2mm, distal 2.1mm; CuA_2 1.16mm with anterior angle well developed, posterior angle absent. CuA_2 to A_1 straight for 1.98mm. r-m joins R_{3+4+5} at well before R_3 divergence. Halter yellow. Prehalter yellow. **Legs.** Coxae yellow. Femur and tibia yellow. First tarsomere yellow proximally, turning

brown distally. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensillae.

Abdomen. Base of segments I-V orange, posterior portion brown, posterior segments brown, moderately covered in elongate brown sensilla. **Male Genitalia.** Epandrial collar complete, epandrial apodemes well developed, extending to lateroanterior apex of hypandrium, extending threadlike across gonocoxal apodeme, prominent break between epandrial collar and epandrial apodeme. Epandrial lobes triangular, anterior margin largely straight, only weak curve near lateral apex; lateral margin weakly convex, convergent apically; medial margin concave, straight and basally, divergent, beyond epiproct curving laterally; anterior apex acutely triangular; epandrial lobe apices extend slightly beyond apex of terminal division. Epandrial claspers absent Epiproct prominent, posterior margin weakly emarginate, epandrial lobes with point contact at anterior apex of epiproct. Posteromedial stylus absent. Ventral surface of epandrial lobe flat. Hypoproct with external portion tongue-like, internal portion plate-like, extended laterally beyond base of external portion; subepandrial membrane otherwise membranous. Parameral bridge nearly straight, narrow. Apices of paramere directed dorsally, triangular with subacute point. Gonocoxal apodeme as per genus. General shape of gonocoxite as per genus. Dorsal gonocoxal lobe located near base of gonostylus, short, recumbent triangular. Medial gonocoxal lobe narrow and straplike, forming broad arc at base, directed dorsomedially, the directed straight dorsally flattening and expanding at apex, medial margin very thin and slightly convex. Gonostylus with basal lobe low knob tilted slightly posterior from vertical, cylindrically petiolate at base, rounded apex with stout trichoid sensilla. Apical stylus subspatulate, flattened, expanding to rounded apex, secondary lobe absent.

Basal division of hypandrium subhemispherical, greater than two times as tall as wide, eversible sac ovoid leaf-like, adhered at dorsal margin, extended ventroposterior, not approaching either dorsal or ventral margin of basal division. Terminal division narrow, broadly attached to basal division as

dorsally directed C-shape with lateral apices acute, medially with elongate medial stylus, extending nearly to epandrial lobes, apex inflated triangle.

Aedeagus oriented 45 degrees from vertical. Aedeagal sclerites obtusely pointed, approximately third length of sperm sac, lateral sclerites expanding convergent; apical apodemes present, apex angled; lateral ejaculatory processes directed laterally, discoid apodeme ovoid, directed ventrally. Sperm sac oblong, much larger than ejaculatory apodeme, extending into segment VII. Ejaculatory apodeme attached dorsally to sperm sac, closely associated with aedeagus, larger than sperm sac, scythe-like paralleling dorsal surface of sperm sac. Subapical sclerite trowel-shaped with medial internal keel, not extending beyond apex of aedeagal sclerites; lateral plates prominent, extending beyond apex of medial portion, base rounded, extended laterally, dorsomedial apex directed dorsomedially and convergent, spinelike.

Female Genitalia. Tergite VII orange medially, brown at lateral margins. Cerci uniformly orange, lateral ridge poorly defined, dorsal furrow well developed, dark orange. Cercal length:width, 3:1. Hypogynium uniformly orange, moderately set with setae, rotated dorsally approximately 45 degrees from vertical; lateral margins flat, dorsal apex not expanded, rounded square, hypogynial valves inevident. Apex rounded square, flat, lateral corner rounded. Lateral margin hidden by Sternite VII.

Figures. Male genitalia 37, Wing 38, Distribution 39.

Taxonomic Notes. The holotype of *P. quadrifasciata* was collected in Pennsylvania (Say provided no further detail) and apparently no longer exists (J. Gelhaus, pers. comm.). The species was widely recognized under the synonym *Ptychoptera rufocincta* Osten Sacken, 1860 (holotype locality also Pennsylvania) which was synonymized by Alexander in 1965. The species is easily distinguishable from other Nearctic Ptychopteridae based on the description of four bands on the wing. In 1959 Alexander described *Ptychoptera osceola* from specimens initially determined as this species collected by J.S.

Rogers, and the current study has found that the western populations of *P. quadrifasciata* represent a distinct species. As there remains the possibility that further cryptic species are contained within the current concept of *P. quadrifasciata* a neotype is merited. The conditions of Article 75.3 are fulfilled thus: 75.3.1, The purpose of this neotype designation is to clarify the taxonomic concept of *Ptychoptera quadrifasciata* Say, 1824; 75.3.2, The species is distinguishable from other Nearctic Ptychopteridae by the four bands on the wing; 75.3.3, The description provided here is sufficient to distinguish *P. quadrifasciata*; 75.3.4, The authors have contacted J. Gelhaus, curator of the Diptera Collection of the Academy of Natural Sciences, Philadelphia and confirmed that the holotype of *P. quadrifasciata* was destroyed; 75.3.5, The diagnosis and the type locality of Pennsylvania allow the recognition of the neotype specimen proposed here as of the same species as the original description; 75.3.6, The locality of *P. quadrifasciata* given in the original description is Pennsylvania, and the proposed neotype was collected in that state; 75.3.7, This neotype will be transferred upon publication to the Diptera collection of the Academy of Natural Sciences, Philadelphia, a publicly accessible research collection and the original repository of Say's holotype.

Material Examined. Neotype. USA, PA, Centre County, Moshannon State Forest, Smays Run @ N Run Rd, 40°53.88'N 81°01.19'W, 580m 27.iii.2012 coll. GW, Courtney, depo. zone (Pinned: 1 m#) (ANSP) **Other Material.** Same as neotype specimen (Pinned: 3 m#, 2 f#; Alcohol: 6 m#, 10 f#, 1 larva, 2 pupa) (ISIC). FLORIDA, Leon County, III-18-1939, J.S. Rogers (Pinned: 1 m#) (ISIC). GEORGIA: Oconee Co. 2mi. N. Watkinsville, 3 October 1977, George W. Byers #1 (Pinned: 2 m#, 2 f#) (KU). KENTUCKY: Whitley Co. Cumberland Falls, St. Pk. 6 June 1960, George W. Byers #2 (Pinned: 1 m#) (KU). MARYLAND Garrett Co. #8. New Germany St. Park, 2300', 8 June, 1977. Byers, May, Young (Pinned: 2 m#) (KU). Montcalm Co. Mich, 8-14.48, R.R. Deisbach (Pinned: 1 m#) (KU). Fayetteville NC, 14 May 59, DL Wray (Pinned: 1 f#) (NCSU). PENNSYLVANIA: Allegheny Co. Schenly Park, Pittsburgh. 40-26-17N, 79-56-44W/ 320m., 22-23

June 2001, PITTSBURGH BIOBLITZ, 2001 staff Carnegie, Museum Natural History (Pinned: 2 m#, 4 f#) (CMNH). PENNSYLVANIA, Franklin Co. No.1, Caledonia St. Park, 2 July 1960, Byers and Party (Pinned: 1 m#) (KU).

Acknowledgements

J. Gassman is thanked for illustrations of the external views of the male genitalia of Bittacomorphinae. We also wish to thank the curatorial staff who facilitated loans or examination of specimens: P.H. Adler & J.C. Morse (CUAC), T. Pape (ZMUC), J. Boone (FMNH), P. Perkins (MCZ), C. Deitrich & D. Dmitriev (INHS), Z. Falin & J. Thomas (KU), G. Parsons (ARC), M. O'Brien (UMMZ), C.J. Marshall (ORSU), S. Fitzgerald (PNDL), G.R. Curler (PERC), and W.N. Mathis (USNM). Collecting at Coweeta Hydrological Laboratory and Olympic National Park was facilitated by J. Love and J. Freilich, respectively. D.R. Fasbender and R.I. Madriz participated on collecting trips with the first author. This project was supported in part by National Science Foundation grants (DEB-0933218 and EF-1115112) to G.W. Courtney and the National Institute of Food and Agriculture, Project No. 6693.

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Table 1: Species Groups of the Nearctic Ptychopteridae

<i>Bittacomorphella sackenii</i> Group	<i>Ptychoptera lenis</i> Group	<i>Ptychoptera pendula</i> Group	<i>Ptychoptera quadrifasciata</i> Group
<i>Bittacomorphella furcata</i>	<i>Ptychoptera bilobata</i>	<i>Ptychoptera espica</i>	<i>Ptychoptera abbreviata</i>
<i>Bittacomorphella pacifica</i>	<i>Ptychoptera byersi</i>	<i>Ptychoptera monoensis</i>	<i>Ptychoptera osceola</i>
<i>Bittacomorphella sackenii</i>	<i>Ptychoptera coloradensis</i>	<i>Ptychoptera pendula</i>	<i>Ptychoptera quadrifasciata</i>
	<i>Ptychoptera lacrimiformis</i>	<i>Ptychoptera townesi</i>	
	<i>Ptychoptera lenis</i>		
	<i>Ptychoptera minor</i>		
	<i>Ptychoptera obscura</i>		
	<i>Ptychoptera uta</i>		

Table II: Common Misidentifications of the Nearctic Ptychopteridae

Species	Misidentification
<i>Bittacomorpha occidentalis</i>	→ <i>Bittacomorpha clavipes</i>
<i>Bittacomorphella fenderiana</i>	→ <i>Bittacomorphella pacifica</i>
<i>Bittacomorphella pacifica</i>	→ <i>Bittacomorphella sackenii</i>
<i>Ptychoptera coloradensis</i>	→ " <i>Ptychoptera lenis lenis</i> ", <i>Ptychoptera uta</i>
<i>Ptychoptera lenis</i>	→ * <i>Ptychoptera minor</i>
<i>Ptychoptera lacrimiformis</i>	→ * <i>Ptychoptera lenis</i>
<i>Ptychoptera pendula</i>	→ <i>Ptychoptera townesi</i>

*Misidentification in Alexander, 1967

Figure Abbreviations

AEA: Ejaculatory Apodeme, AES: Aedeagal Sclerite, AEV: Ventral Apical Apodeme of Aedeagus, ALP: Lateral Ejaculatory Process AS: Sperm Sac, ASA, Subapical Sclerite of Aedeagus, ASP: Lateral Plate of Subapical Sclerite, AVA: Ventral Arm of Subapical Sclerite, CRC: Cercus, ECA: Epandrial Apodeme, ECB: Epandrial clasper basal lobe, ECL: Epandrial Collar, ECP: Epandrial Clasper, ECV: Epandrial Clasper Ventral Lobe, EL: Epandrial Lobe, EMS: Epandrial Clasper medial swelling, EPI: Epiproct, EPG: Epigynium, EPP: Epandrial Plate, EPS: Posteromedial Stylus of Epandrium, ESS, Subapical Spine of Epandrium, EVL: Ventromesal Lobe of Epandrium, GAS: Apical stylus of gonostylus, GAT: Tertiary lobe of Apical Stylus of Gonostylus, GBA: Anterior lobe of basal lobe of gonostylus, GBL: Basal lobe of gonostylus, GBM: Medial lobe of basal lobe of gonostylus, GBP: Posterior lobe of basal lobe of gonostylus, GCT: Gonocoxite, GCA: Gonocoxal Apodeme, GDS: Dorsal spur of gonocoxal apodeme, GLD: Dorsal Gonocoxal Lobe, GLM: Medial Gonocoxal Lobe, GLV: Ventral Gonocoxal Lobe, GSL: Secondary lobe of Apical Stylus of Gonostylus, GFK: Genital Fork, GST: Gonostylus: HBD: Basal Division of Hypandrium, HBS: Basal scale of Hypandrium HES: Eversible sac of Hypandrium, HLT: Lateral lobule of terminal division, HMW: Membranous Window of Terminal Division, HPG: Hypogynium, HSL: Spathate Lobe of Hypandrium, HTD: Terminal Division of Hypandrium, HTE: Lateral Extension of Terminal Division, HVL: Hypogynial Valves, HYP: Hypoproct, PMB: Paramere Base, PME: Posteromedial Extension of Paramere, PPA: Apical Process of Paramere

Figures

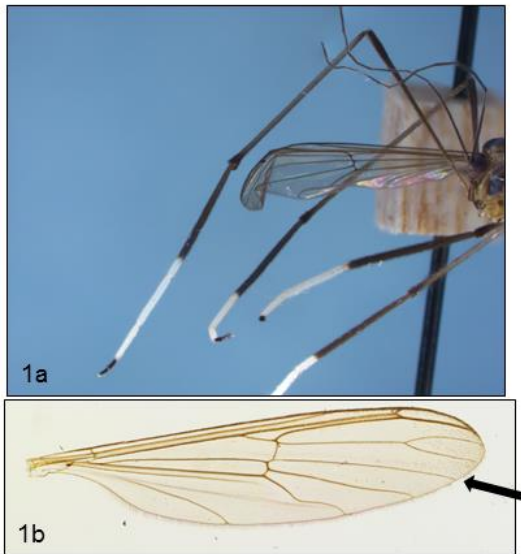


Fig 1. *Bl. fenderiana* a. Legs b. Wing

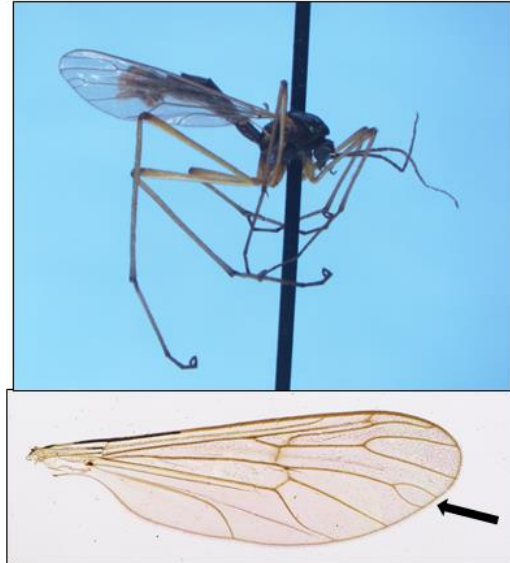


Fig 1. *P. metallica* c. Legs d. Wing

1a.	Legs banded with white (Fig. 1a). Wings lacking cell m1 (vein M unbranched) (Fig. 1b). Antenna with 17 or more flagellomeres... Subfamily Bittacomorphinae	<u>2</u>
1b.	Legs not banded with white (Fig. 1c). Wings with cell m1 present (vein M branched) (Fig. 1d). Antenna with 13 flagellomeres... Subfamily Ptychopterinae, <i>Ptychoptera</i>	<u>8</u>

Figure 1. Couplet 1.

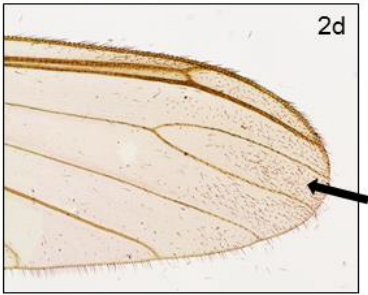
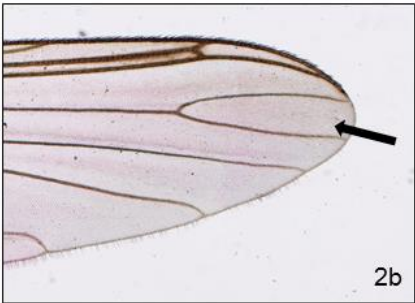


Fig 1. *B. clavipes* a. Legs b. Wing

Fig 1. *Bl. jones* c. Legs d. Wing

2a. (1)	All legs with first tarsomere conspicuously expanded (Fig. 2a). Wing with distal radial and medial cells without macrotrichia (Fig. 2b). Antenna with 17-19 flagellomeres... <i>Bittacomorpha</i> Fabricius	<u>3</u>
2b.	All legs with first tarsomere not expanded (Fig. 2c). Wing with distal radial and medial cells with macrotrichia (Fig. 2d). Antenna with 20+ flagellomeres... <i>Bittacomorphella</i> Alexander	<u>4</u>

Figure 2. Couplet 2.

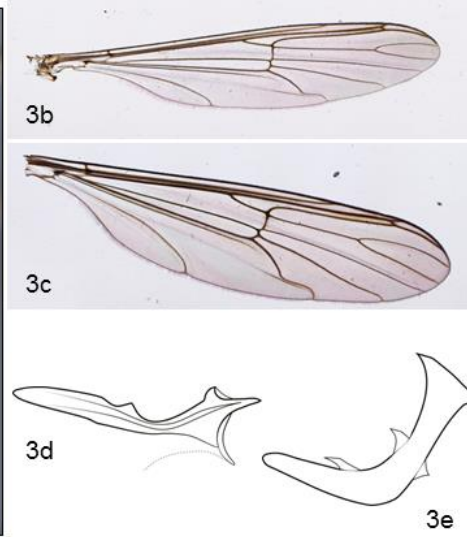


Fig 3. *B. clavipes*, a. Scutum, b. Wing, d. Paramere

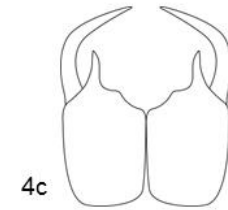
Fig 3. *B. occidentalis*, c. Wing, e. Paramere f. Scutum

3a. (2)	Scutum dull black with silver-grey tomentum in lateral and ventrolateral views and with distinct, narrow, silver-grey, medial stripe expanded postsuturally (Fig. 3a). Cell r4 about one-third the length of cell r5 (Fig. 3d). Male terminalia with apex of paramere weakly furcate (Fig. 3c). Widespread east of Rocky Mountains... <i>Bittacomorpha clavipes</i> Fabricius	
3b.	Scutum shining black; pale medial stripe absent, but patch of silver-grey tomentum present on postsutural midline (Fig. 3f). Cell r4 about one-half the length of cell r5 (Fig. 3ec. Male terminalia with apex of paramere spatulate (Fig. 3e). Western... <i>Bittacomorpha occidentalis</i> Aldrich	

Figure 3. Couplet 3.



4b



4d

Fig 3. *Bl. fenderiana*, c. Epandrium, b. Habitus

4a. (2)	Legs with broad white band on proximal portion of tibia (Fig. 3a). Male terminalia with posterior margin of epandrium not emarginate, epandrial claspers with basal lobe (Fig. 3b). Eastern... <i>Bittacomorphella jonesi</i> Johnson	
4b.	Legs without white band on proximal portion of tibia (Fig. 3d). Male terminalia with epandrium emarginate, epandrial claspers lacking basal lobe (Fig. 3c). Western...	<u>5</u>

Figure 4. Couplet 4.

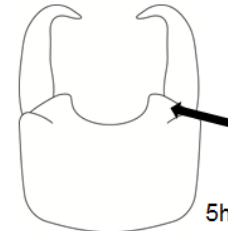
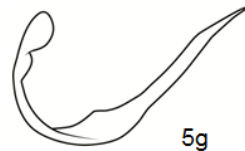
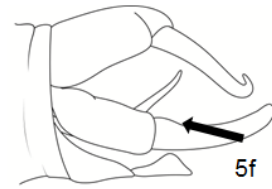
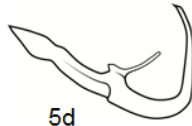
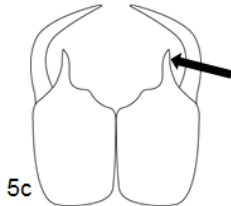
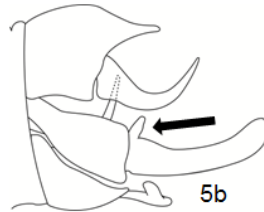
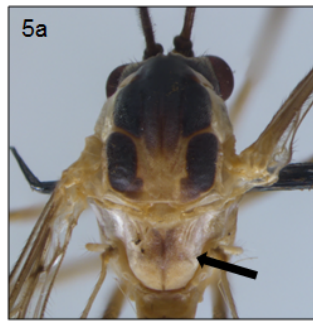


Fig 5. *Bt. pacifica*: a. Mediotergite, b. Male Lateral, c. epandrium, d. paramere

Fig 5. *Bt. pacifica*: e. Mediotergite, e. Male Lateral, g. paramere, h. epandrium

5a. (4)	Mediotergite of postnotum yellow (Fig. 5a). Male terminalia with epandrial lobes prominent and pentagonal in dorsal view, capped with a narrow, stylate posteromedial stylus (Fig. 5c). Gonostylus with a slender basal lobe directed dorsally (Fig. 5b). Paramere a long, slender, sickle-shaped hook curving dorsomedially; lobule at base (Fig. 5d) Coast Range... <i>Bittacomorphella fenderiana</i> Alexander	
5b.	Mediotergite of postnotum dark (Fig 5e). Male terminalia with articulated lobes of epandrium bearing setae throughout their length; epandrial lobes not apparent, posteromedial stylus of epandrium forming low knob directly medial to epandrial clasper (Fig. xx). Gonostylus without a basal lobe (Fig. xx). Paramere straight, curved ventrally, or bifurcate; basal lobule absent. (Fig. 5g). <i>Bittacomorphella sackenii</i> Group...	<u>6</u>

Figure 5. Couplet 5.

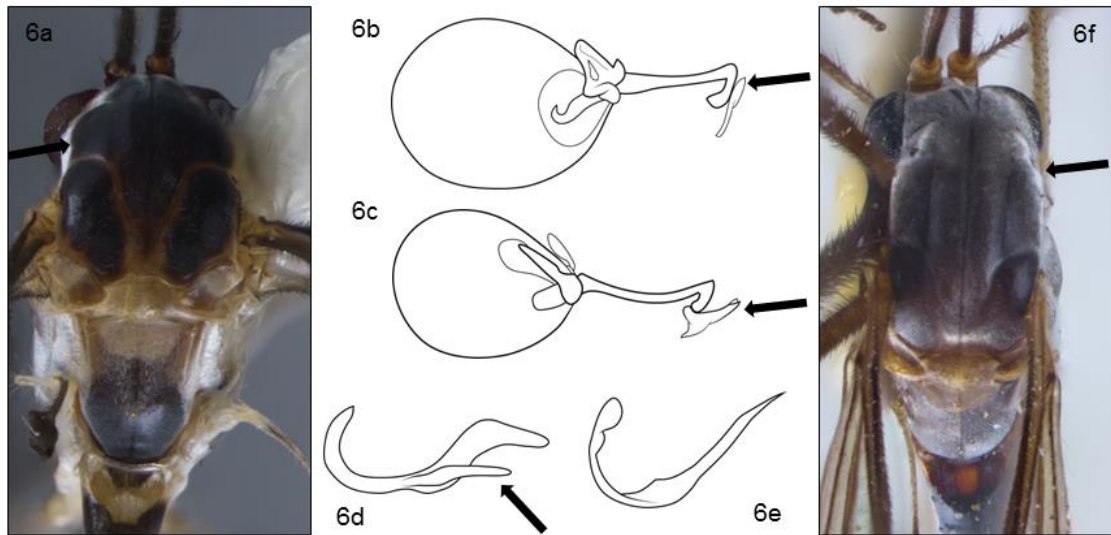


Fig 6. *Bl. furcata*: **a.** scutum, **b.** aedeagus, **d.** paramere

Fig 6. *Bl. furcata*: **c.** aedeagus, **e.** paramere, **f.** scutum

6a. (5)	Scutum glabrous (Fig. 6a). Male terminalia with posterior margin of epandrium strongly emarginate, subapical sclerite reduced to a poorly distinguished plate at apex of aedeagus (Fig. 6b), paramere bifurcate (Fig. 6d). Olympic Peninsula and Coast Range... <i>Bittacomorphella furcata</i> Fasbender & Courtney	
6b.	Scutum covered in silver-grey tomentum (Fig. 6f). Male terminalia with posterior margin of epandrium weakly emarginate, subapical sclerite of aedeagus conical (Fig. 6c), extending beyond phallotrema, Paramere simple (Fig. 6e)...	<u>I</u>

Figure 6. Couplet 6.

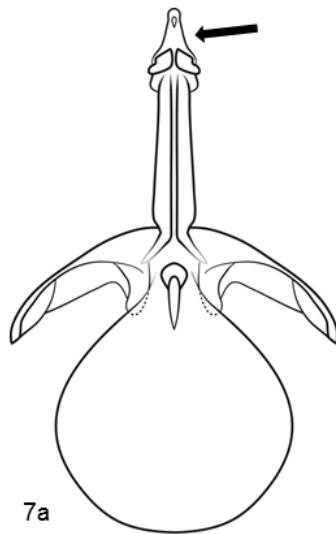


Fig 7. *Bl. pacifica*: **a.** aedeagus dorsal, **b.** aedeagus lateral, **c.** paramere

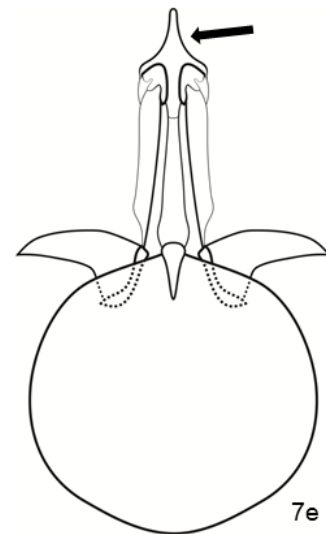
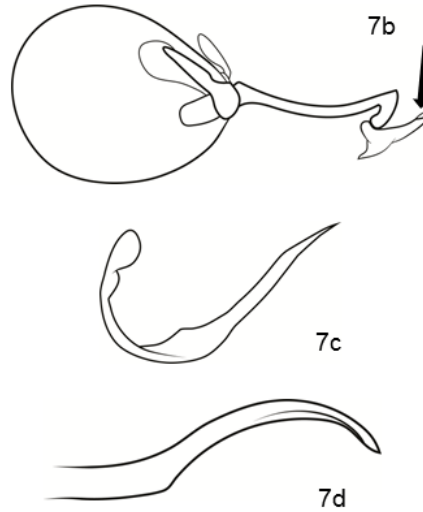
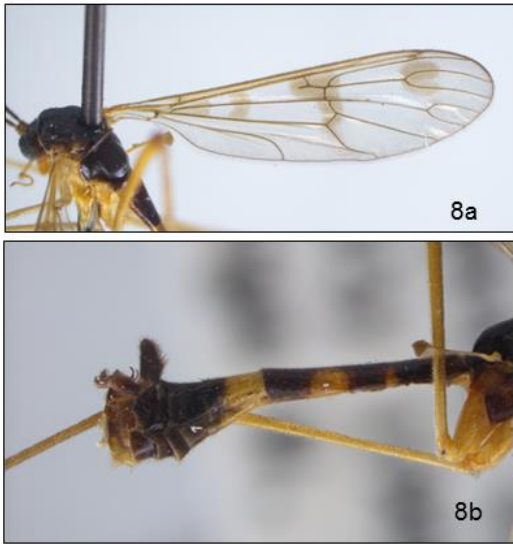
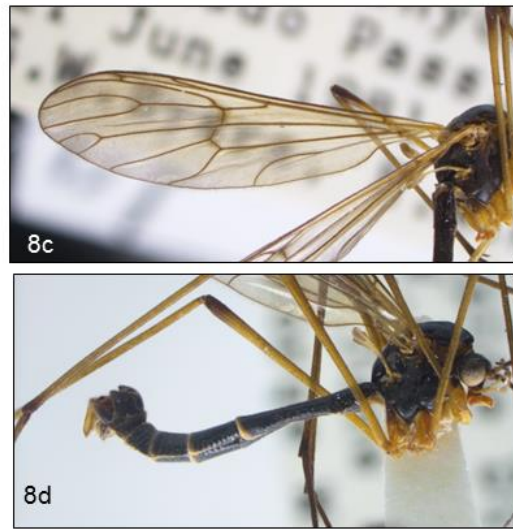


Fig 7. *Bl. sackenii*: **a.** aedeagus dorsal, **b.** aedeagus lateral, **c.** paramere

7a. (6)	Male terminalia with subapical sclerite of aedeagus tapering triangular (Fig. 7a), apex with triangular tooth dorsally (Fig. 7b). Paramere simple or with weak sigmoidal curvature. (Fig. 7c). Coast and Cascade Ranges... <i>Bittacomorphella pacifica</i> Alexander	
7b.	Male terminalia with subapical sclerite of aedeagus pin-like, apex simple (Fig. 7e). Paramere forming semicircular curve dorsally. (Fig. 7d). Sierra Nevada Range... <i>Bittacomorphella sackenii</i> von Röder	

Figure 7. Couplet 7.

Fig 8a: *P. quadrifasciata* wing; 8b: *P. quadrifasciata* abdomenFig 8c: *P. pendula* wing; 8d: *P. pendula* abdomen

8a. (1)	Wing with three or more distinct dark bands (Fig. 8a). Abdomen with light bands on anterior margins of abdominal segments. (Fig. 8b)	<u>9</u>
8b.	Wing hyaline or with faint infuscation near cord and R4+5 and M1+2 (Fig. 8c). If light bands are present on abdomen, confined to posterior margins of abdominal segments (Fig. 8d).	<u>12</u>

Figure 8. Couplet 8.

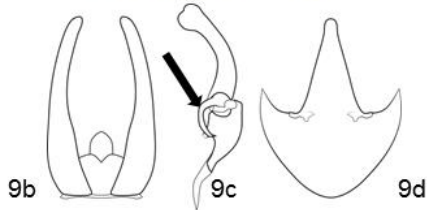


Fig 9. *P. alexanderi*: **a.** laterotergite, **b.** epandrium
c. gonopod, dorsal **d.** hypandrium, posterior

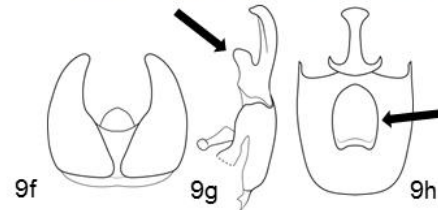
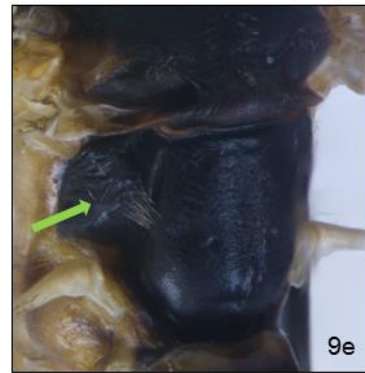
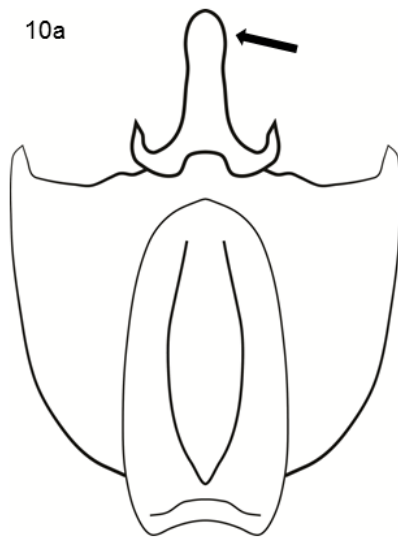
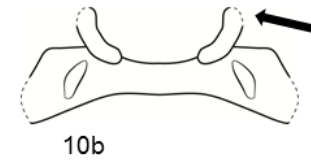


Fig 9. *P. quadrifasciata*: **e.** laterotergite, **f.** epandrium
g. gonopod, dorsal **h.** hypandrium, posterior

9a. (8)	Mediotergite of postnotum orange-yellow medially, laterotergite orange yellow (Fig. 9a). Male terminalia with epandrial lobes elongate, nematoform (Fig. 9b); gonostylus with basal lobe narrow-sickle-shaped, glabrous, directed anterior (Fig. 9c); basal division of hypandrium without eversible sac. (Fig. 9d) Central America... <i>Ptychoptera alexanderi</i> Hancock	
9b.	Mediotergite of postnotum completely dark, laterotergite dark (Fig. 9e). Male terminalia with epandrial lobes short, triangular (Fig. 9f); gonostyle with basal lobe knob-like, directed posterior, heavily provided with stout sensillae (Fig. 9g); basal division of hypandrium with eversible sac. (Fig. 9h) Eastern...	<u>10</u>

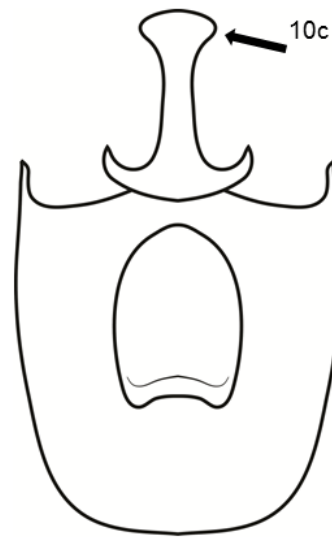
Figure 9. Couplet 9.

Fig 9. *P. osceola*: a. hypandrium, b. paramere

10b



10c

Fig 9. *P. quadrifasciata*: c. paramere, d. hypandrium

10c

10a. (9)	Male terminalia with apex of terminal division of hypandrium tapering (Fig. 10a), medial gonocoxal lobe fused to paramere. (Fig. 10b). Florida and Georgia... <i>Ptychoptera osceola</i> Alexander	
10b.	Male terminalia with apex of terminal division of hypandrium expanded (Fig. 10d), medial gonocoxal lobe free of paramere. (Fig. 10c)...	<u>11</u>

Figure 10. Couplet 10.

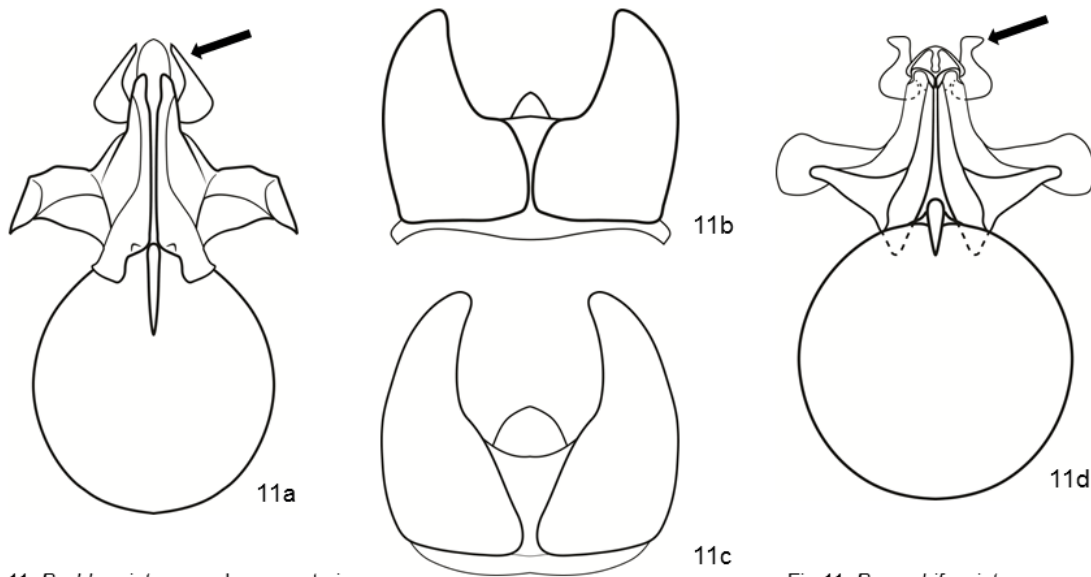


Fig 11. *P. abbreviata*: **a.** aedeagus anterior, **b.** epandrium

Fig 11. *P. quadrifasciata*: **c.** epandrium, **d.** aedeagus anterior

11a. (10)	Male terminalia with apex of epandrial lobe blunt, not convergent, not extending beyond apex of terminal division; lateral apices of subapical sclerite convergent, spine-like. (Fig. xx) Central and western Midwest... <i>Ptychoptera abbreviata</i> sp. n.	
11b.	Male terminalia with apex of epandrial lobe tapering, convergent, extending beyond apex of terminal division; lateral apices of subapical sclerite divergent, flag-like. (Fig. xx) Eastern seaboard, eastern Midwest... <i>Ptychoptera quadrifasciata</i> Say	

Figure 11. Couplet 11.



Fig 12. *P. sculleni*: a. thorax,
b. epandrium



Fig 12. *P. pendula*: c. thorax,

12a. (8)	Scutum with at least <u>prescutal suture</u> outlined in yellow, often with larger yellow areas present as well (Fig. 12a). <u>Mediotergite of postnotum</u> yellow, dark posteriorly (Fig. 12a). Pleural sclerites with at least dorsal portion yellow (Fig. 12a). Male <u>terminalia</u> with <u>epandrial lobes</u> elongate, gently arcing <u>nematoform stylus</u> , foot-shaped apically and bearing a short ventral lobe at about two-thirds the length (Fig. 12b). Cascade and Coast Ranges <i>Ptychoptera sculleni</i> Alexander	
12b.	Scutum uniformly dark (Fig. 12c). <u>Mediotergite of postnotum</u> dark, often with small yellow marks basally (Fig. 12c). Pleural sclerites uniformly dark (Fig. 12c). Male <u>terminalia</u> lacking elongate stylus associated with the <u>epandrial lobe</u> OR if elongate stylus present bladelike, with a distinct angle medially and a ventral lobe at the base...	<u>13</u>

Figure 12. Couplet 12.

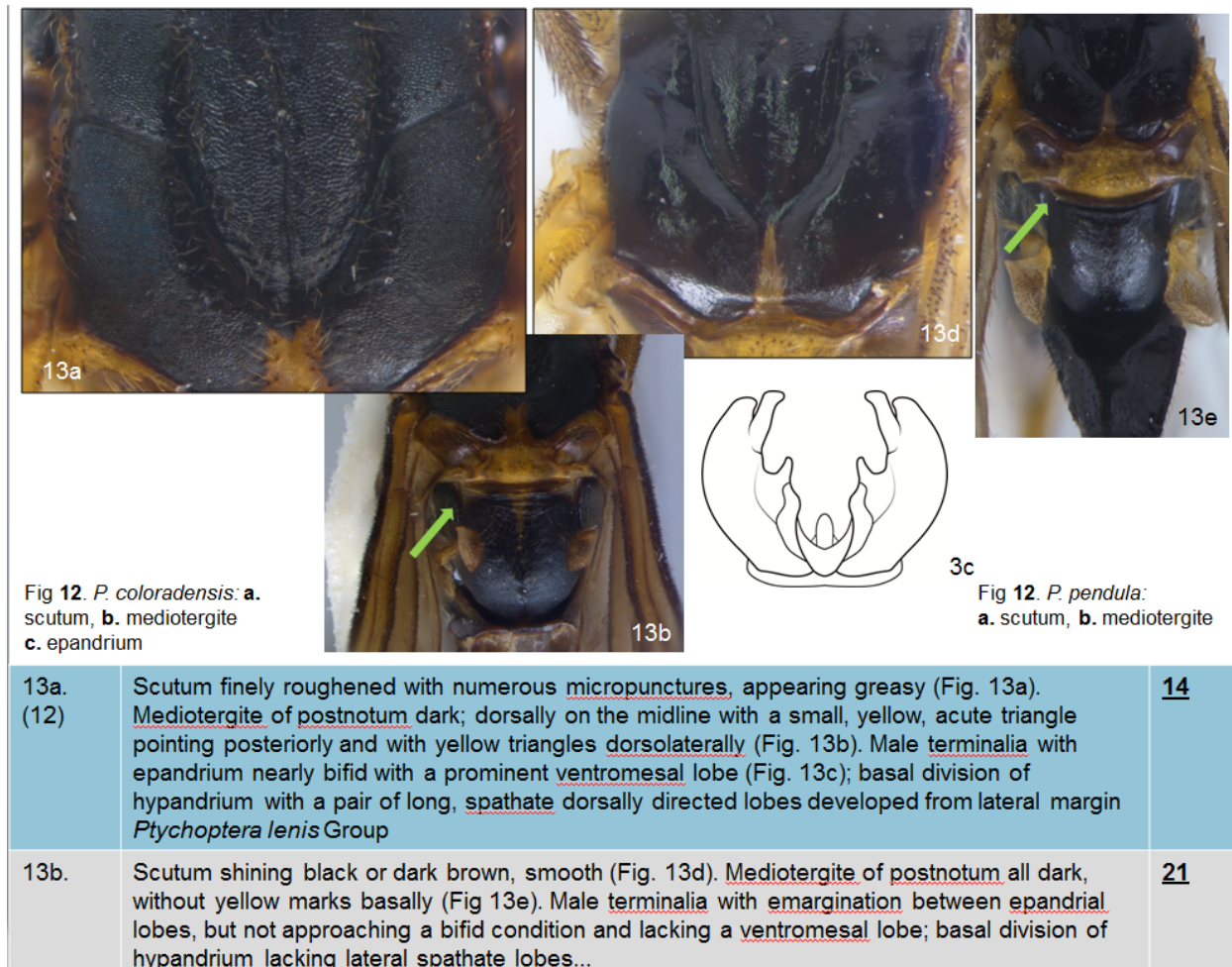
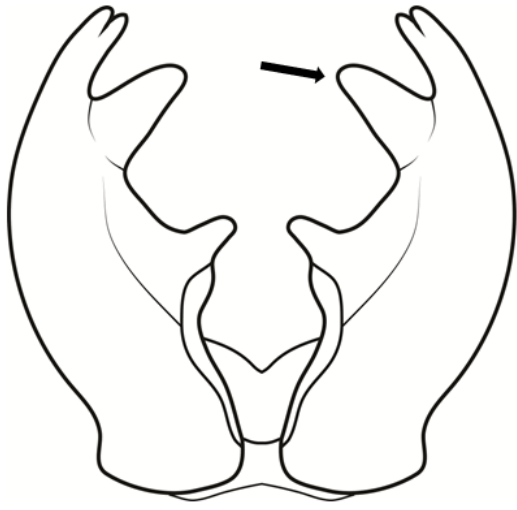
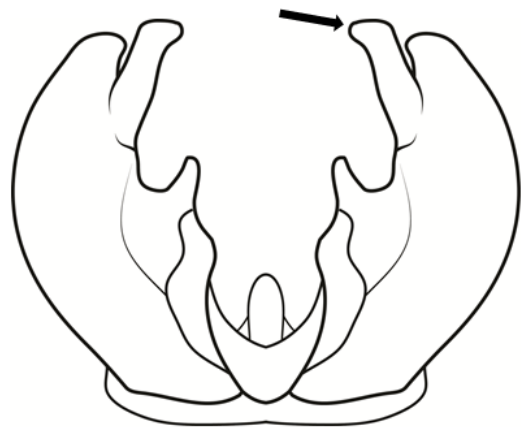


Figure 13. Couplet 13.

Fig 14a. *P. byersi* epandriumFig 14b. *P. coloradensis* epandrium

14a. (13)	Epandrium with ventromesal lobe a simple, tapering cone (Figs. 14a). Medial margin of hypandrial spathate lobes touching...	<u>15</u>
14b.	Epandrium with ventromesal lobe not tapering and flattened to varying degrees (Fig. 14b). Medial margin of hypandrial spathate lobes not in contact...	<u>16</u>

Figure 14. Couplet 14.

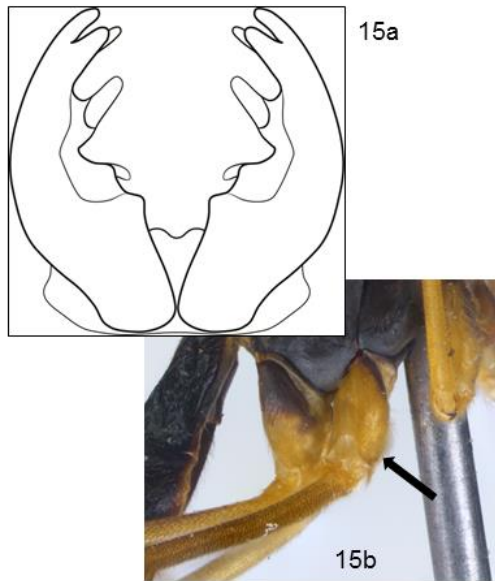


Fig 15. *P. bilobata*: a. epandrium, b. midcoxa

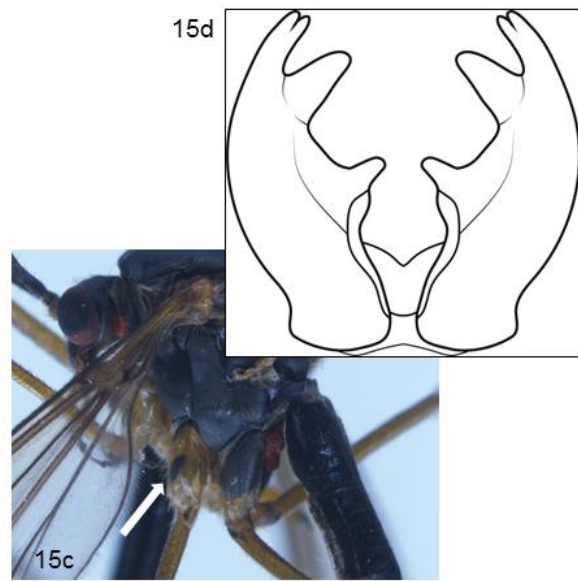


Fig 15. *P. byersi*: c. midcoxa d. epandrium

15a. (14)	Midcoxa lacking brown ventral stripe anterolaterally (Fig. 15b). Apex of epandrial lobe with finger-like spine present ventrally at base of dorsal lobe and extending a little past apices of lobes (Fig. 15a). Northern WA & Southern BC... <i>Ptychoptera bilobata</i> sp. n.	
15b.	Midcoxa with brown ventral stripe anterolaterally (Fig. 15c). Apex of epandrial lobe lacking lateral fingerlike spine (Fig. 15d). Great Basin... <i>Ptychoptera byersi</i> Alexander	

Figure 15. Couplet 15.

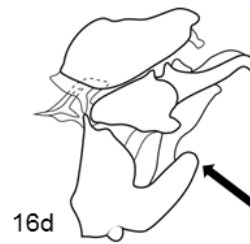
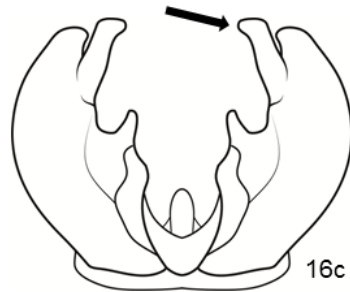
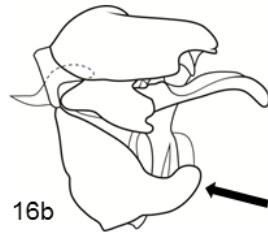
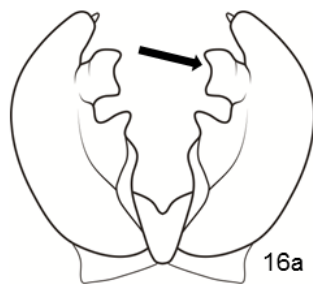
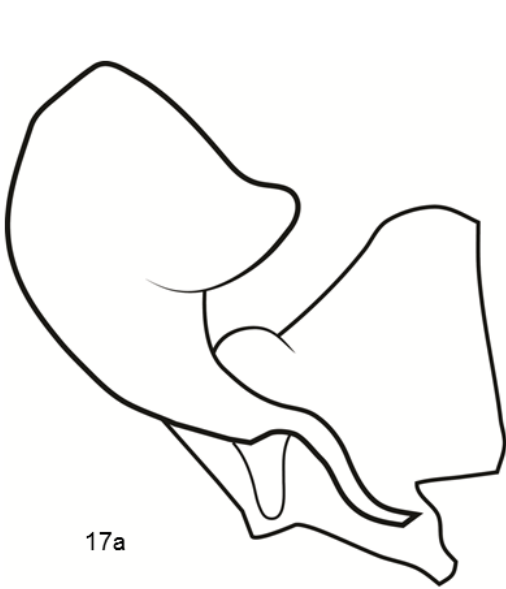


Fig 16. *P. lenis*: a. epandrium, b. male genitalia lateral

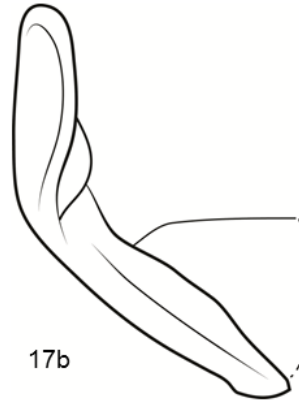
Fig 16. *P. coloradensis*: a. epandrium, b. male genitalia lateral

16a. (14)	Male terminalia orange-red, epandrial lobe with ventromesal lobe broadly attached at base obtusely crescent shaped (Fig. 16a); hypandrium with spathate lobes not extending dorsally to gonopods (Fig. 16b). Sierra Nevada mountains... <i>Ptychoptera lenis</i> Osten Sacken	
16b.	Male terminalia dark to orange-red, epandrial lobe with ventromesal lobe forming a distinct pedicel at base, shape variable from ovoid shaped to scythelike (Fig. 16c); hypandrium with spathate lobes extending dorsally to gonopods (Fig. 16d)...	<u>17</u>

Figure 16. Couplet 16.



17a

Fig 17. *P. uta*: a. paramere dorsal

17b

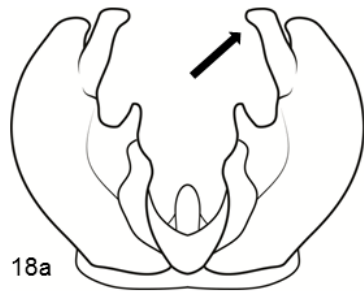


17c

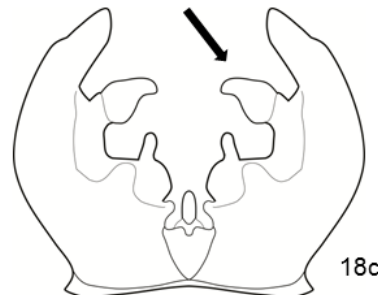
Fig 17. *P. minor*: a. paramere dorsal,
b. paramere lateral

17a. (16)	Male terminalia with paramere flattened in transverse plane, without apparent sagittal ridge (Fig. 17a). Northern Utah. <i>Ptychoptera uta</i> Alexander	
17b.	Male terminalia with paramere often laterally compressed, with at minimum a distinct sagittal ridge (Fig. 17 b&c)...	<u>18</u>

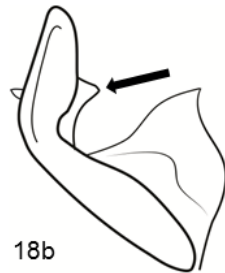
Figure 17. Couplet 17.



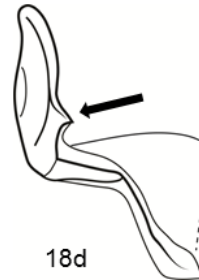
18a



18c



18b



18d

Fig 17. *P. coloradensis*:

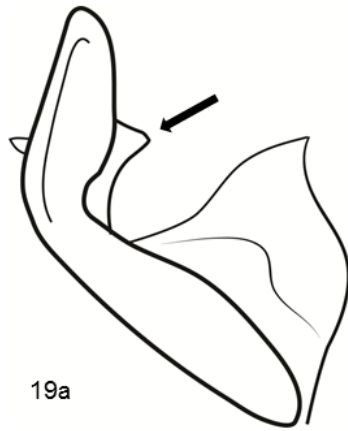
a. epandrium,
b. paramere dorsal

Fig 18. *P. lacrimiformis*:

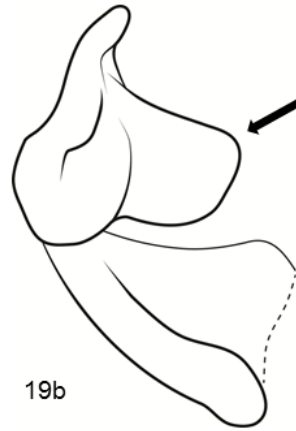
c. epandrium,
d. paramere dorsal

18a. (17)	Male terminalia ventromesal lobe of epandrial lobe having bluntly scythelike shape and the apical portion directed posterior at pedicel (Fig. 18a). Parameres with prominent lateral lobe (Fig. 18b).	<u>19</u>
18b.	Male terminalia with ventromesal lobe of epandrial lobe sub-ovoid or lacrimiform, apical portion directed ventrally (Fig. 18c). Parameres with at most a weak lateral ridge (Fig. 18d)	<u>20</u>

Figure 18. Couplet 18.



19a

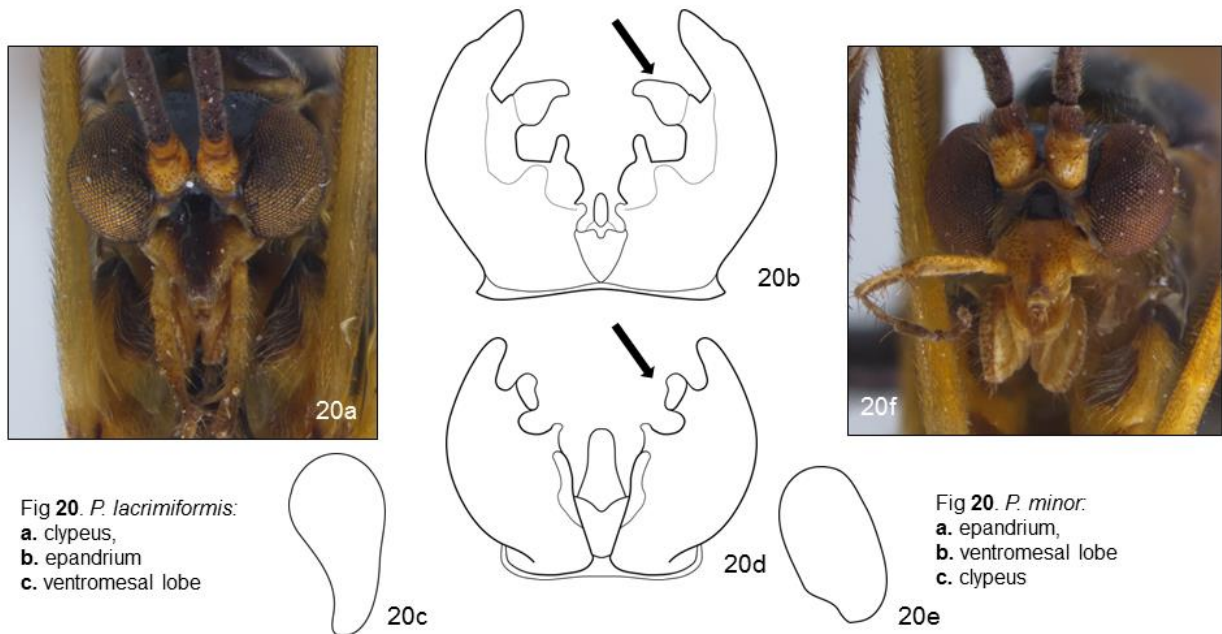
Fig 19. *P. coloradensis*: a. paramere dorsal

19b

Fig 19. *P. coloradensis*: b. paramere dorsal

19a. (18)	Male terminalia with lateral lobe of paramere shorter than apical portion of paramere. (Fig. 19a). Intermountain West... <i>Ptychoptera coloradensis</i> Alexander	
19b.	Male terminalia with lateral lobe of paramere longer than apical portion of paramere. (Fig. 19b). Southern Rocky Mountains... <i>Ptychoptera obscura</i> Peus	

Figure 19. Couplet 19.



20a. (18)	Clypeus completely dark or with vertical brown band medially (Fig. 20a). Male terminalia with ventromesal lobe of epandrial lobe lacrimiform (Fig. 20b), apical section extending at least 2x the width of the pedicel ventrally (Fig. 20c) Pacific Northwest... <i>Ptychoptera lacrimiformis</i> sp. n.	
20b.	Clypeus yellow, at most slightly fumose at apex (Fig. 20f). Male terminalia with ventromesal lobe of epandrial lobe sub-ovoid (Fig. 20d), extending less than 2x the width of the pedicel ventrally (Fig. 20e) Costal California... <i>Ptychoptera minor</i> Alexander	

Figure 20. Couplet 20.

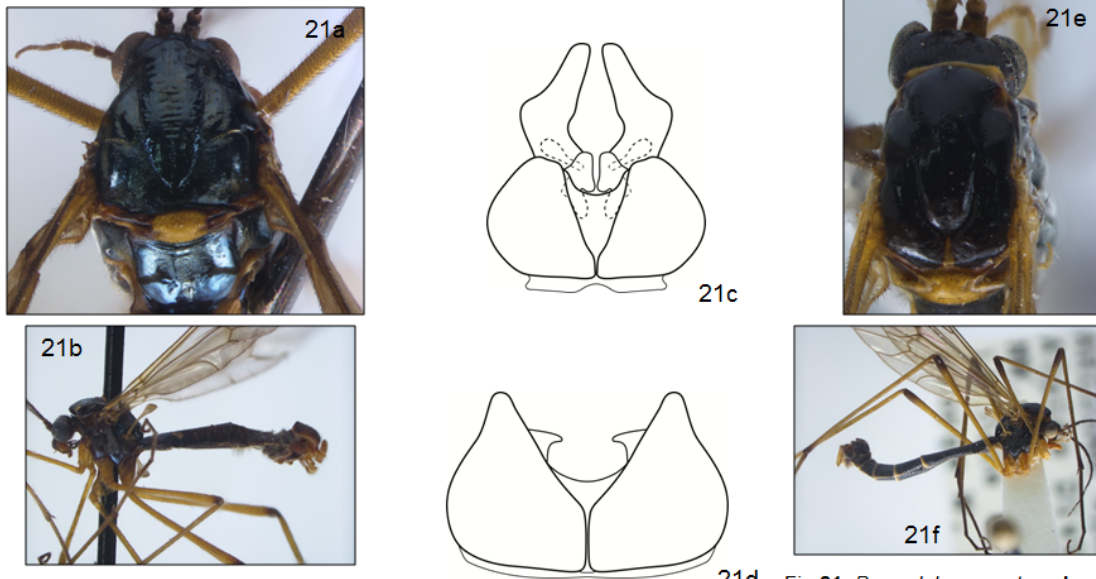


Fig 21. *P. metallica*: **a.** scutum, **b.** abdomen
c. epandrium

21d Fig 21. *P. pendula*: **a.** scutum, **b.** abdomen
c. epandrium

21a. (13)	Scutum dark ruddy brown with metallic blue sheen (Fig. 21a), abdomen uniform chocolate brown (Fig. 21b). Male terminalia with subhemispherical epandrial lobes terminating in prominent well-articulated styus, gonostyle without ventral lobe (Fig. 21c) Canadian Shield and Prairie pothole Region... <i>Ptychoptera metallica</i> Walker	
21b.	Scutum shining black (Fig. 21e), abdomen black with light yellow bands on posterior margin of anterior abdominal segments (Fig. 21f). Male terminalia with flattened triangular epandrial lobes without a posterior stylus, gonostyle with prominent pendant ventral lobe. (Fig. 21d)... <i>Ptychoptera pendula</i> Group	<u>22</u>

Figure 21. Couplet 21.

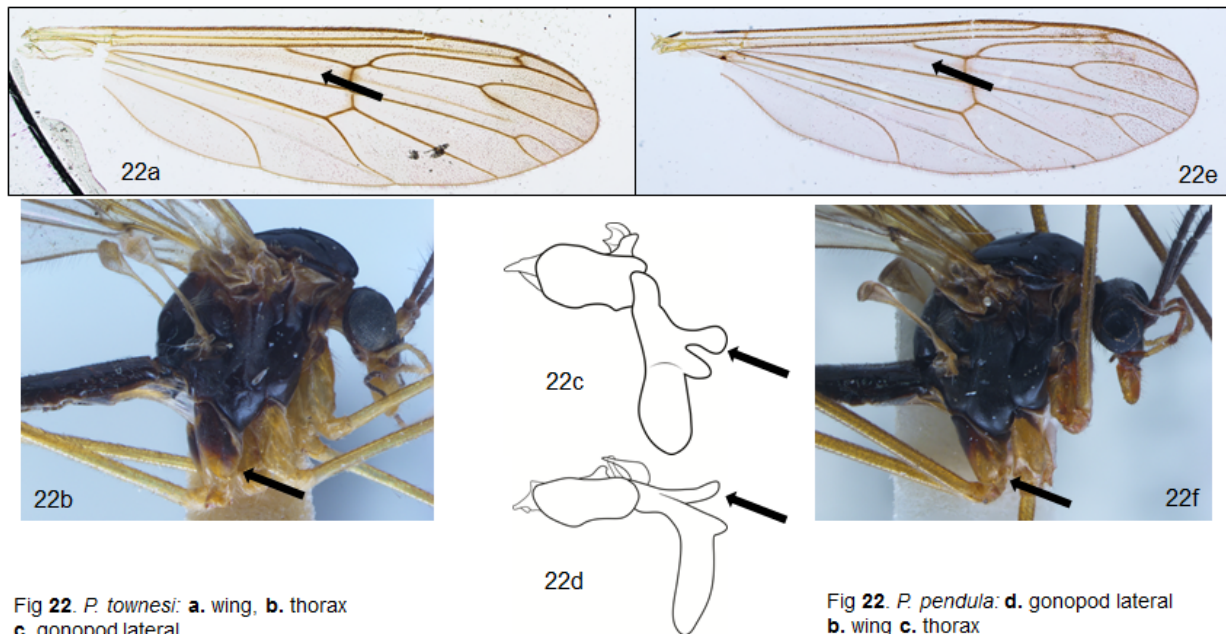
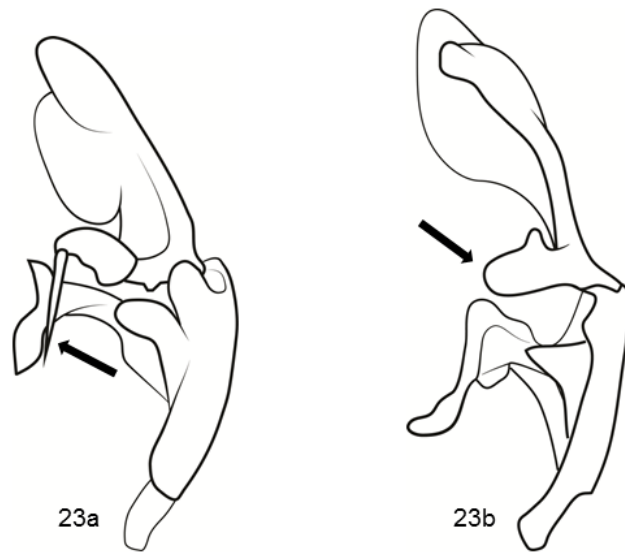


Fig 22. *P. townesi*: a. wing, b. thorax
c. gonopod lateral

Fig 22. *P. pendula*: d. gonopod lateral
b. wing c. thorax

22a. (21)	Wing with <u>macrotrichia</u> distributed almost the entire length of costal, radial and medial cells and a third of the length of cubital and anal cells (Fig. 22a). The small yellow mark on <u>scutum</u> anterior to <u>scutellum</u> has anterior apex truncate or bifid. Fore- and <u>midcoxae</u> yellow, narrowly darkened basally; <u>hindcoxae</u> mostly dark and often sparsely grey tomentose (Fig. 22b). Male <u>terminalia</u> with gonostylus with medial lobe paddle-like, directed dorsally; ventral lobe with rounded lobule on dorsal surface, lobule <u>subequal</u> to medial lobe. (Fig. 22c)...	<u>23</u>
22b.	Wing with <u>macrotrichia</u> mostly distal to the fork of R4 and R5 (Fig. 22e). The small yellow mark on <u>scutum</u> anterior to <u>scutellum</u> a triangle with anterior apex acute. All <u>coxae</u> yellow, narrowly darkened basally, the <u>hindcoxae</u> often with a dark smudge dorsally on the posterior face (Fig. 22f). Male <u>terminalia</u> with gonostylus with medial lobe <u>digitiform</u> directed medially; ventral lobe with singular triangular lobule on medial surface proximally, lobule much smaller than medial lobe. (Fig. 22d)...	<u>24</u>

Figure 22. Couplet 22.

Fig 23. *P. townesi*: a. gonopod dorsalFig 23. *P. espica*: b. gonopod dorsal

23a. (22)	Male terminalia with gonostylus basal lobe ending in single moveable apical spine (Fig. 23a), gonocoxal lobe with lateral lobe sloping ventrally. Olympic Peninsula... <i>Ptychoptera townesi</i> Alexander	
23b.	Male terminalia with gonostylus basal lobe ending without apical spine (Fig. 23b), gonocoxal lobe with lateral lobe squared ventrally. Coast Range... <i>Ptychoptera espica</i> sp. n.	

Figure 23. Couplet 23.

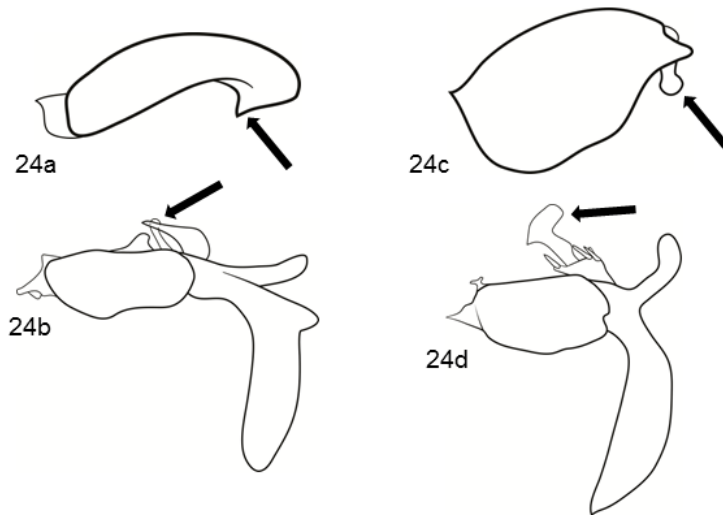


Fig 24. *P. pendula*: **a.** epandrium lateral
b. gonopod lateral

Fig 24. *P. monoensis*: **c.** epandrium lateral
d. gonopod lateral

24a. (22)	Male epandrium with ventral spine simple (Fig. 24a). Apex of medial gonocoxal lobe subcircular (Fig. 24b). Intermountain West... <i>Ptychoptera pendula</i> Alexander	
24b.	Male epandrium with ventral spine clavate (Fig. 24c). Apex of medial gonocoxal lobe hammer-shaped (Fig. 24d). Sierra Nevada Range... <i>Ptychoptera monoensis</i> Alexander	

Figure 24. Couplet 24.

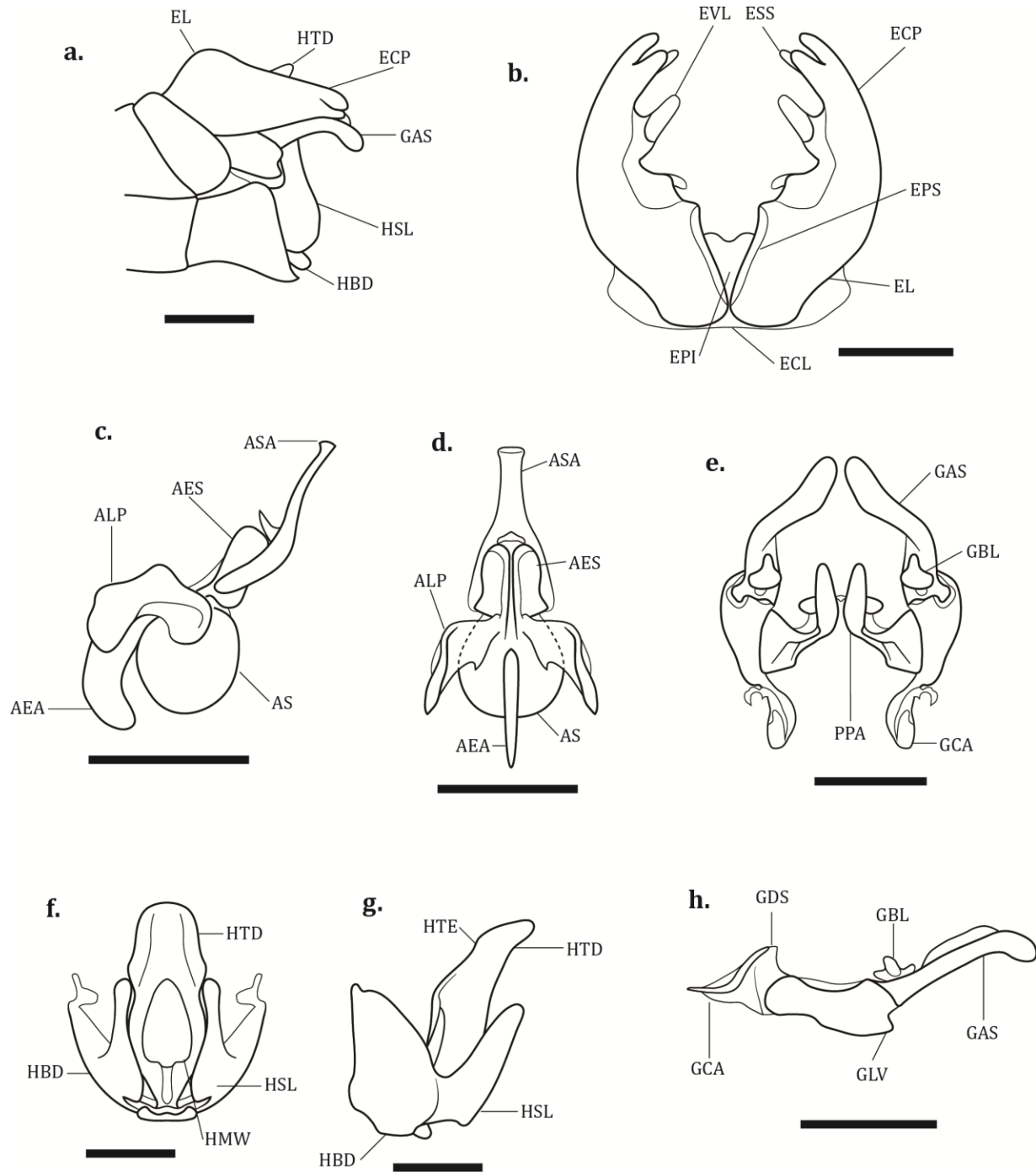


Figure 25. *Ptychoptera bilobata* Male Genitalia Plate; a. male genitalia lateral view, b. epandrium dorsal view, c. aedeagus anterior view, d. aedeagus lateral view, e. gonopods and parameres, dorsal view, f. hypandrium posterior view, g. hypandrium lateral view, h. gonopod lateral view.

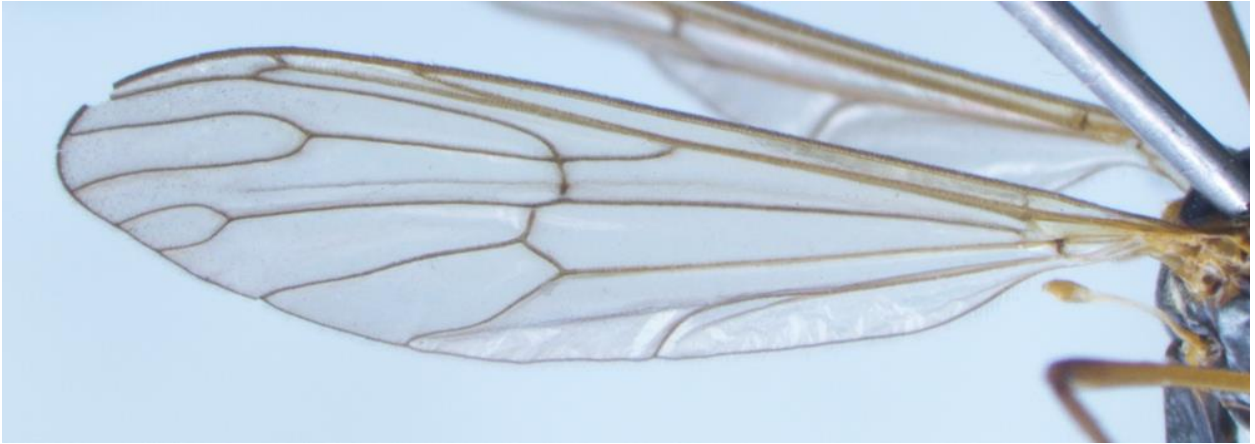


Figure 26. *Ptychoptera bilobata* Wing.



Figure 27. Distribution of *Ptychoptera bilobata*.

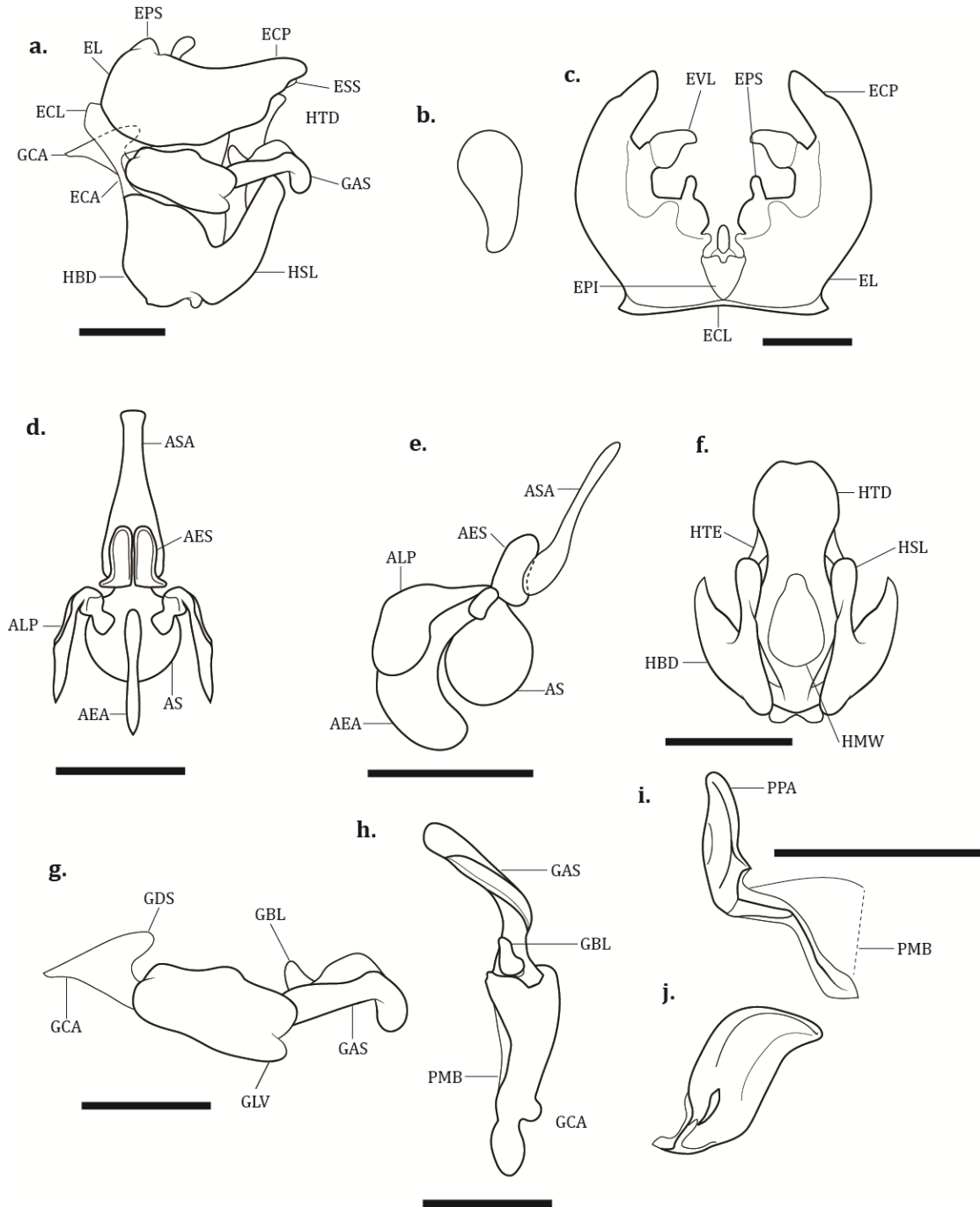


Figure 28. *Ptychoptera lacrimiformis* Male Genitalia Plate; a. male genitalia lateral view, b. ventromesal lobe medial view, c. epandrium dorsal view, d. aedeagus anterior view, e. aedeagus lateral view, f. hypandrium posterior view, g. gonopod lateral view, h. gonopod dorsal view, i. paramere dorsal view, j. paramere apex lateral view.



Figure 29. *Ptychoptera lacrimiformis* Wing.



Figure 30. Distribution of *Ptychoptera lacrimiformis*.

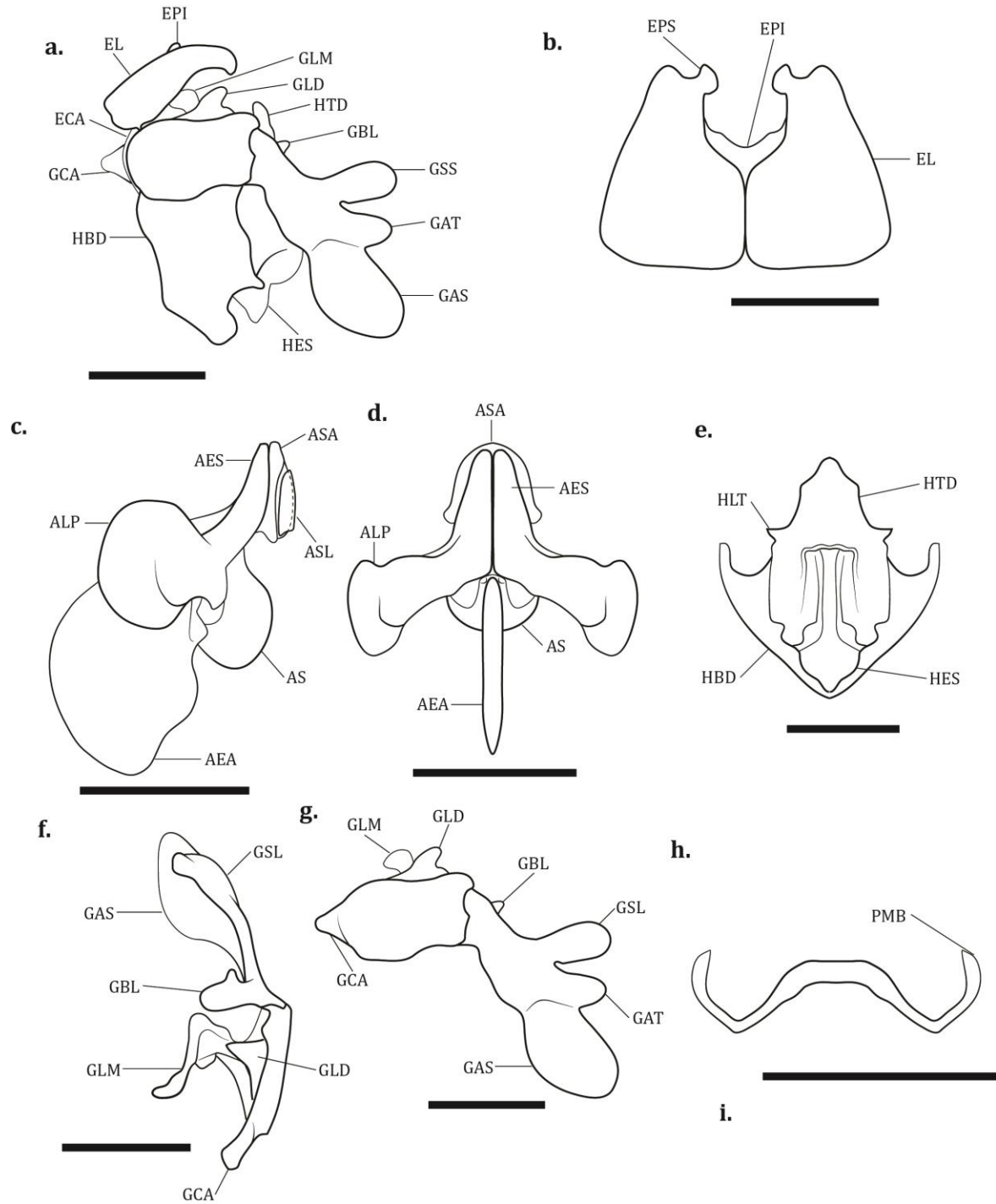


Figure 31. *Ptychoptera espica* Male Genitalia Plate; a. male genitalia lateral view, b. epandrium dorsal view, c. aedeagus anterior view, d. aedeagus lateral view, e. hypandrium posterior view, f. gonopod dorsal view, g. gonopod lateral view, h. paramere lateral view.

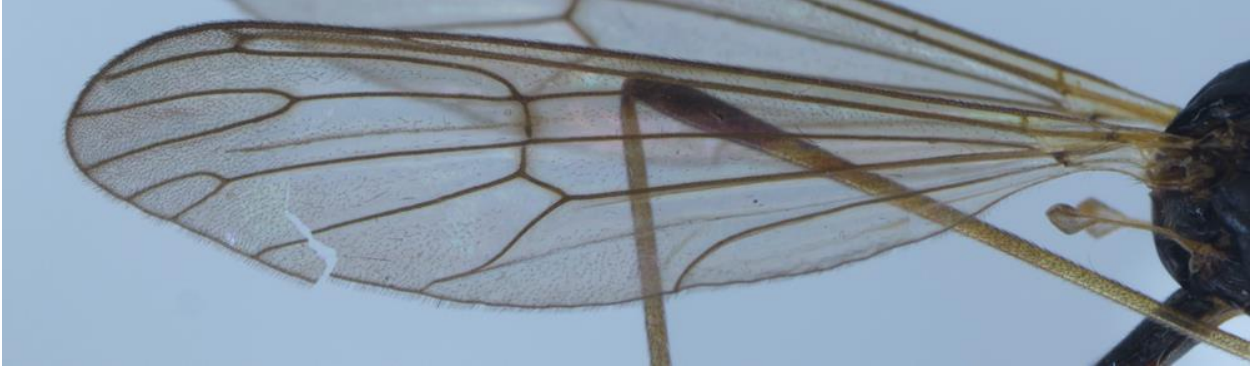


Figure 32. *Ptychoptera espica* Wing.



Figure 33. Distribution of *Ptychoptera espica*.

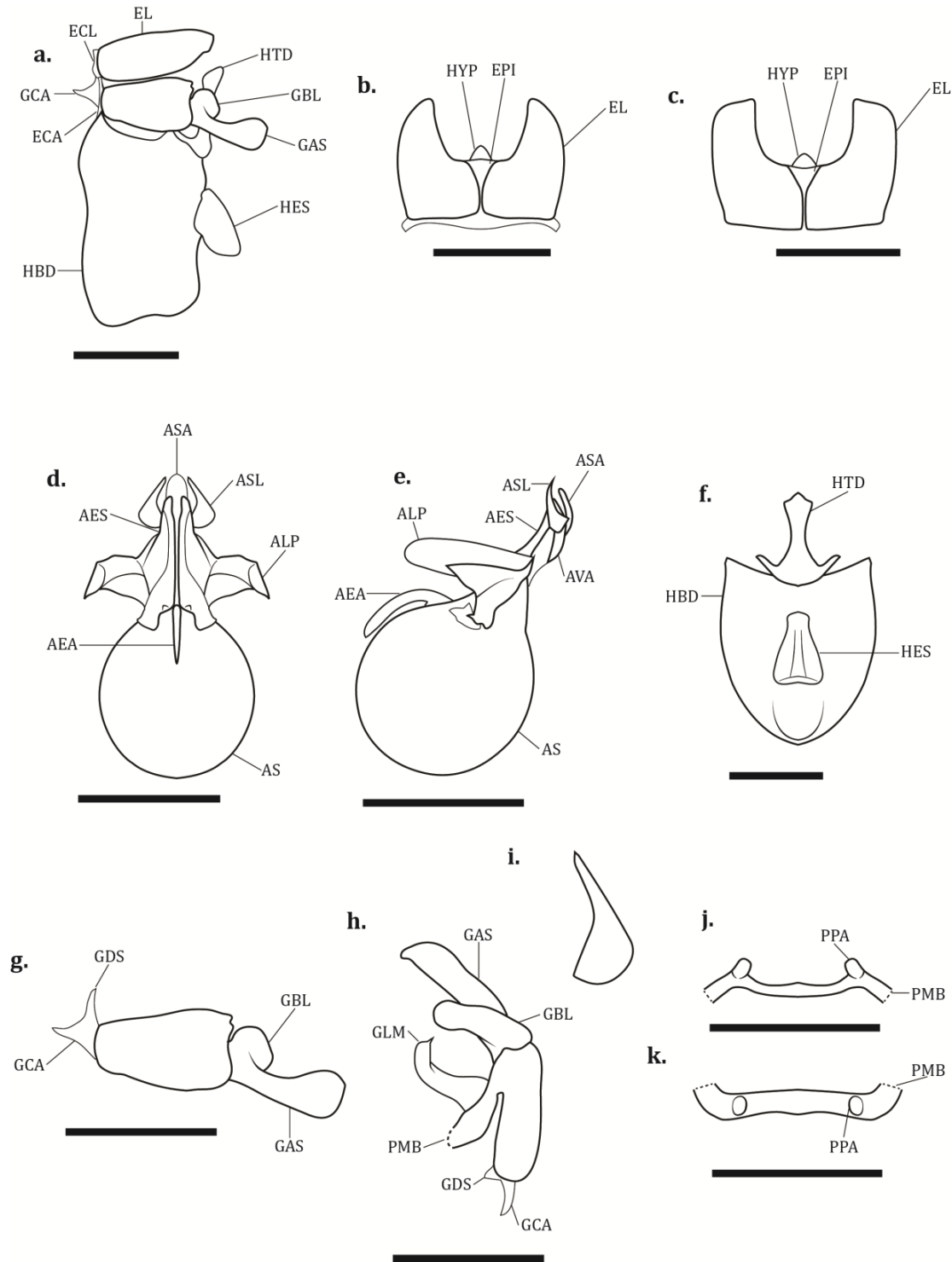


Figure 34. *Ptychoptera abbreviata* Male Genitalia Plate; a. male genitalia lateral view, b. epandrium dorsal view, c. alternate epandrium form, dorsal view, d. aedeagus anterior view, e. aedeagus lateral view, f. hypandrium posterior view, g. gonopod lateral view, h. gonopod dorsal view, i. lateral plate posterior view, j. paramere posterior view, k. paramere dorsal view.



Figure 35. *Ptychoptera abbreviata* Wing.



Figure 36. Distribution of *Ptychoptera abbreviata*.

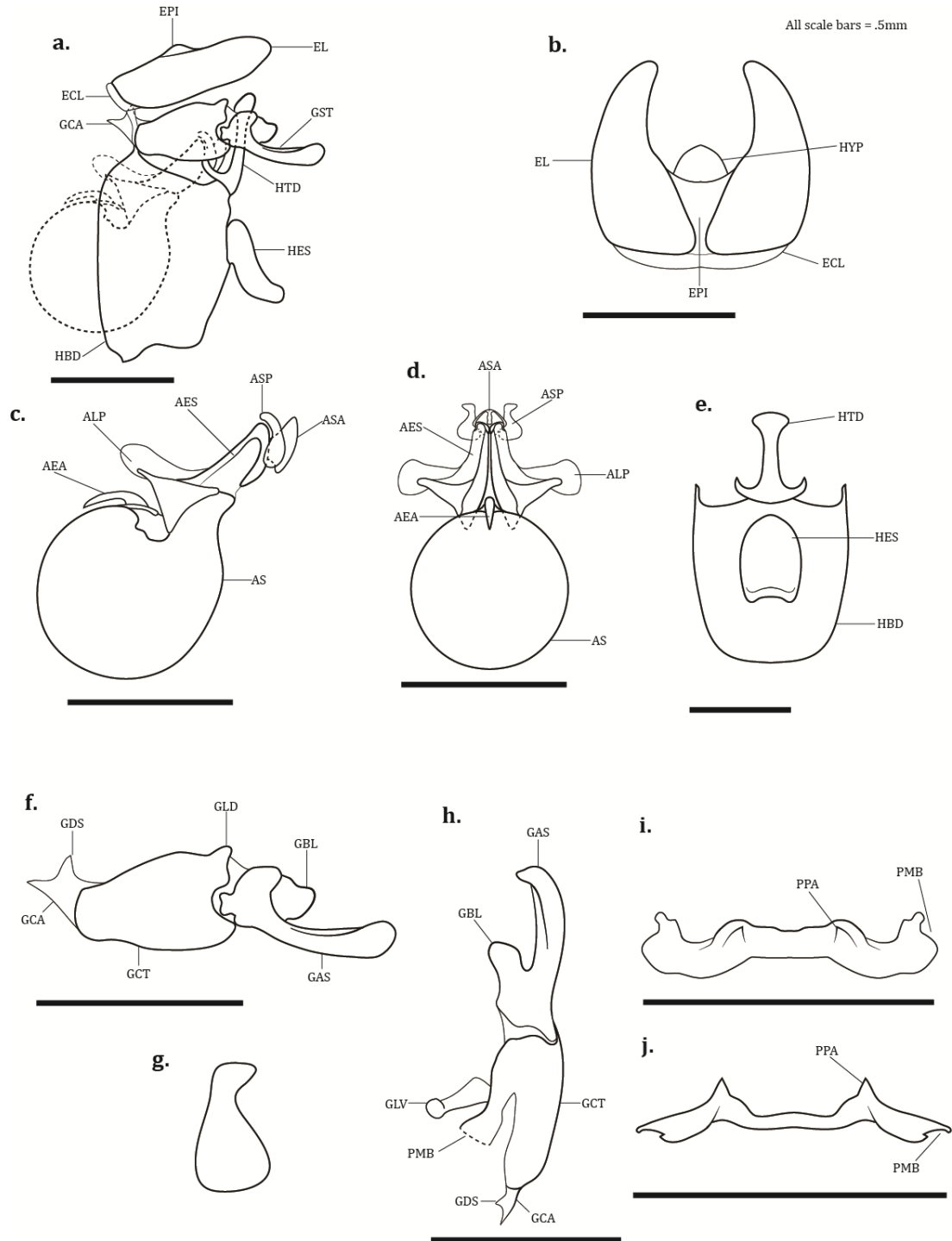


Figure 37. *Ptychoptera abbreviata* Male Genitalia Plate; a. male genitalia lateral view, b. epandrium dorsal view, c. aedeagus anterior view, d. aedeagus lateral view, e. hypandrium posterior view, f. gonopod lateral view, g. lateral plate posterior view, h. gonopod dorsal view, i. paramere dorsal view, k. paramere posterior view.



Figure 38. *Ptychoptera quadrifasciata* Wing.



Figure 39. *Ptychoptera quadrifasciata* Distribution.

CHAPTER SIX: A REVISION OF BITTACOMORPHINAE WITH A REVIEW OF THE MONOPHYLY OF THE EXTANT SUBFAMILIES OF PTYCHOPTERIDAE (DIPTERA)

Submitted to *Zootaxa*

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ABSTRACT

The phylogenetic relationship between the two extant subfamilies of Ptychopteridae is examined using morphological characters. Bittacomorphinae is supported as a monophyletic group with several synapomorphies. Monophyly of the Ptychopterinae is less certain. Descriptions are provided for the family and subfamilies. The genera and species of Bittacomorphinae are reviewed, and phylogenetic relationships within the subfamily are discussed. While *Bittacomorpha* is a monophyletic group, *Bittacomorphella* is probably paraphyletic. Redescriptions of the species of *Bittacomorpha* and most of *Bittacomorphella* are presented. A new species, *Bittacomorphella furcata* **n. sp.**, is described from the Olympic Peninsula of Washington State, USA. The range of Bittacomorphinae is found to extend into the Neotropical region with a reliable record of *Bittacomorpha clavipes* from Costa Rica. A key to the world species of Bittacomorphinae is provided.

INTRODUCTION

Ptychopteridae, whose members are often colloquially called “Phantom Craneflies,” is a family of lower Diptera associated with saturated organic sediments, which serve as the larval habitat (Alexander 1920, Harris & Carlson 1978, Alexander 1981, Bowles 1998). The larvae burrow in these saturated sediments, feeding on fine particulate organic matter (FPOM) (Mattingly 1987, Mattingly

1988, Wolf *et al* 1997, Wolf & Zwick 2001). After pupation near the surface of the sediment the emerging adults typically stay in close proximity to the larval habitat, usually resting on nearby vegetation. The extant members of the family have a generally Holarctic distribution, extending into the Afrotropical region.

Ptychopteridae is a readily diagnosed group in all life stages. The larva is eucephalous, with distinct labral and mandibular brushes as well as a biarticulated mandible. The body is vermiform, with a pair of small prolegs on the ventral surface of abdominal segments I, II and III. The most notable feature of the larva is a partially to fully retractable siphon composed of the posterior abdominal segments, with a pair of spiracular openings at the tip. The pupae of Ptychopteridae are generally cigar shaped, with the abdomen covered in tubercles capped with dentitions, and a set of asymmetrically developed thoracic respiratory organs, one hypertrophied and longer than the rest of the pupa. The adult ptychopterid is generally crane fly-like in appearance, but lacking a second anal vein and with a reduced medial sector compared to most Tipuloidea. There also is a trend toward fusion of the thoracic sclerites (Lukashevich 2008) and a unique lobe located at the base of the halter, known as the prehalter. The male genitalia of Ptychopteridae are highly complex and exhibit numerous apomorphies, leading to some misinterpretation of homologies in previous works. A future publication will examine these homologies in greater detail.

The phylogenetic position of Ptychopteridae has been unstable within the wider context of Diptera. Initially considered a member of Tipulidae, Osten Sacken proposed the subfamily Ptychopterinae for the genus *Ptychoptera* Meigen (Osten Sacken 1862). Osten Sacken also recognized this group as a separate clade containing *Bittacomorpha* Westwood, *Ptychoptera*, and *Protoplasa* Osten Sacken earlier (Osten Sacken 1860), but did not provide a name for the group at the time. Two years later Osten Sacken (1862) formally proposed the subfamily Ptychopterinae (as Ptychopterina) as a

constituent of Tipulidae, which was initially accepted by Schiner (1864). The view of Ptychopteridae as a separate family was first proposed by Hart (1895), which would gradually become widely accepted in the early twentieth century (Handlirsch 1908, Alexander 1916, Alexander 1919). Following Osten Sacken's example, many authors included Tanyderidae as a subfamily within Ptychopteridae until the 1920s (Osten Sacken 1877, Alexander 1919, Alexander 1927b). Early phylogenies placed Ptychopteridae near Tipulidae (Alexander 1920), however Hennig's landmark 1973 (Hennig 1973) phylogeny placed the family into a heterogeneous Psychodomorpha as sister to Tanyderidae.

Later morphological studies continued to place Tanyderidae as sister to Ptychopteridae in the infraorder Ptychopteromorpha (Wood & Borkent 1989, Oosterbroek & Courtney 1996). Many of the characters "uniting" these two families are tenuous. They include a probable symplesiomorphy (five malpighian tubules), while others exhibit homoplasy with other families of lower Diptera (non-retractile anal papillae, malpighian tubules terminate in anal papillae). The synapomorphy of a foldable fifth tarsomere is not exhibited in all ptychopterids (Griffiths 1990), nor even in all *Ptychoptera*. In both Wood and Borkent (1989) and Oosterbroek and Courtney (1996), Ptychopteromorpha was placed as sister to Culicomorpha, primarily based on characters of the larval mouthparts (labral brushes present, premandibles present, hypostoma serrate), gastric caecae and metapneustic respiratory system. The mouthpart synapomorphies may be convergent, independently derived structures used for sifting organic material, while the metapneustic respiratory system may be a convergent adaptation for living in anoxic habitats. The sole adult character uniting the clades is the lack of ocelli, which is also found in several unrelated families of Diptera. Molecular analyses have further shed doubt on the placement of Tanyderidae in Ptychopteromorpha (Bertone *et al* 2008, Wiegmann *et al* 2011). Furthermore, a molecular phylogeny of Psychodidae including *Protoplasia fitchii* and *Ptychoptera quadrifasciata* did not

group them, and in fact recovered *Protoplasia* as an ingroup of Psychodidae (Curler & Moulton 2012).

The most recent large scale morphological study (Lambkin *et al* 2013) did not include a representative of Ptychopteridae.

Ptychopteridae is divided into five subfamilies, two of which are extant (Lukashevich 2008, Lukashevich 2012). These subfamilies, Bittacomorphinae Alexander 1919 and Ptychopterinae Osten Sacken 1860, have never been described in detail and the distributions and polarity of diagnostic characters have only been briefly examined (Alexander 1920, Alexander 1927, Alexander 1981, Lukashevich 2012). The only thorough investigation of the relationships of the subfamily was by Lukashevich (2012). This study focused on the interrelationships of the various genera, without substantial investigation of the monophyly of extant genera or subfamilies. Bittacomorphinae is defined by apomorphic characters (vein M unforked, CuA₂ sigmoidal, banded legs) (Lukashevich 2012), but many of the characters given as diagnostic for Ptychopterinae (vein M forked, legs without banding) (Alexander 1981, Lukashevich 2008, Lukashevich 2012) are plesiomorphic when compared with outgroups. Other characters used to define Ptychopterinae are not consistently distributed across the family or are difficult to interpret as discrete character states (the formation of the wing “cord” (alignment of r-m, base of CuA₁ and CuA₂). However, there are a large number of previously unexamined morphological characters that are informative at the subfamilial level.

Similarly, within Bittacomorphinae there has never been thorough examination of species placement within the accepted genera. Interpretation and phylogenetic inferences of Bittacomorphinae have assumed the monophyly of *Bittacomorpha* and *Bittacomorphella*. However, there has been no definitive evidence that *Bittacomorphella* is a monophyletic group.

Several species of Ptychopteridae were described in the 18th century in the genus *Tipula* (Linnaeus 1758, Fabricius 1781), with Meigen distinguishing these from *Tipula* species under the genera

Liriope and *Ptychoptera* in his 1800 and 1803 publications, respectively. The priority of the name *Liriope* was not widely known until the early 20th century, whereupon there was a division between those authors using *Ptychoptera* (such as C. P. Alexander) and those using *Liriope* (including F. Peus). The 1800 Meigen publication was suppressed by the ICZN in 1960 (Melville, 1960), leaving *Ptychoptera* and Ptychopteridae as the valid names for these taxa. Tonnoir (1919) erected the genus *Parapterychoptera* Tonnoir for a group of European *Ptychoptera* with an auxiliary sexual organ on the 3rd abdominal sternite. Later authors (Alexander 1927, Freeman 1950, Peus 1958) considered *Parapterychoptera* a synonym of *Ptychoptera*. Zwick and Stary (2003) resurrected *Parapterychoptera* as a subgenus of *Ptychoptera*, citing the distinctness of the group and the need for wider phylogenetic study of *Ptychoptera*.

Bittacomorpha was described in 1835 by Westwood for (at the time) *Ptychoptera clavipes* Fabricius, to which the species *Bittacomorpha sackenii* von Röder, *Bittacomorpha occidentalis* Aldrich, and *Bittacomorpha jonesi* Johnson were added, though *Bittacomorpha sackenii* and *Bittacomorpha jonesi* would later be transferred to *Bittacomorphella*. *Bittacomorphella* was described as a subgenus of *Bittacomorpha* by Alexander (1916). Though he never explicitly elevated it to generic rank, Alexander (1920) treated *Bittacomorphella* as a genus in *The Crane-flies of New York*, and all later authors have followed suit. To the present day the generic structure of extant Bittacomorphinae is essentially unchanged.

Bittacomorpha currently contains only *B. clavipes* and *B. occidentalis*, and the genus is largely confined to the Nearctic though the combined distributions of these species cover much of the North American continent (*B. clavipes* has also been collected in Costa Rica). *B. clavipes*, in particular, is one of the most common ptychopterids of the eastern Nearctic, recognized even by many non-dipterists. *B.*

occidentalis replaces *B. clavipes* west of the Cascade and Sierra Nevada mountains in the US states of Washington, Oregon, and California, as well as the Canadian province of British Columbia.

Bittacomorphella has a wider geographical distribution, including both the Nearctic, eastern Palaearctic, and Oriental regions. However, in the Nearctic *Bittacomorphella* species have far more limited ranges than *Bittacomorpha*. *Bl. jonesi* is associated with the Appalachian Mountains and the Canadian Shield, while *Bl. fenderiana* Alexander and *B. pacifica* Alexander inhabit the Pacific Coast of North America. *Bl. sackenii* is endemic to the Sierra Nevada range, though many specimens of *Bl. pacifica* are mislabeled as this species. The remainder of North America is bereft of *Bittacomorphella*.

In East Asia *Bittacomorphella* is recorded from Japan, Taiwan, China, and Thailand (Alexander 1953, Nakamura & Saigusa 2009, Young & Fang 2011, Kang *et al* 2012). *Bittacomorphella esakii* Tokunaga and *Bittacomorphella nipponensis* Alexander are endemic to Japan, with *Bl. nipponensis* restricted to Honshu and *Bl. esakii* more widespread (Nakamura & Saigusa 2009). *Bittacomorphella lini* Young & Fang is recorded from Taiwan and mainland China (Young & Fang 2011, Kang *et al* 2012). *Bittacomorphella gongshana* Kang, Wang & Yang and *Bittacomorphella zhaotongensis* Kang, Wang & Yang are also recorded from mainland China. *Bittacomorphella thaiensis* Alexander is known only from two female specimens from Thailand.

Bittacomorphella is defined by plesiomorphic characters (lack of inflated tarsomeres) or characters not distributed across all species (abundant macrotrichia at wing apex). At a larger scale there have only been limited attempts to homologize structures across the family, and examine the distribution of character state transformations. A detailed examination of the morphology and function of the male genitalia of Ptychopteridae is outside the scope of this manuscript, and will be presented in detail in a future publication. Instead a chart of various author's terminology and homologies of structures is provided in Table 1.

There were three goals of this study. The first was evaluation of the purported relationship between Tanyderidae and Ptychopteridae using expanded sampling in Ptychopteridae and a more comprehensive set of morphological characters. The second component was a morphological evaluation of the monophyly of the subfamilies of Ptychopteridae, combined with explicit descriptions of the subfamilies. The third was examining the species level phylogeny of Bittacomorphinae, with emphasis on examining the monophyly of Bittacomorphinae. As part of this objective comprehensive descriptions and illustrations of the species of Bittacomorphinae were produced, excepting the recently described *Bl. gongshana*, *Bl. lini*, and *Bl. zhaotongensis*. Finally a key to the extant members of Bittacomorphinae was constructed.

Materials and Methods

The material examined in this study was collected by the authors (deposited in ISIC) or obtained on loan from the following institutions: Clemson University Arthropod Collection (CUAC), Natural History Museum of Denmark (ZMUC), the Field Museum of Chicago (FMNH), Harvard Museum of Comparative Zoology (MCZ), Illinois Natural History Survey (INHS), Iowa State Insect Collection (ISIC), University of Kansas Snow Entomological Museum (KU), Michigan State University Arthropod Research Collection (ARC), University of Michigan Museum of Zoology (UMMZ), Oregon State University (ORSU), Pacific Northwest Diptera Research Lab (PNDL), Purdue University Entomology Research Collection (PERC), Smithsonian National Museum of Natural History (USNM), Washington State University James Entomological Collection (WSU). Additional comparative material from the FLYTREE project (Lambkin *et al*, 2013) stored at ISIC was examined for the phylogenetic analysis. Line breaks in label data of the specimens examined are denoted by a “,”, and separate labels are designated using a “/”.

Specimens were examined in this study using Olympus SZX12 and SZX9 stereomicroscopes and a Nikon E800 compound microscope. A Nikon DS-Fi1 camera on a detachable mount was used to capture

photomicrographs from the SZX12 and E800 microscopes; these microscopes were additionally fitted with camera lucida devices for rendering illustrations.

Taxonomic Methods. Male genitalia was dissected and cleared for observation with the following technique. The posterior abdominal segments were cut from the specimen using a set of dissecting scissors. The genitalia of dried specimens was hydrated for 18 hours prior to clearing to assure complete and even action of the clearing agent. Specimens preserved in alcohol were similarly hydrated for 20 minutes to ensure even clearing. Shell vials were prepared by adding a dry KOH pellet to a measured amount of deionized water. The vials were capped and the KOH allowed to dissolve, at which point the vials were shaken vigorously to ensure a uniform concentration within the vial. The hydrated specimens were then individually placed in a marked vial and recapped and set on a warming plate, with the solution reaching approximately 60C. Specimens were individually observed at five minute intervals until sufficient clearing had occurred, at which point the specimen were transferred twice to a fresh container of deionized water for ten minutes to dilute any remaining KOH. Specimens would then be taken through a series of ethanol solutions from 30-50-70-95%, further rinsing the specimen and preparing it for transfer to glycerin. Glycerin transfer was accomplished by placing a small amount of pure glycerin into a well of a spot plate for each sample and filling the remainder of the well with 95% ethanol and vigorously stirring the well to bring the glycerin into solution. The genitalia were then transferred to the wells and the plate was placed under an incandescent lamp to evaporate ethanol from the solution. The genitalia were then transferred to a glycerin filled watch glass for observation and finally to microvials associated with the originating specimen.

Descriptive terminology is based on Cumming & Wood (2009). Illustrations were produced by either sketching a specimen using the camera lucida and scanning them for tracing in Adobe Illustrator CS5, or taking a series of photomicrographs and tracing them in Adobe Illustrator. Photomicrographs

were produced by taking a stack on images in varying focal planes using the Nikon DS-Fi1. These images were then aligned and stacked in Adobe Photoshop CS5 12.0.4.

Measurements were taken using an ocular micrometer mounted on the SZX12 dissecting scope. Reference points of measurements are as follows: Overall length is average of combined head, thorax, and abdomen measurements; **Head.** Width is measured between lateral apices of the eyes, Height is measured from vertex to apex of clypeus, Length is measured from occiput to anterodorsal margin of clypeus, Flagellum length is from the base of the first flagellomere to apex of ultimate flagellomere, Flagellomere proportions: are based on the first flagellomere, Maxillary palpus length is the sum of individual segment lengths, Maxillary palpus segment proportions are based on the second segment; **Thorax.** Length is measured from anterior apex of the prescutum to the posterior surface of the mediotergite, Height is measured from the dorsal apex of scutum to the ventral apex of the episternum, Wing length is measured from base to apex, Wing width is measured across the widest part of the wing, Leg proportions are all based on the fore-femur; **Abdomen.** Length is measured from the anterior margin of tergite I to apex of epandrium, Male tergite proportions are based on the length of Tergite I; **Male Genitalia.** Width is measured across the basal division of hypandrium below gonocoxites, Height is measured from the basal division to epandrium. For measurements based on an average a range is given in parentheses.

Phylogenetic Methods. The basis of the phylogeny component of this project was the FLYTREE data matrix produced by Lambkin *et al* (2013). Initial work consisted of removing unnecessary taxa for evaluating the phylogenetic relations of Ptychoptermorpha, primarily Brachyceran Diptera. Nannochoristidae was chosen as an outgroup based on the lack of autapomorphic characters compared with other Mecoptera (Griffiths 1990). With the removal of a significant portion of the FLYTREE matrix

there were numerous uninformative characters remaining, requiring the deletion of these characters. Additional characters informative to the relationships within Ptychopteridae were then added to the matrix.

The rationale for the selection of ptychopterids for the analysis differed between subfamilies. In Bittacomorphinae all species with available males were utilized, excluding *Bl. gongshana*, *Bl. lini*, *Bl. thaiensis*, and *Bl. zhaotongensis*. *Bl. thaiensis* is known only from females, while no material from the other excluded bittacomorphines was available to the authors at the time of this analysis. Exemplars across several species groups were selected from Ptychopterinae to provide a broad sampling of the morphological diversity of that subfamily.

All data in the matrix were reviewed against specimens in this analysis, including those taxa already recorded in the matrix. The matrix was then analyzed using TNT 1.1 for Maximum Parsimony (Swofford 2003) and MrBayes 3.2 for Bayesian Inference (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003). The Markov Chain Monte Carlo analysis was undertaken with two runs with four chains each, with the temperature set to 0.2. Sample frequency was set at 100, swap frequency was set to one and the number of swaps set to two. The initial burn-in for the analysis was set using the “burninfrac” parameter to 0.15. After the analysis was complete the sampled trees were compiled into a consensus tree using the “sumt” function with a burn-in of 25000.

TNT searches were undertaken using a “New Technology Search” using the “Driven Search” option, with “Init. Adseqs.” set at five and “Find min. Length” set at thirty. Bootstrap values were calculated using a “Standard Search” with 100 replicates. Bremer support was calculated using TBR from existing trees.

Figure Abbreviations. ADA: Dorsal apical apodeme of aedeagus, AEA: Ejaculatory Apodeme, AES: Aedeagal Sclerite, AEV: Ventral Apical Apodeme of Aedeagus, ALP: Lateral Ejaculatory Process AS: Sperm

Sac, ASA, Subapical Sclerite of Aedeagus, AVA: Ventral Arm of Subapical Sclerite, CRC: Cercus, ECP: Epandrial Clasper, EL: Epandrial Lobe, EPI: Epiproct, EPG: Epigynium, EPP: Epandrial Plate, EPS: Posteromedial Style of Epandrium, GBL: Basal lobe of gonostylus, GCT: Gonocoxite, GCA: Gonocoxal Apodeme, GFK: Genital Fork, GST: Gonostylus, HBD: Basal Division of Hypandrium, HLT: Lateral lobule of terminal division, HPG: Hypogynium, HTD: Terminal Division of Hypandrium, HVL: Hypogynial Valves, HYP: Hypoproct, PM: Paramere, ST7: Sternite 7, TG7: Tergite 7

Results

Results for the phylogenetic analyses are presented as cladograms in Figures 1-6. Figures 1 and 2 represent two equally parsimonious trees produced by the Maximum Parsimony analysis. Figure 3 is a strict consensus of these two trees with Bootstrap and Bremer support values indicated. Figure 4 traces character state changes from the Maximum Parsimony consensus tree across the Ptychopteridae. Figure 5 is the consensus tree produced by the Bayesian Inference analysis, with posterior probabilities noted. Figure 6 traces character state changes from the Bayesian Inference consensus tree across the Ptychopteridae.

A key is provided to the adults of all described species of Bittacomorphinae, and descriptions and illustrations for the genera and most species of Bittacomorphinae follow. For descriptions of the recently described species *Bl. gongshana*, *Bl. lini*, and *Bl. zhaotongensis* readers are encouraged to consult Young and Fang (2011) and Kang, Wang & Yang (2012). Immatures are still poorly known for the group, and further collections and research are required for a full understanding of the morphological diversity present. Diagnoses are provided for the immatures which the authors were able to examine.

Family Ptychopteridae Osten Sacken, 1862

Ptychopterinae Osten Sacken, 1862: 12 (original description)

Ptychopterinae Schiner, 1862: 495 (description)

Ptychopteridae Osten Sacken, Hart 1895: 189 (elevation to full family rank)

Liriopeidae Brues & Melander, 1915: 62 (replacement name)

Diagnosis

Larva. Vermiform, eucephalous, metapneustic. Abdominal segments 1-3 with ventral prolegs.

Anal division with prominent retractile respiratory siphon and two small, simple anal papillae.

Adult. Head without ocelli, antenna with 13-21 flagellomeres. Wing with four branches of R reaching margin, 1-2 branches of M, 2 of CuA, 1 anal vein. Halter with prehalter at anterior base. Second abdominal segment extended. Male genitalia with distinctive epandrial claspers, prominent lateral ejaculatory processes, subapical sclerite of aedeagus.

Description

Larva. Head. Cranium well developed with distinct frontoclypeal apotome and genae. Subgenal sclerite present. Single stemmata present. Antenna present, two-three segmented. Labrum triangular, with two prominent labral brushes, epipharynx with premandible. Mandible with molar and incisor lobe, molar lobe massive, subquadrate or semicircular, incisor lobe triangular; prostheca and mandibular comb present. Maxilla with well sclerotized cardo and stipes, maxillary palpus peg-like; lacinia large, with prominent brushes, galea present. Prementum bottleneck shape, with prominent denticles at apex, postmentum forming bridge or fused to subgenal sclerite.

Thorax and abdomen. Thoracic segments readily distinguishable, cylindrical or weakly fusiform. Abdominal segments I-VI free, I-III each with pair of ventral prolegs. Abdominal segments VII-IX formed into anal division housing respiratory siphon. Anal papillae paired, developed laterally as ribbon-like lobes on either side of anal division at the base of the terminal respiratory siphon.

Adult Male. Head. inverse triangular in anterior view, greater in height than depth, hypognathous, deflexed; chaetotaxy variable. Vertex weakly convex, with or without medial suture, broadly trapezoidal, ocelli absent. Compound eyes prominent, hemispherical, forming lateral margin of head, never holoptic. Occiput closely conforming to posterior margin of eye, weakly convex to foramen. Foramen of moderate size, approximately $1/3$ of head diameter. Antennae elongate; scape cylindrical tapering weakly at apex with prominent trichoid sensillae; pedicel subglobular with or without trichoid sensillae; flagellum with 13-20 flagellomeres, 1st flagellomere longest, decreasing in length towards apex, densely clothed with fine trichoid sensillae. Facial sclerite small, trapezoidal, often indistinct. Clypeus prominent, undivided, triangular to sub trapezoidal, somewhat inflated. Gena bandlike under compound eye to clypeus, or reduced medially; subgena well developed with medial suture, anteriorly emarginated for base of labium. Labrum abbreviated, closely associated with apex of clypeus, externally forming small triangular or semicircular sclerotized node protruding anterior between clypeus and labium. Hypopharynx not apparent externally, closely fused with labium, forming moderately sclerotized trough extending to apex of clypeus, ending at base of external portion of labrum, equal in width to labrum; apex square, with salivary canal prominent. Mandibles absent. Maxillae not externally developed; maxillary palpus elongate, with five segments, first segment short, approximately same length as width, produced laterally to remaining palpus segments; second segment shorter than following two subequal segments, length of terminal segment variable, highly elongate in some taxa; palpus with thick vestiture of trichoid sensillae, but no modified sensillae. Labium with base fused to underside of clypeus; overall U-shaped in cross section, very lightly sclerotized; in some taxa the

prementum extends a short distance beyond the apex of clypeus, in others it terminates in the labellae subapically. Labellae prominent, may be fused or unfused medially, dorsal surface glabrous, lateral surfaces with prominent large trichoid sensillae, ventral surface with well-developed pseudotracheae.

Thorax. Boxlike, narrow, approximately as tall as long, with variable but sparse setae. Cervix short but distinct; no sclerites dorsally or ventrally, laterocervicale weakly developed and lightly sclerotized. Antepnotum prominent, variable between subfamilies, often with dorsomedial lobules; antepnotal lobe well developed, fingerlike, subglobose at apex, postnotum produced as narrow strip obscured by antepnotum. Basisternum I fused medially into precoxal bridge, complete fused structure forming inverse trapezoid. Scutum quadrate in dorsal view, prescutum, presutural and postsutural scutum well delineated, medial suture prominent or weakly defined. Prescutum expanded forming anterior margin of scutum, rapidly narrowed to median strip extending posterior at least $2/3^{\text{rd}}$ length of scutum but never reaching posterior margin of scutum. Prescutal suture complete or incomplete posteriorly, with prominent prescutal pits. Presutural scutum quadrate, completely divided by posterior section of prescutum. Transverse suture distinct, straight, merging with prescutal suture. Postsutural scutum with prominent anterolateral lobes created by medial emargination of prescutum, antero-lateral lobes with square apex, lateral margins straight, posterior margin slightly convex. Supra-alar setae present in the form of patch of trichoid sensillae produced at lateral margin of anterolateral lobe near anterior base of wing. Suprasquamal ridge very prominent, rhomboid in shape, with cluster of post-alar trichoid sensillae produced dorsolaterally. Scutellum prominent, bulbously convex, shape from subcircular to elliptical ovoid, provided with a distinct vestiture of trichoid sensillae. Mediotergite of postnotum longitudinally extended hemispherical, with or without medial suture; Laterotergite of postnotum undivided, anterior margin rounded, posterior margin largely straight, with low node rising above halter, provided with a prominent patch of trichoid sensillae antero-dorsally. Metanotum narrow, bandlike. Pleuron of thorax nearly sheer, not convex, largely glabrous, with setae on the posterior

sclerites in some taxa. Paratergite narrow, tapering at extremities. Episternum generally rectangular in shape, anteroventral corner extended ventrally, episternal cleft prominent, often nearly obliterating anterodorsal section of anepisternum, some taxa with protuberance associated with anterior basalare; anepisternal suture partially developed to completely inevident. Metapleural suture straight, with deep narrow invagination below posterior basalare. Posterior basalare beanshaped, convex. Epimeron undivided, indistinguishably fused with meron, narrowly pentagonal in shape with ventral pointed apex between mid and hind coxae. Metapleuron subtrapezoidal, metapleural suture presence variable. **Wing.** Elongate, base narrow for approximately $1/8^{\text{th}}$ length, expanding to uniform width to obtusely rounded apex, longitudinal wing venation relatively straight and parallel. Wing membrane with dense vestiture or fine evenly spaced microtrichia, macrotrichia present in some taxa. C strong along anterior margin, provided with evenly spaced stout trichoid sensillae in multiple rows, becoming weak or ending after apex, with elongate fine macrotrichia in single row. Sc extended approximately $1/2$ - $3/4$ the length of wing, arcing anterior to margin at apex; crossvein h located in basal $1/4^{\text{th}}$ of wing. R initially branching approximately $1/2$ of wing length, R_{1+2} paralleling margin, terminating subapically to wing apex, R_1 extending anterior to margin, R_2 directed posterior fusing with R_3 ; R_5 short, R_3 paralleling margin reaching margin near apex of wing, r-m developed near R_3 fork, short; R_{4+5} elongate, forking approximately midway along length, R_4 and R_5 reaching wing margin at apex. M straight, m-cu emerging approximately $2/3$ of length to apex. CuA straight, deflected slightly posterior, forking near m-cu, base of CuA_1 angled anterior to junction with m-cu, then deflexed slightly posterior in straight line to wing margin; CuA_2 bent medially or sigmoidal anterolateral to wing margin. A_1 reaching wing margin at $2/5$ of length of wing, straight basally, then gently curved to wing apex distally. Halter large, length approximately equal to width of thorax, base with distinctive fingerlike lobe called the prehalter. **Legs.** narrow, elongate; similar form with length slightly increasing posteriorly. Coxae tapering cylindrical, longer than width of pleural sclerites, with distinct setal patterns on surface. Trochanter lopsided

cylindrical, posteroventral margin emarginate. All posterior leg segments round in cross-section densely clothed in stout trichoid sensillae. Femur expanded slightly near distal apex, longest leg segment. Tibia slightly shorter than femur, expanded slightly at proximal apex; tibial spur formula 1-2-2. Tarsomere with five segments, acropod well developed; 1st tarsomere elongate, $1/3^{\text{rd}}$ - $2/3^{\text{rd}}$ length of tibia, tarsomeres 2-5 much shorter, segments moderately decreasing in length distally. 1st tarsomere capable of folding back on 2nd in some taxa. Acropod with two opposed scythe-shaped claws, prominent pulvilliform empodium.

Pregenital abdomen. elongate, narrowed at base. Segment I of moderate length, segment II elongate at least twice as long as next longest segment with sternite II subdivided approximately halfway along length, segments III-VII successively decreasing in length. Male genitalia forming distinct capsule, composed of segments VIII-XI, unrotated. Epandrium strongly developed, often bilobate, with distinct anterolateral epandrial claspers. Cerci probably not developed (see remarks). Epiproct distinct or indistinct, hypoproct always distinct with form variable. Parameres associated with base of gonocoxite, highly variable. Gonopods well developed, laterally produced, free from epandrium and hypandrium. Gonocoxite with prominent apodeme extending anterior beyond anterior margin of epandrium and hypandrium, gonocoxal lobe present or absent. Gonostylus well developed, simple or complex. Hypandrium subdivided into basal and terminal division. Aedeagal complex well sclerotized, composed of several discrete substructures. Sperm sac large, subglobular, ejaculatory apodeme well developed and laterally compressed. Aedeagal shaft composed of two lateral sclerites joined medially by a membranous region, lateral ejaculatory process present at base of aedeagal sclerite. Apex of aedeagus with distinct subapical sclerite articulated on ventral surface.

Subfamily Ptychopterinae Osten Sacken, 1862

Ptychopterinae Osten Sacken, 1862: 12 (description)

Ptychopterinae Schiner, 1862: 495 (description)

Liriopeinae Brues & Melander, Peus 1958: 11 (first usage of coordinate name)

Diagnosis

Larva. Head capsule broadly trapezoidal, with genae expanded posteriorly. Postmentum not fused with subgenal sclerite, anterior margin serrate. Three antennal segments, Larval integument without tubercles or cuticular extensions. Prolegs not more than small bumps on posteroventral margin of anterior abdominal segments. Abdomen with prominent annular creeping welts.

Adult. Medium to large, robust crane fly, variable in color. Antennae with 13-14 flagellomeres, mouthparts with short labium and prominent teardrop-shaped labella. Scutum with complete transverse suture, metapleuron without metapleural suture. Wing with M forking to M₁ and M₂. Legs with at most weak yellow bands, tibial spur of foreleg a simple spine. Posterior abdominal segments at least partially telescoped. Male genitalia highly variable, epandrial lobes always prominent, aedeagus rotated dorsally and shielded by terminal division of hypandrium. Female genitalia with tergite VII concealing epigynium, cerci curved ventrally and heavily sclerotized.

Description

Larva. Head. Head capsule not deflexed, broadly triangular with straight posterior margin. Dorsal surface of cranium flattened; posterolateral corners of genae expanded, forming rounded subacute angle; subgenal sclerite separate from postmentum, simple. Antennae with three articles, apex with variable configuration of sensilla. Postmentum floating in membrane, forming “bridge” beneath maxillae, dorsal surface serrated with rounded dentitions.

Thorax and abdomen. Cuticle translucent to transparent, glabrous, with only isolate patches of sensillae and other setiforms. Prolegs weakly developed, little more than low bumps on ventral surface of abdominal segments I-III with scythe-like claw. Abdominal segments I-V with prominent annular creeping welts on posterior margin. Anal division with respiratory siphon variable in length, never fully retractile in remainder of anal division.

Adult. Head. Head weakly deflexed, broadly. Frons wider than long, especially in *Bittacomorphella*, may be slightly convex or concave, median suture present, sparsely provided with setae. Scape subcylindrical, pedicel sub-spherical, 13-14 flagellomeres, proximal flagellomeres elongate (variable between species), distal flagellomere subequal in size to penultimate flagellomere; verticillate trichoid sensilla present on all flagellomeres, well provided with fine setae. Face rectangular, in some species distinct from clypeus which incises it. Clypeus broadly triangular, labrum variable from broad point to hidden by clypeus, Maxillary palpus long, with 5 segments, ultimate segment often extremely elongate. Labium broad, not extending beyond apex of clypeus, teardrop -haped labella free medially, with ventral surfaces directed posteriorly at rest, pseudotrachae present. Genae with or without setae.

Thorax. Cervical sclerites well developed. Anteprenotum strap-like behind head, teardrop-shaped above forecoxa. Post pronotum small, triangular, does not meet membranous region around anterior spiracle. Prescutum prominent, anterior section rising above pre-sutural area of scutum, forming broad arrowhead-shape anteriorly. Pre-scutal suture distinct, forming triangular point at posterior apex of prescutum; sagittal suture distinct, ending at terminus of prescutum. Prescutum terminating approximately 7/8ths length of scutal complex. Transverse suture complete, curving sharply posteriorly after merging with prescutal suture. Scutum heavily incised by prescutum, with lateral sections prominent, and a low medial ridge linking lateral sections in all but *Bittacomorphella sackenii* complex. Prescutellum small, ovoid in *Bittacomorpha*. Scutellum ovoid, with postalar ridge forming

triangular pattern pointed anteriorly. Postalar wall straight. Mediotergite prominent, domelike, with weak patch of clear setae at anterior margin; sagittal suture weak, extending from anterior margin. Episternum broadly rectangular at ventral 2/3rds, upper third rapidly narrowing in post spiracular area to anterior portion of wing base; sometimes with scattered setae. Anepisternal cleft variously developed - sclerotized post spiracular membrane separated from episternum by suture. Anepisternal inevident, instead a prominent ridge extends from the anterior basalare transversely across the episternum. Paratergite well developed, oval shaped, not provided with any setae. Epimeron with straight anterior margin, ventrally bulging posterior margin. Subalifer ovoid. Laterotergite ovoid, slightly domed, upper portion freckled with sparse setae, without prominence over halter. Metapleuron trapezoidal, roughly square in proportion, tapering ventrally; metapleural suture inevident. Posterior pleural sclerites sometimes with sparse setae, sometimes pollinose. Base of halter anteriorly with pre-halter, post halter absent. Pre-halter fingerlike, setose. Halter stem narrow, round in cross-section, provided with stout setae (~.03mm) along anterior margin, longer setae (~.06mm) provided basally at medial margin, otherwise lacking setiforms. Knob of halter with setae (~.06mm) only along margins. **Wing.** Length subequal to body length. Infuscated or hyaline, abundant microtrichia and macrotrichia on wing membrane. All veins with macrotrichia, Sc, R, M, and anterior margin of C with stout setae. Posterior margin of C with fringe of long microtrichia. R₃-R₄₊₅ fork variably associated with rm. M₁-M₂ fork present, CuA₂ sigmoidal. Anal lobe well developed. **Legs.** Legs light in color, sometimes with dark bands. Arrangement of coxal setae variable. Femur only weakly narrowing towards trochanter, radically in *Bittacomorpha*. Foreleg with single peg-like tibial spur. Mid- and hind-leg each with two tibial spurs, spurs narrow, acutely pointed, with elongate macrotrichia.

Pre-Genital Abdomen. Basally narrow in males, broad in females. Males with distinctive telescoping of posterior sclerites. **Male Genitalia.** Epandrium bilobate, strongly emarginate, sometimes provided with stylets at posteriolateral apices; epiproct distinct between epandrial lobes, hypoproct

tongue-like; epandrial claspers articulated, variably developed. Hypandrium with terminal division rotated into vertical plane, joint between basal and terminal divisions with varying degrees of articulation. Basal division band-like to obtusely hemispherical. Gonostylus highly variable, complex, always with basal lobe dorsally. Gonocoxite cylindrical, mounted laterally between epandrium and hypandrium, often expanding to gonostylus. Gonocoxal lobe often present. Parameres variable, separate in some taxa (*Ptychoptera lenis* group) or fused to bridge, point of articulation shifted posteriorly along the dorsal surface of the gonocoxite. Aedeagus short, lateral ejaculatory processes directed laterally or anteriorly, often broader than sperm sac, ventral portion of process weakly developed. Apex of aedeagus simple. Sperm sac variably developed, from filling most of VIIth segment of abdomen to small globular structure contained entirely within the hypandrium, ovoid to subspherical – narrowing slightly at endophallus; membranous windows absent. Ejaculatory apodeme small and spine-like to massive and flag-like, correlated to size of sperm sac. **Female Genitalia.** 7th tergite covers epigynium. Epigynium platelike, well sclerotized, generally rectangular in shape, without lateral apices. Cerci beak-like, largely glabrous, heavily sclerotized. Hypogynium shape variable, longer than wide, with medial emargination variably developed. Spermathecae three in number, round, well sclerotized.

Subfamily Bittacomorphinae Alexander (1919)

Bittacomorphinae Alexander, 1919: 779, 790 (first usage)

Bittacomorphinae Alexander, 1920: 779 (diagnosis)

Diagnosis

Larva. Integument with either tubercles or cuticular extensions. Head capsule broadly trapezoidal to rounded, with genae variable in shape. Two antennal segments present, postmentum fused with subgenal sclerite, at most two lobes. Prolegs well developed. **Adult.** Large, delicate fly with dark coloration and prominent banded white legs. Antennae with >18 flagellomeres, mouthparts

with well distinguished labium and labellae. Scutum without complete transverse suture, metapleuron with at minimum superficial division to metanepisternum and metkatepisternum. Wing with M unbranched. Legs with prominent white bands of variable pattern, tibial spur of foreleg modified to pair of fleshy lobes. Only Abdominal Segments VI-VII telescoped. Male genitalia with prominent epandrial claspers and simple gonostylus. Female genitalia with exposed subpentagonal epigynium and flexible tab-like cerci.

Description

Larva. Head. Head capsule weakly to strongly deflexed, trapezoidal to oblong, with posterior margin straight to rounded. Dorsal surface of cranium flattened or domed; posterolateral corners of genae expanded, forming rounded subacute angle; subgenal sclerite fused to postmentum. Antennae with two articles, apex with variable configuration of sensilla. Postmentum and subgenal sclerite with variable anterior margin, never serrate.

Thorax and abdomen. Cuticle translucent, absorbing or adhering iron oxide and sometimes other particles from the substrate giving it a distinctly orange or brown appearance; integument covered in prominent tubercles or cuticular extensions, often forming ordered rows. Prolegs strongly developed, distinctly cylindrical protrusions on ventral surface of abdominal segments I-III, with scythe to sickle shaped claw. Abdominal segments I-V lacking creeping welts. Anal division with respiratory siphon variable in length, fully retractile in some taxa.

Adult Head. Head heavily deflexed, broadly triangular (*Bittacomorphella*) to subovoid (*Bittacomorpha*). Frons wider than long, especially in *Bittacomorphella*, may be slightly convex or concave, median suture present, sparsely provided with setae. Scape subcylindrical, pedicel sub-spherical, 18-20 flagellomeres, proximal flagellomeres elongate, shortening distally, distal flagellomere reduced to button-like structure; verticillate trichoid sensillae not present, well provided with fine

setae. Face small, indistinct from clypeus which incises it. Clypeus roughly triangular, moderate (*Bittacomorphella*) to narrow width (*Bittacomorpha*), with or without fine setae, labrum small, spear-like to pin-like, Maxillary palpus long, with five segments. Labium prominent, extending beyond sclerotized portion of clypeus, Semicircular to teardrop shaped labellae fused or unfused medially, ventral surfaces folded against each other at rest, pseudotrachae present. Genae with sparse setae, if any at all.

Thorax. Cervical sclerites very reduced. Antepronotum thin plate behind head, widening slightly above forecoxa where it is provided with sparse setae, not teardrop shaped as in some Ptychopterinae. Post pronotum small, triangular, does not meet membranous region around anterior spiracle. Prescutum prominent, Anterior section rising above pre-sutural area of scutum, forming broad T-shape anteriorly. Pre-scutal suture often indistinct. becoming completely obscure at medial-posterior margin of prescutum; sagittal suture distinct anteriorly, fading out at terminus of prescutum. Prescutum terminating approximately 7/8ths length of scutal complex (*Bittacomorpha*), or terminating at scutellum (*Bittacomorphella pacifica*, *Bittacomorphella* sp. n.) Transverse suture incomplete, curving sharply posteriorly after merging with prescutal suture. Scutum heavily incised by prescutum, with lateral sections prominent, and a low medial ridge linking lateral sections in all but *Bittacomorphella sackenii* complex. Small, ovoid prescutellum present in *Bittacomorpha*. Scutellum ovoid, with postalar ridge forming rounded pattern pointed anteriorly. Postalar wall straight, more prominent, slightly folded anteriorly. Mediotergite prominent, domelike, with dense prominent patch of clear setae (~.08mm) at anteriolateral margin; sagittal suture extending from anterior margin, fading out approx. midway across mediotergite. Episternum broadly rectangular at ventral 2/3rds, upper third rapidly narrowing in post spiracular area to anterior portion of wing base; not provided with any setae. Membranous region behind anterior spiracle variously developed -some species large and membranous (*Bittacomorpha clavipes*), others almost entirely sclerotized (*Bittacomorphella esakii*), sclerotized post spiracular membrane separated from episternum by suture. Anepisternal suture faintly evident, does not reach

anterior margin of episternum. Paratergite well developed, oval shaped, not provided with any setae. Epimeron with straight anterior margin, subtriangular posterior margin. Subalifer ovoid. Laterotergite ovoid, slightly domed, upper portion freckled with sparse setae, without prominence over halter. Metapleuron rectangular, taller than wide, tapering somewhat ventrally; with metapleural suture variably developed: weakly in *Bittacomorphella*, definitively in *Bittacomorpha*. Metepisternum narrow, much taller than wide, tapering somewhat ventrally, extending from posterior spiracle to hind coxa, with cudgel shape; metepimeron triangular, widest under halter, terminating in point at half length of metepisternum. All pleural sclerites without setae, heavily pollinose. Base of halter with pre-halter anterior, and smaller post halter posterior. Pre-halter fingerlike, setose. Post-halter knob-like to peg-like, setose. Halter stem narrow, round in cross-section, provided with stout setae (~.03mm) all along anterior margin, longer setae (~.06mm) provided basally at medial margin, otherwise lacking setiforms. Knob of halter with setae (~.06mm) only along margins. **Wing.** Less than ½ body length. Hyaline, abundant microtrichia, sometimes with macrotrichia on the anterior and distal margins. All veins provided with microtrichia, Sc, R, M, and the anterior margin of C provided with stout setae. Posterior margin of C with fringe of long microtrichia. R3-R4+5 fork contiguous with rm. M1-M2 fork not present, CuA2 sigmoidal. Anal lobe heavily reduced. **Legs.** Legs dark in color, variably banded with white. Fore coxa and mid coxae with single row of setae stretching from antero-ventral margin medial-dorsal margin, fore coxa with additional setae at posterior-ventral margin. Hind coxa setae variable. Femur strongly narrowing towards trochanter, radically in *Bittacomorpha*. Tibial spur on foreleg heavily modified, fleshy, bifurcated to two unequal lobes, which converge apically. Two tibial spurs on each mid and hind-leg, spurs narrow, acutely pointed, glabrous. 1st Tarsomere expanded (*Bittaconorpha*) or normal (*Bittacomorphella*).

Pre-Genital Abdomen. Very narrow in both sexes, petiolate proximally, without telescoping of sclerites until after 5th segment. **Male Genitalia.** Epandrium bilobate or platelike, posterior margin

shallowly emarginated (except *Bittacomorphella jonesi*), often provided with stylets at posterior-lateral apices; epiproct indistinct, hypoproct ovoid, closely associated with epandrium; two prominent epandrial claspers attached ventrally. Epandrial claspers simple, well-articulated with distinct basal joint, directed posteriorly or postero-ventrally. Hypandrium in horizontal plane, divided into basal and terminal divisions by well-developed joint. Basal division broadly triangular, band-like, obtusely hemispherical. Terminal division significantly smaller than basal division, either narrow and pouch-like or foliiform, often with acute lateral apices. Gonostylus simple tapering lobe, apex rounded (*Bittacomorphella*) to flattened on medial margin (*Bittacomorpha*). Gonocoxite cylindrical, mounted laterally between epandrium and hypandrium, comparatively larger than Ptychopterines in relation to overall genitalia. Parameres elongate, either entirely sclerotized (*Bittacomorphella*) or with heavily sclerotized spine supporting lightly sclerotized lateral sections (*Bittacomorpha*). Parameres simple, narrow, without membranous association medially or broad with apical enlargement and medial connective membrane (*Bittacomorpha clavipes*). Aedeagus elongate, lateral ejaculatory processes wing-like and directed laterally and provided with lobe-like ventral portion. Apex with apical apodemes, closely associated with subapical sclerite articulating on hypandrium. Sperm sac well developed, filling most of VIIth segment of abdomen, subspherical – narrowing slightly at juncture with aedeagal sclerites; two membranous windows formed at junction with ventral apodemes of aedeagus, which protrude into the sac. Ejaculatory apodeme small, apex rounded or pointed. **Female Genitalia.** 7th tergite does not cover epigynium. Epigynium platelike, well sclerotized, generally pentagonal in shape, with prominent lateral apices. Cerci tablike roughly subquadrate to rounded, well provided with setae, without the heavy sclerotization displayed in Ptychopterinae. Hypogynium roughly rounded, nearly as wide as long, with deep medial emargination, lateral apices of emargination rounded. Spermathecae absent or unsclerotized.

Key to the species of Bittacomorphinae

Adults

This key was developed from the one published in Kang *et al* (2012) and a publication in progress by Fasbender, Cannings, Copley, and Courtney.

1. All legs with first tarsomere conspicuously expanded. Wing with distal radial and medial cells without macrotrichia. Antenna with 19 flagellomeres ... *Bittacomorpha*

Westwood ... **2**

- All legs with first tarsomere not expanded. Wing with distal radial and medial cells with or without macrotrichia (Fig. xx). Antenna with 18-20 flagellomeres ... *Bittacomorphella* Alexander ... **3**

2. Scutum dull black with silver-grey tomentum in lateral and ventrolateral views and with distinct, narrow, silver-grey, medial stripe expanded postsuturally. Cell m1 about one-third the length of cell r5 (Fig. 7). Male terminalia with apex of paramere weakly furcate (Fig. 6f). Widespread east of Rocky Mountains.

... *B. clavipes* Fabricius

- Scutum shining black; pale medial stripe absent, but patch of silver-grey tomentum present on postsutural midline. Cell m1 about one-half the length of cell r5 (Fig. 13). Male terminalia with apex of paramere spatulate (Fig. 12f). Western.

... *B. occidentalis* Aldrich

3. Legs with light band on proximal portion of tibia ... **4**

- Legs without light band on proximal portion of tibia ... **9**

4. Legs with 4th & 5th tarsomeres cream colored ... **5**

- Legs with 4th & 5th tarsomeres dark brown ... **6**

5. Legs with white band on proximal apex of 1st tarsomere. Japan ... *Bl. esakii* Tokunaga

- Legs without light band on proximal apex of 1st tarsomere ... **7**

6. Foreleg with distal apex of first tarsomere brown. Male genitalia with epandrial lobe semicircular, parameres tapering and curving medially, subapical sclerite of aedeagus conical. China ... *B. gongshana* Kang, Wang & Yang

- Foreleg with distal apex of first tarsomere white. Male genitalia with epandrial lobe rectangular, parameres clavate and straight, subapical sclerite of papiliform. Taiwan and China ... *B. lini* Young & Fang

7. Foreleg with distal apex of first tarsomere white. China ... *Bl. zhaotongensis* Kang, Wang & Yang

- Legs with 4th & 5th tarsomeres dark brown ... **8**

8. Legs with broad white band subapically on proximal portion of tibia. Male terminalia with posterior margin of epandrium not bilobate or emarginate, epandrial claspers with basal lobe (Fig. 36a). Eastern North America ... *Bl. jonesi* Johnson

- Legs with narrow white band at proximal apex of tibia. Male terminalia with epandrium bilobate, emarginate, epandrial claspers lacking basal lobe (Fig. 40a). Japan ... *Bl. nipponensis* Alexander

9. Wing without macrotrichia (Fig. 43). Thailand ... *Bl. thaiensis* Alexander

- Wing with abundant macrotrichia (Figs. 19, 22, 25, 31) ... **10**

10. Scutum with anterior of prescutum and presutural lateral portion of scutum shining dark brown/black, posterior apex of prescutum and medial portion of scutum with yellow stripe. Male terminalia with articulated lobes of epandrium curved medially, acute, almost glabrous, with only a few setae on distal third; epandrial lobes prominent and triangular in dorsal view, capped with a narrow, truncate posteromedial style (Fig. 30a). Gonostylus with a slender basal lobe directed dorsally (Fig. 30b). Paramere a long, slender, sickle-shaped hook curving dorsomedially; lobule at base (Fig. 30f)

... *Bl. fenderiana* Alexander

- Scutum black. Male terminalia with articulated lobes of epandrium bearing setae throughout their length; epandrial lobes not apparent, posteromedial style of epandrium forming low knob directly medial to epandrial clasper (Fig. 18a, 21a, 24a). Gonostylus without a basal lobe (Fig. 18b, 21b, 24b). Paramere straight, curved ventrally, or bifurcate; basal lobule absent. (Figs. 18f, 21f, 24e) ... **11**

11. Scutum glabrous. Male terminalia with posterior margin of epandrium strongly emarginate, subapical sclerite reduced (Figs. 18d, 18e), a poorly distinguished plate at apex of aedeagus, paramere bifurcate. (Fig. 24e) ... *Bl. furcata* sp. n.

- Scutum covered in silver-grey tomentum. Male terminalia with posterior margin of epandrium weakly emarginate, subapical sclerite of aedeagus conical, extending beyond phallotreme (Figs. 21d, 21e, 24d), Paramere simple. (Figs. 21f, 24e) ... **12**

12. Male terminalia with subapical sclerite of aedeagus tapering, apex with triangular tooth dorsally (Fig. 21d). Paramere simple or with weak sigmoidal curvature. (Fig. 21f) ... *Bl. pacifica* Alexander

- Male terminalia with subapical sclerite of aedeagus pin-like, apex simple (Fig. 24d). Paramere forming semicircular curve dorsally. (Fig. 24e)... *Bl. sackenii* Von Röder

Larvae

The larvae of few species Bittacomorphinae are known, so this key should be used circumspectly.

1. Head capsule with cranium rounded, hypostoma with two lobes laterally (Figs. 10, 16); thorax and abdomen with cylindrical tubercles (Figs. 8, 14); anal division conical, respiratory siphon partially retractable ... *Bittacomorpha* Westwood ... **2**

- Head capsule with cranium flat, hypostoma with broad blade medially (Fig. 34); thorax and abdomen with finger-like cuticular extensions, often with hardened substrate attached (Fig. 32); anal division cylindrical, respiratory siphon fully retractable ... *Bittacomorphella* Alexander ... **3**

2. Head capsule with genae not expanded posterior, olive colored with dark spots, hypostoma with lateral lobes rounded (Figs. 9, 10). Most of North America.

... *B. clavipes* Fabricius

- Head capsule with genae expanded posterior, uniform black color, hypostoma with lateral lobes triangular (Figs. 15, 16). Western.

... *B. occidentalis* Aldrich

3. Posterolateral apex of head capsule simple angle ... *Bl. jonesi* Johnson

- Posterolateral apex of head capsule with small hook (Fig. 33) ... *Bl. fenderiana* Alexander

***Bittacomorpha* Westwood, 1835**

Bittacomorpha Westwood, 1835: 281 (original description, type species *Bittacomorpha clavipes* Fabricius)

Bittacomorpha Westwood, Alexander 1919: 790 (catalog)

Bittacomorpha clavipes Fabricius, Alexander 1920: 783–784 (redescription)

Bittacomorpha Westwood, Alexander 1927: 9–10 (catalog)

Bittacomorpha Westwood, Alexander 1965: 98 (catalog)

Diagnosis.

Larva. Head rounded, well separated from prothorax, cranium rounded, hypopharynx with two lateral lobes on anterior margin. Thorax and abdominal segments with cylindrical tubercles, anal division conical, respiratory siphon partially retractile.

Adult. Head ovoid, Clypeus extremely narrow and acute, 1st Tarsomere inflated on all legs.

Description

Adult. Head. Head ovoid in shape, closely pressed to thorax, frons broad with vertex at same level as dorsal margin of eye, medial suture moderately to clearly distinct, extending between antennal bases to dorsal margin of face. Antennal scape subovoid, compressed in cross-section, provided with 5–8 socketed sensilla subdorsally along anterior margin; pedicel subspherical, with scattered dorsally directed setae; 20 Flagellomeres. Face trapezoidal, not incised by clypeolabrum, suture with clypeolabrum indistinct. Clypeolabrum small to moderate, extremely acute, lateral margins straight, around 2.5x longer than wide, not inflated. Maxillary palpusi as in subfamily. Hypopharynx variable. Labium prominent, partially hidden to largely exposed by clypeolabrum. Labella fused medially, forming circular pad.

Thorax. Antepronotum platelike, narrowing obtusely dorsally. Scutum glabrous, shining or pollinose, black with white marking posteromedial to prescutum. Prescutellum absent. Scutellum pale yellow, with dense group of setae medially, ovoid with parallel lateral margins. Mediotergite ruddy-brown, dense patches of setae at anteriodorsal margin, as well as two parallel lines of setae medially. Paratergite well developed, crescent-shaped, subacute anterior, broad posterior. Sub-paratergal membrane inverse triangular, with sclerotized band near anterior spiracle, otherwise poorly sclerotized. Episternum flat, without prominence, rectangular in shape; anepisternal suture poorly developed, denoted by low ridge emerging from posterior margin, incomplete. Epimeron subtrapezoidal, surface slightly convex, rising to prominence at wing base, posterior heavily incised by laterotergite. Laterotergite D-shaped, largely flat, ventral portion depressed towards halter. Suture between epimeron and metapleuron distinct dorsally and ventrally, obscure medially; metapleural suture well developed, complete, emerging from posteroventral margin, straight to halter; no prominence or setae below halter. All pleurites with opaque sky blue pollinosity, surface black. **Wing.** Wing length 5x width, anal lobe undeveloped. Macrotrichia absent. Halter and prehalter as per subfamily, posthalter well developed, nearly twice as long as wide, largely free of webbing to posterior membranous association of halter. **Legs.** Coxae pollinose blue, fading to light yellow at trochanter, lateral surfaces with long setae; proximal portion of femur yellow, darkening to black at tibial joint. White band sub-proximally on tibia, expanding slightly to 1st tarsomeres. First tarsomere greatly expanded, ovoid, upper margin with white band. 2nd & 3rd tarsomeres white, 4th & 5th black. Empodium loosely associated with acropod, rounded-off diamond-shaped, heavily provided with short clear setae, notched proximally.

Pre-genital Abdomen. Segments 2–7 black, with posterior margins yellow. **Male Genitalia.** Epandrium over twice as wide as long; broadly hexagonal in shape, broadly and deeply emarginate on posterior margin; posterior apices obtusely rounded, with small downward directed triangular lobe medially; mediosagittal suture absent; epiproct not apparent, hypoproct closely associated with ventral

surface of epandrium, ovoid, well sclerotized, with several setae of moderate length. Dorsal surface provided with scattered long setae (0.10–0.25mm), becoming more numerous toward margins.

Epandrial claspers emergent from anterior margin, directed posteriorly, curved medially; tapering to blunt apex, medial surface flattened with numerous short blunt sensilla; lateral surface with long setae.

Parameres broad, glabrous sclerotized medial margin and poorly sclerotized sheet-like lateral margin; basal section adhered to membrane above aedeagus, with acute spine directed dorsomedially arising near gonocoxite; distal portion of paramere curving back to a nearly straight vertical spine tapering to an acute point. Gonocoxite conical, expanding to gonostylus, 2/3rds length of gonostylus. Gonostylus rounded at tip, medial surface well provided with long setae, dense ovoid cluster of blunt sensilla at inner apex. Basal division of hypandrium a hemispherical band, provided sparsely with long setae, dull yellow in color; junction with terminal division membranous; gonocoxite not closely associated.

Terminal division articulated, foliform, margins cupped dorsally. Short, rounded lateral apices present, posterior margin ranging from slightly emarginated to slightly convex. Ventral surface sparsely provided with setae, dorsal surface glabrous. Aedeagus with sperm sac as per subfamily, lateral ejaculatory process variable. Ejaculatory apodeme spathate, does not taper to rounded apex. Apex of aedeagus with medial emargination where sclerites meet. Dorsal apical apodemes present; ventral apical apodemes large, expanding round, directed posteroventrally. Subapical sclerite triangular, directed dorsally. **Female Genitalia.** Epigynum flat, subtrapezoidal tapering towards posterior margin; posterior margin with triangular medial extension. Cerci comparatively elongate, >3x length vs. height, slight ventral curvature, apex rounded. Hypogynium broad, especially at base, medial emargination width ~.5x length.

***Bittacomorpha clavipes* Fabricius (1781)**

Tipula clavipes Fabricius, 1781: 404 (original description)

Tipula clavipes Fabricius, Fabricius 1787: 323 (redescription)

Ptychoptera clavipes Fabricius, Fabricius 1805: 22 (catalog, redescription)

Bittacomorpha clavipes Fabricius, Westwood 1835: 282 (set as type species of *Bittacomorpha*)

Bittacomorpha clavipes Fabricius, 1890: 230 (key)

Bittacomorpha clavipes Aldrich, 1895: 200 (original description)

Bittacomorpha clavipes Fabricius, Johnson 1905: 75 (key)

Bittacomorpha (Bittacomorpha) clavipes Fabricius, Alexander 1916: 546 (key)

Bittacomorpha clavipes Fabricius, Alexander 1920: 784–787 (redescription)

Bittacomorpha clavipes Fabricius, Alexander 1927: 9 (catalog)

Bittacomorpha clavipes Fabricius, Peus 1968: 11 (catalog)

Bittacomorpha clavipes Fabricius, Alexander 1965: 98 (catalog)

Bittacomorpha clavipes Fabricius, Alexander 1967: 171 (illustration)

Diagnosis

Larva. Larval cranium domed, genae round and abbreviate, olive-colored and spotted with black. Abdominal segments with linear, transverse rows of fleshy tubercles dorsally and ventrally, longitudinal rows laterally, each tubercle with a single branching sensillum. Prolegs prominent. Thoracic and abdominal segments often incorporating iron oxide and appearing orange-brown in color, though this characteristic not developed in specimens inhabiting iron-oxide deficient environments.

Adult. Scutum with longitudinal white stripe on scutum. Male with paramere apex weakly furcate.

Description

Larva. Head. Dorsal surface weakly flattened, hemispherical, olive-colored with rows of dark spots posteriorly on frontoclypeal apotome and dorsal surface of genae. Frontoclypeal apotome narrow, 2.5x as long as wide, narrowing weakly anterior to antennae, anterior margin blunt; occipital margin narrowing acutely posterior to antenna, reaching nearly to posterior margin of cranium; ecdysial stem line short, obscured by prothorax, only on collar of genae. Genae rounded in dorsal view, not expanded posteriorly, do not meet medioventrally, anterior margin square, short collar present on posterior margin, ventroposterior margin weakly and broadly emarginate; subgenal sclerite fused with hypopharynx, narrowed at midpoint of length, apex with semicircular anterolateral lobes. Single stemmata present. Antenna two-segmented, base recessed at anterior terminus of ecdysial suture: basal segment cylindrical, apical segment weakly fusiform, apex rounded, apical sensilla cluster directed laterally. Labrum triangular, dorsally with heavily sclerotized trapezoidal plate, ventral surface membranous, slightly expanded, ventral margins heavily sclerotized, narrow medially, broadening flag-like dorsolaterally; labral brushes round, macrotrichia elongate; medioventral apex with conical, ventrally directed, obtuse point, with stout ventrally directed sensilla. Premandible ventral to labrum, well developed, with serrate medioventral margin. Mandible with molar lobe semicircular, ventrolaterally with triangular lobule, mandibular comb well developed, surrounding incisor lobe, becoming a weakly serrated lobe on inner ventral margin; incisor lobe triangular, ventral margin unserrated; prosthema prominent on inner lateral margin, heavily modified: ventromedially with elongate thick trunk ending in knob, laterodorsal two blunt, thick sensilla, followed by four narrower sensilla. Maxillae with cardo in form of an inverse, acute triangle, ventral point heavily rounded; stipes

culvert-like over lacinia, without brushes, maxillary palpus apical; lacinia elliptical. Prementum broadly bottleneck-shaped, dentition at apex blunt.

Thorax and abdomen. Thoracic segments weakly increasing in size posteriorly, tubercles in irregular pattern, mound-like, each tubercle with elongate branching sensillum. Abdominal segments cylindrical, homogenous in width, delineations between segments weak; tubercles mound-like with medial cylindrical apex, apex with elongate branching sensillum, lateral margins of tubercle each with smaller branching sensilla; tubercles arranged in regular pattern, transverse rows on dorsal and ventral surface, longitudinal rows laterally. Anal division conical, with lightly sclerotized exsertable tube containing siphon; siphon with annulations weakly developed if at all.

Adult. Measurements (n=5). Overall length: 10.82mm (10.51–11.16mm) **Head.** Width: 1.06mm (1.02–1.12mm); Height: 0.95mm (0.88–1.0mm); Length: 0.61mm (0.57–0.67mm); Flagellum length: 5.17mm; Flagellomere proportions: 1.00, 0.82, 0.89, 1.00, 1.00, 0.89, 0.94, 0.89, 0.76, 0.76, 0.64, 0.64, 0.64, 0.51, 0.43, 0.43, 0.38, 0.38, 0.17; Maxillary palpus length: 1.49mm; Maxillary palpus segment proportions: 0.24, 1.0, 1.3, 0.96, 1.0 **Thorax.** Length: 1.96mm (1.65–2.22mm); Height: 1.78mm (1.65–1.91mm); Wing length: 7.26mm (6.7–7.9mm); Wing width: 1.42mm (1.31–1.6mm); Leg: Femur: 1.0, 1.12, 1.27; Tibia: 0.98, 0.95, 1.19; Tarsomeres: Foreleg 0.53, 0.22, 0.14, 0.05, 0.04, Midleg 0.54, 0.21, 0.12, 0.05, 0.03, Hindleg 0.58, 0.25, 0.16, 0.04, 0.06. **Abdomen.** Length: 11.87mm (10.85–13.15mm); Male tergite proportions 1.00, 3.13, 2.20, 2.23, 1.88, 0.89, 0.28; Male Genitalia: Width: 1.03mm; Height: 0.71mm.

Head. Head closely pressed to thorax, generally triangular in shape, frons broadly domed with vertex well above dorsal margin of eye, medial suture clearly evident, extending between antennal bases to dorsal margin of face. Antennal scape ovoid in cross-section, provided with five-socketed sensilla subdorsally along anterior margin; 19 Flagellomeres. Face narrow, incised by clypeus nearly to

dorsal margin. Clypeus large, sub-acutely triangular, lateral margins somewhat pinched at junction with face, around 2x longer than wide, somewhat inflated. Maxillary palpi as in subfamily. Hypopharynx subconical triangular, directed anteroventrally. Labium largely hidden by clypeolabrum. Labellae free medially, not forming pad.

Thorax. Antepronotum with two small fleshy semicircular lobes emergent from dorsal margin, each provided with several setae. Scutum glabrous, shining, ruddy-brown with broad muddy yellow highlighting of transverse suture. Distinct fold at rear of scutum, but no prescutum present. Scutellum muddy yellow, with dense group of setae medially, subcircular. Mediotergite ruddy-brown, dense patches of setae at anteriodorsal margin, as well as two parallel lines of setae medially. Paratergite well developed, broad, blunt crescent-shaped. Sub-paratergal membrane elliptical in shape with tapered apices, well sclerotized. Episternum flat with prominence above midcoxa, rectangular in shape; anepisternal suture well developed. Epimeron rectangular in shape, with shallow sulcus located midway dorsally, posterior margin straight. Laterotergite lacrimiform, depressed dorsally with a few long setae along dorsal margin rising to slight prominence towards halter. Halter and prehalter as per subfamily, posthalter well developed, nearly twice as long as wide, largely free of webbing to posterior membranous association of halter. Metapleuron with incomplete suture, emerging from posterior ventral margin in a broad arc and terminating well before halter; immediately below halter low prominence with cluster of long clear setae. All pleurites muddy yellow, fading to ruddy brown at ventral margin. **Wing.** Wing without macrotrichia. Apex of $R_{1 \text{ and } 3}$, with macrotrichia, all other veins bare. Costa weakening significantly at wing apex, faint along posterior margin. R_{3+4+5} stem 0.60mm, straight; R_{4+5} stem 2.00mm; R_4 after fork 1.25mm, R_5 after fork 1.23mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 3.33 : 2.08$. r-m 0.30mm; M distal to r-m 2.97mm; Mdistal: $R_{3+4+5} = 4.95:1.00$, $R_4:Mdistal = 0.42:1.00$. CuA_2 1.78mm, loosely sigmoidal, proximal bend approximately 140° , distal bend very near wing margin, nearly 90° . A_1 faint basally, paralleling Cu for a short distance before broadly curving to anal margin, arc becoming

more acute apically. M-Cu joins M at r-m. Anal lobe poorly developed, angle obtuse; alula undeveloped.

Halter: length: 1.14mm; stem elongate, medial furrow shallow at base becoming obscure distally, long clear macrotrichia laterally, knob pale yellow with dark stout trichoid sensilla laterally, apex of knob bare; prehalter elongate, sparsely provided with elongate clear trichoid sensilla; posthalter well developed, palpusiform, with several long translucent sensilla apically, free of webbing posteriorly. **Legs.**

Coxae yellow, overall leg coloration brown. White banding confined to distal tip of 1st, 2nd & 3rd tarsomeres. Empodium closely associated with acropod, heavily provided with setae, notched posteriorly.

Pre-genital Abdomen. As per genus. **Male Genitalia.** Epandrium subquadrate, posterior margin strongly emarginate medially. Dorsal surface evenly covered with trichoid sensilla of moderate length. Anterior margin straight to lateral extremity, gently curving posterior to lateral margin. Lateral margins straight, forming a subobtuse angle with posterior margin above epandrial clasper. Lateral extremities of posterior margin straight, perpendicular to lateral margin, medial section of posterior margin with prominent semicircular emargination; posteriomedial style directed ventrally at lateral termination of emargination, short and triangular. Internal folds above epandrial clasper prominent and well sclerotized, originating at rear margin of epandrial clasper and extending in a straight line medially with slight posterior deflection. Epiproct indistinguishable, hypoproct a central sclerotized plate surrounded by membrane. Epandrial clasper cylindrical, tapering only at apex, weakly curved medially; medial apex flattened and provided with thick covering of conical sensilla. Subepandrial sclerite divided, broadly sickle-shaped structure fused to medial margin of the base of the epandrial clasper, extending towards the hypoproct, additionally a small crescent-shaped weak sclerotization exists between the subepandrial sclerites in the subepandrial membrane in some specimens. Parameres complex, arising near dorsal margin of gonocoxite. Dorsal margin heavily sclerotized scaffold supporting medial membrane reaching

nearly to apex, as well as lateral membrane extending posterior to lateral spine. Apex of sclerotized portion subacute spine, with prominent dorsal tooth subapically. Lateral spine directed lateroventrally, curving posteriorly towards apex, set at $2/3$ the length of paramere. Medial membrane fused medially with membrane of opposing paramere, heavily emarginate. Gonocoxite directed completely posterior, weakly expanding to gonostylus, shorter than gonostylus. Gonostylus weakly curving medially, slightly tapered rounded at tip, medial surface from base to apex covered in dense, moderately sclerotized trichoid sensilla. Heavily sclerotized apicomedial sensilla weakly developed at apex of gonostylus in some populations. Basal division of hypandrium roughly triangular, expanded, subhemispherical, posterior margin weakly emarginate, lateral margins without emargination or sulci; surface sparsely scattered with sensilla. Terminal division well-articulated, variable foliform shape, always with petiolate base and two lateral lobes of small size, posterior margin highly variable, ventral surface provided with short setae. Superaedeagal membrane highly inflated, with medial division evident, extending well beyond apex of aedeagus. Aedeagus with sperm sac as per subfamily, membranous window distinct. Ejaculatory apodeme spathate, with rounded apex. Basal lateral apodeme complex; dorsolateral portion emergent from peduncle, associated with lateral surface of ventral portion and lateral aedeagal sclerite, loose triangular dorsally directed crescent in outline, lateral apex broadly triangular in lateral view, medial apex acutely triangular and fingerlike, sclerotized ridge trailing lateral and dorsal margin, extending ventrally to ventral section; ventral section elongate, larger than dorsolateral section, forming subacute quadrilateral towards blunt anterior apex, apex with lightly sclerotized region directed laterally, deeply inserted into sperm sac. Ejaculatory apodeme spathate, slightly tapering towards apex. Lateral sclerites of aedeagus of moderate width, widely separated at base. Apical apodemes of aedeagus prominent; dorsal lobe large, directed dorsally curving anteriorly at apex; ventral lobe sickle-shaped, fusing with posterior section of subapical sclerite, with sclerotization reduced posteriorly. Subapical sclerite complex, internal section divided with prominent anterolateral apex and ventral arm,

anterolateral apex forming flat plate expanding to emarginated posterior margin, ventral arm a relatively short rod emerging from lateral margin of dorsal section curving weakly ventrally. External portion of subapical sclerite large, triangular directed posterodorsally, extending dorsally beyond apex of aedeagus. **Female Genitalia.** Epigynium flat, posterior margin straight, angle to lateral margin square, lateral margins straight, posterior margin indistinct, emarginated with distinct angle. Medial suture present, faint. Cerci fused at base, one-segmented: dorsal margin straight, apex rounded, ventral margin swollen, potbellied anteriorly, tapering posteriorly. Apex of cercus with short, cylindrical nodule with stout elongate trichoid sensilla medially, ring of three finer sensilla arranged equidistant around central sensillum. Hypoproct broad, tongue-like, with sclerotized triangular boat-like sclerite located ventrally, anterolateral apex with triangular lobe. Genital fork spatulate, posterior margin weakly emarginate. Hypogynium a hemi-ring, hypogynial valve a short triangular lobe medially, lateral margins straight and angled dorsally, medial notch square: 0.75x as deep as broad.

Material Examined. COSTA RICA. Guanacoste, Prov.. Bijagua, 22-II-1991, D.W. Webb & M.E. Irwin (Pinned: 1 m#) (INHS); **UNITED STATES.** ALABAMA Hale Co. #1, Payne Lake, 24 mi., SE. of Tuscaloosa, 25 May 1978 G.W., Byers & C.W. Young (Pinned 1 m#, 1 f# on same pin) (KU); ALABAMA Lee Co. #3, Chewacia State Park/ 4 mi. SW. of Auburn, 26 May 1978. G.W., Byers & C.W. Young (Pinned: 1 f#) (KU); ARKANSAS Hot Spring, Co. #1, Malvern, City park. 22 May '78, G.W. Byers, C.W. Young (Pinned: 3 m#) (KU); ARKANSAS Montgomery, Co. #2, Gap Creek, 1.3mi. SE. of Joplin, 22 May 1978. G.W., Byers & C.W. Young (Pinned: 1 m#) (KU); ARKANSAS:, Montgomery Co., Gap Creek Picnic Grd., 1 mi SE Joplin, 700 ft., 1 June 1984, S.A. Teale (Pinned: 1 m#) (KU); ARKANSAS:, Montgomery Co., 800 ft., 2 mi NW Mount Ida, 1 June 1984, S.A. Teale (Pinned: 1 m#) (KU) COLORADO Fremont Co., #1, Hayden Creek, 4, mi. SW. Coaldale, 13 July 1974 7200', G.W. Byers, C.W. Young (Pinned: 8 m#, 1 f#) (KU); COLORADO, Gunnison Co., Gothic 10000ft., July 23 1952, B. Pruitt #29 (Pinned: 6 m#, 1 f#) (UMMZ); COLORADO Mineral Co., #3, Wolf Creek Cpg., San Juan Natl. Forest, 25 July 1981. 7830', G.W. Byers & S.A. Teale

(Pinned: 3 f#) (KU); COLORADO San Juan, Co. #1, 30 mi. N., Durango, 9400 ft., 13 August 1965, George W. Byers (Pinned: 1 f#) (KU); Colo. | S (Pinned: 1 m#) (WSU); Redding, CT, 2 Aug. '28, AL Melander (Pinned: 1 m#) (USNM); Butts Co. G.a., V-6-73 (Pinned: 2 m#) (FMNH); GEORGIA, Fulton Co., East Point 15 May, 1965 Bruce Harrison (Pinned: 1 f#) (KU); GEORGIA Lumpkin Co., #5 De Soto Falls, 23 June 1967 2000', George W. Byers (Pinned: 2 m#) (KU); GEORGIA: Oconee Co., 2mi. N. Watkinsville, 3 October 1977, George W. Byers (Pinned: 2 m#) (KU); GEORGIA Union Co., #8 Lake Winfield, Scott 3000 ft., 23 June 1967, George W. Byers (Pinned: 1 m#) (KU); ILL.: Dupage Co., Argonne Natl. Lab, IX-11-1974, D. Pearson (Pinned: 1 m#) (FMNH) ILL.: Kane Co., VII:23:1972, leg. D. Pearson (Pinned: 2 m#, 4 f#, various dates July 23, 1972 – July 27, 1973) (FMNH); Palos Park., VI:20:09 ILL / Col. by, W.J. Gerhard (Pinned: 1 m#) (FMNH); INDIANA, Lagrange Co., Pigeon River, 4 Sept. 1928 B.E.M. (Pinned: 1 f#) (UMMZ); Mich. City., 2-IX-55 Ind / H. Dybas, Collector (Pinned: 1 m#) (FMNH); IN, Tippecanoe Co., Ross Hills Park, Malaise 1-8.vi.2013, coll. G. Curler, 40°24'08.22"N, 87 °09'18.80"W (Pinned: 1 f#) (PERC); Ames, IOWA, V-17 1964, W.S. Craig (Pinned: 43 m#, 2 f#) (ISIC); Iowa Lakeside Lab., Dickinson Co., Iowa, July 18, 1959, Jean L. Laffoon (Pinned: 1 m#) (ISIC); USA Iowa, Dickinson Co., Iowa Lakeside Lab, sampling in seep May-17-2010, Hillside Seep nr. Marsh, 43.383374N, 95.179974W, GW Courtney + A Fasbender (Pinned: 2 f#) (ISIC); USA Iowa, Dickinson Co., Silver Lake Fen May-17-2010, Hillside Seep nr. Marsh, 43.437472N, 95.365009W, GW Courtney + A Fasbender (Pinned: 11 m#, 9 f#; Alcohol: 4 m#, 3 f#, 3 larvae; adults reared) (ISIC); Springbrook St.Pk., Guthrie Co., IOWA, August 24, 1972, A. Stewart Cott (Pinned 1 m#, 1f#) (ISIC); Springbrook St. Park, w.1/2Sec. 33 T8IN, R3IW, Guthrie Co., IOWA, VII-19-1960 J. Laffoon (Pinned: 1 m#) (ISIC); KANSAS Douglas Co., Lawrence vicinity, VII-8-1987, J. Gelhaus Snow Hall (Pinned: 2 f#, also 19 May 1986, BN Danforth) (KU); Bar Harbor, Maine, Aug. 5, 1936, A.E. Brower (Pinned: 2 m#) (USNM); Maine:, Ellsworth, IX.12.1967, PJ Spangler (Pinned: 1 f#) (USNM); Maine: Orono, Penobscot Co., 18 VIII 1981, Coll. S. Struad (Pinned: 1 m#) (KU); Battle Creek, Mich. (Pinned: 3 m#, 5 f#) (WSU); MICHIGAN: Calhoun Co., Battle Creek, 5 July 1979, George W. Byers #1 (Pinned: 1 f#) (KU); Cheboygan

Co, Mich. 7/31 (Pinned: 1 m#) (KU); MICHIGAN Cheboygan, Co., Cochran Lake, 19 July 1957, R.E. Beer (Pinned: 1 m#) (KU); 4mi. N. of, Topinbee, Cheb. Co. Mich., VII-8-1961, H. Willis (Pinned: 1 f#) (KU); 4mi. W. Pell-, ston, Emmet, Co., Mich., VII-15 1969 (Pinned: 3 m#, 2 f#) (UMMZ); MICH: Gratiot Co., Ithaca, 13 VII 1959, Victor Potter (Pinned: 3 m#, 5 f#) (UMMZ); Jackson Co., Mich. V.7.39, F. Awnerman (Pinned: 1 f#) (UMMZ); Gull Lake Biol. Sta., Kalamazoo Co., MICH, 4 July 1965, B. & T. Hlavac (Pinned: 1 f#) (FMNH); MICHIGAN, Schoolcraft Co., Aug 14 1951, J.S. Rogers+ 2 (Pinned: 1 m#) (UMMZ); Itasca State, Park, Minn, IX-2 1950, Jean Laffoon (Pinned: 6m#, 1 f#) (ISIC); MISSISSIPPI Lafay-, ette Co. #1, Puskus, Lake, 8mi. NE. Oxford, 23 May 1978, G.W., Byers & C.W. Young (Pinned: 1 f#) (KU); MISSISSIPPI, Vicksburg, 23 Sept 1977, G.W. Byers (Pinned: 1 m#) (KU); Rushville, Nebr., Malaise Trap / R.W. Dawson, July 12 1967 (Pinned: 1 m#) (WSU); Valentine, Nebraska, June 9 1950, Hicks, Slater, Laffoon (Pinned: 6 m#, 5 f#; multiple dates June 9-11 1950) (ISIC); 7 miles S. of, Long Lake, N.Y., 26-VIII-1956, W.E. LaBerge (Pinned: 2 m#); North Rose, VI:17:27 N.Y. / Rawson-Mac, Millan Exped / Col. by, A.C. Weed (Pinned: 1 f#) (FMNH); Saranac Inn, N.Y., 1900 / OS Wescott, Collection (Pinned: 5 m#) (KU); Smyrna, VIII:16:25 N.Y. / Col. & pres. by, A.C. Weed | (Pinned: 1 f#) (FMNH); Asheville, N.C., 4-29-62, R.D. Peterson / ON Store, Window, (Mello's card nr., cards) (Pinned: 1 f#) (ISIC); NORTH CAROLINA, Swain Co. #11, 1.2, mi. NE. Clingman'sDm., GSMNP 15 June '67, G.W. Byers 6000' (Pinned: 1 m#) (KU); 4 mi. E Kent, OH, AUG 8, 1967, M. Duckenonod (Pinned: 1 f#) (USNM); PENNSYLVANIA, Berks Co. No. 3, French Creek Park, 7 July 1960, George W. Byers (Pinned: 3 m#, 1 f#; 21 m#, 1 f# at No. 4, July 9 1960; 2 m# at No. 5, July 9 1960; 1 m# at No. 6 9 July 1960; 3 m# at No. 7 10 July 1960) (KU); PENNSYLVANIA: Berks, Co., 1mi. SE. Reading 15 August 1956, George W. Byers (Pinned: 3m#, 1 f#) (KU); PENNSYLVANIA, Franklin Co. No.1, Caledonia St. Park, 2 July 1960, Byers and Party (Pinned: 2 m#) (KU); PENNSYLVANIA: Luzerne, Co., Hazelton, 8 July 1979, George W. Byers #8 (Pinned: 1 m#) (KU); SOUTH CAROLINA, Abbeville Co. #1, 5 mi. S. Abbeville, 29 May 1978 G.W., Byers & C.W. Young (Pinned: 2 m#, 1 f#) (KU); SOUTH CAROLINA, Oconee Co. #1, Westminster 820ft., 30 May 1978. G.W., Byers & C.W. Young (Pinned: 1 f#) (KU); S. CAR:

Oconee Co., Oconee State Park, (Small lake) 20Aug1939, #3974 B.E. Montgomery (Pinned: 1 m#) (UMMZ); USA, SC, Pickens Co., Clemson U. Experimental, Forest, Six-Mile Creek, 34°45'N 82°51'W, 17 iii 2005, coll. G.W. Courtney (Alcohol: 5 pupae; 1 m# 2 pupae coll. MJ Petersen) (ISIC); South Dakota Black Hills, Nat. For. Stream nr. South, Rochford Road, Sweeping, 44.109621N103.734564W, A Fasbender June-29-2010 (Alcohol: 3 m#) (ISIC); USA, SD, Custer Co., Custer SP, French Crk Picnic, 43.7180°N 103.4891°W, 30.vi.2008 3373' 95%EtOH, coll.: J.D. Petersen (Alcohol: 1 f#) (ISIC); USA, SD, Custer Co., Custer SP, Sylvan Lake, 43.8459°N 103.5602°W, 30.vi.2008 6068' 95%, EtOH, coll.: J.D. Petersen (Alcohol: 1 f#) (ISIC); TENNESSEE Fentress, Co. #1, Allardt, 2 June 1978, G.W., Byers & C.W. Young (Pinned: 2 m#) (KU); Fighting Creek, 1600', Great Smoky Mts., 35°40.7'N, 83°33.3'W, VII-7-1958 J. Laffoon (Pinned: 1 m#) (ISIC); TEXAS Bastrop Co.// Bastrop St. Park// 20 MAR 1976// Ernest M. May (Pinned: 1 m#) (KU); TEXAS: Nacogd. Co., Nacogdoches, X 12 1960 / COLLECTOR, Royce Oliver (Pinned: 7 m#, 1 f#, various dates April 8, 1960 – May 6, 1962) (KU); VERMONT Orleans Co., #1. 5 mi. NNE. Orleans, 19 June 1982 925', George W. Byers (Pinned: 1 f#) (KU); Alexandria, VIRGINIA, June 15, 1973, B.M. O'Connor, coll. (Pinned: 1 f#) (UMMZ); Lake Accotink, Fairfax Co., VA, VIII-5-1972 / Collector:, Barry M. O'Connor (Pinned: 1 f#) (UMMZ); VIRGINIA: Giles Co., Mt. Lake Biol. Stn. 6-12 August 1979, George W. Byers #163 (Pinned: 1 m#) (KU); Woodbridge, Va, 8-28-1946, L.D. Beamer (Pinned: 1 m#) (KU); Squaw Lake, Vilas, County, Wisconsin, August 16 1954, Jean L. Laffoon (Pinned: 2 m#) (ISIC); USA Wyoming, Medicine Bow, Nat. For. North Laramie River, at Sand Lk. Rd. Beaver Dam, 41.351557N, 106.166511W, A Fasbender June-21-2012 (Pinned: 1 f#) (ISIC)

Figures. Adult. 6, 7; **Larva.** 8-10; **Material Examined.** 11.

Taxonomic Notes.

This species can be easily differentiated from its congener *Bittacomorpha occidentalis* by the medial white stripe on the scutum, shortened and narrowed clypeus, and paramere with lateral spur and apical

dorsal tooth. Overall the morphology of *Bittacomorpha clavipes* exhibits two definite autapomorphic characters when compared the *Bittacomorpha occidentalis* and *Bittacomorphella*: the absence of stout trichoid sensillae at the apex of the gonostylus and the aforementioned apical tooth of the paramere. The lateral spur of the paramere is somewhat similar in form to the lateral style of the paramere in *Bittacomorphella furcata*, but the placement of these two species in separate clades suggests this is a homoplasy. An abbreviate clypeus is found in *Bittacomorpha clavipes*, *Bittacomorphella jonesi*, and *Bittacomorphella thaiensis*. However, the clypeus is further narrowed in *Bittacomorpha clavipes*, again suggesting that this character is homoplastic.

The holotype of *Bittacomorpha clavipes* is not listed in the collection of Fabricius type material at ZMUC, and may be lost or destroyed. Fortunately, the distinctive character of the inflated 1st tarsomere allows the determination of the species to genus without contention, and material from the range of *Bittacomorpha occidentalis* would not have been available to Fabricius at the time.

The current concept of *Bittacomorpha clavipes* probably represents a species complex. There is some minor variation in the male genitalia (such as the shape of the posterior margin of the terminal division of the hypandrium), but it is difficult to correlate this into distinct metapopulations. Other characters which at first appear distinctive have turned out to be variable within a population, such as the shape of the anterior apex of the ventral portion of the lateral ejaculatory process. An unpublished molecular phylogeny utilizing the COI gene found internal clades of *Bittacomorpha clavipes* that probably correspond to cryptic species, but the dataset was localized to Pennsylvania and West Virginia (C.W. Young, pers. comm.). To resolve this issue will require extensive molecular sampling across the range of *Bittacomorpha clavipes*, which should be supplemented by examination of larval morphology, which been largely absent in previous studies of Bittacomorphinae.

Ecological Notes. *B. clavipes* is associated with habitats exhibiting minimal water flow (Harris & Carlson 1978) and deep substrates. These locations also typically have emergent vegetation and often a canopy of trees or brush, though these features are not essential. The “classic” *B. clavipes* habitat is a seepage with saturated soil, with at most shallow film of water covering the substrate and typically heavily infused with iron oxide. There is some variance from this stereotype: *Bittacomorpha clavipes* can be found in shallow, slow flowing streams along the margin and the presence of iron oxide is not a determinant factor in the presence of the species.

B. clavipes is the dominant species of Ptychopteridae in much of eastern North America, with a range covering over half the continent. The range can be roughly bounded by Newfoundland in the northeast (Tjeder 1960), eastern British Columbia in the northwest (R. Cannings, pers. comm.), western Wyoming and northeast Utah in the Rocky Mountain West (Alexander 1945, Alexander 1948) and the Atlantic Ocean to the east and southeast. A remarkable specimen from Costa Rica is present in the Illinois Natural History Survey collection, extending the range of the species (and the subfamily) into the Neotropical region.

Two questions are raised by the extensive range of this species: What mechanism promoted such range expansion in *B. clavipes*, and what factors are acting to constrain the range to its current limits? While there is not sufficient quantitative data to make any conclusive assertions, examining external biotic factors and the patterns of interaction with sympatric and allopatric species allows some hypotheses to be proposed.

The northern limit of the range is relatively simple to explain. Higher latitudes probably limit the range of *B. clavipes* due to two factors: the short summer, and the reduction of organic sediments.

The true western limits of the range are difficult to ascertain, as collection localities become increasingly sparse moving across the eastern Intermountain West. There likely are a number of factors

that contribute to this phenomenon. Perhaps two of the most important are the reduction of the climatic envelope in which *B. clavipes* is competitive and the reduction of deep organic substrates. When rearing western Nearctic *Ptychoptera* in a laboratory setting there is often considerable mortality in the larval and pupal stages, while *B. clavipes* can be reared quite readily in the same conditions (pers. obs.). The western *Ptychoptera* develop in larval habitats that often remain very cool through the year, while many *B. clavipes* localities have significantly warmer summer temperatures, suggesting that *B. clavipes* is heat tolerant. This may also indicate that the *Ptychoptera* which dominate the western fauna in similar habitats (the *Ptychoptera lenis* species group) outcompete *B. clavipes* at lower temperatures. In the west the warmer lower elevations are xeric, with limited habitat suitable for ptychopterids. The mesic higher elevations typically have cool summers and long winters, which may allow species of the *Ptychoptera lenis* group to outcompete *B. clavipes*.

There is some support for this hypothesis of niche overlap between *B.* and the *Ptychoptera lenis* group from sympatric associations of the two groups collected by the authors. One of these was an association of *B. occidentalis* with *Ptychoptera byersi*, which is discussed in the ecological notes of the *B. occidentalis* description. The other notable locality is located in eastern Wyoming at high elevation, 2775m, in the Snowy Range of the Rocky Mountains. Along the North Fork of the Little Laramie River in the Medicine Bow National Forest (denoted by an asterisk in the material examined above), both *Ptychoptera lenis coloradensis* Alexander and *B. clavipes* were collected in a marshy area below a beaver dam with extensive emergent grasses and willows. This locality was collected twice in the same season, once on June 5th, and a second time on June 21st. On the initial June 5th date only *P. l. coloradensis* was collected from the emergent vegetation, but on June 21st one female *B. clavipes* was collected along with numerous *P. l. coloradensis*, with an additional *B. clavipes* individual sighted in thick vegetation.

This phenological pattern with *P. l. coloradensis* emerging earlier in the season than *B. clavipes* appears to indicate the adaptation of this *Ptychoptera* species to the cooler climate and shorter summer that limits the active period of insects at high elevation.

An interesting addendum to the North Fork of the Laramie River site is that a nearby collection locality at a beaver meadow on Nash Fork lacked any emerging ptychopterids on June 5th, but had large numbers of *P. l. coloradensis* (as well as *Ptychoptera pendula* Alexander in a depositional zone downstream) on June 21st. The Nash Fork site is at 3000m of elevation, and with attendant delay of the emergence period of *P. l. coloradensis*. Unfortunately it was not possible to sample the locality at a later date that season, so inferences cannot be drawn about the impact of the altitudinal gradient on the phenology of *B. clavipes*.

The habitats where the *Ptychoptera lenis* group is found in the west share many features with habitats preferred by *B. clavipes*. Most significantly, *Ptychoptera lenis* group habitats have low rates of water flow, deep organic sediments, and often emergent vegetation. Indeed, the authors have sampled *Ptychoptera lenis* group species from iron oxide seepages which appear nearly identical to productive *B. clavipes* sites in the eastern Nearctic.

The southern limits of the species complex are also difficult to ascertain due to fragmentary locality data. With the exception of the Costa Rican specimen, the most southern records are from central and eastern Texas. It seems probable that the species ranges down the coastal plain along the Gulf of Mexico to Neotropical Central America, but the authors could find no material to confirm this. It is difficult to state the prevalence of *B. clavipes* in Central America, as collecting and curation of the fauna of the region is still in the preliminary stages, with large gaps in current knowledge (Brown 2009). There has been an oft cited historical report of *Bittacomorpha* in Brazil (Osten Sacken 1878, Alexander

1919, Alexander 1927). To date, this record has never been confirmed, and with the lack of comprehensive sampling of southern Central America and northern South America makes any statements of the southern extremity of the range tenuous.

The southwestern boundary is also poorly known. The ptychopterid fauna of the southwest United States and Mexico is extremely poorly known, and it is not unreasonable that *B. clavipes* would be present in mesic habitats, particularly with regards to possible heat tolerance in the species. It is possible that *B. clavipes* may be found at higher elevations in New Mexico, Arizona and the Sierra Madre Orientale and Sierra Madre Occidental in Mexico. The southernmost records of the *Ptychoptera lenis* group are from the White Mountains of eastern Arizona and the Mongollon Mountains of western New Mexico. It is highly unlikely that the *Ptychoptera lenis* group extends to Central America, where the only known ptychopterine is *Ptychoptera alexanderi* Hancock, known from the Chiapas in southern Mexico and Costa Rica (Hancock *et al* 2006, Fasbender: unpublished data). The ranges and potential sympatric associations of *B. clavipes* and the *Ptychoptera lenis* group in the southwestern United States and Mexico will likely be informative with regard to the niche overlap hypothesis and the biotic factors influencing the distribution of each group.

One mechanism which may facilitate the wide distribution of *B. clavipes* was described to Alexander (1920) by J.G. Needham, who observed an individual drifting on an air current out of a deep ravine up into the atmosphere beyond the range of sight. Air currents at higher altitude could carry these drifting *Bittacomorpha* over extended distances, including minor geographic barriers. This may facilitate gene flow across the extensive geographic range of *B. clavipes*, resulting in the largely homogenous morphology of the species across populations. However, this hypothesis is undermined by the probable unrecognized cryptic species within the current concept of *B. clavipes*.

***Bittacomorpha occidentalis* Aldrich (1895)**

Bittacomorpha occidentalis Aldrich, 1895: 201 (original description)

Bittacomorpha occidentalis Aldrich, Johnson 1905: 75 (key)

Bittacomorpha occidentalis Aldrich, Alexander 1916: 546 (key)

Bittacomorpha occidentalis Aldrich, Alexander 1927: 9 (catalog)

Bittacomorpha occidentalis Aldrich, Peus 1958: 11 (catalog)

Bittacomorpha occidentalis Aldrich, Alexander 1965: 98 (catalog)

Bittacomorpha occidentalis Aldrich, Alexander 1967: 171 (illustration)

Diagnosis

Larva. Larval cranium domed, genae expanded posterior, completely black. Abdominal segments heavily provided with linear longitudinal rows of fleshy tubercles each with a single branching sensillae. Prolegs prominent.

Adult. Prescutum black, shining; apex of parameres spatulate.

Description

Larva. Head. Dorsal surface weakly flattened hemispherical, uniform black. Frontoclypeal apotome narrow, 2.5x as long as wide, narrowing subacutely anterior to antennae, anterior margin blunt; broad, forming acute triangle posteriorly, reaching nearly to posterior margin of cranium; ecdysial stem line short, obscured by prothorax, only on collar of genae. Genae triangular in dorsal view, expanded posteriorly, do not meet medioventrally, anterior margin square, short collar present on posterior margin, ventroposterior margin weakly and broadly emarginate; subgenal sclerite fused with

hypopharynx, trapezoidal in shape, apex with triangular anterolateral lobes. Single stemmata present. Antenna two segmented, base recessed at anterior terminus of ecdysial suture: basal segment button-like, apical segment weakly pyriform, apex rounded, apical sensillae cluster directed apically. Labrum triangular, dorsally with heavily sclerotized trapezoidal plate, ventral surface membranous, slightly expanded, ventral margins heavily sclerotized, narrow medially, broadening flag-like laterodorsally; labral brushes round, macrotrichia elongate; medioventral apex with conical ventrally directed obtuse point, with stout ventrally directed sensillae. Premandible ventral to labrum, well developed, with serrate medioventral margin. Mandible with molar lobe semicircular, ventrolaterally with triangular lobule, mandibular comb well developed surrounding incisor lobe, becoming weakly serrated lobe on inner ventral margin; incisor lobe triangular, ventral margin unserrated; prosthema prominent on inner lateral margin, heavily modified: ventromedially with elongate thick trunk ending in knob, laterodorsal two blunt, thick sensillae, followed by four narrower sensillae. Maxillae with cardo inverse acute triangle, ventral point heavily rounded; stipes culvert-like over lacinia, without brushes, maxillary palpus apical; lacinia elliptical. Prementum broadly bottle-neck shape, dentition at apex blunt.

Thorax and abdomen. Thoracic segments weakly increasing in size posterior, tubercles in irregular pattern, mound-like, each tubercle with multiple elongate branching sensilla. Abdominal segments cylindrical, homogenous in width, delineations between segments weak; tubercles mound-like with medial cylindrical apex, apex with elongate branching sensilla, lateral margins of tubercle each with smaller branching sensilla; tubercles arranged in regular pattern, transverse rows on dorsal and ventral surface, longitudinal rows laterally. Anal division conical, with lightly sclerotized exertable tube containing siphon; siphon with annulations weakly developed if at all.

Adult. Measurements (n=2): Overall length: 10.82mm (10.51–11.16mm) **Head.** Width: 1.53mm (1.41–1.59mm); Height: 1.47mm (1.37–1.63mm); Length: 0.87mm (0.86–0.88mm); Flagellum length: 6mm; Flagellomere proportions: 1.00, 0.48, 0.55, 0.55, 0.51, 0.54, 0.54, 0.54, 0.54, 0.48, 0.41, 0.39, 0.37, 0.31, 0.33, 0.33, 0.31, 0.22, 0.18; Maxillary palpus length: 2.16mm; Maxillary palpus segment proportions: 0.17, 1.0, 1.05, 0.66, 0.89 **Thorax.** Length: 2.97mm (2.72–3.2mm); Height: 2.67mm (2.44–3.04mm); Wing length: 11.4mm (10.42–12.43mm); Wing width: 2.52mm (2.8–2.25mm); Leg Proportions: Femur: 1.0, 1.08, 1.25mm; Tibia: 0.97, 1.02, 1.24; Tarsomeres: Foreleg 0.48, 0.22, 0.14, 0.06, 0.07, Midleg 0.49, 0.23, 0.13, 0.06, 0.05, Hindleg 0.58, 0.25, 0.15, 0.05, 0.06. **Abdomen.** Length: 15.66mm (17.50–14.29mm); Male tergite proportions 1.00, 2.97, 2.02, 2.29, 1.9, 0.80, 0.26; Male Genitalia: Width: 1.1mm; Height: 0.76mm

Head. Head extremely closely pressed to thorax, generally triangular in shape, frons broadly domed with vertex well above dorsal margin of eye, medial suture clearly evident, extending between antennal bases to dorsal margin of face. Antennal scape ovoid in cross-section, provided with five socketed sensillae subdorsally along anterior margin; 19–20 Flagellomeres. Face narrow, incised by clypeo-labrum nearly to dorsal margin. Clypeo-labrum large, sub-acutely triangular, lateral margins somewhat pinched at junction with face, around 2x longer than wide, somewhat inflated. Maxillary palpus as sub-family. Hypopharynx subconical triangular, directed anterior-ventrally. Labium not very prominent, largely hidden by clypeo-labrum. Labellae free medially, not forming pad.

Thorax. Antepronotum with two small fleshy semicircular emergent from dorsal margin, each provided with several setae. Scutum glabrous, shining, ruddy-brown with broad muddy yellow highlighting of transverse suture. Distinct fold at rear of scutum, but no prescutum present. Scutellum muddy yellow, with dense group of setae medially, subcircular. Mediotergite ruddy-brown, dense patches of setae at anteriodorsal margin, as well as two parallel lines of setae medially. Paratergite well

developed, broad, blunt crescent shape. Sub-paratergal membrane elliptical in shape with tapered apices, fairly well sclerotized. Episternum fairly flat with prominence above midcoxa, rectangular in shape; anepisternal suture fairly well developed. Epimeron rectangular in shape, with shallow sulcus located midway dorsally, posterior margin straight. Laterotergite lacrimiform, deject dorsally with a few long setae along dorsal margin rising to slight prominence towards halter. Halter and prehalter as per subfamily, posthalter well developed, nearly twice as long as wide, largely free of webbing to posterior membranous association of halter. Metapleuron with incomplete suture, emerging from posterior ventral margin in a broad arc and terminating well before halter; immediately below halter low prominence with cluster of long clear setae. All pleurites muddy yellow, fading to ruddy brown at ventral margin. **Wing.** Wing without macrotrichia. Apex of R_1 and R_3 , with macrotrichia, all other veins bare. Costa weakening significantly at wing apex, faint along posterior margin. R_{3+4+5} stem 0.82mm, slightly curved medially; R_{4+5} stem 2.2mm; R_4 after fork 2.59mm, R_5 after fork 2.5mm; $R_{3+4+5}:R_{4+5}$ -stem: $R_4 = 1.00 : 2.68 : 3.15$. r-m 0.36mm; M distal to r-m 4.35mm; Mdistal: $R_{3+4+5} = 5.3 : 1.00$, $R_4:Mdistal = 0.59 : 1.00$. CuA_2 2.14mm, tightly sigmoidal, proximal bend approximately 140° , distal bend well away from wing margin, nearly 90° . A_1 faint basally, paralleling Cu for a short distance before broadly curving to anal margin, arc becoming more acute apically. M-Cu joins M slightly medial to r-m. Anal lobe very poorly developed, angle obtuse; alula undeveloped. Halter: length: 1.6mm; stem elongate, medial furrow shallow at base becoming obscure distally, long clear macrotrichia laterally, knob pale yellow with dark stout trichoid sensillae laterally, apex of knob bare; prehalter elongate, sparsely provided with elongate clear trichoid sensillae; posthalter well developed, palpusiform, with several long translucent sensillae apically, free of webbing posteriorly. **Legs.** Coxae yellow, overall leg coloration brown. White banding confined to distal tip of 1st, 2nd & 3rd tarsomeres. Empodium closely associated with acropod, heavily provided with setae, notched posteriorly.

Pre-genital Abdomen. As per genus. **Male Genitalia.** Epandrium subquadrate, posterior margin strongly emarginate medially. Dorsal surface evenly covered with trichoid sensillae of moderate length. Anterior margin straight, forming nearly right angle with lateral margin. Lateral margins straight to base of epandrial clasper, very weakly angled medially above epandrial clasper, forming nearly a right angle with posterior margin above epandrial clasper. Lateral extremities of posterior margin straight, perpendicular to lateral margin, medial section of posterior margin with prominent semicircular emargination; posteriomedial style directed medially at lateral termination of emargination, weak and obtuse. Internal fold above epandrial clasper very prominent and well sclerotized, originating at rear margin of epandrial clasper and extending in a straight line medially with slight posterior deflection. Epiproct inevident, hypoproct consisting a central sclerotized plate surrounded by membrane. Epandrial clasper cylindrical, tapering only at apex, weakly curved medially; medial apex flattened and provided with thick covering of conical sensillae. Subepandrial sclerite divided, bladelike with base directed medially and a subobtuse angle directed anterior, fused to medial margin of the base of the epandrial clasper, extending posteriomedially. Parameres ribbon-like, laterally compressed, arising near dorsal margin of gonocoxal apodeme, forming broad arc along length before straightening to dorsoposterior orientation shortly before spatulate apex. Dorsal and ventral margin with opposed short triangular spines approximately 2/3rds along length. Gonocoxite directed completely posterior, weakly expanding to gonostylus, shorter than gonostylus. Gonostylus weakly curving medially, slightly tapered rounded at tip, medial surface from base to apex covered in dense, moderately sclerotized trichoid sensillae. Heavily sclerotized apicomedial sensillae present, forming irregularly spaced cluster at medial apical surface. Basal division of hypandrium roughly triangular, moderately expanded subhemispherical, posterior margin weakly emarginate, lateral margins without emargination or sulci, angling dorsally in a band at lateral extremity, posterior margin narrow, emarginated, medially with suture extending from posterior margin weakening anteriorly; surface sparsely scattered with trichoid sensillae. Terminal division well-

articulated arrow-like in shape, base very narrow and petiolate, apex dominated by two lateral lobes directed slightly anteriodorsally, dorsal surfaces heavily sclerotized at lateral extremity becoming membranous medially, posterior margin forming broad angle centered on median, ventral surface provided with short trichoid sensillae medially, lateral lobe with large hooked trichoid sensillae. Supraedeagal membrane highly inflated, with medial division evident, covering apex of aedeagus. Aedeagus with sperm sac as per sub-family, membranous window distinct. Ejaculatory apodeme spathate, rounded apex. Basal lateral apodeme complex; Dorsolateral portion emergent from broad peduncle associated with lateral surface of ventral portion and lateral aedeagal sclerite, loose triangular dorsally directed crescent in outline, lateral apex broadly triangular in lateral view, medial apex broadly triangular, not extended, sclerotized ridge trailing lateral and dorsal margin, extending ventrally to ventral section; ventral section elongate, larger than dorsolateral section, forming acute triangle with pointed anterior apex, apex with lightly sclerotized region directed laterally, deeply inserted into sperm sac. Ejaculatory apodeme spathate, slightly tapering towards apex. Lateral sclerites of aedeagus of moderate width, closely approximated at base. Apical apodemes of aedeagus prominent; dorsal lobe large, directed dorsally curving anteriorly at apex; ventral lobe broad, apex subacute and well sclerotized, directed slightly lateral, not fused with subapical sclerite. Subapical sclerite complex, internal section divided to anterolateral apex and ventral arm, anterolateral apex forming flat plate expanding to straight posterior margin, ventral arm relatively short rod emerging from lateral margin of dorsal section curving weakly ventrally. External portion of subapical sclerite large, prominent, triangular directed dorso-posteriorly, extending dorsally to apex of aedeagus. **Female Genitalia.** Epigynum rounded dorsally, posterior margin straight, angle to lateral margin convex with apex apodeme, lateral margins straight, posterior margin indistinct, minimal medial suture present. Cerci with base indistinct, dorsal margin straight, apex rounded, ventral margin swollen, potbellied anteriorly tapering posterior. Apex of cercus with short, cylindrical nodule with stout elongate trichoid sensillae medially, ring of three

finer sensillae arranged equidistant around central sensilla; cercus epigynium ratio 0.54 : 1. Hypoproct broad triangular, fused to ventral surface of epigynium, with sclerotized conical sclerite located ventrally, anterolateral apex with acute lobe. Genital fork spatulate, posterior margin weakly emarginate. Hypogynium quadrate, lacking lateral lobes, hypogynial valves distinct, square, medial notch square: 2.4x as deep as broad.

Figures. Adult. 12, 13; **Larva.** 14–16; **Material Examined.** 17.

Material Examined.Lectotype. Seattle, Wash / Collection, JM Aldrich / Cotype, No. 52263, U.S.N.M , *Bittacomorpha occidentalis*, Type Aldrich (Pinned: 1 m#) (USNM); **Paralectotype.** Same as lectotype. (Pinned: 1 m#) (USNM); **Other Material Examined. UNITED STATES.** USA, CA, Plumas Co., Lassen Nat Frst, Humbug, 40.107°N 121.373°W, 19.vi.2007 alt 2007m, coll.: JD Davis, MJ Petersen (Pinned: 4 m#) (ISIC); CALIFORNIA, Tehama Co. #1, nr. Lassen N.P., 15 June 1959, G.W. Byers (Pinned: 1 m#, 1 f#) (KU); Oregon, Benton Co., VI-8-85 Muddy Swamp, n.r Oak Creek Lab, Col. & I.D. J.K. FURNISH, *Bittacomorpha clavipes*, (Fabricius) (Incorrect Identification) (Alcohol: 6 larvae) (ISIC); USA, Oregon, Benton Co., Sulphur Springs, Baker Ck Trail, 44°38.37'N 123°18.74'W 165m, 21 May 2012 coll. GW Courtney, from seeps along trail near Xing (Alcohol: 14 2nd instar larvae; 1 4th instar larva) (ISIC); 3 mi. below summit, of Mary's Peak, Ore. 4-20-41., col: Schih & Gray (Pinned: 1 f#) (WSU); USA Oregon Fremont Nat. For., Gilbert Spring at NF3360, Hillside Seeps with vegetation, 42.42599N 120.755315W, A Fasbender June-11-2012 (Alcohol: 2 m#) (ISIC); OREGON Lane Co., No.1 2.7 mi. NW, Salt Creek Falls, 24 June 1959, George W. Byers (Pinned: 2 m#) (KU); OREGON – Lane Co., #1, Salt Creek, 24 June 1959, George W. Byers (Pinned: 2 m#, 1 f#) (KU); 12 mi. S. of, Parkdale, Ore, July 29 1938, Coll. K. Gray, J. Schuh (Pinned: 1 f#) (WSU); ORE TillamookCo, 2mi W. Sandlake, 1 May 1973, John D Lattin (Pinned: 1 m#, 1 f#) (ORSU); USA, OR, Wasco Co., Mt. Hood NF, Warm Springs, Mdw 44.9888°N 121.7901°W, 9.vii.2008 3700' 95%EtOH, coll. J.D. Petersen (Pinned: 1 m#; Alcohol: 1 m#) (ISIC); 6 2 95 / Olympia,

Wash (Pinned: 3 m#; 5-25-95 1 m#; no date 1 m#) (WSU); Mt. Rainier, Nat. Pk. WASH, D. W. Smith / Kautz Creek, June 19, 1966 (Pinned: 3 m#) (WSU); Yakima, Wash / Collector, C.V. Piper (Pinned: 1 m#) (WSU)

Taxonomic Notes. *B. occidentalis* is often confused for *B. clavipes*, although the species distributions are allopatric. There are several morphological characters which distinguish the species: *B. occidentalis* has a shining black scutum without a median white stripe, the clypeus is elongate, and the male genitalia has the parameres with a spatulate apex. The larvae are also distinctive, with the head capsule triangular in dorsal view versus the rounded head capsule of *B. clavipes*. *B. occidentalis* is also the largest species among the extant Ptychopteridae.

Many of the character states observed in *B. occidentalis* represent plesiomorphies when compared with *B. clavipes* – in particular the elongate clypeus in the adult as well as the trapezoidal head capsule with posteriorly expanded genae in the larvae are similar to *Bittacomorphella*. Unlike *B. clavipes*, there is no current evidence to suggest that *Bittacomorpha occidentalis* represents a species complex.

Ecological Notes. *B. occidentalis* is restricted to the Pacific Coast region of the Nearctic. There are no records to the species from east of the Cascade or Sierra Nevada ranges, though the northern and southern limits of the range are less well defined. The habitats characteristic of the species extend north to British Columbia, though specimens have yet to be collected from the region (C. Copley & R. Cannings, pers. obs.). In the south the species has been collected as far as the Lassen National Forest in the northern Sierra Nevadas, but west-central and southern California has not been sufficiently sampled for ptychopterids to draw any further conclusions.

Although *B. occidentalis* has an affinity for iron oxide seepages much like its sister species, it has been collected in other seepage habitats, though again never in areas with significant flow. Unlike *B.*

clavipes, *B. occidentalis* does not dominate the ptychopterid fauna of the region, which is one of the most diverse for the family outside of southeast Asia. *B. occidentalis* has been collected in sympatry with several other ptychopterids, including *Bl. fenderiana*, *Ptychoptera byersi* Alexander, and another undescribed species of the *Ptychoptera lenis* group. Mechanisms facilitating sympatry between these species are not yet evident.

***Bittacomorphella* Alexander (1916)**

Bittacomorpha (*Bittacomorphella*) Alexander, 1916: 545 (Original description) Type species:

Bittacomorpha jonesi Johnson (Original designation)

Bittacomorphella Alexander, Alexander 1919: 790 (elevated to full generic rank)

Bittacomorphella Alexander, Alexander 1920: 779-780 (description of immature stages)

Bittacomorphella Alexander, Alexander 1927: 8–9 (catalog)

Bittacomorphella Alexander, Alexander 1965: 98 (catalog)

Diagnosis

Larva. Head subquadrate, well separated from prothorax, cranium flat, hypopharynx with median rectangular blade on anterior margin. Thorax and abdominal segments with fingerlike cuticular extensions, often covered in hardened substrate, anal division cylindrical, respiratory siphon fully retractile.

Adult. Head triangular, Clypeus triangular and subacute, 1st tarsomere cylindrical.

Description

Adult. Head. Head triangular in shape, closely pressed to thorax, frons broad with vertex at same level as dorsal margin of eye, medial suture moderately to clearly distinct, extending between antennal bases to dorsal margin of face. Antennal scape sub-ovoid compressed in cross-section, provided with 5–8 socketed sensillae subdorsally along anterior margin; pedicel subspherical, with scattered dorsally directed setae; 18–21 Flagellomeres. Face trapezoidal or indistinct, often incised by clypeolabrum, suture with clypeolabrum indistinct. Clypeus dominant, subacute, lateral margins straight, around 2.5x longer than wide, not inflated. Maxillary palpus as sub-family. Hypopharynx variable. Labium prominent or weak, partially hidden to largely exposed by clypeo-labrum. Labella fused or separate, teardrop shaped.

Thorax. Antepronotum platelike, narrowing obtusely dorsally. Scutum glabrous, shining or pollinose, color from black to chocolate brown to ruddy. Prescutellum sometimes present. Scutellum pale yellow, with dense group of setae medially, ovoid or subcircular. Mediotergite variable, dense patches of setae at anteriodorsal margin, as well as two parallel lines of setae medially. Paratergite shape variable, crescent or razor shaped. Sub-paratergal membrane shape variable, sclerotization variable. Episternum flat or somewhat depressed, rectangular in shape; anepisternal suture complete to inevident never prominent. Epimeron subtrapezoidal, surface slightly convex, rising to prominence at wing base, posterior heavily incised by laterotergite. Laterotergite D-shaped, largely flat, ventrally heavily deject to halter towards halter. Suture between epimeron and metapleuron indistinct; metapleural suture inevident or weakly developed, not complete, emerging from posterior margin curving to halter; often a weak prominence with setae below halter. Pleurites ruddy to yellow, with variously colored pollinosity. **Wing.** Wing length 5x width, anal lobe undeveloped. Macrotrichia absent or present. Halter and prehalter as per subfamily, posthalter weak or well developed, often with distinct

membranous webbing extending to halter. **Legs.** Coxae pollinose blue, fading to light yellow at trochanter, lateral surfaces covered with long setae; proximal portion of femur yellow, darkening to black at tibial joint. White band sub-proximally on tibia, expanding slightly to 1st tarsomeres. First tarsomere greatly expanded, ovoid, upper margin with white band. 2nd & 3rd tarsomeres white, 4th & 5th black. Empodium loosely associated with acropod, rounded diamond shaped, heavily provided with short clear setae, notched proximally.

Pre-genital Abdomen. Black to ruddy, posterior margins of segs 2–7 yellow. **Male Genitalia.** Epandrium variable in shape, platelike or bilobate; posterior apices obtusely rounded, posteromedial style variable; epiproct prominent or inevident, hypoproct ovoid or tonguelike. Dorsal surface provided scattered long setae (.1–.25mm), becoming more numerous towards margins. Epandrial claspers emerge from lateral apex to posterior margin, directed posteriorly, curved medially; tapering to pointed apex. Parameres variable, heavily sclerotized, medial membrane never extending more than half length of paramere. Gonocoxite variable shape and length. Gonostylus pointed or rounded at tip, medial surface with rows of stout trichoid sensillae at inner posterior apex. Basal division of variable in shape, gonocoxite often fitting into trough. Terminal division articulation variable, shape variable. Lateral apices present or absent. Ventral surface sparsely provided with setae, dorsal surface glabrous. Aedeagus with sperm sac as per sub-family, lateral ejaculatory process variable. Ejaculatory apodeme variable, apex often rounded. Apex of aedeagus with medial emargination where sclerites meet. Ventral apical apodemes present, some species with dorsal apical apodemes. Subapical sclerite variable. **Female Genitalia.** Epigynium flat, subtrapezoidal tapering towards posterior margin; posterior margin with triangular medial extension. Cerci comparatively elongate, >3x length vs. height, slight ventral curvature, apex rounded. Hypogynium broad, especially at base, medial emargination relatively wide ~.5x length.

Bittacomorphella sackenii* Species Group*Diagnosis**

Adult. Clypeus elongate, 2x as long as wide; scutum black or dark brown, uniform coloration; epandrium quadrate with epandrial claspers at lateral apices, without medial suture, epiproct not apparent; hypandrium acutely triangular, basal division narrowing well before terminal division.

Description

Adult. Head. Fringe of postocellar setae present. Clypeus elongate, 2x as long as wide. Shelf over maxillary palpus prominent, triangular. Hypopharynx highly reduced or narrow and acute. Labium elongate, extending past apex of clypeus, labellae small (shorter than labium), adhered medially.

Thorax. Antepronotum without lobes. Scutum dark brown or black, with at most a weak light colored patch adjacent to scutellum. Metapleural suture complete. **Legs.** Single white band covering distal apex of the 1st-3rd tarsomeres, 4th & 5th tarsomeres infusate. **Male Genitalia.** Epandrium quadrate, epandrial lobes inevident, posterior margin at most weakly emarginated with epandrial claspers placed at posterior corners. Epandrial claspers strongly curved medially, pointed. Epiproct inevident, hypoproct ovoid. Parameres separate, simple or bifurcate. Gonopods with elongate cylindrical gonocoxite, apex of gonostylus rounded. Hypandrium acutely triangular, basal division blending seamlessly into terminal division, very narrow. Aedeagus with lateral ejaculatory processes curving posterior, ventral portion weakly developed. Apical apodemes of aedeagus simple, subapical sclerite variable.

Larvae and pupae unknown.

Taxonomic Notes. The *Bittacomorphella sackenii* species group is erected to contain *Bl. sackenii*, *Bl. furcata*, and *Bl. pacifica*. The most compelling characters uniting these species are in the male

genitalia: primarily the massive, quadrate epandrium with epandrial claspers located apically, and the hypandrium forming a narrow, acute triangular shape when viewed ventrally.

Ecological Notes. The *Bl. sackenii* group is confined to the Pacific Region of the United States and Canada, with the eastern boundary largely delimited by the Cascade and Sierra Nevada mountain ranges. Two of the species are endemic to particular mountain ranges (*Bl. furcata* in the Olympic Peninsula, *Bl. sackenii* in the Sierra Nevada range), while *Bl. pacifica* is found in both the Coast and Cascade ranges from northern California to British Columbia.

The majority of the range of the *Bittacomorphella sackenii* group is sympatric with *Bl. fenderiana*, which is far more common in collections. Indeed, the author's collection efforts during this project have not succeeded in collecting any of the *Bittacomorphella sackenii* group, and not for lack of effort. Whether this means that the *Bittacomorphella sackenii* group is rare, or utilizes a different microhabitat than other ptychopterids, is open to debate.

It appears that within this group species distributions are essentially allopatric. *Bl. sackenii* and *Bl. pacifica* appear to be well separated, though more sampling of the Lassen National Forest and northern Sierra Nevada range to determine the limits of the range of each particular species. *Bl. furcata* is known from the Olympic Peninsula and northern Coast Range of Oregon; there are records of *Bl. pacifica* across Puget Sound, but none on the Olympic Peninsula itself. There are some records of *Bl. pacifica* in the Oregon Coast range, but they are south of the *Bl. furcata* locality. Further sampling is merited to better delineate the ranges of these species.

Bittacomorphella furcata* Fasbender & Courtney (sp. nov.)*Diagnosis**

Adult. Legs with white confined to distal part of 1st, 2nd & 3rd tarsomeres, 4&5th tarsomeres pale brown. Epandrium subquadrate, platelike, posteriorly emarginate; gonostylus subequal to gonocoxite, curved dorsally; basal apical sclerite platelike; parameres bifurcated, medial section convergent, laterally compressed.

Description.

Adult. Measurements (n=2): Overall length: 10.82mm (10.51–11.16mm); **Head.** Width: 0.90mm (0.84–0.97mm); Height: 0.88mm (0.88–0.88mm); Length: 0.50mm (0.44–0.55mm); Flagellum length: 6.7mm; Flagellomere proportions: 1.00, 0.72, 0.88, 1.06, 1.02, 1.02, 1.06, 1.02, 1.00, 0.83, 0.81, 0.76, 0.67, 0.67, 0.67, 0.60, 0.58, 0.53, 0.46, 0.14; Maxillary palpus length: 1.57mm; Maxillary palpus segment proportions: 1, 1.27, 1.33, 1.15; **Thorax.** Length: 1.62mm (1.55–1.68mm); Height: 1.58mm (1.56–1.60mm); Wing length: 8.25mm (8.00–8.50mm); Wing width: 1.88mm (1.88–1.88mm); Leg Proportions: Femur: 1.0, 1.01, 1.09mm; Tibia: 0.96, 0.96, 1.17; Tarsomeres: Foreleg 0.6, 0.19, 0.12, 0.04, 0.04, Midleg 0.51, 0.17, 0.13, 0.04, 0.04, Hindleg 0.56, 0.20, 0.13, 0.04, 0.04. **Abdomen.** Length: 10.13mm; Male tergite proportions 1.00 : 4.11, 2.55, 2.05, 1.88, 0.65, 0.40. **Male Genitalia.** Width: 0.63mm; Height: 0.69mm.

Head. Head closely pressed to thorax, broadly triangular in shape, frons broadly domed with vertex well above dorsal margin of eye, medial suture indistinct, most prominent between antennal bases; triangular field of trichoid sensillae emerging from anterior occipital margin, expanding posteriorly. Antennal scape ovoid in cross-section, with four regularly spaced socketed sensillae in transverse line midway along anterior surface; pedicel with single equatorial line of trichoid sensillae; 20

flagellomeres, ultimate flagellomere minute. Face narrow, incised by clypeus nearly to dorsal margin. Clypeus large, acutely triangular, approximately 2x longer than wide, slightly inflated, sparsely provided with clear macrotrichia, lateral margins straight, lateral extension of labrum visible as shelf over maxillary palpus. Maxillary palpus as in subfamily. Labrum subconical triangular, directed anteroventrally. Labium prominent, extending beyond clypeolabrum. Labella elongate elliptical shape, yellow, anterolateral margins with elongate sensillae, pseudotracheae prominent, not fused medially.

Thorax. Antepronotum platelike, thin, rising trapezoidally and closely appressed to thorax, two small setose lobes extend anterior at dorsolateral apices. Scutum glabrous, pollinose, fuscous with lateral margins and sutures straw yellow; sagittal scutal suture dark, well developed, becoming indistinct beyond terminus of transverse suture; anterior apex of prescutum blunt, nearly transverse, posterior portion incising anterior portion of scutum, merging with scutum posteriorly; anterior portion of prescutal suture moderately developed, becoming indistinct near merger with transverse suture, prescutal pit bilaterally with distinct respiratory organ scar anteriorly; transverse suture well developed laterally, turning posteriorly, subparallel and terminating from posterior margin of scutum, incomplete; distinct cluster of dark trichoid sensillae produced posterolateral to transverse suture, ending above wing base. Scutellum ovoid muddy yellow, with dense group of translucent trichoid sensillae medially. No postscutum present. Mediotergite ruddy brown, dense lateral patches of trichoid sensillae at anterodorsal margin, as well as two parallel lines of sensillae medially, medial suture distinct, overall color fuscous. Paratergite indistinct, narrow, scythe-like. Anepisternal cleft subquadrate, lightly sclerotized. Episternum with dorsal portion depressed rising to midcoxa, rectangular in shape; ridge rising from midpoint of anterior margin to posterodorsal corner; anepisternal suture indistinct, incomplete, reaching neither anterior nor posterior margin, located on ventral surface of anepisternal ridge. Epimeron rectangular in shape, tapering ventrally, posterior margin straight. Suture of epimeron and metapleuron indistinct, especially ventrally. Laterotergite D-shaped, flat, with sparse cluster of long

setae across dorsal surface. Metapleural suture complete, emerging from ventral margin above coxa, running indistinctly to the level of the base of the abdomen, then becoming distinct in a broad arc and terminating at halter; immediately below halter low prominence with cluster of long clear setae. All pleurites ruddy brown. **Wing.** Length: 8.25mm. Scattered macrotrichia on distal $\frac{1}{4}$ of wing, in cells Sc, R_{1+2} , R_3 , R_4 , R_5 , with macrotrichia apically in cell M. Vein C to wing apex, Sc, R_1 , R_3 , and R_4 & R_5 after forking with macrotrichia, all other veins bare. Costa weakening significantly at wing apex, faint along posterior margin. R_{3+4+5} stem 0.60mm, slight anterior turn at fork from R_{1+2} ; R_{4+5} stem 2.00mm; R_4 after fork 1.70mm, R_5 after fork 1.05mm; $R_{3+4+5}:R_{4+5}$ -stem: $R_4 = 1.00 : 3.33 : 2.83$. r-m 0.30mm; M distal to r-m 3.25mm; Mdistal: $R_{3+4+5} = 5.41:1.00$, $R_4:Mdistal = 0.52:1.00$. CuA_2 1.57mm, loosely sigmoidal, proximal bend approximately 140° , distal bend very near wing margin, nearly 90° . A_1 faint basally, paralleling Cu for a short distance before broadly curving to anal margin, arc becoming more acute apically. M-Cu joins M at r-m. Anal lobe very poorly developed, angle obtuse; alula undeveloped. Halter: length: 1.28mm; stem elongate, medial furrow shallow at base becoming obscure distally, long clear macrotrichia laterally, knob pale yellow with dark stout trichoid sensillae laterally, apex of knob bare; prehalter elongate, sparsely provided with elongate clear trichoid sensillae; posthalter moderately developed, triangular, with several long translucent sensillae apically, largely free of webbing posteriorly. **Legs.** Coxae yellow. Forecoxa: anterolateral surface with expansive cluster of yellow trichoid sensillae, ventroposterior margin with single row of yellow trichoid sensillae. Midcoxa with sparse yellow sensillae on anterior surface, posterior surface as forecoxa. Hindcoxa with anterior surface free of setiforms, lateral surface with yellow sensillae, posterior surface free of setiforms. Overall leg coloration consistent across fore-, mid- and hindlegs, proximal surfaces with dark brown stout trichoid sensillae, sensillae white on distal pale surfaces: femur straw yellow apically, becoming light brown at joint with tibia, tibia pale yellow basally becoming light brown distally, tarsomeres with white confined to distal tip of 1st, and complete 2nd & 3rd tarsomeres, base of 1st tarsomere dull brown and 4th & 5th tarsomeres yellow-

brown. Empodium prominent, yellow, closely associated with acropod, provided with dense stout trichoid sensillae, notched posteriorly.

Pre-genital Abdomen. Most surfaces dark olive to fuscous, posterior margins of tergites with narrow dull straw yellow band, tergite VII completely straw yellow. **Male Genitalia.** Epandrium about 1.25x as wide as long; subquadrate, not bilobate, heavily bowed dorsally, anterior and lateral margins straight joining at right angle, strongly emarginate across entire posterior margin, posteromedial style formed to obtuse subconical lobe dorsomedial to epandrial clasper, internal suture extending posteromedially from lateral margin of posteromedial style; epiproct not readily apparent, hypoproct largely membranous with ovoid sclerotized plate and large posteriorly directed setae. Dorsal surface sparsely provided with long setae (.1–.25mm), fringe lining posterior margin. Epandrial claspers emergent from posterior apices, directed medioposteriorly, dorsal surface bulging, abruptly tapering to sub-acute point, apically curved anterodorsally, dorsal and medial surfaces with long setae. Subepandrial sclerite undivided, posterior margin heavily emarginated; lateral margins forming broad arms extending to base of epandrial clasper; anterior margin abbreviate, slightly convex. Parameres glabrous, arising from dorsomedial portion of posterior margin of gonocoxite, basal section adhered to membrane above aedeagus, bifurcating after 1/3 of total length; lateral style short, straight, gradually tapering to subacute point; medial style laterally compressed to become nearly ribbon-like, basal portion directed posteromedially nearly to convergence and rising radically dorsally, distal portion parallel with opposite paramere, dorsal margin tapering to subacute point. Gonocoxite conical, expanding to gonostylus. Gonostylus sub-equal to gonocoxite, expanded at base, curving dorsally at slightly expanded apex, sensillae along inner apex: single row of 8–9 along dorsomedial margin, arcing around margin at apex. Gonopod not closely associated with hypandrium. Basal division of hypandrium broadly triangular, narrowing at lateral margins, posterior margin emarginated at terminal division - joint highly membranous. Terminal division distinct from basal division, well-articulated, narrow with

sides parallel, cupped dorsally forming pouch, obtusely rounded apex enclosed broadly; lateral surfaces heavily provided with setae. Aedeagal complex with massive sperm sac filling most of abdominal segment VII, globular anterior, narrowing slightly posterior towards aedeagus, two ovoid membranous windows penetrated by anterior protrusion of lateral ejaculatory process. Lateral ejaculatory process winglike, slightly swept-back, laterally compressed and angled anteromedially, ventral margin heavily sclerotized lateral apex trapezoidal-rounded; ventral protrusion of lateral ejaculatory process small, rounded, directed posterior; anterior protrusion of ejaculatory process bar-like, straight sided without overall angle to apex, apex heavily recurved laterally forming nearly a semicircle, protrusion directed anterior into sperm sac nearly horizontal. Ejaculatory apodeme broadly teardrop shaped, expands to rounded apex. Sclerites of aedeagus narrowly sclerotized, not tapered. Apical apodemes simple, upper lobe reduced, ventral lobe relatively square, arcing anteroventrally, flaglike, apex broad; lateral apodemes absent. Subapical sclerite poorly developed, association with ventral apical apodeme reduced, ventral arms articulate to basal division of hypandrium, merging to form trapezoidal plate covering posterior surface of apex of aedeagus. **Female Genitalia.** Epigynium trapezoidal, flat dorsally, posterior margin straight, lateral margins straight, posterior margin indistinct, medial suture indistinct. Cerci with base indistinct, dorsal margin weakly convex, apex broadly rounded, ventral margin slightly convex, with an even arc. Hypoproct not visible on specimen examined Apex of cercus with short, cylindrical nodule with single elongate trichoid sensillae medially; cercus epigynium ratio 0.76 : 1. Genital fork not visible on specimen examined. Hypogynium quadrate, hypogynial lobes indistinct, lateral margins formed into lateroposterior triangular lobes , posterior margin forming V shape becoming acute medially, medial notch narrow, incising hypogynium nearly 1/3rd of length.

Larva and pupa unknown.

Figures. Adult. 18, 19; **Material Examined.** 20.

Material Examined. Holotype. USA: OR: Benton Co., 4 mi. up Woods Crk. Rd., jct. Hwy 20; sweep banks, of Woods Creek, 9 May 2013, S. Fitzgerald (Pinned: 1 m#) (PNDL); **Paratypes:**

Same as holotype (1m#, also 1m# (2 May 2013) (PNDL); LakeCushman, Wash.June 27 1917, HGDyar, Collector (Pinned: 2 m#, 1 f#) (USNM)

Etymology. The specific epithet refers to the distinctive bifurcate structure of the paramere as viewed dorsally.

Taxonomic Notes. *Bl. furcata* is a member of the *Bittacomorphella sackenii* group, probably representing the sister species to *Bl. pacifica* + *Bl. sackenii*. However, the chief characteristics supporting this relationship are probably apomorphies of *Bl. furcata*, primarily the furcate and medially directed parameres (151 & 152) and the reduction of the subapical sclerite (176). The potential synapomorphies for the *Bl. sackenii* + *Bl. pacifica* relationship are the labium extending well beyond the apex of the clypeus (57) and the fusion of the labellae (60). However, these character states show homoplasy in Bittacomorphinae and should be looked at circumspectly in defining relationships.

Bittacomorphella furcata can be separated from the remaining *Bittacomorphella sackenii* group by the lack of pollinosity of the scutum, as well as the furcate paramere and reduced subapical sclerite of the aedeagus in the male genitalia.

Ecological Notes. *Bittacomorphella furcata* has been collected only from the northern Oregon Coast Range, and the Olympic Peninsula of Washington. The only historical collection was on June 27, 1919 by H.G. Dyar near Lake Cushman, Washington, but the species was recently recollected in western Oregon by S. Fitzgerald in early May, 2013. There is some range overlap with *Bittacomorphella pacifica* in the Oregon Coast Range, but the limit of each species in the region is not clearly defined. The only inferences that can be drawn currently are that the locality with *Bittacomorphella pacifica* is located

south of *Bittacomorphella pacifica* in the Coast Range, but another locality in the Willamette Valley near Dayton is north of the 2013 collection locality of *Bittacomorphella furcata*. In the Cascade Range *Bittacomorphella pacifica* ranges north of the Olympic Peninsula locality representing the northern most record of *Bittacomorphella furcata*. It is difficult to make any assertions about the limits of *Bittacomorphella furcata*'s range based on the extremely limited collection data, although sampling in the Cascade Range by the second author has not collected any individuals.

As neither of the authors have collected *Bittacomorphella furcata*, further ecological inferences are impossible to draw.

***Bittacomorphella pacifica* Alexander (1958)**

Bittacomorphella pacifica Alexander, 1958: 49–50 (original description)

Bittacomorphella pacifica Alexander, Alexander 1965: 98 (catalog)

Bittacomorphella pacifica Alexander, Alexander 1967: 171 (illustration)

Diagnosis. Legs with white confined to distal tip of 1st, 2nd & 3rd tarsomeres. Gonostyli with basal lobe.

Description

Adult. Measurements (n=5). Overall length: 10.45mm (9.68–1.16mm); **Head.** Width (n=3): 0.85mm (0.82–0.89mm); Height: 0.81mm (0.74–0.87mm); Length: 0.45mm (0.38–0.53mm); Flagellum length: 6.78mm; Flagellomere proportions: 1.00, 0.70, 0.70, 0.70, 0.70, 0.70, 0.67, 0.67, 0.56, 0.56, 0.51, 0.48, 0.43, 0.43, 0.43, 0.40, 0.40, 0.35, 0.35, 0.08; Maxillary palpus length: 1.95mm; Maxillary palpus segment proportions: 0.28, 1, 1.52, 0.96, 3.68; **Thorax.** Length: 1.49mm (1.31–1.67mm); Height: 1.42mm (1.34–1.55mm); Wing length: 7.38mm (6.70–8.30mm); Wing width (n=4): 1.59mm (1.41–

1.85mm); Leg Proportions: Femur: 1.0, 1.01, 1.04mm; Tibia: 0.96, 0.94, 1.04; Tarsomeres: Foreleg 0.53, 0.18, 0.13, 0.03, 0.03, Midleg 0.56, 0.20, 0.14, 0.03, 0.03, Hindleg 0.68, 0.23, 0.15, 0.03, 0.03. **Abdomen.** Length: 8.81mm (8.00–9.96mm); Male tergite proportions 1.00, 3.37, 1.98, 1.87, 1.53, 0.78, 0.14; **Male Genitalia.** Width: 0.76mm; Height: 0.71mm.

Head. Head extremely closely pressed to thorax, generally triangular in shape, frons broadly domed with vertex well above dorsal margin of eye, medial suture indistinct, most prominent between antennal bases. Antennal scape ovoid in cross-section, provided with three socketed sensillae midway along anterior margin; 20 Flagellomeres. Face narrow, incised by clypeo-labrum nearly to dorsal margin. Clypeo-labrum large, sub-acutely triangular, lateral margins straight, around 2x longer than wide, somewhat inflated. Maxillary palpus as sub-family. Hypopharynx subconical triangular, directed anterior-ventrally. Labium prominent, extending beyond clypeo-labrum. Labellae partially fused medially.

Thorax. Antepronotum platelike, dorsal margin rounded. Scutum glabrous, pollinose, fuscous. Scutellum muddy yellow, with dense group of setae medially, ovoid. No postscutum present. Mediotergite ruddy-brown, dense patches of setae at anteriodorsal margin, as well as two parallel lines of setae medially. Paratergite poorly developed, narrow, scythe-like. Sub-paratergal membrane subquadrate, lightly sclerotized. Episternum with dorsal portion depressed rising to midcoxa, rectangular in shape; anepisternal suture inevident; ridge rising from midpoint of anterior margin to dorso-posterior corner. Epimeron rectangular in shape, with sulcus located midway at posterior margin, posterior margin straight. Suture of epimeron and metapleuron very indistinct. Laterotergite D-shaped, flat, with a sparse cluster of long setae dorsal across dorsal surface. Halter and as per subfamily; prehalter elongate; posthalter poorly developed protrusion, largely free of webbing to posterior membranous association of halter. Metapleural suture complete, emerging from posterior ventral

margin in a broad arc and terminating at halter; immediately below halter low prominence with cluster of long clear setae. All pleurites ruddy brown. **Wing.** Length: 8.25mm. Scattered macrotrichia on distal $1/10^{\text{th}}$ of wing, in cells R_{1+2} , R_3 , R_4 , R_5 , M. Vein C to wing apex, Sc, R_5 , R_1 , R_3 , R_4 & R_5 after forking and distal portion of M with macrotrichia, all other veins bare. Costa ending at wing apex. R_{3+4+5} stem 0.54mm straight; R_{4+5} stem 1.55mm; R_4 after fork 1.16mm, R_5 after fork 1.13mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 3.03 : 2.3$. r-m 0.25mm; M distal to r-m 2.50mm; Mdistal: $R_{3+4+5} = 5.13:1.00$, $R_4:M\text{distal} = 0.06:1.00$. CuA_2 1.08mm, loose medial curve, longer and weak marginal curve. A_1 faint basally, paralleling Cu for a short distance before broadly curving to anal margin, arc becoming more acute apically. M-Cu joins M at r-m. Anal lobe very poorly developed, angle obtuse; alula undeveloped. Halter: length: 1.22mm; stem elongate, medial furrow shallow at base becoming obscure distally, long clear macrotrichia laterally, knob pale yellow with dark stout trichoid sensillae laterally, apex of knob bare; prehalter elongate, sparsely provided with elongate clear trichoid sensillae; posthalter moderately developed, triangular, with several long translucent sensillae apically, largely free of webbing posteriorly. **Legs.** Coxae yellow, overall leg coloration brown. White banding confined to distal tip of 1st, 2nd & 3rd tarsomeres. Empodium closely associated with acropod, heavily provided with setae, notched posteriorly.

Pre-genital Abdomen. As per genus. **Male Genitalia.** Epandrium about 1.5x as wide as long; subquadrate, slightly bowed dorsally, rarely with weak internal suture present; dorsal surface sparsely provided with long trichoid sensillae (.1–.25mm), denser fringe lining posterior margin; anterior margin straight, without emargination, forming right angles with lateral margins; lateral margins straight without convergence until posterior apex, forming subobtuse angle at posterior margin near epandrial clasper origin, with internal fold of cuticle over epandrial clasper present and arcing weakly anteriorly, ending near medial margin of posteriomedial style; posterior margin emarginate, posteriomedial style formed to blunt triangular lobule medially adjacent to epandrial clasper; epiproct not readily apparent, hypoproct largely membranous with round sclerotized plate and short posteriorly directed trichoid

sensillae. Epandrial claspers emergent from posteriolateral apical angle, directed medio-posteriorly, evenly tapering along length to sub-acute point, curved sub-circularly dorso-anteriorly, dorsal and medial surfaces with long trichoid sensillae. Parameres glabrous, arising from dorso-medial portion of posterior margin of gonocoxite; basal section forming ventral arc adhered to supraedeagal membrane, dorsoventrally flattened; distal portion of paramere acute straight spine tapering to fine point, directed posteriodorsally. Gonocoxite conical, expanding to gonostylus. Gonostylus 1.5x length of gonocoxite, moderately expanded at base, sensillae along inner apex: single row of 10-11 along distal-medial surface, arising from dorsal margin anteriorly and shifting ventrally posterior; three sensillae at medial base. Gonopod not closely associated with hypandrium. Basal division of hypandrium broadly triangular, anterior margin weakly emarginated, medial suture present to membranous region. Membranous region lacrimiform, emarginating posterior portion of terminal division. Terminal division well-articulated, basal portion cupped dorsally forming pouch longer than wide; apical portion with lateral margins fused dorsally forming narrow tube, narrowed considerably from basal portion, shorter than basal portion with end closed. Lateral surface before apical portion provided with trichoid sensillae, apical portion with similar sensillae scattered across surface. Aedeagus with sperm sac as per sub-family, except lateral membranous windows highly reduced. Basal lateral apodeme broad and triangularly winglike, swept-anterior, apex rounded, dorso-laterally compressed at base, rotating to completely laterally compressed distally, low longitudinal ridge present on posterior surface emerging from ventral section; ventral section of apodeme small, rounded, directed posterior, not incising sperm sac. Ejaculatory apodeme broadly teardrop shaped, expands to rounded apex. Sclerites of aedeagus narrowly sclerotized, not tapered. Apical apodemes simple, upper lobe absent, ventral portion square, dorsoanterior extension of subapical sclerite articulating only on posterior margin; ventral apodemes moderate, acutely triangular, directed anteriorly. Subapical sclerite well developed, internal portion with anterolateral apex trapezoidal in dorsal view, flattened, contiguous with upper surface of external

portion, ventral arm forming sclerotized rods extending to margins of joint between basal and terminal division of hypandrium; external portion narrow tapering, curved dorsally towards apex, dorsal surface with broadly triangular denticle immediately prior to apex. **Female Genitalia.** Epigynum trapezoidal, flat dorsally, posterior margin straight, lateral margins straight, posterior margin indistinct, medial suture indistinct. Cerci with base indistinct, dorsal margin weakly convex, apex broadly rounded, ventral margin slightly convex, with an even arc. Apex of cercus with short, cylindrical nodule with single elongate trichoid sensillae medially; cercus epigynum ratio 0.46 : 1. Hypoproct trapezoidal, narrowing posterior, base with heavily sclerotized subtriangular lobe directed posterior. Genital fork T-shaped, lateral apices weakly curved anteriorly. Hypogynium quadrate, basal and terminal division indistinct, basal division with lateral margins formed into lateroposterior triangular lobes, posterior margin forming V shape becoming acute medially, medial notch extremely weak.

Figures. Adult. 21, 22; **Material Examined.** 23.

Material Examined. Holotype. Mt. Rainier, Wash. 4700 ft., Jul. 21, 1940, H.&M. Townes / Lower, spec. m#, = Holotype / HOLOTYPE, *Bittacomorphella pacifica*, C.P. Alexander / PARATYPE, *Bittacomorphella pacifica*, C.P. Alexander (Pinned: 1 m#, head and genitalia on slide) (USNM);

Paratypes. Mt. Rainier, Wash. 4700 ft., Jul. 21, 1940, H.&M. Townes / Lower, spec. m#, = Holotype (Pinned: 1 f#, same pin as holotype, head and genitalia on slide) (USNM); California, Castle Crags, 2000', VII-6-53, Alexander (Pinned: 2 m#, on same pin; Slide: 1 m#) (USNM); Oregon, Dayton, 9-19-46, Fender (Pinned: 1 m#) (USNM); **Other Material. CANADA.** Brit.Columbia, Robson, VI.5.1938, H.H. Foxlee (Pinned: 1 m#, 1 f#, incorrectly determined as *Bittacomorphella sackenii*) (UMMZ); **UNITED STATES.**

Mt.Hood OR, 3000ft., 29 July 21, AL Melander / AL Melander, Collection, 1961 (Pinned: 1 m#, incorrectly determined as *Bittacomorphella sackenii*) (USNM); Ore, Benton Co., Mid Parker Cr., Aug 8 1981 (163), Coll. G.W. Courtney (ISIC); 3 mi. E. Reedsport, Or.; Schofield Slough, April 23, 1964, J.D. vertrees; J Schuh

(Pinned: 1 m#) (WSU); Everett WN, 4 July 1924, AL Melander / AL Melander, Collection, 1961 (Pinned: 2 m#, incorrectly determined as *Bittacomorphella sackenii*) (USNM); 6 10 91- / Olympia, Wash (Pinned, 1 f#, incorrectly determined as *Bittacomorphella sackenii*) (WSU)

Taxonomic Notes. *Bl. pacifica* is a member of the *Bittacomorphella sackenii* group. Within the group *Bl. pacifica* can be identified by the pollinose scutum and details of the male genitalia: the straight, needle-like parameres and the dorsal tooth on the subapical sclerite of the aedeagus.

Phylogenetic analyses have placed *Bl. pacifica* as sister to *Bl.*, though without strong support. Most of the characters supporting the clade are symplesiomorphies compared with *Bl. furcata*. There are additional conflicting characters supporting a sister-group relationship between *Bl. sackenii* and *Bl. furcata*, detailed in the taxonomic notes of the latter species.

Ecological Notes. *Bl. pacifica* inhabits the Pacific Coast region of the Nearctic, inhabiting the Cascade and Pacific Coast ranges and the Willamette Valley. It is by far the most commonly collected of the *Bl. sackenii* group, likely due to its extensive range. That being said, *Bl. pacifica* is still rare when compared with *Bl. fenderiana*, which shares much of the range. Like the rest of the western Nearctic Bittacomorphinae, the eastern and western limits of the range are delimited by the Great Basin Desert and Pacific Ocean. *Bl. pacifica* is present as far north as British Columbia (Copley & Cannings, pers. comm.), extends south into California as far as the terminus of the Cascade Range. The southern limits in the Coast Range are unknown at this time, with more surveys of the California Coast needed.

The authors have been unable to collect this species during the course of this study, so further inferences about ecology are currently impossible to draw.

***Bittacomorphella sackenii* von Röder (1890)**

Bittacomorpha sackenii von Röder, 1890: 230 (original description)

Bittacomorpha sackenii von Röder, 1895: 200 (redescription, key)

Bittacomorpha sackenii von Röder, Johnson 1905: 75 (key)

Bittacomorpha (*Bittacomorphella*) *sackenii* von Röder, Alexander 1916: 546 (key)

Bittacomorphella sackenii von Röder, Alexander 1927: 9 (catalog)

Bittacomorphella sackenii von Röder, Peus 1958: 11 (catalog)

Bittacomorphella sackenii von Röder, Alexander 1965: 98 (catalog)

Bittacomorphella sackenii von Röder, Alexander 1967: 171 (illustration)

Diagnosis.

Adult. Legs with white confined to distal tip of 1st, 2nd & 3rd tarsomeres. Epandrium quadrate nearly flat, basal apical sclerite of aedeagus spiniform, distal portion of paramere formed to semi-circular arc.

Description.

Adult. Measurements (n=1). Overall length: 10.45mm (9.68–11.16mm); **Head.** Width: 0.75mm; Height: 0.71mm; Length 0.43mm; Flagellum length: 6.95mm; Flagellomere proportions: 1.00, 0.81, 0.87, 0.87, 0.87, 0.87, 0.77, 0.72, 0.68, 0.64, 0.64, 0.59, 0.59, 0.50, 0.55, 0.46, 0.42, 0.09; Maxillary palpus length: 1.16mm; Maxillary palpus segment proportions: 0.16, 1.0, 1.1, 0.8, 0.8; **Thorax.** Length: 1.38mm (1.43–1.53mm); Height: 1.23mm (1.29–1.45mm); Wing length: 6.7mm; Wing width: 1.5mm; Leg Proportions: Femur: 1.0, 1.05, 1.15mm; Tibia: 0.96, 0.99, 1.21; Tarsomeres: Foreleg 0.56, 0.18, 0.12,

0.04, 0.04, Midleg 0.54, 0.19, 0.13, 0.03, 0.04, Hindleg 0.66, 0.24, 0.16, 0.03, 0.04; **Abdomen.** Length: 8.26mm; Male tergite proportions 1.00, 3.55, 2.14, 1.97, 1.63, 0.89, 0.13; **Male Genitalia.** Width: 0.54mm; Height: 0.57mm.

Head. Head extremely closely pressed to thorax, generally triangular in shape, frons broadly domed with vertex well above dorsal margin of eye, medial suture weakly developed. Antennal scape ovoid in cross-section, provided with three socketed sensillae midway along anterior margin; 19–20 Flagellomeres. Face narrow, incised by clypeo-labrum to antennal bases. Clypeo-labrum large, sub-acutely triangular, lateral margins straight, around 2x longer than wide, somewhat inflated. Maxillary palpus as sub-family. Hypopharynx triangular flattened, directed anteriorly. Labium prominent, extending beyond clypeo-labrum. Labellae D-shaped partially fused medially, forming ovoid pad.

Thorax. Antepronotum weakly developed, narrow low ridge. Scutum glabrous, pollinose, fuscous. Scutellum muddy yellow, with dense group of setae medially, ovoid. No postscutum present. Mediotergite ruddy-brown, dense patches of setae at anteriodorsal margin, as well as two parallel lines of setae medially. Paratergite poorly developed, narrow, scythe-like. Sub-paratergal membrane subquadrate, lightly sclerotized. Episternum with dorsal portion depressed rising to midcoxa, rectangular in shape; anepisternal suture inevident; ridge rising from midpoint of anterior margin to dorso-posterior corner. Epimeron rectangular in shape, with sulcus located midway at posterior margin, posterior margin straight. Suture of epimeron and metapleuron sinuous, rapidly becoming indistinct ventrally. Laterotergite lacrimiform, flat, with a sparse cluster of long setae dorsal across dorsal surface. Halter and as per subfamily; prehalter elongate; posthalter poorly developed protrusion, inevident. Metapleural suture complete, emerging from posterior ventral margin in a broad arc and terminating at halter; immediately below halter low prominence with cluster of long clear setae. All pleurites ruddy brown. **Wing.** Length: 8.25mm. Sparse macrotrichia along apical 1/6th of wing in cells Sc, R₁, R₃, R₄, R₅, M.

Vein C to wing apex, Sc, R_s, R₁, R₃, R₄ & R₅ after fork with macrotrichia, all other veins bare. Costa ending at wing apex. R₃₊₄₊₅ stem 0.39mm straight; R₄₊₅ stem 1.53mm; R₄ after fork 1.23mm, R₅ after fork 1.21mm; R₃₊₄₊₅:R₄₊₅-stem:R₄ = 1.00 : 3.92 : 2.52. r-m 0.23mm; M distal to r-m 2.45mm; Mdistal:R₃₊₄₊₅ = 5.90:1.00, R₄:Mdistal = 0.42:1.00. CuA₂ 1.27mm, moderate medial curve, moderately long and loose marginal curve. A₁ faint basally, paralleling Cu for a short distance before broadly curving to anal margin, arc becoming more acute apically. M-Cu joins M medial to r-m. Anal lobe very poorly developed, angle obtuse; alula undeveloped. Halter: length: 1.03mm; stem elongate, medial furrow shallow at base becoming obscure distally, long clear macrotrichia laterally, knob pale yellow with dark stout trichoid sensillae laterally, apex of knob bare; prehalter elongate, sparsely provided with elongate clear trichoid sensillae; posthalter weakly developed, broadly triangular, with several long translucent sensillae apically, webbing to halter well-developed. **Legs.** Coxae yellow, overall leg coloration brown. White banding confined to distal tip of 1st, 2nd & 3rd tarsomeres. Empodium closely associated with acropod, heavily provided with setae, notched posteriorly.

Pre-genital Abdomen. As per genus. **Male Genitalia.** Epandrium about 1.5x as wide as long, not bilobate; subquadrate, nearly flat across surface, anterior margin straight, lateral margins slightly bowed laterally, curvature becoming more pronounced towards posterior margin, internal fold in epandrium above epandrial clasper at most weakly developed (often absent), posterior margin very weakly emarginate medially, posteriomedial lobule formed to obtuse triangle medial to base of epandrial clasper; epiproct not readily apparent, hypoproct ovoid sclerotized plate with cluster of posterior directed setae. Dorsal surface sparsely provided with long setae (.1–.25mm), fringe lining posterior margin. Epandrial claspers emergent from posteriolateral apices, directed medio-posteriorly, abruptly tapering to sub-acute point, curved sub-circularly dorso-anteriorly, dorsal and medial surfaces with long setae. Parameres glabrous, arising from dorso-medial portion of posterior margin of gonocoxite; basal section adhered to membrane above aedeagus, laterally compressed, moderately sclerotized, becoming

weakly sclerotized anteriorly; distal portion of paramere narrow style, curved semicircular ventrally, tapering slightly to subacute point, heavily sclerotized. Gonocoxite conical, expanding to gonostylus. Gonostylus 1.5x length of gonocoxite, slightly expanded at base, sensillae along inner apex: single row of 10-11 along dorsomedial margin, shifting from directly medial posterior towards dorsal anterior; three sensillae at medial base. Gonopod not closely associated with hypandrium. Basal division of hypandrium broadly triangular, anterior margin weakly emarginated, medial suture present to membranous region. Membranous region lacrimiform, emarginating posterior portion of terminal division. Terminal division well-articulated, basal portion cupped dorsally forming pouch longer than wide; apical portion with lateral margins fused dorsally forming narrow tube, narrowed considerably from basal portion, shorter than basal portion with end closed. Lateral surface before apical portion provided with trichoid sensillae, apical portion with similar sensillae scattered across surface. Aedeagus with sperm pump as per subfamily, membranous windows weakly developed. Ejaculatory apodeme spathate, dorsal margin expanding $\frac{1}{3}$ rd along length, apex tapering to point. Basal lateral apodeme with lateral section triangular winglike, swept-back; apex pointed; ventral section of apodeme small, rounded, directed posterior, largely contiguous with remainder of apodeme, medial margin heavily sclerotized continuing in curve to anterior margin, sclerotization stopping abruptly at confluence with lateral margin, lateral margin arcing posterior, rising to merger with anterior margin of lateral section. Lateral sclerites of aedeagus moderately broad, weakly tapered. Apical apodemes simple, upper lobe absent, ventral lobe apodemes moderately developed, heavily rounded, becoming distinctly less sclerotized distally. Subapical sclerite well developed, internal portion rectangular, weakly sclerotized anteriorly, more sclerotized posteriorly; external portion spinelike, directed posterior. **Female Genitalia.** (only available from a lateral slide mount) Epigynium subtrapezoidal tapering towards posterior margin; posterior margin straight. Cerci short, 1.78x length vs. height, ovoid, ventral margin not potbellied. Hypogynium broad,

especially at base, not well delineated into basal and terminal divisions; posterolateral apices of posterior margin formed to rounded triangular lobes, medial emargination very weakly developed.

Figures. Adult. 24, 25; **Material Examined.** 26.

Material Examined: UNITED STATES. MonoLake, Cal., July 24, 1911 / Collection, J M Aldrich (Pinned: 1 m#) (USNM); California, Yosemite, Mar-, iposa grove, VII-22-46, (Alexander) (Slide: 1 f#) (USNM); California, Sierra Nevadas, Big Pine Creek, 9000' VII-11-'57, (Alexander) (Slide: 3 m#) (USNM).

Taxonomic Notes. The holotype of *Bl. sackenii* is not located in the collection of the Martin Luther Universität Halle-Wittenberg (where the majority of von Röder's type material is housed), but probably resides with the collection of H. K. Morrison (Karla Schneider, pers. comm.). The authors were unable to determine where the Morrison collection is housed, therefore the holotype was unavailable for examination. Alexander (1967) also notes he was unable to locate the holotype. However, von Röder records the specimen as being collected in: (*Sierra Nevada. America septentrionalis.* (H. K. Morrison). There is only one species of *Bittacomorphella* present in the Sierra Nevada Mountains, which does not overlap in range with other species of *Bittacomorphella*, so the assignment of this species is not problematic.

Bittacomorphella sackenii is the nominate member of the *Bittacomorphella sackenii* group, which includes *Bl. pacifica* and *Bl. furcata*. Before the description of *Bl. pacifica* and *Bl. fenderiana*, all of western Nearctic *Bittacomorphella* were determined to *Bl. sackenii*, and many of these incorrect determination labels remain in collections. *Bl. sackenii* can be distinguished from these species by the structure of the male genitalia: the epandrium is platelike and square (versus bilobate and hexagonal in *Bl. fenderiana*) and the parameres are undivided (versus bifurcate in *Bl. furcata*) and arced dorsally (versus straight in *Bl. pacifica*).

Ecological Notes. The authors were unable to collect fresh specimens of *Bl. sackenii*, and are limited to the inferences that can be made from museum material and general observations from a 2012 collecting trip in eastern California. The recorded collection localities are from the Sierra Nevada Mountains south of Lake Tahoe (Alexander 1958, Fasbender pers. obs.), on both sides of the range. The eastern slope of the range is highly xeric, the driest seen of the North American *Bittacomorphella*. The eastern and southern limits of the species appear to be limited by the Great Basin and Mojave deserts; the western border of the range is the California central valley. The northern extent of the range of *Bl. sackenii* is not clearly defined: all known records are recorded from south of Lake Tahoe, but there are no notable geographic barriers preventing the species range from extending to the northern portion of the Sierra Nevadas.

Unplaced *Bittacomorphella*

Bittacomorphella esakii Tokunaga (1938)

Bittacomorphella esakii Tokunaga, 1938: 189–190 (original description)

Bittacomorphella esakii Tokunaga, Peus 1958: 42 (redescription, illustration)

Bittacomorphella esakii Tokunaga, Nakamura & Saigusa 2009: 278–279 (redescription, illustration)

Diagnosis

Adult. Legs with three white bands, broad proximal band around upper portion of tibia; subdistal band at proximal extremity of 1st tarsomere; distal band distal tip of 1st, 2nd, 3rd & 4th tarsomeres. Epandrium with prominent epiproct dividing to two lobes, epandrial lobes rounded.

Description

Adult. Measurements (n=2). Overall length: 10.45mm (9.68–11.16mm); **Head.** Width (n=1): 0.75mm; Height: 0.72mm (0.71–0.73mm); Length: 0.43mm (0.40–0.46mm); Flagellum length: 8.96mm;

Flagellomere proportions: 1.00, 0.73, 0.96, 1.04, 1.04, 1.00, 0.93, 0.93, 0.89, 0.84, 0.76, 0.68, 0.68, 0.68, 0.60, 0.54, 0.50, 0.10; Maxillary palpus length: 1.34mm; Maxillary palpus segment proportions: 0.18, 1, 1.59, 1.22, 2.09; **Thorax.** Length: 1.48mm (1.43–1.53mm); Height: 1.37mm (1.29–1.45mm); Wing length (n=1): 6.6mm; Wing width (n=1): 1.36mm; Leg Proportions: Femur: 1.0, 1.03, 1.15mm; Tibia: 0.98, 0.91, 1.07; Tarsomeres: Foreleg 0.70, 0.23, 0.15, 0.03, 0.04, Midleg 0.64, 0.22, 0.14, 0.03, 0.04, Hindleg 0.73, 0.25, 0.17, 0.03, 0.03. **Abdomen.** Length: 8.84mm (8.16–9.53mm); Male tergite proportions 1.00, 4.31, 2.01, 1.85, 1.66, 0.74, 0.22. **Male Genitalia.** Width: 0.67mm; Height: 0.78mm.

Head. Head extremely closely pressed to thorax, generally triangular in shape, frons broadly domed with vertex well above dorsal margin of eye, medial suture absent. Antennal scape ovoid in cross-section, provided with three socketed sensillae subdorsally along anterior margin; 18 Flagellomeres. Face indistinct. Clypeolabrum large, sub-acutely triangular, margins straight, extending nearly to antennal base, surface relatively flat and uninflated; margins do not cover maxillary palpus. Maxillary palpus as sub-family. Hypopharynx conical, directed ventrally. Labium prominent, elongate, extending well beyond clypeolabrum. Labellae fused medially, large and bean-shaped, forming foldable pad.

Thorax. Antepronotum closely pressed to thorax, dorsal margin relatively straight edge. Scutum glabrous, shining, sienna lightening slightly at medial apices of transverse suture; prescutal pit not prominent. No prescutellum evident. Scutellum light yellow, with compact group of setae medially, ovoid. Mediotergite light chocolate brown, dense patch of setae at anteriolateral margin. Paratergite well developed, broad, semi-circular narrowing anteriorly. Sub-paratergal membrane heavily sclerotized, generally triangular narrowing to anterior point ventrally. Episternum fairly flat, overall rectangular in shape with dorsal edge formed to an acute point posteriorly; anepisternal suture not evident. Epimeron subrectangular in shape, convex, posterior margin heavily incised by laterotergite. Laterotergite broadly

lacrimiform, deject near center, free of setae. Halter and prehalter as per subfamily, posthalter moderately developed triangular lobule, post halter membrane poorly developed. Metapleuron with very fine incomplete suture, almost unnoticeable in some individuals, emerging from medio-posterior margin in straight line; immediately below halter low prominence with cluster of long clear setae, with a ridge looping posterior up to join the halter. Pleurites color uniform from sienna to muddy yellow based on individual variation. **Wing.** Length: 8.25mm. Single row of macrotrichia at extreme apex of cells R_1 , R_3 , R_4 . Vein C to wing apex, Sc, R_5 , R_1 , R_3 , R_4 & R_5 after forking with macrotrichia, all other veins bare. Costa ending at wing apex. R_{3+4+5} stem 0.39mm straight; R_{4+5} stem 1.53mm; R_4 after fork 1.18mm, R_5 after fork 1.05mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 3.92 : 2.52$. r-m 0.27mm; M distal to r-m 2.56mm; $M\text{distal}:R_{3+4+5} = 5.90:1.00$, $R_4:M\text{distal} = 0.42:1.00$. CuA_2 1.15mm, tight medial curve, longer and tight marginal curve. A_1 faint basally, paralleling Cu for a short distance before broadly curving to anal margin, arc becoming more acute apically. M-Cu joins M medial to r-m. Anal lobe very poorly developed, angle obtuse; alula undeveloped. Halter: length: 0.98mm; stem elongate, medial furrow shallow at base becoming obscure distally, long clear macrotrichia laterally, knob pale yellow with dark stout trichoid sensillae laterally, apex of knob bare; prehalter elongate, sparsely provided with elongate clear trichoid sensillae; posthalter weakly developed, broadly triangular, with several long translucent sensillae apically, webbing to halter well-developed. **Legs.** Coxae yellow, femur yellow fading to overall leg coloration of brown. Three white bands, first on tibia near femoral joint, second on proximal end of 1st tarsomere, third distal tip of 1st, 2nd & 3rd & 4th tarsomeres as well as acropod. Empodium closely associated with acropod, heavily provided with setae, unnotched.

Pre-genital Abdomen. As per genus. **Male Genitalia.** Epandrium bilobate and emarginate posterior margin, overall 2x wide vs. long (measured from anterior margin to base of stylet), internal folds above epandrial clasper absent; epandrial lobes semicircular, wider than long, , shining, provided heavily with long setae; epandrial lobe with posterior margin straight, rounding at medial and lateral

margins; lateral and medial margins evenly rounded, forming simple semicircular arc, with posteriomedial stylet at apex; epiproct prominent, dividing epandrial lobes medially, reminiscent of webbing with slight emargination on posterior margin; hypoproct platelike, ovoid, located immediately underneath epiproct with several stout setae directed posterior. Epandrial claspers emergent from lateral extremity of epandrial lobe, directed medio-ventrally, tapering to acute glabrous point, curved hooklike medially; provided heavily with long setae from base to $\frac{1}{4}$ length from apex. Subepandrial sclerite divided, articulated at mediobasal apex of epandrial clasper, broad ovoid plate directed medioanteriorly. Parameres glabrous, arising from dorso-medial portion of posterior margin of gonocoxite, laterally compressed, narrowing slightly dorsoventally near midpoint, straight; medial margin adhered to supraedeagal membrane from base to near midpoint, distal portion free. Apex subacutely triangular, curving dorsally. Gonocoxite conical, expanding to gonostylus, shorter than gonostylus. Gonostylus rounded at tip, outer surface heavily provided with long setae, sensillae along inner apex setiform: single row of 8 traversing from directly medial at posterior apex towards dorsal surface anteriorly. Basal division of hypandrium narrow band, with emargination below gonocoxite, evenly provided with long setae across anterior margin. Terminal division marginally articulated, pouchlike in shape, tapering to broad point. Ventral surface provided with long setae, dorsal surface glabrous, lateral margins folded dorsally. Aedeagus with sperm sac as per sub-family. Ejaculatory apodeme very large for Bittacomorphinae, dorsal margin arcing heavily basally tapering anteriorly to pointed apex. Basal lateral apodeme with lateral section broadly triangular, swept anterior laterally, lateral apices rounded, as broad as $\frac{1}{2}$ length of aedeagal sclerites, anterior margin with triangular tooth about midway along length; ventral section heavily sclerotized on medial margin, posterior apex rounded, ridge traversing from posterior apex dorsolaterally to merge with lateral section. Ejaculatory apodeme very large for Bittacomorphinae, dorsal margin arcing heavily basally tapering anteriorly to pointed apex. Sclerites of distophallus broad, narrowing toward apex; apical apodemes not readily

distinguished in specimen examined. Subapical sclerite heavily sclerotized, internal portion largely square, dorsal section platelike, trapezoidal with posterior margin weakly emarginate, lateral extremities heavily rounded, lateral margins convergent posteriorly constricting at junction with external section, ventral section heavily sclerotized, earlike in shape; external section roughly turnip-shaped, flattened, tip slightly curved dorsally. **Female Genitalia.** Epigynum broadly semicircular, arched dorsally, fusion with epiproct very weakly evident as U-shaped change of color at posterior margin, lateral margins broadly rounded at base, straight distally, medial suture inevident; epiproct with margin between cerci convex. Cerci broad with base tapered slightly, dorsal margin weakly convex, apex obtusely rounded, ventral margin convex, especially posteriorly. Apex of cercus with short, cylindrical nodule with single elongate trichoid sensillae medially; cercus epigynum ratio 0.66 : 1, cercus length to height 2 : 1. Hypoproct not visible on specimen. Genital fork not visible on specimen examined. Hypogynium trapezoidal, hypogynial lobe base distinct as straight sulcus across hypogynium, hypogynium lobes with square margins on either side of medial notch; medial notch small, narrow V-shape, slit-like.

Figures. Adult. 27, 28; **Material Examined.** 29.

Material Examined: JAPAN. Japan, Echigo, Mt. Amaka-, zari, Vi-25-35, Baba AM31 (Pinned: 3 m#, 2 f#; Slide: 1 m#)

Taxonomic Notes. *Bl. esakii*, like the other Asian *Bittacomorphella*, exhibits many plesiomorphic character states. The Japanese *Bittacomorphella* receive only weak support as a monophyletic group, and further examination of the remainder of the Asian *Bittacomorphella* may show that the Japanese species are not particularly closely related. Indeed, whether the Asian species of the genus represent a clade is debatable, and further examination and analysis is required before any assertions can be made. The only synapomorphy for the East Asian “group” is the restricted distribution of absence of

macrotrichia on the wing membrane, with the other characters defining the group either plesiomorphic or homoplastic. *Bl. esakii* can be easily identified by the distinctive three white bands present on each leg, with the distal band including all of the tarsomeres.

***Bittacomorphella fenderiana* Alexander (1947)**

Bittacomorphella fenderiana Alexander, 1947: 22–24

Bittacomorphella fenderiana Alexander, Peus 1958: 11 (catalog)

Bittacomorphella fenderiana Alexander, Alexander 1965: 98 (catalog)

Bittacomorphella fenderiana Alexander, Alexander 1967: 171 (illustration)

Diagnosis

Larva. Head capsule trapezoidal, posterolateral corners with small hook. Thoracic and abdominal segments annulated, with prominent cuticular extensions which typically have hardened clumps of detritus attached.

Adult. Legs with white confined to distal tip of 1st, 2nd & 3rd tarsomeres. Gonostyli with basal lobe.

Description

Larva. Head. Cranium well separated from prothoracic segment, trapezoidal in shape from above; dorsal surface flat, black. Frontoclypeal apotome broad, 2.5x as long as wide, expanding to apex, anterior margin blunt; occipital margin narrowing considerably posterior, forming narrow point reaching nearly to posterior margin of cranium, posterior portion of cranium directed ventrally, forming dorsoposterior surface; ecdysial stem line short, obscured by prothorax. Genae triangular in dorsal view, anterior point blunt, lateral margin narrowing anterior, lateroposterior apex forming blunt hook-

like spine directed anterior, medioventrally nearly convergent, anterior margin square, no collar on posterior margin, ventroposterior margin broadly obtuse angle; subgenal sclerite fused with hypopharynx, triangular, narrowing posterior, anterior margin with rectangular lobe medially. Single stemmata present, large, triangular, located far posterior to anterior margin. Antenna two segmented, base recessed at anterior terminus of ecdysial suture: basal segment cylindrical, apical segment weakly fusiform, apex rounded, apical sensillae cluster directed laterally. Labrum triangular, dorsally with heavily sclerotized trapezoidal plate with rounded anterior margin, ventral surface membranous, slightly expanded, ventral margins heavily sclerotized, narrow medially, broadening flag-like laterodorsally; labral brushes round, macrotrichia elongate; medioventral apex with conical ventrally directed obtuse point, with stout ventrally directed sensillae. Premandible ventral to labrum, well developed, with serrate medioventral margin. Mandible with molar lobe semicircular, ventrolaterally with triangular lobule, mandibular comb well developed surrounding incisor lobe, becoming weakly serrated lobe on inner ventral margin; incisor lobe triangular, ventral margin unserrated; prosthema prominent on inner lateral margin, heavily modified: ventromedially with elongate thick trunk ending in knob, laterodorsal two blunt, thick sensillae, followed by four narrower sensillae. Maxillae with cardo inverse acute triangle, ventral point heavily rounded; stipes culvert-like over lacinia, without brushes, maxillary palpus apical; lacinia elliptical. Prementum broadly bottle-neck shape, dentition at apex blunt.

Thoracic segments not increasing in size posteriorly, largely indistinguishable from abdominal segments, elongate cuticular extensions present, typically covered in hardened substrate from habitat, apically with elongate branching sensilla. Abdominal segments cylindrical, homogenous in width, delineations between segments extremely weak; cuticular extensions also present, arranged in regular longitudinal rows on dorsal and lateral surface, absent ventrally. Prolegs well developed, apical claw with basal angle, sythe-like apex. Anal division cylindrical, with lightly sclerotized exsertable tube containing siphon; siphon with annulations weakly developed if at all.

Adult. Measurements (n=5). Overall length: 11.92mm (11.36–12.6mm); **Head.**Width (n=3): 0.90mm (0.88–0.92mm); Height: 0.81mm (0.75–0.89mm); Length: 0.51mm (0.49–0.54mm); Flagellum length: 7.84mm; Flagellomere proportions: 1.00, 0.56, 0.64, 0.73, 0.8, 0.83, 0.83, 0.76, 0.67, 0.64, 0.67, 0.59, 0.55, 0.53, 0.49, 0.46, 0.43, 0.43, 0.02; Maxillary palpus length: 1.43mm; Maxillary palpus segment proportions: 0.56, 1, 1.56, 1.08, 2; **Thorax.** Length: 1.61mm (1.55–1.71mm); Height: 1.47mm (1.43–1.57mm); Wing length: 7.6mm (6.70–8.20mm); Wing width: 1.56mm (1.50–1.69mm); Leg Proportions: Femur: 1.0, 0.99, 1.04mm; Tibia: 1.02, 0.99, 1.15; Tarsomeres: Foreleg 0.64, 0.27, 0.17, 0.05, 0.04, Midleg 0.60, 0.26, 0.18, 0.04, 0.04, Hindleg 0.63, 0.26, 0.18, 0.04, 0.03; **Abdomen.** Length: 9.8mm (9.32–10.35mm); Male tergite proportions 1.00, 2.9, 1.88, 1.94, 1.62, 0.53, 0.1; **Male Genitalia.** Width: 0.69mm; Height: 0.9mm

Head. Head extremely closely pressed to thorax, generally triangular in shape, frons broadly domed with vertex well above dorsal margin of eye, medial suture clearly evident, extending between antennal bases to dorsal margin of face. Antennal scape ovoid in cross-section, provided with five socketed sensillae subdorsally along anterior margin; 19–20 Flagellomeres. Face narrow, incised by clypeo-labrum nearly to dorsal margin. Clypeo-labrum large, sub-acutely triangular, lateral margins somewhat pinched at junction with face, around 2x longer than wide, somewhat inflated. Maxillary palpus as sub-family. Hypopharynx subconical triangular, directed anterior-ventrally. Labium not very prominent, largely hidden by clypeo-labrum. Labellae free medially, not forming pad.

Thorax. Antepronotum with two small fleshy semicircular emergent from dorsal margin, each provided with several setae. Scutum glabrous, shining, ruddy-brown with broad muddy yellow highlighting of transverse suture. Distinct fold at rear of scutum, but no prescutum present. Scutellum muddy yellow, with dense group of setae medially, subcircular. Mediotergite ruddy-brown, dense patches of setae at anteriodorsal margin, as well as two parallel lines of setae medially. Paratergite well

developed, broad, blunt crescent shape. Sub-paratergal membrane elliptical in shape with tapered apices, fairly well sclerotized. Episternum fairly flat with prominence above midcoxa, rectangular in shape; anepisternal suture fairly well developed. Epimeron rectangular in shape, with shallow sulcus located midway dorsally, posterior margin straight. Laterotergite lacrimiform, deject dorsally with a few long setae along dorsal margin rising to slight prominence towards halter. Halter and prehalter as per subfamily, posthalter well developed, nearly twice as long as wide, largely free of webbing to posterior membranous association of halter. Metapleuron with incomplete suture, emerging from posterior ventral margin in a broad arc and terminating well before halter; immediately below halter low prominence with cluster of long clear setae. All pleurites muddy yellow, fading to ruddy brown at ventral margin. **Wing.** Length: 8.25mm. Scattered macrotrichia on distal $1/10^{\text{th}}$ of wing, in cells R_{1+2} , R_3 , R_4 , R_5 . Vein C to wing apex, Sc , R_1 , R_3 , and R_4 & R_5 after forking with macrotrichia, all other veins bare. Costa weakening significantly at wing apex, faint along posterior margin. R_{3+4+5} stem 0.68mm straight; R_{4+5} stem 1.9mm; R_4 after fork 1.57mm, R_5 after fork 1.56mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 2.79 : 2.3$. $r\text{-m}$ 0.32mm; M distal to $r\text{-m}$ 3.36mm; $M\text{distal}:R_{3+4+5} = 4.94:1.00$, $R_4:M\text{distal} = 0.46:1.00$. CuA_2 1.63mm, strong medial curve, short and weak marginal curve. A_1 faint basally, paralleling Cu for a short distance before broadly curving to anal margin, arc becoming more acute apically. $M\text{-}Cu$ joins M at $r\text{-m}$. Anal lobe very poorly developed, angle obtuse; alula undeveloped. Halter: length: 1.22mm; stem elongate, medial furrow shallow at base becoming obscure distally, long clear macrotrichia laterally, knob pale yellow with dark stout trichoid sensillae laterally, apex of knob bare; prehalter elongate, sparsely provided with elongate clear trichoid sensillae; posthalter moderately developed, triangular, with several long translucent sensillae apically, largely free of webbing posteriorly. **Legs.** Coxae yellow, overall leg coloration brown, with an especially dark band at the apex of the femur in some individuals. White banding confined to distal tip of 1^{st} , 2^{nd} & 3^{rd} tarsomeres. Empodium closely associated with acropod, heavily provided with setae, notched posteriorly.

Pre-genital Abdomen. As per genus. **Male Genitalia.** Epandrium broadly hexagonal in shape, bilobate, emarginate on posterior margin; anterior margin forming broad W-shape, with medial emargination and lateral extremities angled obliquely posterior; lateral margin angled laterally to base of epandrial clasper approximately 2/3rds of length, posterior portion arcing broadly medially to posteriomedial style; posteriomedial style formed to elongate spine, parallel directed posterior; posterior margin with semicircular emargination medially. with prominent lateral apices obtusely pointed, posterior apices with pin like stylets with acute glabrous points, faint medio-sagittal suture distinguishable; epiproct not readily apparent, hypoproct largely membranous with sclerotized plate and large dorsally directed setae medially. Dorsal surface provided with long setae (.1-.25mm), becoming more numerous approaching posterior margin. Epandrial claspers emergent from lateral apices, directed medio-posteriorly, tapering to acute point, curved semi-circularly dorsally, glabrous except for several long setae sub-apically. Parameres glabrous, arising from dorso-medial portion of posterior margin of gonocoxite; basal section adhered to membrane above aedeagus, with acute spine directed dorso-medially arising near gonocoxite; distal portion of paramere curving dorsoanterior to a nearly straight vertical spine tapering to an acute point. Gonocoxite conical, expanding to gonostylus, subequal to gonostylus. Gonostylus longer than gonocoxite, expanding along length to distinctly round apex, basal lobe present at dorsal juncture of gonostylus and gonocoxite, rounded, less than 1/8 length of gonostylus, provided with setae at tip; heavily sclerotized trichoid sensillae along inner apex of gonostylus: dorsal row with 5 sensillae extending from apex anteriorly along distal 3rd, ventral row with 9-10 extending from apex along distal half, both rows located along medial surface at apex, shifting to dorsal surface anteriorly. Basal division of hypandrium roughly triangular, expanded subhemispherically, with minimal taper to straight posterior margin at joint with terminal division, anterior margin heavily emarginated in obtuse arc, lateral margins broadly emarginated near gonocoxite with gonocoxite set in emargination, medial suture absent, scattered trichoid sensillae only at extreme lateral margin. Terminal

division well-articulated, foliform, posterior margin strongly emarginated; lateral margins heavily cupped dorsally, parallel anteriorly, posteriorly arcing medially to form broad apex, rounded medial apex indistinct in some specimens; lateral lobes present subapically, flat in cross-section, broad with apex subobtusate, posterior margin with less severe angle than anterior; ventral surface heavily provided with setae along lateral margins and lateral lobes, medial surface glabrous. Superaedeagal membrane closely not inflated, taut over aedeagus. Aedeagus with sperm sac as per subfamily, membranous windows prominent, ejaculatory apodeme relatively large for subfamily, ventral margin straight basally, weakly dorsally arced terminally, dorsal margin strongly arced dorsally. Basal lateral apodeme without pedicel, emerging directly from base of aedeagal sclerite, lateral portion winglike, heavily laterally compressed, expanding to broad rounded apex, dorsal margin heavily sclerotized, broad sinuous W-shape in dorsal view, ventral margin broadly connected with ventral portion; ventral portion subquadrate, anteroventral apex extended anteriorly, inserted moderately into sperm sac. Lateral sclerites of aedeagus short, broad, compact; expanded at both anterior and posterior extremity. Apical apodemes of aedeagus without dorsal lobe, ventral lobe well developed, narrow, apex acute. Subapical sclerite with internal dorsal section forming sclerotized plate closely associated with ventral margin of apical apodeme, posterior margin acutely divided medially nearly to apex, posterior following dorsal curve of apical apodeme nearly to dorsal apex, forming two posteriorly directed blade-like ridges where it emerges from the supraedeagal membrane to form the external section, merging dorsomedially with distinct suture which opens posteriorly to a triangular emargination of the posterior margin; ventral arm emerging from dorsal curve of internal dorsal section as a dorsally arced rod extending to margin at the joint of the terminal and basal divisions. **Female Genitalia.** Epigynium rounded dorsally, lateral margins forming broad curving arc, posterior margin distinct with strong triangular emargination between base of cerci, medial suture present as gap in chaetotaxy. Cerci with base distinctly joined with epiproct, dorsal margin rounded, apex circular, ventral margin evenly rounded. Apex of cercus with one especially

stout trichoid sensilla; cercus to epigynium ratio 0.66 : 1. Hypoproct broad triangular, fused to ventral surface of epigynium, anterior hook low and broad. Genital fork complex, medial apex rounded point, lateral apices quadrate. Hypogynium quadrate, posterolateral apices with triangular posteriorly directed lobe, hypogynial valves indistinct, rounded, medial notch sub-V-shaped: 0.53x as deep as broad.

Figures. Larva. 32, 33, 34 **Adult.** 30, 31 **Material Examined.** 35.

Material Examined. Holotype. Peavine Ridge, Or., nr. McMinnville, V-15-1946, Kenneth M. Fender / HOLOTYPE *Bittacomorphella fenderiana* C.P. Alexander (Pinned: 1 m#, genitalia mounted on slide) (USNM); **Paratypes.** Oregon- Yamhill, co.; Peavine Ridge, nr. McMinnville, VI-5-1945, (K. M. Fender) (Slide: 1 m#) (USNM); Oregon, Peavine, Ridge, V-26 45, Fender (Pinned: 1 m#) (USNM); m# Oregon, Peavine Ridge, nr. McMinnville, Aug 22- 1946, (K. M. Fender) (Slide: 1#) (USNM); m# Washington, Keyport, July 1905, (R.W. Doane) (Slide: 1 m#) (USNM); Washington, Ashford, Aug. 18, 1940 (H.&M. Townes) (Slide: 1 m#) (USNM); Stanley Park, Vancouver B.C., Sept. 3, 1930, Hugh B. Leach (Pinned: 1 f#) (USNM) **Other Material Examined. UNITED STATES. CALIFORNIA** Humboldt, Co., 6 km. NE. Arcata, 14 June 1982, Robert W. Brooks (Pinned: 1 m#, 1 f#) (KU); Oregon, Benton Co., VI-8-85 Muddy Swamp, n.r Oak Creek Lab, Col. & I.D. J.K. FURNISH, *Bittacomorpha clavipes*, (Fabricius) (Incorrect Identification) (Alcohol: 1 larva) (ISIC); 4-25-1962, OREGON, Benton Co., 5 mi. NW Corvallis; McDonald For., Oak, Crk. gate--el. 500' / Collected By, David L. Mays (Pinned: 2 m#) (ORSU) April 10, 1963// OREGON, Benton Co.,// 5 mi. NW Corvallis;// McDonald For., Oak// Crk. gate--el. 500' | Collected By// David L. Mays (Pinned: 13 m#) (ORSU); Oregon, Benton Co., 5 mi.N.E. Corvallis, McDonald Forest, Oak, Cr.Gate in shady, marsh D.L. Mays, April 1965 (Pinned: 2 m#, 2 f#) (ORSU); USA, OR, Hood River Co., Mt. Hood NF. Nr. Horsethief, Mdw. 45.3366°N 121.573°W, 9.vii.2008 3570' 95%EtOH, coll.: J.D. Petersen (Alcohol: 1 m#) (ISIC); OREGON – Lane Co., #1, Salt Creek, 24 June 1959, George W. Byers (Pinned: 1 m#, 2 f#) (KU); OREGON, Yamhill County, Peavine Ridge, VI-13 1953, Fender Sta.3A (also June 16, 1953, July

7, 1953) (Pinned: 2 m#, 1 f#) (UMMZ); USA, Oregon, Yamhill Co., Peavine Rd, upper Deer Creek, 45°14.38'N 123°23.15'W 400m, 13.vii.2011 coll. G.W. Courtney, from roadside seepage (Alcohol: 2 f#) (ISIC); WA King Co., Issaquah: nr. L. Sammamish, 26/APR-17/MAY/1998/, Brian K. Urbain, Malaise Trap (Pinned: 1 m#) (ORSU); Longmire's Springs, Mt. Rainer, Wash., Aug. 2, 05 (Pinned: 1 m#) (USNM); WASHINGTON, Olympic Nat.Pk., Olympic HotSpgs., July 20, 1953, K.M. Fender (Pinned: 1 m#) (UMMZ); USA, Washington, Jefferson Co., Olympic National Park, Queets River Valley, mile 2.0, 47°33.06'N 124°11.80'W 45m, 28 May 2011 coll. GW Courtney, from roadside seepage (Alcohol: 1 m#, 1f#) (ISIC); USA, Washington, Jefferson Co., Olympic National Park, Queets River Valley, mile 2.0, 47°33.06'N 124°11.80'W 45m, 28 May 2012 coll. GW Courtney, from roadside seepage (Alcohol: 23 larvae) (ISIC) Seattle, King Co. WASH. 9 May 1927, M. & N. Deyrup / PERC 0051944 (Pinned: 1 m#) (PERC)

Taxonomic Notes. *Bl. fenderiana* is one of the most interesting species of Bittacomorphinae from the standpoint of morphology, as it exhibits plesiomorphic characters. The most notable character is the distinctly bilobate epandrium with posteromedial styles.

Bl. fenderiana can be easily separated from the other Nearctic *Bittacomorphella* by the combination of legs with a single white band at tarsomeres 1, 2, and 3 with the margins of the scutum outlined in yellow, the yellow forming a distinct patch posteromedially. Additionally, *Bl. fenderiana* is the only species of Bittacomorphinae in the Nearctic with a strongly bilobate epandrium and a basal lobe on the gonostylus.

Ecological Notes. The stronghold of *Bl. fenderiana* is the Pacific Coast Range of the western Nearctic, including the Olympic Peninsula. Specimens have also been collected in the Cascade Range in Washington and Oregon. The species range appears to be delimited by the Pacific Ocean to the west and the Great Basin Desert to the east. The northern and southern limits of the range are not as easily defined, likely due to limited sampling. The southern extent of the range likely follows the California

Coast Range south until the prevailing climatic envelope becomes too xeric, probably near San Francisco Bay. The northern range limit is even more difficult to ascertain: coastal temperate rainforest extends north through British Columbia to the Alaska Panhandle, as extreme northwestern North America has seen only cursory sampling for ptychopterids.

Bl. fenderiana is associated primarily with the temperate rainforests of the Nearctic Pacific coast. It is regularly found in association with *Ptychoptera sculleni* Alexander and an undescribed species in the *Ptychoptera lenis* group. Unfortunately the knowledge of the larval habitat of *Bl. fenderiana* is known only from one site on the Olympic Peninsula and one in the Oregon Coast Range. These sites consisted of stream seepages along road cuts, with deposits of organic particulate matter upon the margins. Distribution of larvae was highly localized, with all larvae collected at the Olympic Peninsula site retrieved from a single sediment sample among many collected that day.

Bl. fenderiana has also been found in sympatric association with *B. occidentalis* in Oregon. Unfortunately there is only a single larval record, which makes it difficult to provide any inferences with regard to the mechanisms facilitating this sympatry.

***Bittacomorphella jonesi* Johnson (1905)**

Bittacomorpha jonesi Johnson, 1905: 75–76 (original description)

Bittacomorpha (Bittacomorphella) jonesi Johnson, Alexander 1916: 546 (key)

Bittacomorphella jonesi Johnson, Alexander 1919: 781, 790 (catalog)

Bittacomorphella jonesi Johnson, Alexander 1920: 780-783 (redescription)

Bittacomorphella jonesi Johnson, Alexander 1927: 9 (catalog)

Bittacomorphella jonesi Johnson, Peus 1958: 11 (catalog)

Bittacomorphella jonesi Johnson, Alexander 1965: 98 (catalog)

Diagnosis

Adult. Legs with two white bands, narrow proximal band around upper portion of tibia, second band distal tip of 1st, 2nd & 3rd tarsomeres. Epandrium sub-quadrate, epandrial claspers with basal lobe.

Description

Adult. Measurements (n=5). Overall length: 10.45mm (9.68–11.16mm); **Head.** Width (n=3): 0.77mm (0.67–0.82mm); Height: 0.70mm (0.67–0.75mm); Length: 0.40mm (0.36–0.43mm); Flagellum length: 6.48mm; Flagellomere proportions: 1.00, 1.00, 1.13, 1.22, 1.19, 1.19, 1.19, 1.05, 1.11, 1.05, 1.00, 1.00, 0.91, 0.91, 0.86, 0.69, 0.61, 0.61, 0.22; Maxillary palpus length: 1.23mm; Maxillary palpus segment proportions: 0.19, 1, 1.26, 0.92, 1.34; **Thorax.** Length: 1.35mm (1.28–1.43mm); Height: 1.31mm (1.29–1.37mm); Wing length: 6.73mm (6.25–7.10mm); Wing width: 1.46mm (1.23–1.61mm); Leg Proportions: Femur: 1.0, 1.06, 1.15mm; Tibia: 0.97, 0.94, 1.06; Tarsomeres: Foreleg 0.57, 0.20, 0.14, 0.04, 0.04, Midleg 0.58, 0.22, 0.14, 0.04, 0.04, Hindleg 0.64, 0.23, 0.15, 0.03mm, 0.04; **Abdomen.** Length: 8.7mm (8.04–9.30mm); Male tergite proportions 1.00, 2.88, 1.85, 1.74, 1.53, 0.75, 0.19; **Male Genitalia.** Width: 0.59mm; Height: 0.59mm.

Head. Head extremely closely pressed to thorax, generally triangular in shape, frons broadly domed with vertex well above dorsal margin of eye, medial suture clearly evident, extending between antennal bases to dorsal margin of face. Antennal scape ovoid in cross-section, provided with three socketed sensillae subdorsally along anterior margin; 18-19 Flagellomeres. Face marginally distinct, shallowly incised by clypeolabrum. . Clypeolabrum large, sub-acutely triangular, margins pinched at junction with face; lateral margins over maxillary palpus expanded to shelf, around 2x longer than wide, somewhat inflated. Maxillary palpus as sub-family. Hypopharynx short, foliform triangular, anteriorly directed and closely associated with apex of clypeolabrum. Labium not very prominent, largely hidden by clypeo-labrum. Labellae free medially, not forming pad.

Thorax. Antepronotum with two small fleshy triangular lobes emergent from dorsal margin, each provided with several setae. Scutum glabrous, shining, russet with limited dull orange highlights of transverse suture; prescutal pit prominent. Narrow prescutellum prominent, preceded by deep fold. Scutellum muddy yellow, with moderate group of setae medially, ovoid. Mediotergite faded yellow, dense patches of setae at anteriodorsal margin. Paratergite well developed, broad, semi-circular narrowing anteriorly. Sub-paratergal membrane inverse triangular in shape, with well sclerotized semicircular disk in antero-ventral apex. Episternum fairly flat, overall rectangular in shape; anepisternal suture fairly well developed, anepisternum roughly triangular with posterior dorsal apex reaching paratergite. Epimeron subrectangular in shape, convex, posterior margin heavily incised by laterotergite. Laterotergite lacrimiform, deject near center, free of setae. Halter and prehalter as per subfamily, posthalter very poorly developed, little more than small bump with several setae, post halter membrane poorly developed. Metapleuron with nearly complete suture, emerging from medio-posterior margin in straight line and terminating nearly at halter; immediately below halter low prominence with cluster of long clear setae. Episternum and epimeron and paratergite russet colored, darkening at ventral apices; laterotergite and metapleuron light yellow. **Wing.** Length: 8.25mm. Scattered macrotrichia on distal $1/10^{\text{th}}$ of wing, in cells R_{1+2} , R_3 , R_4 , R_5 , M. Vein C to wing apex, Sc, R_5 , R_1 , R_3 , R_4 & R_5 after forking and distal portion of M with macrotrichia, all other veins bare. Costa ending at wing apex. R_{3+4+5} stem 0.53mm straight; R_{4+5} stem 1.61mm; R_4 after fork 1.22mm, R_5 after fork 1.27mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 3.03 : 2.3$. r-m 0.18mm; M distal to r-m 2.72mm; Mdistal: $R_{3+4+5} = 5.13:1.00$, $R_4:M\text{distal} = 0.06:1.00$. CuA_2 1.29mm, strong medial curve, short and weak marginal curve. A_1 faint basally, paralleling Cu for a short distance before broadly curving to anal margin, arc becoming more acute apically. M-Cu joins M at r-m. Anal lobe very poorly developed, angle obtuse; alula undeveloped. Halter: length: 1.22mm; stem elongate, medial furrow shallow at base becoming obscure distally, long clear macrotrichia laterally, knob pale yellow with dark stout trichoid sensillae laterally, apex of knob bare; prehalter elongate,

sparsely provided with elongate clear trichoid sensillae; posthalter moderately developed, triangular, with several long translucent sensillae apically, largely free of webbing posteriorly. **Legs.** Coxae yellow, femur yellow fading to overall leg coloration of brown. Two white bands, first on tibia near femoral joint, second distal tip of 1st, 2nd & 3rd tarsomeres. Empodium closely associated with acropod, heavily provided with setae, unnotched.

Pre-genital Abdomen. As per genus. **Male Genitalia.** Epandrium 1.5x wide vs. long; subquadrate in shape with convex posterior margin, heavily bowed; not emarginate, no medio-sagittal suture distinguishable; epiproct not readily apparent, hypoproct well developed, broadly triangular tongue-like, extending posterior from medial posterior margin. Dorsal surface evenly provided with long setae (.1–.25mm). Epandrial claspers emergent from lateral portions of posterior margin, directed medio-posteriorly, tapering to acute point, curved hooklike medially; mediobasal margin with short triangular lobe; provided sparsely with long setae. Subepandrial sclerite well sclerotized, V-shaped, not fully divided basally, extending entire length of epandrium. Parameres glabrous, arising from dorso-medial portion of posterior margin of gonocoxite, laterally compressed; medial margin adhered to supraedeagal membrane nearly to apex; approximately halfway along length paramere bifurcated, divergence rounded, dorsal spine longer, directed at oblique dorso-posterior angle with slight sinuosity; ventral spine 75% length of upper spine, directed posterior. Spine tips broadly triangular. Gonocoxite conical, expanding to gonostylus, shorter than gonostylus. Gonostylus rounded at tip, outer surface heavily provided with long setae, sensillae along inner apex setiform: dorsal row 4, ventral row 3. Basal division of hypandrium sub-hemispherical band slightly emarginated on anterior margin and extended to terminal division, sparsely provided with setae laterally, slightly emarginate below gonocoxite, medial suture absent. Terminal division well-articulated with small membranous region, spadelike in shape, narrowly ovoid in cross-section. Two dorsolateral lobes prominent near posterior apex, fingerlike with apex heavily provided with setae. Aedeagus with sperm pump as per sub-family; Ejaculatory apodeme

comparatively large for family, approximately half the length of lateral ejaculatory processes, scythe like, with pointed apex, heavily sclerotized rhomboid plate forming base. Lateral ejaculatory process broadly triangular, lateral lobe swept anterior and slightly dorsally with apex rounded, mediodorsal margin extended dorsally as a thin square ridge, lower margin relatively straight; ventral lobe subquadrate, swept back anteriorly, lower edge very straight. Lateral sclerites of aedeagus moderately broad, very weakly curving dorsally at posterior extreme to apical apodeme, with medial membranous region narrow widening somewhat near base and apex; apical apodemes prominent, dorsal portion well developed, sub-conical projecting dorsally curving sharply posterior at apex, convergent and narrow, becoming narrower than shaft of aedeagus immediately anterior; ventral portion of apical apodeme broadening ventrally and divergent, becoming platelike and very thin, ventral apex closely articulated with sub-apical sclerite. Sub-apical sclerite present, complex; anteriorly a flat dorsal transverse plate articulated with the apical apodemes of aedeagus, two fine rod-shaped processes emergent from posterior margin directed antero-dorsal, the lateral edges of the plate extended laterally nearly to the ventral spine of the paramere, tapering to apex; dorsal plate forming roof of ringlike complex, sides and base formed by two parallel tongue-like lateral lobes extending posterior over terminal division, forming trough ventrally, curving slightly dorsally to a broadly rounded apex; anterior base of lateral lobes with ventral arm formed as triangular lobe emergent latero-ventrally, tapering and curving weakly ventrally towards apex, apex articulated at point of articulation between basal and terminal division. **Female**

Genitalia. Epigynium, trapezoidal, flat dorsally, posterior margin straight, lateral margins straight, posterior margin indistinct, medial suture indistinct. Cerci with base indistinct, dorsal margin weakly rounded, apex rounded, ventral margin swollen: weakly potbellied anteriorly, tapering posterior. Apex of cercus with single subelongate trichoid sensillae medially; cercus epigynium ratio 0.46 : 1. Hypoproct broad triangular, fused to ventral surface of epigynium. Genital fork not visible on specimens examined.

Hypogynium trapezoidal, dorsoanterior lobe present hypogynial valves with base indistinct, hypogynial valves triangular, medial notch square: 1.4x as deep as broad.

Figures. Adult. 36, 37; **Material Examined.** 38.

Material Examined. Holotype. Mt. Toxaway, aug N.C., alt 3000-4000 Ft. | Type, 7482 / C.W. Johnson, Collector (Pinned: 1 m#) (MCZ); **Other material examined: UNITED STATES.** USA, Georgia Gilmer Co., Chattahoochee Nat. For., seepage off Wilderness Rd., 34°48.779'N 84°35.023'W, May-15-2013: A. Fasbender (Alcohol: 1 m#) (ISIC); GEORGIA Lumpkin Co., #4 De Soto Falls, 21 June 1967 2000', George W. Byers (Pinned: 4 m#) (KU); Neel Gap Ga., 6-6-46, P. W. Fattig (Pinned: 1 m#) (USNM); GEORGIA Union Co. # 5, Neel's Gap 3050 ft., 21 June 1967, George W. Byers (Pinned: 1 m#) (KU); Bar Harbor, VII.21 Me (Pinned: 1 m#) (USNM); Cheboygan Co., Mich. 7/8 1940, R. I. Sailer (Pinned: 3 m#) (KU); Cheboygan Co., Mich. 7/4 1949, J. D. Lattin (Pinned: 1 m#) (ISIC); Michigan – Gogebic, Co. aug. 8, 1920, (J.S. Rogers) (Slide: 1 m#) (USNM); Woodworth's Lake, Fulton, Co NY, alt. 1650 ft., June 15, 1911, C.P. Alexander (Slide: 1 m#) (USNM)// Gloversville, N.Y., Alexander. (Pinned: 1 m#) (USNM); NORTH CAROLINA, Burke Co. #3, Linville Falls, 10 June 1960, George W. Byers (Pinned: 2 m#); Highlands, Macon, Co., N.C. 3850', 35°3.2'N 83°11.3'W, June 16, 1958, Jean L. Laffoon (Pinned: 6 m#; dates June 16 – July 15, 1958) (ISIC); NORTH CAROLINA, Macon Co. #3, Van Hook Glade, 11 June 1960, George W. Byers (Pinned: 8 m#, dates 11-12 June, 1960) (KU); NORTH CAROLINA Macon, Co. #8, VanHook Glade, 30 May 1977, 3250 ft., Byers, May & Young (Pinned: 2 m#) (KU); USA, NC, Macon Co., Nantahala Nat. For. 1005m, seepage @ Van Hook Glade, 35°04.39'N 83°14.31'W, May-13-2013: A. Fasbender (Alcohol: 1 f#) (ISIC); North Carolina, Linville Falls, 3200' VI-21-1939, (Slide: 1 m#) (C.P. Alexander) (USNM); NORTH CAROLINA Yancey, Co. #21. Crabtree, Meadows Camp, BRP mi., 339.5 31 May 1977, Byers, May & Young (Pinned: 2 m#) (KU); near Indian Gap, 5000', Great Smoky Mts, Sevier Co. Tennessee, 35°36.6'N 83°27.1'W// VII-7-1958 J. Laffoon (Pinned: 1 m#) (ISIC); VIRGINIA Giles Co.// #76 White Rock Br.// 1.5

mi.SE Kire// 4 July 1969 3000ft.// George W. Byers (Pinned: 1 m#, 1 f#); WEST VIRGINIA// Preston Co.
 #4// Cathedral St. Pk.// 28 June 1960// George W. Byers (Pinned: 1 m#) (KU)

Taxonomic Notes. *Bl. jonesi* is easily distinguished from other Nearctic *Bittacomorphella* by the distinctive white band located proximally on the tibia, as well as features of the male genitalia such as the posterior margin of the epandrium being convex (a character novel for the entire family) and the epandrial claspers having a small basal lobule. Placement of the species is problematic: analyses have either placed *Bl. jonesi* as sister to *Bl. fenderiana* + *Bittacomorpha*, or sister group to the remaining Bittacomorphinae. Much of this problematic placement is probably due to the large number of autapomorphic character states found in *Bl. jonesi*. One compelling synapomorphy placing *Bl. jonesi* near *Bittacomorpha* is the presence of a dorsal apical apodeme of the aedeagus (164).

Ecological Notes. Alexander believed that *Bl. jonesi* was closely associated with “Canadian woods” (Alexander 1920), which would currently be labeled the “Mixed Wood Plains Ecozone” (CFS 2013; NFI 2013). Indeed, the northern part of the range is closely associated with this habitat, with records as far north as coastal Maine and extending to the western extreme of the Upper Peninsula of Michigan (though more sampling in northern Wisconsin and possibly Minnesota would probably uncover additional localities). In contrast, the holotype was collected in North Carolina and in the intervening decades substantial material of this species has been collected from the southern Appalachians. The general extent of *Bl. jonesi* in the southern extent of the range is closely associated with the Appalachian Mountains, not extending to lower elevations.

The authors have only collected adults in western North Carolina and northern Georgia, near what appeared to be larval habitat. Alexander (1920) asserted that larvae of this species were typically found in “rich organic mud in shaded woods.” Both collection localities were located deep within deciduous woodland, with the western North Carolina site heavily overgrown with *Rhododendron*

maximum. The North Carolina locality also had very shallow organic substrate atop decomposing rock, covered in fallen leaves with a gentle flow of water flowing from a seepage area in the hillside across the substrate to a small (partially hyporrheic) stream. The north Georgia locality was in a large forested seepage off a roadside with expanses of open saturated organic sediment tinted with iron oxide. In general this site had the appearance of a classic *Bittacomorpha* site, and *Bittacomorpha* larvae were collected in sediment samples, though no *Bittacomorphella* larvae were found.

Despite the wide range, there is not currently morphological evidence to suggest the presence of a cryptic species complex, though there are no current molecular analyses of the species. *Bl. jonesi* has only been found in sympatric association with *B. clavipes*, though more extensive collection in the Appalachians may uncover associations with species in the *Ptychoptera quadrifasciata* Say complex, as both species may be somewhat tolerant of flowing water systems.

***Bittacomorphella nipponensis* Alexander (1924)**

Bittacomorphella nipponensis Alexander 1924: 51–52 (catalog)

Bittacomorphella nipponensis Alexander, Alexander 1927: 9 (catalog)

Bittacomorphella nipponensis Alexander, Peus 1958: 42–43 (redescription, illustration)

Bittacomorphella nipponensis Alexander, Nakamura & Saigusa 2009: 275, 277 (redescription, illustration)

Diagnosis

Adult. Legs with two white bands, first located at proximal apex of tibia, second of 1st, 2nd 3rd & 4th tarsomeres. Epandrium bilobate, lateral margins largely straight with convergent angle towards posterior margin; parameres spinelike, extend posteriorly past aedeagus.

Description

Adult. Measurements (n=3). Overall length: 10.45mm (9.68–11.16mm); **Head.** Width: 0.70mm (0.58–0.89mm); Height: 0.66mm (0.52–0.80mm); Length: 0.44mm (0.38–0.51mm); Flagellum length: 8.96mm; Flagellomere proportions: 1.00 : 0.73 : 0.96 : 1.04 : 1.04 : 1.00 : 0.93 : 0.93 : 0.89 : 0.84 : 0.76 : 0.68 : 0.68 : 0.68 : 0.60 : 0.54 : 0.50 : 0.10; Maxillary palpus length: 1.95mm; Maxillary palpus segment proportions: 0.28 : 1 : 1.52 : 0.96 : 3.68 **Thorax.** Length: 1.36mm (1.20–1.61mm); Height: 1.27mm (1.10–1.51mm); Wing length: 6.45mm (5.19–8.30mm); Wing width: 1.20mm (0.94–1.58mm); Leg Proportions: Femur: 1.0, 1.03, 1.14mm; Tibia: 0.95, 0.94, 1.11; Tarsomeres: Foreleg 0.76, 0.24, 0.14, 0.03, 0.04, Midleg 0.63, 0.23, 0.14, 0.03, 0.03, Hindleg 0.75, 0.27, 0.17, 0.02, 0.03; **Abdomen.** Length (n=2): 9.27mm (8.32–10.23mm); Male tergite proportions 1.00, 3.63, 2.22, 1.92, 1.75, 0.81, 0.27; **Male Genitalia.** Width: 0.67mm; Height: 0.81mm.

Head. Head extremely closely pressed to thorax, generally triangular in shape, frons broadly domed with vertex well above dorsal margin of eye, medial suture faint extending between antenna bases, two sulci extending posterior from antennae. Antennal scape ovoid in cross-section, provided with five socketed sensillae subdorsally along anterior margin; 18 Flagellomeres. Face subquadrate, shallowly incised by clypeo-labrum. Clypeo-labrum large, sub-acutely triangular, lateral margins somewhat pinched at junction with face, around 2x longer than wide, not inflated. Maxillary palpus as sub-family. Hypopharynx subconical triangular, directed anterior-ventrally. Labium prominent, extending beyond clypeo-labrum. Labellae fused medially, forming pad.

Thorax. Anteprenotum with U-shaped dorsomedial- notch. Scutum glabrous, shining, ruddy-brown to black sometimes with muddy yellow highlighting at anterior corners. Distinct fold at rear of scutum, small ovoid postscutum present. Scutellum muddy yellow, with dense group of setae medially, ovoid. Mediotergite olivaceous, dense patches of setae at anteriodorsal margin. Paratergite well

developed, narrow, ovoid. Sub-paratergal membrane triangular in shape, anterior point slightly tapered, fairly well sclerotized. Episternum fairly flat with prominence above midcoxa, rectangular basally with posterior-dorsal apex extended; anepisternal suture complete, not readily evident. Epimeron rectangular in shape, convex, posterior margin incised by laterotergite. Laterotergite lacrimiform, relatively flat with slight prominence towards halter. Halter and prehalter as per subfamily, posthalter fairly short, closely associated with posterior membranous association of halter. Metapleuron with complete suture, emerging from posterior ventral margin in a straight line and terminating at halter; immediately below halter low prominence with cluster of long clear setae. All pleurites ruddy brown to black. **Wing.** Length: 8.25mm. Very limited macrotrichia at extreme apex of cells R_1 , R_3 , R_4 , R_5 . Vein C to wing apex, Sc , R_5 , R_1 , R_3 , R_4 & R_5 after forking and distal portion of M with macrotrichia, all other veins bare. Costa ending at wing apex. R_{3+4+5} stem 0.53mm straight; R_{4+5} stem 2.08mm; R_4 after fork 1.34mm, R_5 after fork 1.21mm; $R_{3+4+5}:R_{4+5}$ -stem: R_4 = 1.00 : 3.92 : 2.52. r-m 0.29mm; M distal to r-m 3.13mm; Mdistal: R_{3+4+5} = 5.90:1.00, R_4 :Mdistal = 0.42:1.00. CuA_2 1.37mm, tight medial curve, longer and weak marginal curve. A_1 faint basally, paralleling Cu for a short distance before broadly curving to anal margin, arc becoming more acute apically. M-Cu joins M at r-m. Anal lobe very poorly developed, angle obtuse; alula undeveloped. Halter: length: 1.22mm; stem elongate, medial furrow shallow at base becoming obscure distally, long clear macrotrichia laterally, knob pale yellow with dark stout trichoid sensillae laterally, apex of knob bare; prehalter elongate, sparsely provided with elongate clear trichoid sensillae; posthalter moderately developed, triangular, with several long translucent sensillae apically, largely free of webbing posteriorly. **Legs.** Coxae yellow, overall leg coloration brown. First white band at proximal apex of tibia, second at 1st, 2nd 3rd & 4th tarsomeres. Empodium loosely associated with acropod, heavily provided with setae, shallowly notched posteriorly.

Pre-genital Abdomen. As per genus. **Male Genitalia.** Epandrium bilobate, trapezoidal in shape, 1.5x as wide as long, internal folds above epandrial clasper absent; epandrial lobe subpentagonal in

shape, posterior margin straight, base of lateral margins straight, parallel, closely pressed medially, medial margin directed laterally at abrupt angle at 1/2 length in straight line, lateral margin angled medially at 2/3 length in straight line, apex of epandrial lobe offset laterally, transitioning into posteriomedial stylet; posteriomedial stylets convergent, spinelike with rounded point. Epiproct prominent, web-like between epandrial lobes, sub-emarginate on posterior margin. Hypoproct moderately sclerotized ovoid plate with large posterior directed trichoid sensillae medially. Dorsal surface provided with long setae (.1–.25mm), becoming more numerous approaching posterior margin. Epandrial claspers emergent from posterior-lateral apex, directed medio-posteriorly, basally broad, tapering to a glabrous style at apex, curved dorsally, long thick setae along lateral margin. Parameres glabrous, laterally compressed, arising from dorso-medial portion of posterior margin of gonocoxite; basal section adhered to membrane above aedeagus; distal portion of paramere curving slightly latero-dorsally tapering to an acute point. Apex of paramere extends beyond terminus of aedeagus.

Gonocoxite conical, expanding to gonostylus, 2/3rds length of gonostylus. Gonostylus rounded at tip, sensillae along inner apex: single row with 11 dark sensillae along distal 2/3rd of style, traversing from directly medial at posterior apex towards dorsal surface anteriorly. Basal division of hypandrium bandlike, with gonocoxite set in trough. Terminal division well-articulated, pouchlike, incising basal division, margins heavily cupped dorsally, terminating in blunt triangular point. Ventral surface heavily provided with setae, dorsal surface glabrous. Aedeagus with sperm pump as per sub-family, Ejaculatory apodeme large for Bittacomorphinae, arcing prominently dorsally at base, only tapering near apex. Basal lateral apodeme with lateral section triangular winglike, not curved anteriorly, medial portion of posterior margin obliquely angled anteriorly towards lateral sclerites of aedeagus, distinct posterior protrusion present on posterior margin; ventral section distinctly triangular, medial margin heavily sclerotized, lateral extremity rising as ridge to merge with lateral section. Lateral sclerites of aedeagus narrow, sclerites widely separated, only 2x length width of Basal lateral apodeme. Apical apodeme

without dorsal lobe, ventral lobes broad rounded lacrimiform when viewed dorsally. Subapical sclerite well developed, internal section with anterolateral apices trapezoidal plate, posterior corners rounded, posterior margin weakly emarginated, ventral arm earlike, posterior-lateral apices extended; external section rounded broadly triangular, terminal section curved weakly dorsally. **Female Genitalia.**

Epigynum broadly trapezoidal, delineation of epiproct inevident, lateral margins broadly rounded at base, straight distally, medial suture inevident; epiproct with margin between cerci straight. Cerci narrow with base tapered heavily, dorsal margin weakly straight, apex narrowly rounded, ventral margin slightly convex, arced posterior. Apex of cercus with short, cylindrical nodule with single elongate trichoid sensillae medially; cercus epigynum ratio 0.75 : 1, cercus height:length 3:1. Hypoproct with apex broadly triangular, base not visible on specimens examined. Genital fork not visible on specimens examined. Hypogynium subhemispherical, base of hypogynial valves distinct as straight sulcus across hypogynium, hypogynial valves with rounded margins on either side of medial notch; medial notch small, narrow V-shape.

Figures. Adult. 39, 40; **Material Examined.** 41.

Material Examined. Holotype. Hinoemata, Japan., alt. 4000 ft., VII-24-1923, T. Esaki / Flying near, surface of, mountain, stream. / HOLOTYPE, *Bittacomorphella nipponensis*, C.P. Alexander (Pinned: 1 f#) (USNM); **Paratype.** Ozenuma, Japan, alt. 6545ft., VII-26-1923, Teise Esaki (Pinned 1 f#) (USNM); Japan, Akita-ken, Lake Tazuara, 260m, VI-13-51, Issiki Ito (Pinned: 1 m#; Slide: 1 m#) (USNM); Japan-Honshu, Akita Prov., Turunoya-650m, VI-14-51, (Issiki-Ito) (Slide: 1 m#) (USNM); **Other material examined. JAPAN.** Japan- Honshu, Kurukawa, Echigo, Aug. 15 1954, (Kintaro Baba) (Pinned: 2 m#; Slide 1 m#) (USNM)

Taxonomic Notes. *Bl. nipponensis* shows the character suite diagnostic of the Asian *Bittacomorphella*, but most of these are plesiomorphic or homoplastic when compared with other members of Bittacomorphinae. For further discussion see *Bl. esakii*.

***Bittacomorphella thaiensis* Alexander (1953)**

Bittacomorphella thaiensis Alexander, 1953: 98–99.

Diagnosis

Adult. Legs with white confined to 2nd & 3rd tarsomeres. Medial emargination of hypogynium not produced, knoblike prominence below posterior margin.

Description

Adult. Measurements (n=1). Overall length (average of combined head, thorax, and abdomen measurements): 10.45mm; **Head.** Width 0.72mm, Height 0.65mm, Length 0.47mm; Flagellum length (female): 2.89mm; Flagellomere proportions: 1.00, 0.90, 0.90, 0.90, 0.90, 0.90 : 0.81, 0.86, 0.72, 0.72, 0.68, 0.72, 0.72, 0.59, 0.59, 0.5, 0.5, 0.14, Maxillary palpus length 0.81mm, Maxillary palpus segment proportions 0.09 : 1 : 1.28 : 1.47; **Thorax.** Length 1.28mm, Height 1.54mm, Wing length 6.80mm, Wing width: 1.37mm, Leg Proportions: Femur 1.0, 1.08, 1.20, Tibia: 0.95, 0.97, 1.06, Tarsomeres: Foreleg 0.65, 0.21, 0.15, 0.02, 0.02, Midleg 0.57, 0.18, 0.12, 0.03, 0.03, Hindleg 0.75, 0.23, 0.15, 0.02, 0.02; **Abdomen.** Length: 7.80mm

Head. Head extremely closely pressed to thorax, generally triangular in shape, frons broadly domed with vertex well above dorsal margin of eye, medial suture weakly developed. Antennal scape ovoid in cross-section, provided with three socketed sensillae midway along anterior margin; 18 Flagellomeres. Face narrow, incised by clypeo-labrum to antennal bases. Clypeo-labrum large, sub-

acutely triangular, lateral margins straight, around 2x longer than wide, somewhat inflated. Maxillary palpus reduced to four segments. Hypopharynx triangular flattened, directed anteriorly. Labium prominent, extending beyond clypeo-labrum. Labellae D-shaped partially fused medially, forming ovoid pad.

Thorax. Antepronotum weakly developed, narrow low ridge. Scutum glabrous, chocolate brown. Scutellum muddy yellow, with dense group of setae medially, round. No postscutum present. Mediotergite ruddy-brown, pollinose, lacking medial setae. Paratergite well developed, ovoid tapering at apices. Sub-paratergal membrane triangular, extending extensively anteroventrally, comparatively well sclerotized. Episternum with dorsal portion depressed rising to midcoxa, rectangular in shape; anepisternal suture inevident; ridge rising from midpoint of anterior margin to dorso-posterior corner. Epimeron subpentagonal in shape, flat except for prominence below wing base and between mid- and hindcoxae posterior margin emarginated by laterotergite. Suture of epimeron and metapleuron indistinct, discernible only ventrally. Laterotergite D-shaped, flat, with a sparse cluster of long setae dorsal across dorsal surface. Metapleural suture complete, emerging from posterior ventral margin in a sinuous arc and terminating at halter; immediately below halter low prominence with cluster of long clear setae. All pleurites glabrous chocolate, with reduced pollinosity. **Wing.** Typical *Bittacomorphella* configuration. Macrotrichia absent from wing. Alula absent. Halter as per subfamily; prehalter spathate; posthalter very poorly developed rise. **Legs.** Coxae yellow, overall leg coloration brown. White banding confined to distal tip of 1st, 2nd & 3rd tarsomeres. Empodium closely associated with acropod, heavily provided with setae, notched posteriorly.

Pre-genital Abdomen. As per genus. **Female Genitalia.** Epigynium flat, with margins folded ventrally, subtrapezoidal tapering towards posterior margin; posterior margin straight. Cerci moderate, 3x length vs. height, nearly narrowing conspicuously at base. Hypogynium narrow, medial emargination

undeveloped, lateral apices of posterior margin formed to short rounded triangular lobes; medial knoblike prominence centrally located just below posterior margin.

Figures. Adult. 42, 43; **Material Examined.** 44.

Material Examined. Holotype. Thailand, Doi Chom, Cheng, 3000 ft., Jan.1.53, Prayoon C;

Paratype. Same as holotype.

Taxonomic Notes. In Alexander's 1953 description he notes that the paratype has a locality of: Near Wat at Doi Suteb, Chengmai, February 1953 (Deed C. Thurman). However, examination of the paratype shows the pinned specimen has the same locality data as the holotype.

This species is interesting morphologically: foremost, there is a complete lack of macrotrichia on the wing membrane, reminiscent of *Bittacomorpha*. The leg banding pattern is very simple and reminiscent of the western Nearctic *Bittacomorphella*. Finally, the clypeus is abbreviate like *Bittacomorpha clavipes*, but is broad unlike the narrow sclerite of that species. It is unfortunate that it is only known from females, as many of the most valuable phylogenetic characters reside in the male genitalia.

Discussion

Classification

One of the most notable outcomes of this analysis is the finding that *Bittacomorphella* is not monophyletic based on current character data. The characters historically used to differentiate *Bittacomorphella*, lack of an inflated 1st tarsomere and wing surface with macrotrichia, are symplesiomorphies. The only other consistent character that could be explained as potential synapomorphies (the apex of the epandrial clasper coming to a point) was not strong enough to form a

clade in this analysis. Indeed, there are numerous characters which are inconsistently distributed in *Bittacomorphella* and suggest the paraphyly of the group, examined in further detail in the morphology section below. In addition, an unpublished analysis by Chen Young of a dataset of ptychopterid COI containing sequences from *B. clavipes*, *Bl. jonesi*, and *Bl. lini* found *Bl. jonesi* as sister to *B. clavipes*.

Although there is strong evidence that *Bittacomorphella* is paraphyletic, it must be noted that this analysis was primarily based on adult morphological characters, heavily biased towards the male genitalia. Only three species (*B. clavipes*, *B. occidentalis*, and *Bl. fenderiana*) were included in the larval analysis; the only other *Bittacomorphella* larva known is *B. jonesi*, for which material was unavailable for this analysis. Additionally, there has been no comprehensive molecular study of the group.

Further, the relationships within *Bittacomorphella* were not well resolved in this analysis, and data from the mainland Asian species was lacking. Based on these considerations, it seems ill-advised to split *Bittacomorphella* at this point. For the time being *Bittacomorphella* will remain in the classification, with the understanding that (rather than a true clade) it represents a grade of bittacomorphine species which do not meet the diagnostic criteria of *Bittacomorpha*.

There are three clades that consistently appear in the analyses: *Bittacomorpha* + *Bl. fenderiana*, the *Bittacomorphella sackenii* group, and the Japanese *Bittacomorphella*. *Bittacomorpha* is an extremely well supported group, with numerous synapomorphies, and needs little more discussion. The inclusion of *Bl. fenderiana* as sister to *Bittacomorpha* is not as clear cut. Some of the most significant probably relate to the structure of the hypandrium, particularly the terminal division (160).

The Japanese *Bittacomorphella* were supported as a clade in both analyses, though often without particularly strong support. One of the most notable characteristics of these species is the presence of a bilobate epandrium, also found in *Bl. fenderiana* and other east Asian *Bittacomorphella*.

Generally there are a number of plesiomorphic character states in the Japanese species, which may confound their placement.

The *Bittacomorphella sackenii* group is easily recognized by its distinctive male genitalia, with the epandrium massively quadrate and the hypandrium acutely triangular (155). It is well supported in the BI analysis, but not in the MP tree. Regardless, the taxon is quite distinctive and benefitting from recognition. All species are found in the Coastal Range, Cascade Range and Sierra Nevada Range of the Nearctic. This group was recovered as sister to the Japanese *Bittacomorphella* in the BI analysis, but support was weak.

Placement of *Bl. jonesi* is variable. In the MP analysis *Bl. jonesi* was sister to *Bittacomorpha* + *Bl. fenderiana*, while in the BI analysis it was placed in a polytomy with *Bittacomorpha* + *Bittacomorphella fenderiana*, and the Japanese *Bittacomorphella* + *Bittacomorphella sackenii* group. There are characters that link *Bl. jonesi* to *Bittacomorpha*, such as the presence of dorsal apical apodemes of the aedeagus (168) and the lateral lobules of the terminal division of the hypandrium (161), but there also are many autapomorphic characters, such as the convex posterior margin of the epandrium.

Bittacomorphinae was recovered as an uncontested monophyletic group with numerous synapomorphies. Ptychopterinae was held as a well-supported clade in the MP analysis, but *Ptychoptera alexanderi* and *Ptychoptera yamato* fell into a polytomy with the remainder of Ptychopterinae as well as Bittacomorphinae in the BI analysis. Both *Ptychoptera alexanderi* and *Ptychoptera yamato* Nakamura & Saigusa show many similarities with Bittacomorphinae, particularly in the structure of the aedeagus. It is probable that these character states represent symplesiomorphies, and the addition of ingroup characters for Ptychopterinae may restore the subfamily as a monophyletic group. An analysis regarding the ingroup relationships of Ptychopterinae is currently underway, which will hopefully resolve this issue.

The sister group to Ptychopteridae remains enigmatic. In neither of the analyses was Tanyderidae supported as a direct sister group, which lends credence to molecular data that has pulled the family out of Ptychopteromorpha. In the parsimony analysis Psychodidae is suggested as sister to Ptychopteridae, but this seems highly unlikely. It is probably that this relationship is based heavily on both taxa having epandrial claspers, which appears to be a case of convergent evolution.

Morphology

Character state transformations relevant to the ingroup relationships of Ptychopteridae are provided in Figures 2&4 for the MP and Bayesian analyses. Synapomorphies for the family are also presented on the stem branch. For selected characters of phylogenetic or taxonomic importance further discussion is merited. Character numbers are given in parenthesis for each character state discussed.

One of the most distinctive differences between Bittacomorphinae and Ptychopterinae is the number of antennal flagellomeres. In Ptychopterinae the flagellum is composed of thirteen to fourteen articles, while in Bittacomorphinae the number can vary between eighteen and twenty one (51). It is difficult to determine whether the shorter or longer flagellum represents the ancestral character state, as both states are present in plausible outgroups. Bittacomorphinae have the ultimate flagellomere strongly reduced, forming a small button at the apex of the antenna (55). Another distinctive feature of the antennae is the development of verticillate sensillae in Ptychopterinae (52), which serve as a synapomorphy of the subfamily.

In *Bittacomorpha* the clypeus is very narrow, about the width of the compound eyes, giving the impression the eyes of *Bittacomorpha* are very large. In general, the clypeus of Bittacomorphinae is narrower than Ptychopterinae. However, this was excluded as a character state based on issues defining distinct character states. Additionally, in Bittacomorphinae the clypeus has a small lateral shelf which extends over the maxillary palpus, a synapomorphy of the subfamily (47).

The thorax is largely homogenous between Bittacomorphinae and Ptychopterinae, but there are significant differences which are useful in comparing the subfamilies. One of the most notable is that the prothorax is attenuated in Bittacomorphinae, with the anteprenotum plate-like and closely appressed to the prescutum (67). This has the effect of directing the head slightly ventral, and constraining its range of motion. This closely appressed state is a synapomorphy of the subfamily, and associated with this state is the flattening of the anterior apex of the prescutum (68). Additionally, *B. occidentalis*, *Bl. fenderiana*, and *Bl. jonesi* have a pair of small lobes near the dorsal apex of the the anteprenotum (66).

The prescutal suture is well defined in Ptychopteridae, merging with the transverse suture. In Ptychopterinae the transverse suture is complete. However, in Bittacomorphinae the transverse suture is incomplete, each side ending shortly after merging with the prescutal suture (70). Cleared specimens of *Bittacomorpha clavipes* and *Bittacomorphella fenderiana* show that even an internal suture is lacking. Again, this is a synapomorphy of Bittacomorphinae, but the alternate state in Ptychopterinae is itself a synapomorphy, as the posterior apex of the transverse suture is distinctly triangular in shape (72).

The pleuron of Ptychopteridae is roughly square in shape, with pleurites forming long rectangular plates. The episternum has a distinct anepisternal cleft below the paratergite, the dorsal margin with a strip of sclerotization extending to the anterior thoracic spiracle (78). In some species in both subfamilies the anepisternal cleft is marginally more sclerotized than the typical membranous state, but this is not consistently distributed. Additionally in most Ptychopterinae the upper extremity of the anepisternum is depressed.

There is a trend towards the elimination of the anepisternal suture in the family, most prominent in Ptychopterinae (77), where the remnant of the the anepisternal suture is only a short spur near the anterior basalare, if present at all. In Bittacomorphinae the anepisternal cleft is variably developed – complete in *Bittacomorpha*, *Bl. jonesi*, *Bl. fenderiana* and *Bl. nipponensis*, inevident in the

Bittacomorphella sackenii group and *Bl. esakii*. Unfortunately this character is only weakly informative for interpreting the relationships of Bittacomorphinae, primarily providing support to the *Bittacomorphella sackenii* group.

In a similar vein, the development of the metapleural suture is part of a wider trend in the reduction of the number of thoracic sclerites in the family (Lukashevich 2008, characters 77, 80, 84). In Ptychopterinae the metapleural suture is completely inevident, while in *Bittacomorpha* the suture is complete and easily distinguishable. In *Bittacomorphella* the suture is weakly developed and often incomplete. In almost all outgroups the anepisternal suture is well developed, suggesting an apomorphic state in Ptychopterinae. Assessing this character in Bittacomorphinae is more problematic, with the presence of a prominent suture possibly a reversal. The interpretation of *Bittacomorphella* provides support to the reversal hypothesis, as the weak development of the suture combined with the paraphyletic nature of the genus support the reversal hypothesis.

Finally, the suture between the epimeron and metapleuron is indistinct in Bittacomorphinae and some species of Ptychopterinae (80). Based on outgroups this is an apomorphic character state, appearing to be independently derived between Bittacomorphinae and those Ptychopterinae.

The wing has been one of the chief sources of diagnostic characters between the subfamilies and genera of Ptychopteridae. A classic diagnostic character between the subfamilies has been the presence of a forked medial vein, which is absent in Bittacomorphinae (95). Based on outgroup comparison the presence of M_2 is plesiomorphic, meaning an unforked M is a synapomorphy of the subfamily. Conversely, the presence of macrotrichia toward the apex of the wing membrane (106), one of the characters used to define *Bittacomorphella*, is probably a plesiomorphy based on presence of a similar character state in Ptychopterinae. Indeed, there are some *Bittacomorphella* with very limited macrotrichia (*Bl. esakii* and *Bl. nipponensis*) and *Bl. thaiensis* is completely lacking macrotrichia.

Bittacomorpha also lacks macrotrichia. Finally, CuA₂ has a distinctive bend in Ptychopterinae, becoming sigmoidal in Bittacomorphinae (100). This character may be independently derived in both taxa as early fossil Ptychopterinae and Bittacomorphinae have a relatively straight CuA₂ (Lukashevich 2008, Lukashevich 2012).

Outside of the prominent leg banding typically cited as diagnostic of Bittacomorphinae, the legs of Ptychopteridae have limited characters of phylogenetic relevance. One of the characters used to associate Ptychopteridae with Tanyderidae has been the presence of a folding 5th tarsomere (115) (Hennig 1973, Wood & Borkent 1989, Oosterbroek & Courtney 1995). However, this character is not consistently distributed in Ptychopteridae (Griffiths 1990). This examination demonstrates that the character of a folding tarsomere is not developed in any of the Bittacomorphinae, and is only found in a subset of Ptychopterinae. Within Ptychopterinae the development of the folding tarsomere does not demonstrate a readily identifiable cladistic pattern. Further investigation into this character is needed. The other significant character of the ptychopterid leg is the modification of the tibial spur of the foreleg into a forked, membranous structure in Bittacomorphinae (114). This character was first described by Young & Fang (2011), and is found throughout the subfamily.

The most striking character of the pregenital abdomen of the extant Ptychopteridae is the extension of the second abdominal segment (120), which is clearly apomorphic for the extant taxa based on the absence of this character state in Mesozoic Ptychopteridae (Lukashevich 2012).

The most prominent character in the female genitalia is the modification of the cerci of Ptychopterinae into a hardened ovipositor (121, 130). This correlates to a difference in oviposition behavior between Bittacomorphinae and Ptychopterinae (see Ecology below). Lukashevich (2012) reports that heavily sclerotized cerci appear to have arisen independently several times in the fossil lineages of Ptychopteridae.

The male genitalia provide the bulk of the characters useful in ascertaining the phylogenetic structure of Ptychopteridae. Another manuscript is in preparation which covers the characters and homologies of the genitalia of the family in more detail. The following discussion primarily is focused on the ingroup character state distributions for Bittacomorphinae.

The epandrium is a rich source of characters for this group. At a fundamental level, the character state polarity between a bilobate and plate-like epandrium is important for determining the distribution of other characters (137). In the extant Ptychopteridae the bilobate character state is part of the ground plan, and thus any transformations to a plate-like epandrium are apomorphic. The plate-like epandrium has arisen three times in Bittacomorphinae: *Bittacomorpha*, the *Bittacomorphella sackenii* group, and *Bl. jonesi*. It appears that the *Bittacomorphella sackenii* group developed this state independent of *Bittacomorpha* or *Bl. jonesi*, between which the character state homology is more ambiguous. If *Bl. jonesi* is sister to *Bittacomorpha* + *Bl. fenderiana* it suggests that *Bl. fenderiana* exhibits a reversal to the bilobate state.

The epiproct is closely associated with the epandrial lobes of Bittacomorphinae. In those taxa with a plate-like epandrium it is inevident, while it is easily distinguishable as a web of sclerotization between the lobes in bilobate taxa (140). On exception is *Bittacomorpha fenderiana*, which is bilobate but lacks a distinguishable epiproct. A distinguishable epiproct is a plesiomorphic state in the subfamily. The hypoproct is modified into an ovoid plate in all Bittacomorphinae except *Bl. jonesi* (141). This lends credence to *Bl. jonesi* being an early diverging bittacomorphine, as the tongue-like state is predominant in Ptychopterinae.

The presence of a pair of posteromedial styli of the epandrium is another potential ground plan character, but this is not well resolved (139). There are several species of Ptychopterinae which have a structure that appears homologous, but the probable ground plan state of the ptychopterine epandrium

appears to lack this characters (pers. obs.). Further, *Bl. jonesi* lacks this structure. If *Bl. jonesi* is a member of the *Bittacomorpha* + *Bl. fenderiana* clade this suggests an autapomorphic loss, but if *Bl. jonesi* is sister to the remainder of Bittacomorphinae this may indicate the similar structure in Ptychopterinae is homoplastic and the posteromedial style is a synapomorphy of the remainder of Bittacomorphinae. The transformation between the states is significant, with *Bittacomorpha* and the *Bittacomorphella sackenii* group having the style knob-like, while the Japanese *Bittacomorphella* and *Bl. jonesi* have the structure developed as an acute stylet.

The epandrial claspers are one of the most striking features of the male genitalia of Ptychopteridae, and they are most well-developed in Bittacomorphinae. At their point of articulation in *Bittacomorpha* and the *Bittacomorphella sackenii* group there is an internal fold in the epandrium (182). This fold may function to increase the range of motion of the clasper, but there is no definitive evidence of this. Based on the current phylogeny it appears that these character states are convergent between the two taxa, possibly based on both of them having developed a plate-like epandrium that does not have the same flexibility as the bilobate type.

The epandrial claspers are articulated by a subepandrial sclerite (183). In the *Bittacomorphella sackenii* group this sclerite is V-shaped and has a point of articulation with the claspers, but in the remainder of Bittacomorphinae the sclerite is divided and fused to the base of the clasper. The V-shaped state is probably a synapomorphy of the *Bittacomorphella sackenii* group, and may be related to the ability of the hypandrium to clasp with the epandrium.

One of the characters of greatest interest in the epandrial claspers of Bittacomorphinae is the configuration of the apex (181). In *Bittacomorpha* this is a pad with numerous stout trichoid sensillae. In *Bittacomorphella* the apex is variable developed to an acute to obtuse point, and this is the only

potential synapomorphy of the group. However, this is not particularly compelling in light of the variance in the exact configuration of the point.

A bifurcate paramere is found in two species of *Bittacomorphella*, *Bl. jonesi* and *Bl. furcata* (151). It is not a compelling character to link the two, based on the distributions of other characters. The medial membrane of the paramere extending nearly to the apex is a synapomorphy of *Bittacomorpha* (153).

The shape of the hypandrium is the most striking character of the *Bittacomorphella sackenii* group (154). In this clade it is triangular and relatively narrow, unlike the subhemispherical structure seen in the remainder of Bittacomorphinae. The epandrium and hypandrium can function together in these taxa to close tightly, probably to enhance clasping during copulation.

The terminal division of the hypandrium also distinguishes between taxa. It is important in defining the *Bittacomorpha* + *Bl. fenderiana* clade, where the terminal division is wider than broad unlike the remainder of the subfamily (159). Similarly, the lateral lobules of the terminal division are the purported synapomorphy linking *Bl. jonesi* to the aforementioned clade (160).

The apical apodemes of the aedeagus are a synapomorphy of Bittacomorphinae. The ventral apodemes are present in all bittacomorphines (166), but the dorsal apodemes are found only in *Bittacomorpha* and *Bl. jonesi*, suggesting their association (167). However, *B. fenderiana* lacks these dorsal apodemes, making this homology assessment uncertain. The inflated membrane over the aedeagus in *Bittacomorpha* is probably related to these apodemes, and the medial membrane between the parameres (168). However, the function of this inflated membrane is unclear.

The aedeagus has many useful characters for delineating species, and is useful in Ptychopterinae for phylogenetics, but is not very informative for intraspecific relationships in Bittacomorphinae. The

ventral portion of the lateral ejaculatory process extends into a membranous window in the sperm sac in most of Bittacomorphinae, but in *Bl. pacifica* and *B. jonesi* it does not (174), though as this state is found in Ptychopterinae this is weak evidence that these represent sister species.

The subapical sclerite of the aedeagus three broad configurations in Bittacomorphinae (176). In the Japanese *Bittacomorphella* and *Bl. sackenii* + *Bl. pacifica* it is conical, while in *Bittacomorpha* it is flattened to a triangular plate. *Bl.* has a highly modified plate that is folded at the lateral margins, while in *Bl. furcata* and *Bl. fenderiana* the sclerite is reduced and is closely associated as a sheath-like structure to the apex of the aedeagus. The wide range of states makes it difficult to interpret the polarity and ranking utility of this character.

Ecology

Bittacomorphinae is a lineage typically associated with seepage habitats and other instances of slow moving water flowing across an organic substrate (Alexander 1920, Harris & Carlson 1978, Bowles 1998). Most of this research has focused on the relatively common *B. clavipes* of the eastern Nearctic. *B. clavipes* is often associated with iron oxide seeps, characteristic for their bright orange color. In fact, bittacomorphine larvae readily integrate iron oxide into the surface of the cuticle, giving them an orange color. Specimens retrieved from environments lacking in iron oxide have a more translucent white tone. In *Bittacomorpha* this iron oxide deposition occurs across the surface of the cuticle. In *Bl. fenderiana* larvae examined there are large clumps of hardened substrate fixed to the thoracic and abdominal cuticular extensions, with less deposition directly on the remaining cuticle. The adaptive significance of this iron oxide deposition is still unknown.

An interesting convergence of morphology and ecology is found in the differences of oviposition between the subfamilies of Ptychopteridae. Female *P. pendula* and *P. quadrifasciata* have been observed ovipositing in both the wild and a lab setting by flying over a suitable larval habitat and then

diving abdomen first to the water surface, depositing a single egg, and returning to flight. In contrast, lab raised *B. clavipes* lay mats of eggs on a flat substrate near the water's surface. This appears to explain the difference in female cerci between the two groups, with ptychopterine species having an elongate, hardened ovipositor to break through surface tension.

While *B. clavipes* typically is found in seepages or slow, shallow streams, the limited evidence provided by localities where *Bittacomorphella* has been collected suggests a more adaptable ecological profile. In the eastern Nearctic *Bl. jonesi* can be found in classic *B. clavipes* seepages with deep organic sediments in the Appalachian Mountains. However, in the same region the species has been collected from shallower sediments found on wet hillsides in New York (Alexander 1920) or adults have been found in similar habitats in North Carolina (Fasbender pers. obs.). In these instances there were deciduous leaves covering the organic substrate, which was fairly shallow in North Carolina. *B. occidentalis* typically is found along the Pacific region in similar habitats to *B. clavipes*. However, *Bl. fenderiana* larvae have been associated with shallow margins of organic material along seepages.

Species of Bittacomorphinae are often sympatric with other ptychopterids, particularly ptychopterines. In some instances of sympatry larvae of multiple species can be extracted from the same sediment sample. *B. clavipes* has been found sympatric with *P. quadrifasciata* across the eastern Nearctic (Harris & Carlson 1978, Fasbender & Courtney pers. obs.). Additionally, there is at least one instance of *B. clavipes* being found in association with *P. l. coloradensis* at 2775 meters elevation. *B. occidentalis* has been recorded in the same seepages as *P. byersi*. *Bl. fenderiana* is has been collected in the same event with *P. townesi*, *P. sculleni*, and another undescribed species of *Ptychopera*. Finally *Bl. jonesi* has been recorded in the same locality as *B. clavipes*, the only example of bittacomorphine sympatry.

B. clavipes, if regarded as a single species, is one of the most widely distributed species in the Nearctic. It is known from Newfoundland (Tjeder 1960) west to eastern British Colombia (R. Cannings, pers. comm.) south throughout the U.S. to Florida, Texas and Arizona. Interestingly, there is a confirmed specimen from Costa Rica, expanding the range of the subfamily into the Neotropics. The sole other species in *Bittacomorpha*, *B. occidentalis*, is confined to the comparatively limited range of the Pacific region.

Bittacomorphella is much more limited in distribution, generally being associated with wet mountain ranges. *Bl. jonesi* is found in the Appalachian Mountains, extending in the north as far west as Cheboygan County Michigan. The *Bl. sackenii* group extends along the west Coast to the Sierra Nevadas, with *Bl. pacifica* being the most widely distributed across the Coast Range and Cascade Range. *Bl. furcata* and *Bl. sackenii* are endemic to the Olympic Peninsula and Sierra Nevada Range, respectively. *Bl. fenderiana* is found across the west coast.

The ranges of the east Asian *Bittacomorphella* are generally much less documented. Nakamura and Saigusa (2009) provide the best range information on the Japanese species, while the other members of the group are known only from a handful of collection localities typically cited in the original descriptions.

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Appendix 1: Modified Bittacomorphinae FLYTREE morphological character list

The FLYTREE morphological dataset (Lambkin *et al*, 2013) was used as a base for the development of this character set. The descriptions of these characters are taken from Lambkin *et al*, 2013, with the character number in that analysis given in parentheses before the text, which is not provided for characters not included in the prior analysis. An asterisk after this number indicates that character states have been either renumbered based on the use of Nannochoristidae as an outgroup, or the character states have been modified to better reflect the features found in lower Diptera (ex. the number of antennal flagellomeres). Character 176 is of uncertain homology to character 360 in the Lambkin *et al* analysis.

LARVAL CHARACTERS

Larva, head

1. (8) Posterodorsal margin of head capsule: (0), incapable of intermolt cuticle deposition; (1), capable of intermolt cuticle deposition
2. (9*) Postgenae: (0); postgenal lobes narrowly in contact or separated by a narrow membranous area; (1), forming a postgenal bridge; (2), widely separated
3. (15) Tentorial bridge (transverse tentorium, tentorium extends transversely to form a posterior bridge): (0), present; (1), absent
4. (16) Antennal segments: (0), none; (1), one; (2), two; (3), three or more
5. (17*) Length of first instar larval antenna: (0), short, about as long as maximum diameter; (1), long, several times longer than maximum diameter
6. (20*) Larval stemmata: (0), none; (1), one; (2), two; (3), five

Larva, mouthparts

7. (27) Labrum: (0), dorsoventrally flattened; (1), conical
8. (28) Brushes on ventral surface of labrum: (0), absent; (1), well-developed; (2), complex
9. (29) Premandibles: (0), absent; (1), present

10. (30) Premandible: (0), a simple unadorned sclerite; (1), with a comb-like row of evenly spaced anteriorly directed teeth
11. (31) Invaginated premandible apodeme: (0), absent; (1), present
12. (32) Premandible: (0), mainly external, with small, invaginated apodeme for insertion of labral retractor muscles; (1), with external portion and invaginated internal portion bearing separate insertions of two labral retractor muscles, movable in anteroposterior direction and capable of forceps-like action resulting from contraction of the labral compressors pulling the intertorma in dorsal direction; (2), mainly internal, serving almost entirely as a point of insertion of labral retractor muscles, with small remnant of external sclerite
13. (35) Torma: (0), fused with the dorsal labral sclerite; (1), articulated
14. (36) Mandibular rotation: (0), horizontal; (1), oblique or vertical
15. (38) Mandibular epicondyle: (0), near junction of genae and frontoclypeal apotome; (1), on tentorial phragma
16. (39) Mandible: (0), uniformly sclerotised; (1), apex and base separated by a zone of membranous cuticle; 2) separated into two distinct articles; (3), subdivided into more than two articles
17. (41) Subapical aboral surface of mandible: (0), bare; (1), with comb-like row of long curved setae
18. (42) Apex of mandible: (0), without comb; (1), with multi-toothed comb
19. (45) Mandibular chela: (0), absent; (1), present
20. (50) Mandibular prosthema: (0), on articulated lobe; (1), arising directly from adoral surface of mandible
21. (51) Cardo: (0), free from anterior margin of head capsule; (1), fused with, or closely appressed to, anterior margin of head capsule
22. (53) Maxillary palpus: (0), palpusiform; (1), flush with the surface of the maxilla and recognizable only by a ring surrounding the sensilla
23. (56) Cibarial filter 'pharyngeal filter': (0), absent; (1), present
24. (57) Cibarium: (0) simple, unmodified; (1), funnel-shaped filter: comb-like, transverse filaments; (2), series of transverse folds with "comb"-like projection used to filter particles from waters; (3), T-shaped ridges; (4), cibarial filter in basal sclerite without t-ridges
25. (59) Prementohypopharyngeal apparatus: (0), absent; (1), present
26. (62) Postmentum (hypostoma): (0), a simple, unadorned sclerite; (1), with serrate anterior margin

27. (63) Postmentum (hypostoma): (0), a separate plate; (1), fused to postgenae

Larva, thorax and abdomen

28. (69) Free abdominal segments (excluding anal division): (0), 9 segments; (1), 8 segments; (2), 7 segments; (3), 6 segments; (4), 5 or fewer segments
29. (70) Body segments: (0), without secondary divisions into annuli or intercalary rings; (1), with complete secondary divisions
30. (74) Crochet tipped proleg(s) on anal division: (0), absent; (1), present
31. (78) Anal papillae: (0), present; (1), absent
32. (79) Number of Malpighian tubules: (0), six; (1), five; (2), four; (3), three or less

Larva, respiratory system

33. (80) Respiratory system of full grown larva: (0), polypneustic (holo-, peri- or hemipneustic); (1), oligopneustic (amphi- or metapneustic); (2), apneustic
34. (83) Spiracles on anal division: (0), Type I; (1), Type II; (2), Type III
35. (85) Position of posterior abdominal spiracle(s): (0), lateral; (1), dorsal or terminal

PUPAL CHARACTERS

36. (87) Stigmatophore (siphon bearing posterior abdominal spiracles) longer than diameter of spiracle: (0), absent; (1), present
37. (97) Body: (0) tergites and sternites darkly sclerotized; (1), tergites darkly sclerotized and sternites lightly sclerotised; (2) tergites and sternites lightly sclerotised
38. (100) Thoracic respiratory organ; a plastron-bearing gill: (0), absent; (1), present
39. (103) Metathoracic leg sheath: (0), extended beyond wing sheath, parallel to sheaths of other two legs or superposed; (1), bent in an S-shape, concealed beneath wing sheath, ending beside apex of mesothoracic leg

ADULT CHARACTERS

Adult-HEAD

Eye

40. (108*) Male eyes; holoptic/dichoptic condition: (0), dichoptic; (1), broadly holoptic, separated by no more than width of median ocellus; (2), eye bridge

41. (110) Ocelli: (0), three; (1), vestigial or absent

42. (111) Ocelli on raised plate: (0), absent; (1), present

Frons

43. Medial suture of frons: (0), absent; (1), present

Face

44. Facial sclerite heavily incised by clypeus: (0), present; (1), absent

Clypeus

45. (127*) Adult clypeus: (0), bulbous and projecting; (1), concave or flattened

46. (129) Clypeus: (0), not divided; (1), divided into postclypeus and anteclypeus

47. Clypeal shelf over base of maxillary palpus: (0), absent; (1) present

Postcranium

48. (135*) Hypostomal bridge: (0), absent; (1), present

49. (136) Well defined row of postocular setae: (0), absent; (1), present

Antennae

50. (142) Antennal pedicel of male: (0), not enlarged; (1), enlarged, globular and much wider than scape because of greatly enlarged Johnston's organ

51. (143*) Flagellar segments (not including the arista/stylus): (0), 20 or more; (1), 16-19; (2), 12-15; (3), 11 or less

52. (144) Antennal flagellum of male: (0), simple; (1), plumose; (2), setae in encircling whorls; (3), Verticillate

53. Cluster of setae on anterior surface of scape: (0), dispersed; (1), single row of setae present; (2), absent

54. Setae encircling pedicel: (0), absent; (1), single row

55. Ultimate flagellomere reduced: (0), absent; (1) present

Mouthparts

56. Mouthpart orientation: (0), hypognathous, (1) prognathous

57. Labium: (0), does not extend beyond clypeus (fused at apex); (1), extends beyond apex of clypeus

58. (158) Labellum: (0), absent; (1), present

59. Labellae size: (0), smaller than clypeus; (1), larger than clypeus

60. Labellae fusion: (0), not fused medially; (1), fused medially

61. (160) Pseudotracheae: (0), absent; (1), present

Adult-THORAX

Prothorax

62. (163) Precervicale: (0), absent; (1), present

63. (164*) Prothorax: (0), elongate; (1), not elongate

64. (170) Episternal lobe: (0), absent; (1), present

65. (171) Precoxal bridge: (0), absent; (1), present

66. Anteprenotal lobes: (0), absent; (1), present

67. Anteprenotum platelike: (0), absent; (1), present

68. Pronotum pressed against prescutum: (0), loose association; (1), closely pressed

Mesothorax

69. (172*) Scutum: (0), without transverse suture; (1), with transverse suture

70. (173) Scutum with transverse suture: (0), incomplete; (1), complete

71. Prescutal suture: (0), well defined; (1), indistinct

72. Posterior apex of prescutum: (0), indistinct; (1), sharply triangular; (2), rounded

73. Medial suture of prescutum: (0), well defined; (1), indistinct

74. (176) Supra-alar bristles: (0), absent; (1), present

75. (177) Post-alar bristles: (0), absent; (1), present

76. (179) Pleural suture of mesothorax between episternum and epimeron: (0), straight or slightly sinuous; (1), bent twice at almost a right angle

77. Anepisternal suture: (0), prominent, complete; (1) obscure, incomplete; (2) inevident

78. Anepisternal cleft: (0), absent; (1), membranous; (2), sclerotized

79. Meron: (0) absent; (1), present

80. Epimeron-metapleuron suture: (0), distinct; (1), indistinct

81. (192) Scutellar bristles: (0), absent; (1), present

82. (197) Dorsal area of anatergite; setosity: (0), bare; (1), setose (infrascapular setulae)

Metathorax

83. (208) Meron of metacoxa: (0), present; (1), absent

84. Metapleural suture: (0), present, prominent; (1), incomplete; (2), inevident

WING

85. (212) Wings on metathorax: (0), present; (1), absent

Axillary area

86. (214) Upper calypter: (0), not developed; (1), developed

Blade

87. (220) Costa: (0), circumambient, continuous around the wing, weakened along the posterior margin; (1), abbreviated, ending at or before M2

88. (224) Humeral crossvein: (0), present; (1), absent

89. (228) Subcosta termination: (0), complete, reaching costa; (1), subcosta incomplete, ending just short of costa; (2), reduced, never longer than half length of basal cells or ending opposite branching of Rs; (3), fused apically to R1

90. (230*) Crossvein sc-r: (0), absent; (1), present

91. (235) Rs: (0), not branched; (1), two-branched; (2), three-branched; (3), four-branched

92. (239) Wing vein R4+5: (0), branched; (1), unbranched or fused

93. (241*) Crossvein r-r between the first and second radial veins, usually named R2: (0), present; (1), absent

94. (244) Vein M: (0), not upcurved at fork of discal cell or at junction with crossvein r-m; (1), upcurved at fork of discal cell or at junction with crossvein r-m

95. (246) M2: (0), present; (1), absent

96. (247) Wing vein M3: (0), present; (1), absent

97. (248) Discal or discal medial: (0), present; (1), absent

- 98.** (250) Basal or basal medial cell: (0), present; (1), absent
- 99.** (251) Crossvein bm-cu: (0), present; (1), incomplete or absent (i.e. cells bm and dm partially united or fused)
- 100.** CuA2: (0), straight; (1), angled; (2), sigmoidal
- 101.** (259) First anal vein (A1 + CuA2 or A1): (0), present; (1), absent
- 102.** (260) First anal vein (A1 + CuA2 or A1): (0), reaching wing margin, even if only as a fold; (1), not reaching wing margin
- 103.** (261) Vein A2 sensu Starý (2008): (0), present; (1), absent or extremely shortened
- 104.** Anal lobe: (0), obtuse, (1), right angle; (2), convex
- 105.** (264) Veins of wing: (0), posterior veins well developed, as distinct as the veins of radial, subcostal and costal sectors; (1), costalised, posterior veins indistinct
- 106.** Macrotrichia on wing: (0), absent; (1), abundant; (2), confined to apex adjacent to costa; (3), scales present

Halter

- 107.** (265) Halteres on metathorax: (0), absent; (1), present
- 108.** Prehalter: (0), absent; (1), present
- 109.** Posthalter: (0), absent; (1), poorly developed; (2) well-developed

Legs

- 110.** Fore coxae closely appressed: (0), absent; (1), present
- 111.** (272) Fore tibial spurs: (0), present; (1), absent
- 112.** (273) Mid tibial spurs: (0), present; (1), absent
- 113.** (274) Hind tibial spurs: (0), present; (1), absent
- 114.** Foretibial spurs: (0), unmodified; (1), bifid, membranous
- 115.** (278) Last tarsomere of male: (0), not capable of being folded proximally; (1), capable of being folded forward against penultimate tarsomere
- 116.** 1st Tarsomere inflated: (0), absent; (1), present
- 117.** (279) Arolium: (0), present; (1), absent

118. (280) Mediolobus (pad like empodium): (0), absent; (1), present

119. (281) Setiform empodium: (0), absent; (1), present

Adult- ABDOMEN, non-genitalic

120. Second abdominal segment extended: (0), absent; (1), present

Adult- female genitalia

121. (298) Ovipositor, shape: (0), unmodified; (1), lance-like; (2) sickle shaped

122. (301) ST8 of ovipositor: (0), undivided; (1), plate-like, partly divided posteriorly, forming hypogynial valves; (2), completely divided longitudinally

123. (305) ST9: (0), external; (1), partially or fully invaginated

124. (306) Female T10: (0), present as separate sclerite; (1), not a separate sclerite

125. Epiproct: (0), Not evident; (1), Easily distinguishable

126. Hypoproct: (0), Present; (1) Absent

127. Epigynal complex: (0), Plate-like; (1), Reduced to heavily sclerotized band

128. (309) ST10: (0), present; (1), absent

129. (313) Female Cerci: (0), two-segmented; (1), one-segmented, free from each other

130. (317) Cercus: (0), lightly sclerotized; (1); heavily sclerotized

131. (318) Spermathecae: (0), absent; (1), 1; (2), 2; (3), 3; (4), 4

Adult-male genitalia

132. (327*) Vasa deferentia configuration: (0), U-shaped, apically approximated; (1), extended caudally, not arching back anteriorly

133. (328*) Accessory gland: (0) continuous with vasa deferentia; (1), separate or not continuous with vasa deferentia

134. (329*) Epididymis: (0), present; (1), absent

135. (330*) Male terminalia; flexion: (0), unflexed, projecting posteriorly; (1), dorsoflexed

136. (331*) Hypopygium: (0), unrotated or not permanently rotated (1), rotated permanently between 90-180°;

- 137.** (334*) Epandrium: (0), shallowly notched or posterior margin straight; (1), bilobate, not heavily incised medially; (2), bilobate, heavily incised medially
- 138.** (335) Epandrium and hypandrium: (0), fused ring; (1), separate
- 139.** Posterior margin of Epandrium with posteromedial style: (0), absent; (1), stylets; (2), low knob; (3), peglike; (4), subdivided
- 140.** Epiproct: (0), not readily apparent; (1), easily distinguishable
- 141.** Hypoproct: (0), completely membranous; (1), ovoid sclerite suspended in membrane; (2), tongue-like; (3), plate
- 142.** (336) Hypandrium and gonocoxites: (0), separate; (1), completely fused, no seams
- 143.** (337*) Gonocoxal apodemes: (0), confined to anterior margin of hypandrium, not extended as narrow process; (1), elongate, extending well beyond anterior margin of hypandrium
- 144.** Gonocoxite shape: (0), tapering to gonostylus; (1), expanding to gonostylus; (2), cylindrical
- 145.** Gonocoxal lobe: (0), absent; (1), present
- 146.** (342) Gonostyli articulation: (0), transverse or oblique; (1), dorsoventral
- 147.** Basal lobule of gonostylus: (0), absent; (1), present
- 148.** Gonopod with stout sensillae on medial apex: (0), absent; (1), present, forming ordered lines; (2) present, scattered
- 149.** Relative lengths of gonocoxite and gonostylus: (0), gonocoxites longer than gonostylus; (1), gonocoxites subequal to gonostylus; (2) gonocoxites shorter than gonostylus
- 150.** (344) Parameres: (0), paired and separate; (1), fused
- 151.** Paramere bifurcate: (0), absent; (1), present
- 152.** Basal portion of paramere directed medially: (0), present; (1), absent
- 153.** Medial membrane of paramere: (0), absent; (1), extending less than $\frac{1}{2}$ length of paramere; (2), extending nearly to apex of paramere; (2), forming hood with fused paramere
- 154.** Shape of hypandrium: (0), indistinct; (1) roughly triangular; (2), sub-hemispherical band; (3) subtrapezoidal; (4) ringlike
- 155.** Eversible sac of hypandrium: (0), absent; (1), present
- 156.** Hypandrial spathate lobes: (0), absent; (1), present

- 157.** Terminal division of hypandrium: (0), absent; (1), present
- 158.** Terminal division articulation: (0), poorly articulated; (1), well-articulated
- 159.** Terminal division shape: (0), terminal division broader than long; (1), terminal division longer than broad
- 160.** Lateral lobules of terminal division: (0), absent; (1), present
- 161.** Terminal division and aedeagus rotated: (0), unrotated; (1), rotated
- 162.** (345) Aedeagus: (0), at least partly sclerotised; (1), entirely membranous
- 163.** (346) Aedeagus or phallus: (0), single tube, terminal opening, apically; (1), with three slender filaments, each with separate opening
- 164.** Aedeagus shortened: (0), more than 2x as long as wide; (1), less than 2x as long as wide
- 165.** Aedeagus medial membrane: (0), aedeagus composed of lateral sclerotized regions joined by medial membrane; (1), aedeagus uniformly sclerotized
- 166.** Ventral apical apodemes of aedeagus: (0), absent; (1), present
- 167.** Dorsal apical apodemes of aedeagus: (0), absent; (1), present
- 168.** Super aedeagal membrane inflated: (0), absent; (1), present
- 169.** (357*) Ejaculatory apodeme: (0), absent; (1), present
- 170.** Shape of ejaculatory apodeme: (0), narrow, tapering; (1), fanlike; (2), reduced
- 171.** Ejaculatory apodeme size: (0), larger than sperm sac; (1), smaller than sperm sac
- 172.** (360) Lateral ejaculatory processes: (0), absent; (1), present
- 173.** Lateral ejaculatory process orientation: (0), directed laterally; (1), directed anterior
- 174.** Ventral portion of lateral ejaculatory process: (0), does not extend into sperm sac; (1), extends into sperm sac
- 175.** (362) Ventral plate/Subapical Sclerite: (0), absent; (1), present
- 176.** Subapical sclerite shape: (0), not present; (1), present, conical; (2), present, platelike; (3), reduced
- 177.** (364) Male tergite 10: (0), present; (1), absent
- 178.** (365) Male sternite 10: (0), present; (1), absent
- 179.** Epandrial claspers: (0), absent; (1), present

- 180.** Epandrial clasper articulation: (0), well-articulated; (1), contiguous
- 181.** Epandrial clasper apex: (0), rounded; (1), pad; (2), point; (3), blunt
- 182.** Internal fold above epandrial clasper: (0), absent; (1), present
- 183.** (368) Subepandrial sclerite: (0), absent (membraneous, at least in part of length); (1), sclerotised along its entire length from base of phallus to hypoproct, forming subepandrial sclerite; (2), sclerotised, divided into bacilliform sclerites (processus longi) laterally
- 184.** (369) Male cerci: (0), present; (1), absent

Appendix II: Character Matrix

Nannochoristidae	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Anopheles gambiae	1	0	1	1	0	0	1	0	1	-	1	0	1	0	?	1	1	1	2	1	0	0	?	1	1	1	0	0	0	0	0	0
Arachnocampa flava	1	1	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	2	0	1	0	1	0	1	0	0	0	0	1	0	1
Bibio longipes	0	?	0	1	0	0	0	1	0	1	0	0	1	1	0	0	0	0	3	0	2	1	0	1	0	1	0	0	0	0	1	0
Bradysia tilicola	0	1	0	1	0	0	0	2	0	0	0	1	1	1	0	1	0	0	2	0	0	1	0	0	0	1	0	0	0	0	1	0
Chironomus tepperi	2	-	-	0	0	1	1	0	1	-	1	1	1	1	0	1	0	1	?	1	2	0	?	1	1	1	0	0	0	0	0	0
Clogmia albipunctata	1	?	1	1	0	0	0	2	1	-	0	1	0	1	0	1	1	0	2	2	0	1	?	0	0	1	0	0	0	0	0	0
Coboldia fuscipes	0	?	1	1	0	0	0	0	0	0	0	1	0	?	0	1	0	0	3	?	1	0	0	1	0	0	1	1	0	0	1	0
Edwardsina gigantea	2	-	-	0	1	1	0	0	0	0	0	0	0	1	1	0	?	0	2	3	1	1	0	0	1	1	0	0	0	0	0	0
Mayetiola destructor	0	?	0	1	0	0	0	0	1	-	?	0	0	?	0	1	0	0	2	2	?	?	?	?	?	?	0	1	?	?	0	1
Trichocera brevicornis	1	1	1	?	0	0	0	0	0	0	0	0	0	0	1	0	1	0	2	0	1	0	?	1	1	1	0	0	0	0	0	0
Protoplasa fitchii	1	?	0	?	0	0	0	0	1	-	0	0	0	1	0	1	0	0	2	3	2	1	0	1	1	1	1	0	1	1	0	0
Sylvicola fenestralis	1	1	1	1	0	0	0	0	0	1	0	1	0	1	0	1	1	0	2	0	1	1	0	0	1	1	0	1	0	1	0	1
Tipula abdominalis	1	1	1	?	0	0	0	0	1	-	0	1	0	1	0	1	0	0	2	3	0	0	0	1	0	1	0	0	1	0	0	1
Bittacomorpha clavipes	1	?	1	1	0	0	0	0	0	-	1	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	1	1	0	1	1	0
Bittacomorpha occidentalis	1	?	1	1	0	0	0	0	0	-	1	0	0	0	1	1	0	0	0	0	1	1	0	1	1	1	1	1	1	1	1	0
Bittacomorphella esakii	?	?	?	?	?	?	?	?	?	-	1	0	0	0	1	1	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1	0
Bittacomorphella fenderiana	1	?	1	1	2	0	0	0	0	-	1	0	0	0	1	1	0	0	0	0	1	1	1	0	1	1	1	0	1	1	0	1
Bittacomorphella jonesi	?	?	?	?	?	?	?	?	?	-	1	0	0	0	1	1	0	0	1	0	1	1	1	0	0	1	0	0	1	0	1	0
Bittacomorphella nipponensis	?	?	?	?	?	?	?	?	?	-	1	0	0	0	1	1	0	0	1	0	1	1	1	1	1	0	1	1	0	1	1	0
Bittacomorphella pacifica	?	?	?	?	?	?	?	?	?	-	1	0	0	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0
Bittacomorphella sackenii	?	?	?	?	?	?	?	?	?	-	1	0	0	0	1	1	0	0	0	0	1	1	1	0	1	1	0	1	1	1	1	0
Bittacomorphella furcata	?	?	?	?	?	?	?	?	?	-	1	0	0	0	1	1	0	0	0	0	1	1	1	1	0	1	1	0	1	1	1	0
Ptychoptera africana	?	?	?	?	?	?	?	?	?	-	0	1	0	0	1	0	0	0	2	3	0	1	0	0	1	1	1	1	1	1	1	0
Ptychoptera albimana	?	?	?	?	?	?	?	?	?	-	0	0	0	0	1	0	0	0	2	3	0	1	0	0	1	1	1	1	1	1	1	0
Ptychoptera alexanderi	?	?	?	?	?	?	?	?	?	-	0	0	0	0	0	1	0	0	2	3	0	1	0	0	1	1	1	1	1	1	1	0
Ptychoptera byersi	1	?	1	1	2	0	0	0	0	-	0	0	0	0	0	1	0	0	2	3	0	0	0	0	0	1	1	0	1	1	0	1
Ptychoptera javensis	?	?	?	?	?	?	?	?	?	-	0	0	0	0	0	1	0	0	2	3	0	1	0	0	1	1	1	1	1	1	1	0
P. (Parapteroptera) lacustris	?	?	?	?	?	?	?	?	?	-	0	0	0	0	0	1	0	0	2	3	0	1	0	0	1	1	1	1	1	1	1	0
Ptychoptera metallica	?	?	?	?	?	?	?	?	?	-	0	1	0	0	0	1	0	0	2	3	0	1	0	0	1	1	1	1	1	1	1	0
Ptychoptera pendula	1	?	1	1	2	0	0	0	0	-	0	0	0	0	0	1	0	0	2	3	0	1	0	0	1	1	1	1	1	1	1	0
Ptychoptera persimilis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ptychoptera quadrifasciata	1	?	1	1	2	0	0	0	0	-	0	1	0	0	0	1	0	0	2	3	0	1	0	0	1	1	0	1	0	1	0	1
Ptychoptera sculleni	1	?	1	1	2	0	0	0	0	-	1	1	0	0	0	1	0	0	2	3	0	1	0	0	1	1	0	1	0	1	0	1
Ptychoptera tibialis	?	?	?	?	?	?	?	?	?	-	0	0	0	0	0	1	0	0	2	3	0	0	0	0	1	1	1	1	1	1	1	0
Ptychoptera yamato	?	?	?	?	?	?	?	?	?	-	0	0	0	0	0	0	0	0	2	3	0	0	0	0	1	1	1	1	1	1	0	1

Appendix II: Character Matrix

	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91
Nannochoristidae	0	0	0	0	?	0	0	-	-	-	-	-	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	0	2
<i>Anopheles gambiae</i>	1	0	1	0	?	0	1	0	1	0	0	0	0	0	0	1	2	0	0	0	1	0	1	1	0	0	0	0	2
<i>Arachnocampa flava</i>	1	1	0	0	0	1	0	0	0	0	1	1	1	0	0	0	1	0	1	0	1	0	1	1	1	0	0	1	0
<i>Bibio longipes</i>	1	1	1	0	0	1	0	0	0	0	1	1	1	0	1	0	1	0	1	0	1	1	1	1	1	0	1	1	0
<i>Bradysia tilicola</i>	1	1	1	0	0	1	0	0	0	0	1	1	1	1	0	1	1	0	1	0	1	2	1	1	1	0	1	0	0
<i>Chironomus tepperi</i>	1	0	1	0	0	1	1	0	0	0	0	0	0	0	1	1	2	1	0	0	1	2	1	1	1	0	1	0	1
<i>Clogmia albipunctata</i>	1	0	1	0	0	1	0	0	1	0	0	1	0	0	0	1	2	0	0	0	1	2	1	1	1	0	1	2	1
<i>Coboldia fuscipes</i>	1	1	0	0	0	1	0	0	1	0	0	0	0	1	0	1	1	1	0	0	1	2	1	0	1	0	2	0	0
<i>Edwardsina gigantea</i>	0	0	0	0	0	1	0	0	1	0	2	1	0	0	0	1	2	0	0	0	1	2	1	1	1	0	1	0	2
<i>Mayetiola destructor</i>	?	1	1	?	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	1	0	0
<i>Trichocera brevicornis</i>	1	0	0	0	0	1	1	0	2	0	0	0	0	0	0	1	1	0	0	0	1	2	1	1	1	0	0	1	2
<i>Protoplasia fitchii</i>	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	1	2	1	1	0	0	0	1	3
<i>Sylvicola fenestralis</i>	1	1	0	0	0	1	1	0	0	0	0	1	1	0	0	2	1	0	1	0	1	2	1	1	1	0	0	1	1
<i>Tipula abdominalis</i>	1	0	0	0	0	1	1	0	2	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	3	1	2
<i>Bittacomorpha clavipes</i>	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	2	1	0	1	1	0	1	1	1	0	0	0	2
<i>Bittacomorpha occidentalis</i>	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	2	1	2	0	0	1	1	0	1	1	0	0	0	2
<i>Bittacomorpha esakii</i>	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	2	1	2	1	0	1	1	1	1	1	0	0	0	2
<i>Bittacomorphella fenderiana</i>	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	1	2	1	0	1	1	1	1	1	1	0	0	0	2
<i>Bittacomorphella jonesi</i>	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	2	2	2	1	0	1	1	1	1	1	0	0	0	2
<i>Bittacomorphella nipponensis</i>	1	0	0	0	1	1	1	0	0	0	0	0	0	0	1	2	2	1	0	1	1	1	1	1	1	0	0	0	2
<i>Bittacomorphella pacifica</i>	1	0	0	0	1	1	1	0	0	0	0	0	0	0	2	1	2	1	0	1	1	1	1	1	1	0	0	0	2
<i>Bittacomorphella sackenii</i>	1	0	0	0	1	1	1	0	0	0	0	0	0	0	2	1	2	1	0	1	1	1	1	1	1	0	0	0	2
<i>Bittacomorphella furcata</i>	1	0	0	0	1	1	1	0	0	0	0	0	0	0	2	2	2	1	0	1	1	1	1	1	1	0	0	0	2
<i>Ptychoptera africana</i>	1	0	0	0	0	1	1	0	1	0	1	0	1	0	0	2	1	2	0	0	1	1	1	1	1	0	0	0	2
<i>Ptychoptera albimana</i>	1	0	0	0	0	0	1	1	0	1	0	1	1	0	2	1	2	1	0	1	1	2	1	1	1	0	0	0	2
<i>Ptychoptera alexanderi</i>	1	0	0	0	0	0	1	1	0	1	0	0	0	0	2	1	2	0	0	1	1	2	1	1	1	0	0	0	2
<i>Ptychoptera byersi</i>	1	0	0	0	0	0	1	1	0	1	0	1	1	0	2	1	2	1	0	1	1	2	1	1	1	0	0	0	2
<i>Ptychoptera javensis</i>	1	0	0	0	0	0	1	1	0	1	0	0	0	0	2	2	2	0	0	1	1	2	1	1	1	0	0	0	2
<i>P. (Paraptychoptera) lacustris</i>	1	0	0	0	0	0	1	1	0	1	0	1	0	0	2	2	2	0	0	1	1	2	1	1	1	1	0	0	2
<i>Ptychoptera metallica</i>	1	0	0	0	0	0	1	1	0	1	0	0	1	0	2	1	2	0	0	1	1	2	1	1	1	0	0	0	2
<i>Ptychoptera pendula</i>	1	0	0	0	0	0	1	1	0	1	0	1	1	0	2	1	2	0	0	1	1	2	1	1	1	0	0	0	2
<i>Ptychoptera persimilis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2
<i>Ptychoptera quadrifasciata</i>	1	0	0	0	0	1	1	0	1	0	1	0	1	1	0	2	1	2	0	0	1	2	1	1	1	0	0	0	2
<i>Ptychoptera sculleni</i>	1	0	0	0	0	1	1	0	1	0	1	0	1	1	0	2	1	2	0	0	1	2	1	1	1	0	0	0	2
<i>Ptychoptera tibialis</i>	1	0	0	0	0	1	1	0	1	0	1	0	1	0	?	?	2	0	0	1	1	2	1	1	1	0	0	0	2
<i>Ptychoptera yamato</i>	1	0	0	0	0	1	1	1	0	1	0	1	0	0	2	1	2	0	0	1	1	2	1	1	1	0	0	0	2

Appendix II: Character Matrix

	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115
Nannochoristidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Anopheles gambiae</i>	1	1	0	0	1	1	0	0	0	0	0	0	1	0	0	3	1	0	2	1	0	0	0	0
<i>Arachnocampa flava</i>	1	1	1	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
<i>Bibio longipes</i>	1	1	1	0	1	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0
<i>Bradysia tilicola</i>	1	1	1	0	1	1	1	1	0	0	1	1	0	1	0	1	0	0	1	0	0	0	0	0
<i>Chironomus tepperi</i>	1	1	0	1	1	1	0	0	0	1	-	1	1	1	0	1	0	0	1	0	0	0	0	0
<i>Glogmia albipunctata</i>	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	1	1	1	1	0	0
<i>Coboldia fuscipes</i>	1	1	1	0	1	1	1	1	1	0	1	1	1	1	0	1	0	0	1	1	1	1	0	0
<i>Edwardsina gigantea</i>	0	1	1	0	1	1	0	0	0	0	0	1	2	0	0	1	0	0	1	0	0	0	0	0
<i>Mayetiola destructor</i>	1	1	0	0	1	1	1	1	0	1	-	1	0	1	0	1	0	?	?	1	1	1	0	0
<i>Trichocera brevicornis</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0
<i>Protoplasa fitchii</i>	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	0	1
<i>Sylvicola fenestralis</i>	1	1	0	0	0	0	0	0	1	0	0	1	2	0	1	1	0	0	0	0	0	0	0	0
<i>Tipula abdominalis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Bittacomorpha clavipes</i>	0	0	0	1	1	1	0	0	2	0	0	1	0	0	0	0	1	1	2	0	0	0	0	1
<i>Bittacomorpha occidentalis</i>	0	0	0	1	1	1	0	0	2	0	0	1	0	0	0	1	1	1	2	0	0	0	1	0
<i>Bittacomorphella esakii</i>	0	0	0	1	1	1	0	0	2	0	0	1	0	0	2	1	1	1	1	0	0	0	1	0
<i>Bittacomorphella fenderiana</i>	0	0	0	1	1	1	0	0	2	0	0	1	0	0	1	1	1	1	2	0	0	0	1	0
<i>Bittacomorphella jonesi</i>	0	0	0	1	1	1	0	0	2	0	0	1	0	0	1	1	1	1	1	0	0	0	1	0
<i>Bittacomorphella nipponensis</i>	0	0	0	1	1	1	0	0	2	0	0	1	0	0	2	1	1	1	1	0	0	0	1	0
<i>Bittacomorphella pacifica</i>	0	0	0	1	1	1	0	0	2	0	0	1	0	0	1	1	1	1	1	0	0	0	1	0
<i>Bittacomorphella sackenii</i>	0	0	0	1	1	1	0	0	2	0	0	1	0	0	1	1	1	1	1	0	0	0	1	0
<i>Bittacomorphella furcata</i>	0	0	0	1	1	1	0	0	2	0	0	1	0	0	1	1	1	1	1	0	0	0	1	0
<i>Ptychoptera africana</i>	0	0	0	1	1	1	0	0	2	0	0	1	0	0	1	1	1	1	1	0	0	0	1	0
<i>Ptychoptera albimana</i>	0	0	0	1	1	1	0	0	1	0	0	1	0	0	1	1	1	1	1	0	0	0	0	0
<i>Ptychoptera alexanderi</i>	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	1	0	0	0	0	1
<i>Ptychoptera byersi</i>	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	1	0	0	0	0	0
<i>Ptychoptera javensis</i>	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	1	0	0	0	0	1
<i>P. (Parapterychoptera) lacustris</i>	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	1	0	0	0	0	0
<i>Ptychoptera metallica</i>	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	1	0	0	0	0	1
<i>Ptychoptera pendula</i>	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	1	0	0	0	0	1
<i>Ptychoptera persimilis</i>	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	?	?	?	?	?	?	?	?	0
<i>Ptychoptera quadrifasciata</i>	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	1	0	0	0	0	1
<i>Ptychoptera sculleni</i>	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	1	0	0	0	0	1
<i>Ptychoptera tibialis</i>	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	1	0	0	0	0	1
<i>Ptychoptera yamato</i>	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	1	0	0	0	0	0

Appendix II: Character Matrix		116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138
Nannochoristidae		0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	1	0	0	0	0	0	0	0
<i>Anopheles gambiae</i>		0	1	0	1	0	0	1	0	0	0	1	1	0	1	0	1	1	1	1	0	1	0	0
<i>Arachnocampa flava</i>		0	1	1	0	0	0	1	1	0	0	?	0	0	0	0	2	0	0	1	0	0	2	1
<i>Bibio longipes</i>		0	1	1	0	0	0	0	1	1	?	?	?	?	0	1	0	3	0	0	1	0	0	0
<i>Bradysia tilicola</i>		0	1	1	0	0	0	1	1	0	?	?	?	?	0	0	?	?	0	0	1	0	0	0
<i>Chironomus tepperi</i>		0	1	0	1	0	0	0	1	0	?	?	?	?	1	1	0	2	0	0	1	0	0	1
<i>Clogmia albipunctata</i>		0	1	1	0	0	0	0	1	1	0	1	0	1	1	1	?	?	1	0	1	0	1	0
<i>Coboldia fuscipes</i>		0	1	1	0	0	0	1	1	1	1	0	0	0	1	0	1	0	1	1	0	0	0	1
<i>Edwardsina gigantea</i>		0	1	?	?	0	0	1	1	0	0	0	0	0	1	0	3	1	1	1	1	0	0	1
<i>Mayetiola destructor</i>		0	1	1	0	0	0	1	1	1	1	?	?	?	0	1	0	2	0	0	1	1	0	0
<i>Trichocera brevicornis</i>		0	0	0	0	0	1	1	1	0	1	1	0	0	1	1	3	0	1	1	0	0	0	0
<i>Protoplasia fitchii</i>		0	1	1	0	0	0	0	1	?	0	0	0	?	0	0	3	?	?	1	0	1	0	1
<i>Sylvicola fenestralis</i>		0	1	1	0	0	0	1	1	1	?	0	?	0	1	0	1	0	1	0	1	0	1	0
<i>Tipula abdominalis</i>		0	0	0	0	1	1	0	1	0	0	0	0	0	1	1	3	0	1	1	0	0	0	0
<i>Bittacomorpha clavipes</i>		1	1	1	0	1	0	1	1	1	1	1	0	0	1	1	0	0	?	?	?	0	0	0
<i>Bittacomorpha occidentalis</i>		1	1	1	0	1	0	1	1	1	1	1	0	0	1	1	0	0	?	?	?	0	0	1
<i>Bittacomorphella esakii</i>		0	1	1	0	1	0	1	1	1	1	1	0	0	1	1	0	?	?	?	?	0	0	1
<i>Bittacomorphella fenderiana</i>		0	1	1	0	1	0	1	1	1	1	1	0	0	1	1	0	0	?	?	?	0	0	1
<i>Bittacomorphella jonesi</i>		0	1	1	0	1	0	1	1	1	1	1	0	0	1	1	0	?	?	?	?	0	0	1
<i>Bittacomorphella nipponensis</i>		0	1	1	0	1	0	1	1	1	1	1	0	0	1	1	0	?	?	?	?	0	0	1
<i>Bittacomorphella pacifica</i>		0	1	1	0	1	0	1	1	1	1	0	0	0	1	1	0	?	?	?	?	0	0	1
<i>Bittacomorphella sackenii</i>		0	1	1	0	1	0	1	1	1	1	0	0	0	1	1	0	?	?	?	?	0	0	1
<i>Bittacomorphella furcata</i>		0	1	1	0	1	0	1	1	1	1	0	0	0	1	1	0	?	?	?	?	0	0	1
<i>Ptychoptera africana</i>		0	1	1	0	1	1	0	1	1	1	0	1	1	1	1	1	3	?	?	?	0	0	2
<i>Ptychoptera albimana</i>		0	1	1	0	1	1	0	1	1	1	0	1	1	1	1	1	3	?	?	?	0	0	2
<i>Ptychoptera alexanderi</i>		0	1	1	0	1	1	0	1	1	1	0	1	1	1	1	1	?	?	?	?	0	0	2
<i>Ptychoptera byersi</i>		0	1	1	0	1	1	?	?	?	?	?	?	?	1	1	?	?	?	?	?	0	0	2
<i>Ptychoptera javensis</i>		0	1	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	2
<i>P. (Parapterychoptera) lacustris</i>		0	1	1	0	1	1	0	1	1	1	0	1	1	1	1	?	?	?	?	?	0	0	1
<i>Ptychoptera metallica</i>		0	1	1	0	1	1	0	1	1	1	0	1	1	1	1	1	3	?	?	?	0	0	1
<i>Ptychoptera pendula</i>		0	1	1	0	1	1	0	1	1	1	0	1	1	1	1	1	3	?	?	?	0	0	2
<i>Ptychoptera persimilis</i>		0	1	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	2
<i>Ptychoptera quadrifasciata</i>		0	1	1	0	1	1	0	1	1	1	0	1	1	1	1	0	?	?	?	?	0	0	2
<i>Ptychoptera sculleni</i>		0	1	1	0	1	1	0	1	1	1	0	1	1	1	1	1	?	?	?	?	0	0	2
<i>Ptychoptera tibialis</i>		0	1	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	2
<i>Ptychoptera yamato</i>		0	1	1	0	1	1	0	1	1	1	0	1	1	1	1	1	?	?	?	?	0	0	2

Appendix II: Character Matrix 139 140 141 142 143 144 145 146 147 148 149 150 151 152 153 154 155 156 157 158 159 160 161

Nannochoristidae	0	0	0	0	-	0	0	0	0	0	0	0	?	0	0	0	0	-	-	-	-
<i>Anopheles gambiae</i>	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	-	-	-	-
<i>Arachnocampa flava</i>	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	-	-	-	-
<i>Bibio longipes</i>	0	1	3	1	0	0	0	0	0	0	0	1	0	0	3	2	0	-	-	-	-
<i>Bradysia tilicola</i>	0	0	0	1	0	0	0	0	0	1	0	1	0	0	3	0	0	-	-	-	-
<i>Chironomus tepperi</i>	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	4	0	-	-	-	-
<i>Clogmia albipunctata</i>	0	1	0	0	0	0	1	0	0	2	1	0	0	0	3	4	0	-	-	-	-
<i>Coboldia fuscipes</i>	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	2	0	-	-	-	-
<i>Edwardsina gigantea</i>	0	1	2	1	0	0	1	0	0	0	1	1	0	3	3	0	0	-	-	-	-
<i>Mayetiola destructor</i>	?	?	?	1	?	?	0	?	?	?	?	1	?	?	?	?	?	-	-	-	-
<i>Trichocera brevicornis</i>	0	0	2	0	0	0	1	0	0	0	1	1	0	1	0	4	0	-	-	-	-
<i>Protoplasa fitchii</i>	0	0	0	1	0	0	0	0	0	0	1	0	0	1	3	3	0	-	-	-	-
<i>Sylvicola fenestralis</i>	0	1	3	1	0	0	1	0	0	0	0	1	?	0	0	3	0	-	-	-	-
<i>Tipula abdominalis</i>	1	0	0	1	0	0	1	0	1	1	0	-	-	-	?	2	0	-	-	-	-
<i>Bittacomorpha clavipes</i>	2	0	1	0	1	0	0	0	0	1	2	0	1	1	2	2	0	1	1	0	1
<i>Bittacomorpha occidentalis</i>	2	0	1	0	1	0	0	0	0	1	2	0	0	1	2	2	0	1	1	0	1
<i>Bittacomorphella esakii</i>	1	1	1	0	1	2	0	0	0	1	0	0	0	1	1	2	0	1	1	0	0
<i>Bittacomorphella fenderiana</i>	1	0	1	0	1	1	0	0	1	1	2	0	0	1	1	2	0	1	1	0	1
<i>Bittacomorphella jonesi</i>	0	0	2	0	1	1	0	0	0	1	2	0	1	1	1	2	0	1	1	1	0
<i>Bittacomorphella nipponensis</i>	1	1	1	0	1	1	0	0	1	2	0	0	1	1	1	2	0	1	1	0	0
<i>Bittacomorphella pacifica</i>	2	0	1	0	1	0	0	0	0	1	1	0	0	1	1	1	0	1	1	0	0
<i>Bittacomorphella sackenii</i>	2	0	1	0	1	2	0	0	1	0	0	0	1	1	1	1	0	1	1	0	0
<i>Bittacomorphella furcata</i>	2	0	1	0	1	2	0	0	1	0	2	1	0	1	1	1	0	1	1	0	0
<i>Ptychoptera africana</i>	0	1	2	0	1	2	0	0	1	0	2	1	1	0	3	4	0	1	1	0	1
<i>Ptychoptera albimana</i>	2	1	2	0	1	1	0	0	1	0	2	1	0	0	3	4	0	1	1	0	1
<i>Ptychoptera alexanderi</i>	0	1	2	0	1	1	0	0	1	2	1	1	0	0	3	2	0	1	0	1	0
<i>Ptychoptera byersi</i>	3	1	2	0	1	1	0	0	1	0	1	0	0	0	2	4	0	1	1	0	1
<i>Ptychoptera javensis</i>	0	1	2	0	?	2	0	0	1	0	2	?	?	?	?	4	0	1	1	0	1
<i>P. (Parapterychoptera) lacustris</i>	0	1	2	0	1	1	1	0	1	0	1	1	0	1	2	2	1	1	1	0	1
<i>Ptychoptera metallica</i>	4	1	0	0	1	1	0	0	1	0	1	1	0	0	3	2	1	0	1	0	1
<i>Ptychoptera pendula</i>	3	1	1	0	1	1	1	0	1	0	2	1	0	0	3	2	1	0	1	0	1
<i>Ptychoptera persimilis</i>	0	1	3	0	1	?	0	0	1	1	1	1	0	0	3	4	0	1	1	0	1
<i>Ptychoptera quadrifasciata</i>	0	1	2	0	1	1	0	0	1	0	1	1	0	0	3	2	1	0	1	0	1
<i>Ptychoptera sculleni</i>	0	1	3	0	1	1	1	0	1	0	0	1	0	0	3	2	1	0	1	0	1
<i>Ptychoptera tibialis</i>	3	1	2	0	1	0	0	0	1	0	0	0	0	0	2	4	0	1	1	1	0
<i>Ptychoptera yamato</i>	0	1	2	0	1	0	0	0	1	0	1	1	1	0	3	2	0	0	1	0	1

Appendix II: Character Matrix 162 163 164 165 166 167 168 169 170 171 172 173 174 175 176 177 178 179 180 181 182 183 184

Nannochoristidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Anopheles gambiae</i>	1	0	-	-	-	0	0	-	-	-	0	-	1	?	0	0	0	-	-	0	0
<i>Arachnocampa flava</i>	0	0	1	0	0	0	0	-	-	-	0	-	0	-	0	0	0	-	-	0	0
<i>Bibio longipes</i>	0	0	0	0	0	0	0	-	-	-	0	-	0	-	0	0	0	-	-	0	0
<i>Bradysia tilicola</i>	0	0	1	1	0	0	0	-	-	-	0	-	0	-	1	0	0	-	-	0	0
<i>Chironomus tepperi</i>	1	0	-	-	-	0	0	-	-	-	0	-	0	-	1	0	0	-	-	0	0
<i>Clogmia albipunctata</i>	0	0	0	0	0	0	1	0	?	0	-	-	0	-	1	0	1	0	1	0	2
<i>Coboldia fuscipes</i>	0	0	0	1	0	0	0	-	0	1	1	0	0	-	1	0	0	-	-	0	0
<i>Edwardsina gigantea</i>	0	2	0	1	0	0	1	1	?	?	-	-	0	-	1	0	0	-	-	0	0
<i>Mayetiola destructor</i>	0	0	?	?	?	?	1	?	?	?	0	-	0	?	1	0	0	-	-	0	0
<i>Trichocera brevicornis</i>	0	0	0	0	0	0	1	0	?	?	0	-	0	-	1	0	0	-	-	0	0
<i>Protoplasa fitchii</i>	0	2	0	1	0	0	1	0	?	?	0	-	0	-	1	1	0	-	-	0	0
<i>Sylvicola fenestralis</i>	0	0	0	1	0	0	1	0	?	?	0	-	0	-	0	0	0	-	-	0	0
<i>Tipula abdominalis</i>	0	0	?	1	0	0	0	-	-	-	0	-	0	-	1	1	0	-	-	0	0
<i>Bittacomorpha clavipes</i>	0	0	0	0	1	1	1	0	1	1	1	0	1	1	1	1	1	0	1	1	2
<i>Bittacomorpha occidentalis</i>	0	0	0	0	1	1	1	0	1	1	1	0	1	1	1	1	1	0	1	1	2
<i>Bittacomorphella esakii</i>	0	0	0	0	1	0	1	0	1	0	1	0	1	0	1	1	0	0	2	0	?
<i>Bittacomorphella fenderiana</i>	0	0	0	0	1	0	1	0	1	0	1	0	1	2	1	1	1	0	2	0	2
<i>Bittacomorphella jonesi</i>	0	0	0	0	1	1	1	0	1	0	1	0	1	1	1	1	1	0	2	0	1
<i>Bittacomorphella nipponensis</i>	0	0	0	0	1	0	1	0	1	0	1	0	1	1	1	1	1	0	2	0	?
<i>Bittacomorphella pacifica</i>	0	0	0	0	1	0	1	0	1	0	1	0	1	0	1	1	1	0	2	1	2
<i>Bittacomorphella sackenii</i>	0	0	0	0	1	0	1	0	1	0	1	0	1	0	1	1	1	0	2	1	2
<i>Bittacomorphella furcata</i>	0	0	0	0	1	0	1	0	1	0	1	0	1	2	1	1	1	0	2	1	1
<i>Ptychoptera africana</i>	0	0	1	0	0	0	1	1	0	1	1	0	1	0	1	1	1	1	0	0	1
<i>Ptychoptera albimana</i>	0	0	1	0	0	0	1	1	0	1	1	0	1	1	1	1	1	1	0	0	?
<i>Ptychoptera alexanderi</i>	0	0	1	0	0	0	1	2	1	1	1	0	1	0	1	1	1	1	0	0	1
<i>Ptychoptera byersi</i>	0	0	1	0	0	0	1	1	0	1	1	0	1	1	1	1	1	1	2	0	2
<i>Ptychoptera javensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	1	0	?	1
<i>P. (Parapterychoptera) lacustris</i>	0	0	1	0	0	0	1	1	0	1	1	0	1	1	1	1	1	0	0	0	1
<i>Ptychoptera metallica</i>	0	0	1	0	0	0	1	1	0	1	1	0	1	1	1	1	1	0	0	0	2
<i>Ptychoptera pendula</i>	0	0	1	0	0	0	1	1	0	1	1	0	1	1	1	1	1	1	3	0	2
<i>Ptychoptera persimilis</i>	0	0	1	0	0	0	1	?	?	?	?	?	?	?	1	1	1	1	0	0	1
<i>Ptychoptera quadrifasciata</i>	0	0	1	0	0	0	1	0	1	1	1	0	1	1	1	1	1	1	3	0	1
<i>Ptychoptera sculleni</i>	0	0	1	0	0	0	1	1	0	1	1	0	1	0	1	1	1	1	0	0	1
<i>Ptychoptera tibialis</i>	0	0	1	0	0	0	1	1	0	1	1	0	1	1	1	1	1	1	3	0	?
<i>Ptychoptera yamato</i>	0	0	1	0	0	0	1	0	1	1	1	0	1	0	1	1	1	1	0	0	1

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Figure Captions

Figure 1. Maximum Parsimony phylogeny based on morphological characters. Bremer support values are shown above the branch, Bootstrap support values below. Bootstrap support under 50 is not shown.

Figure 2. Maximum Parsimony phylogeny tracing character state changes of the data set within Ptychopteridae.

Figure 3. Bayesian Inference phylogeny based on morphological characters. Posterior probabilities are shown below the branch.

Figure 4. Bayesian Inference phylogeny tracing character state changes of the data set within Ptychopteridae.

Figure 5. *Bittacomorpha clavipes* thoracic sclerites, right lateral view.

anclf: Anepisternal cleft, anest: Anepisternal suture, antbs: Anterior basallare, aprnt: Anteprenotum; aspr: Anterior spiracle, epmpl: episternum of metapleuron, epmrn: Epimeron, epstr: Episternum, hltr: Halter, ltgt: Laterotergite of postnotum; mdtg: Mediotergite of postnotum, mplst: Metapleural suture, mrmpl: Meron of metapleuron, mtn: Metanotum, phltr: Prehalter, pprnt: Postpronotum, prsct: Prescutum, pspr: Posterior spiracle, ptg: Paratergite, sbasl: Subalar sclerite, sct: Scutum, sctl: Scutellum wngbs: Wing base

Figure 6. *Bittacomorpha clavipes* Fabricius, 1781. a. Male genitalia, dorsal view; b. Male genitalia, lateral view; c. Male head, anterior view; d. Aedeagus, lateral view e. Aedeagus, dorsal view; f. Paramere, lateral view; g. Female genitalia, lateral view; h. Hypogynium, ventral view; i. Epigynium, dorsal view. All scale bars 0.5mm.

Figure 7. *Bittacomorpha clavipes*, Male wing. Scale bar 1mm.

Figure 8. *Bittacomorpha clavipes*, Larval habitus, lateral view. Scale bar 1mm.

Figure 9. *Bittacomorpha clavipes*, Larval head capsule, dorsal view. Scale bar 0.5mm.

Figure 10. *Bittacomorpha clavipes*, Larval postmentum/subgenal sclerite, ventral view. Scale bar 0.25mm.

Figure 11. *Bittacomorpha clavipes* distribution. a. Nearctic; b. Central America.

Figure 12. *Bittacomorpha occidentalis* Aldrich, 1895. a. Male genitalia, dorsal view; b. Male genitalia, lateral view; c. Male head, anterior view; d. Aedeagus, lateral view e. Aedeagus, dorsal view; f. Paramere, lateral view; g. Female genitalia, lateral view; h. Hypogynium, ventral view; i. Epigynium, dorsal view. All scale bars 0.5mm.

Figure 13. *Bittacomorpha occidentalis*, Male wing. Scale bar 2mm.

Figure 14. *Bittacomorpha occidentalis*, Larval habitus, lateral view. Scale bar 1mm.

Figure 15. *Bittacomorpha occidentalis*, Larval head capsule, dorsal view. Scale bar 0.5mm.

Figure 16. *Bittacomorpha occidentalis*, Larval postmentum/subgenal sclerite, ventral view. Scale bar 0.25mm.

Figure 17. *Bittacomorpha occidentalis* distribution. Star indicates cotype locality.

Figure 18. *Bittacomorphella furcata* sp. n. a. Male genitalia, dorsal view; b. Male genitalia, lateral view; c. Male head, anterior view; d. Aedeagus, lateral view e. Aedeagus, dorsal view; f. Paramere, lateral view; g. Female genitalia, lateral view; h. Epigynum, dorsal view. All scale bars 0.5mm.

Figure 19. *Bittacomorphella furcata*, Male wing. Scale bar 1mm.

Figure 20. *Bittacomorphella furcata* distribution. Star indicates holotype locality.

Figure 21. *Bittacomorphella pacifica* Alexander, 1958. a. Male genitalia, dorsal view; b. Male genitalia, lateral view; c. Male head, anterior view; d. Aedeagus, lateral view e. Aedeagus, dorsal view; f. Paramere, lateral view; g. Epigynum, dorsal view; h. Female genitalia, lateral view; i. Hypogynium, ventral view. All scale bars 0.5mm, except Figure 20:i set at 0.25mm.

Figure 22. *Bittacomorphella pacifica*, Male wing. Scale bar 1mm.

Figure 23. *Bittacomorphella pacifica* distribution. Star indicates holotype locality.

Figure 24. *Bittacomorphella sackenii* Von Röder, 1888 a. Male genitalia, dorsal view; b. Male genitalia, lateral view; c. Male head, anterior view; d. Aedeagus, dorsal view (scale bar = .25mm); e. Paramere, lateral view; f. Female genitalia, lateral view. All scale bars 0.5mm, except e. which is set at 0.25mm.

Figure 25. *Bittacomorphella sackenii*, Male wing. Scale bar 1mm.

Figure 26. *Bittacomorphella sackenii* distribution.

Figure 27. *Bittacomorphella esakii* Tokunaga, 1938. a. Male genitalia, dorsal view; b. Male genitalia, lateral view; c. Male head, anterior view; d. Aedeagus, dorsal view; e. Paramere, lateral view; f. Female genitalia, lateral view. All scale bars 0.5mm, except e. which is set at 0.25mm.

Figure 28. *Bittacomorphella esakii*, Male wing. Scale bar 1mm.

Figure 29. *Bittacomorphella esakii* distribution.

Figure 30. *Bittacomorphella fenderiana* Alexander, 1947. a. Male genitalia, dorsal view; b. Male genitalia, lateral view; c. Male head, anterior view; d. Aedeagus, lateral view e. Aedeagus, dorsal view; f. Paramere, lateral view; g. Paramere, dorsal view; h. Female genitalia, lateral view; i. Hypogynium, ventral view; j. Epigynum, dorsal view. All scale bars 0.5mm.

Figure 31. *Bittacomorphella fenderiana*, Male wing. Scale bar 1mm.

Figure 32. *Bittacomorphella fenderiana*, Larval habitus, dorsal view. Scale bar 2mm.

Figure 33. *Bittacomorphella fenderiana*, Larval head capsule, dorsal view. Scale bar 0.5mm.

Figure 34. *Bittacomorphella fenderiana*, Larval postmentum/subgenal sclerite, ventral view. Scale bar 0.25mm.

Figure 35. *Bittacomorphella fenderiana* distribution. Star indicates holotype locality.

Figure 36. *Bittacomorphella jonesi* Johnson, 1905. a. Male genitalia, dorsal view; b. Male genitalia, lateral view; c. Male head, anterior view; d. Aedeagus, lateral view e. Aedeagus, dorsal view; f. Paramere, lateral view; g. Epigynium, dorsal view, h. Female genitalia, lateral view; i. Hypogynium, ventral view. All scale bars 0.5mm.

Figure 37. *Bittacomorphella jonesi*, Male wing. Scale bar 1mm.

Figure 38. *Bittacomorphella jonesi* distribution. Star indicates holotype locality.

Figure 39. *Bittacomorphella nipponensis* Alexander, 1924. a. Male genitalia, dorsal view; b. Male genitalia, lateral view; c. Male head, anterior view; d. Aedeagus, dorsal view; e. Paramere, lateral view; f. Female genitalia, lateral view. All scale bars 0.5mm.

Figure 40. *Bittacomorphella nipponensis*, Male wing. Scale bar 1mm.

Figure 41. *Bittacomorphella nipponensis* distribution. Star indicates holotype locality.

Figure 42. *Bittacomorphella thaiensis* Alexander, 1953. a. Female genitalia, lateral view; b. Female head. All scale bars 0.5mm.

Figure 43. *Bittacomorphella thaiensis*, Female wing. Scale bar 1mm.

Figure 44. *Bittacomorphella thaiensis* distribution. Star indicates holotype locality.

Abbreviations

ADA: Dorsal apical apodeme of aedeagus, AEA: Ejaculatory Apodeme, AES: Aedeagal Sclerite, AEV: Ventral Apical Apodeme of Aedeagus, ALP: Lateral Ejaculatory Process AS: Sperm Sac, ASA, Subapical Sclerite of Aedeagus, AVA: Ventral Arm of Subapical Sclerite, CRC: Cercus, ECP: Epandrial Clasper, EL: Epandrial Lobe, EPI: Epiproct, EPG: Epigynium, EPP: Epandrial Plate, EPS: Posteromedial Style of Epandrium, GBL: Basal lobe of gonostylus, GCT: Gonocoxite, GCA: Gonocoxal Apodeme, GFK: Genital Fork, GST: Gonostylus: HBD: Basal Division of Hypandrium, HLT: Lateral lobule of terminal division, HPG: Hypogynium, HTD: Terminal Division of Hypandrium, HVL: Hypogynial Valves, HYP: Hypoproct, PM: Paramere, ST7: Sternite 7, TG7: Tergite 7

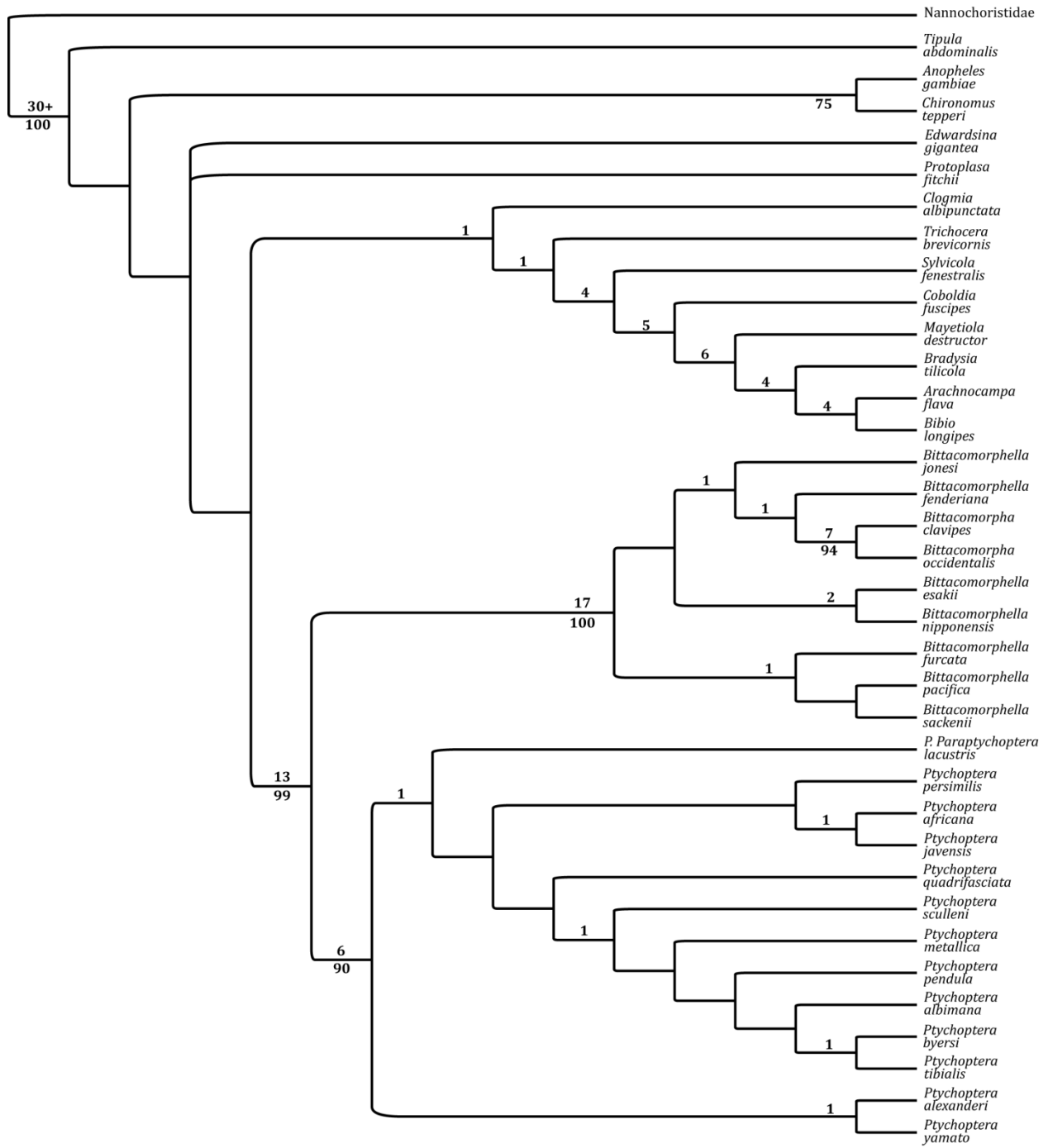


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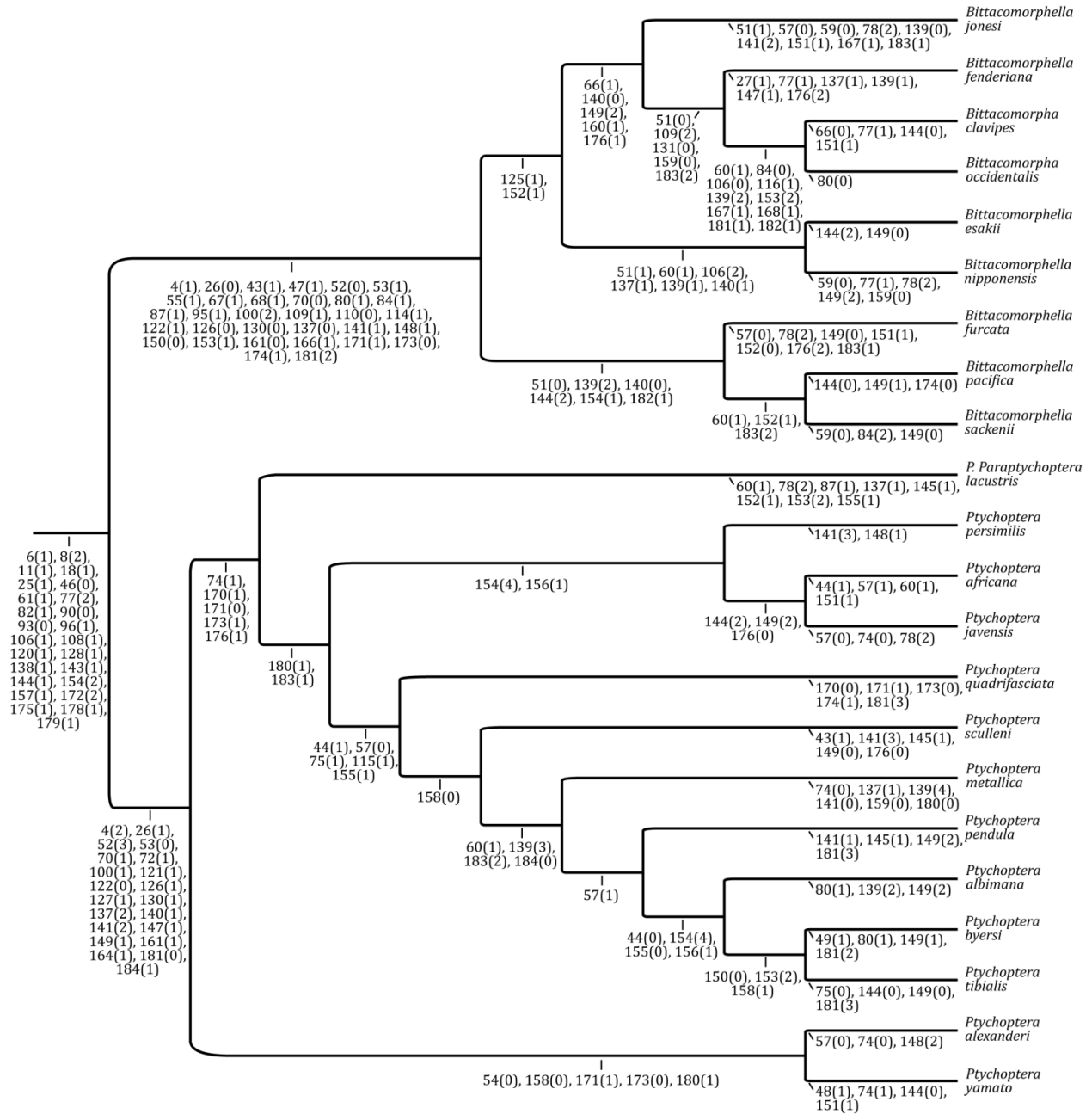


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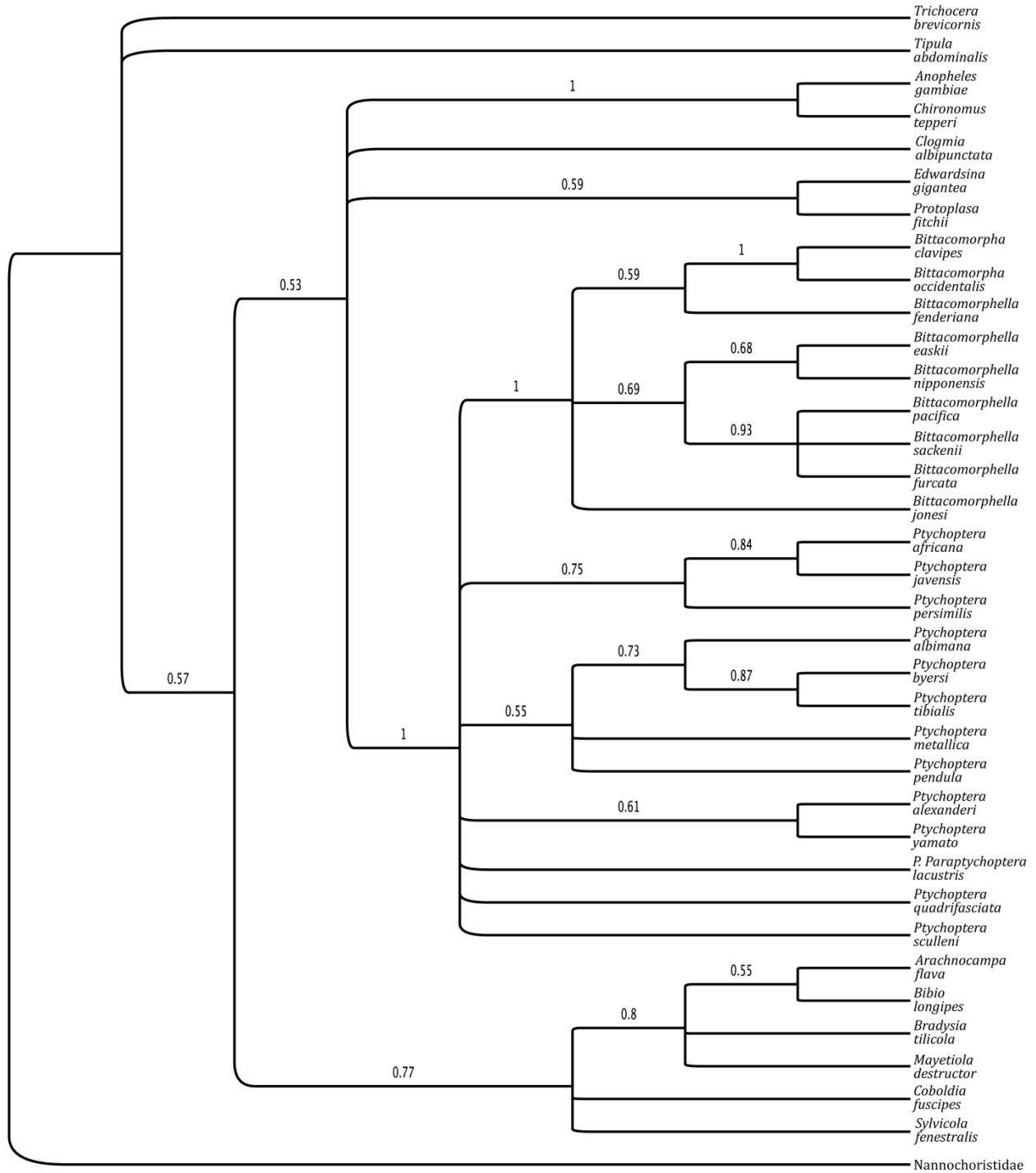


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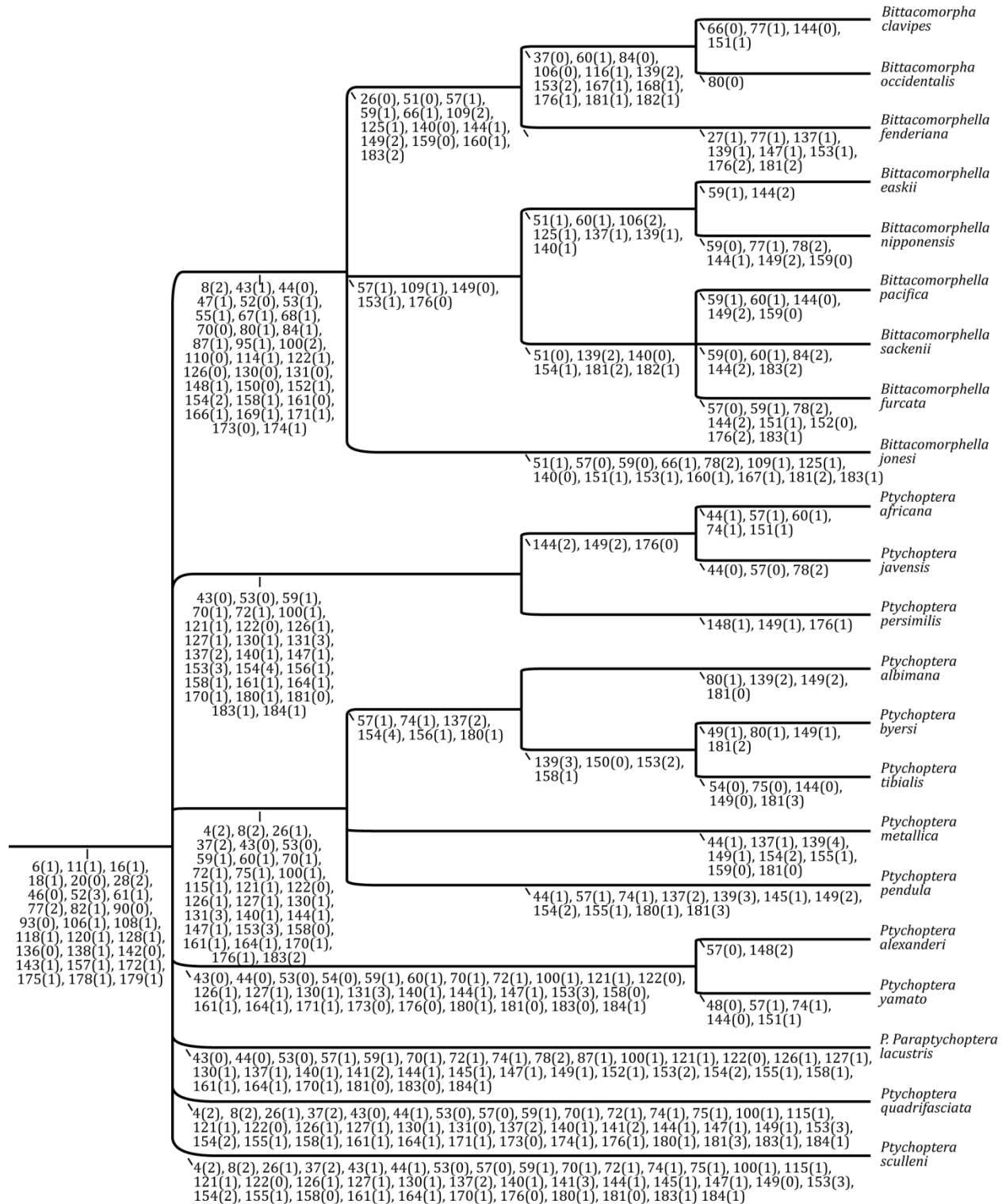


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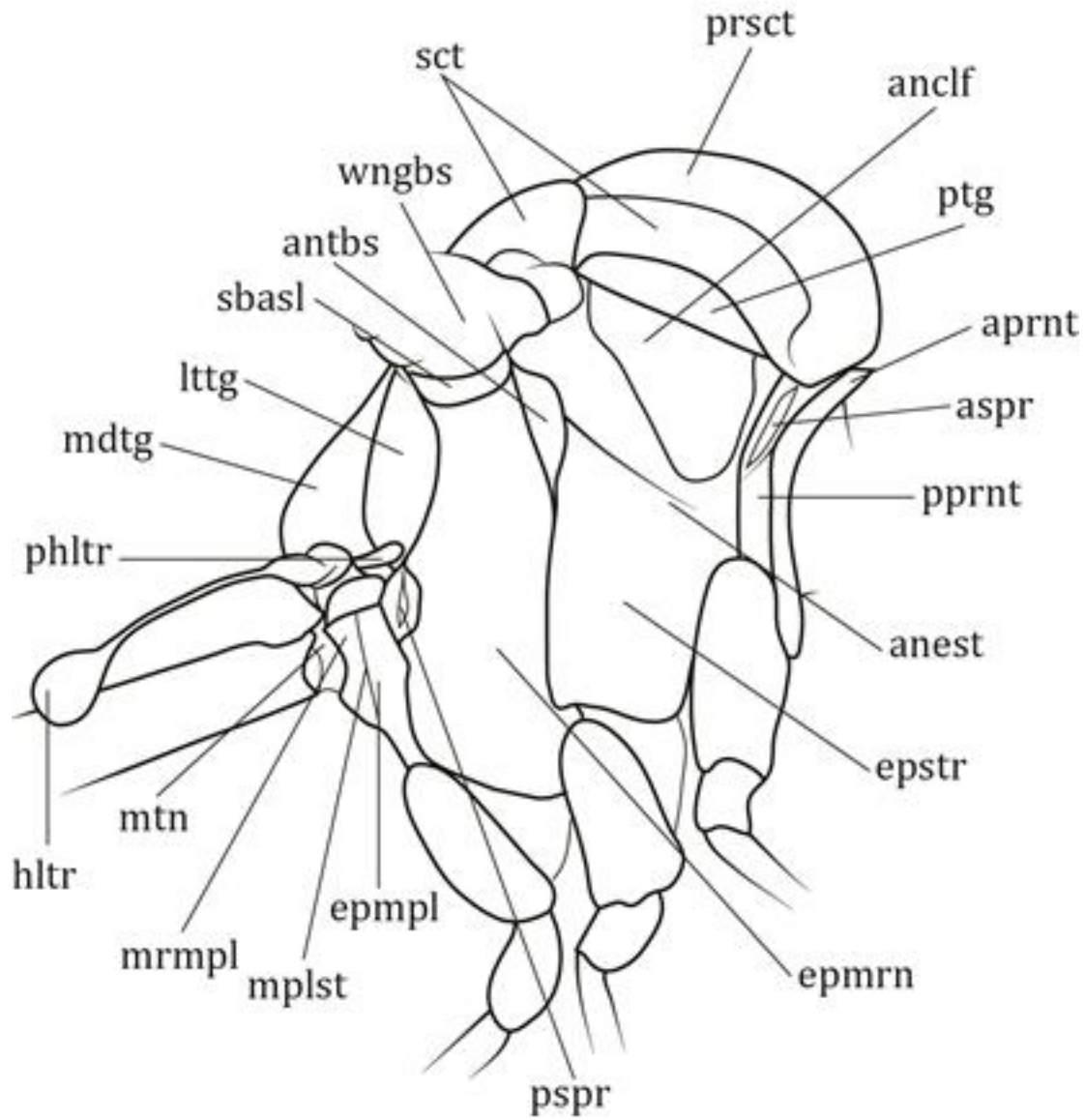


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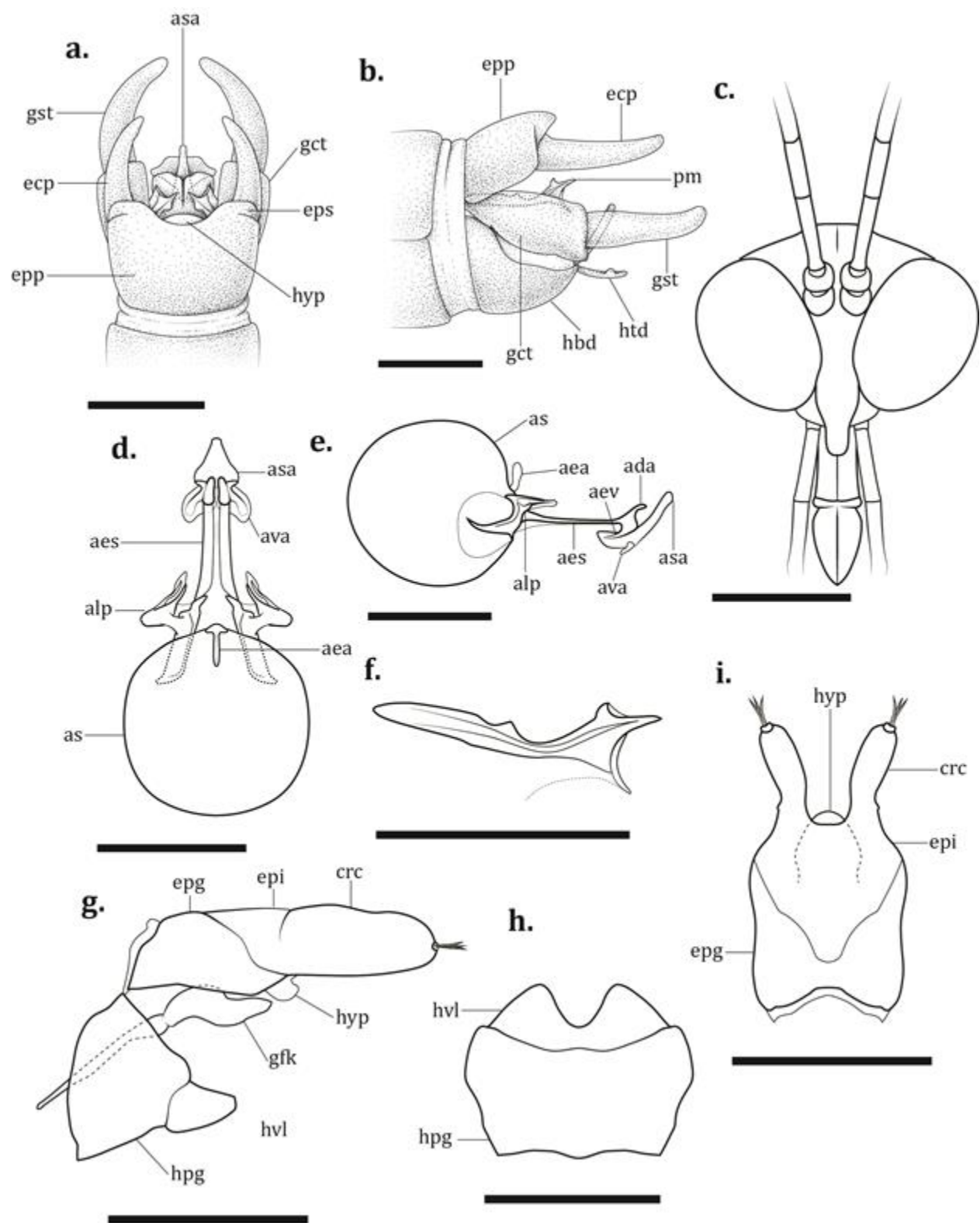


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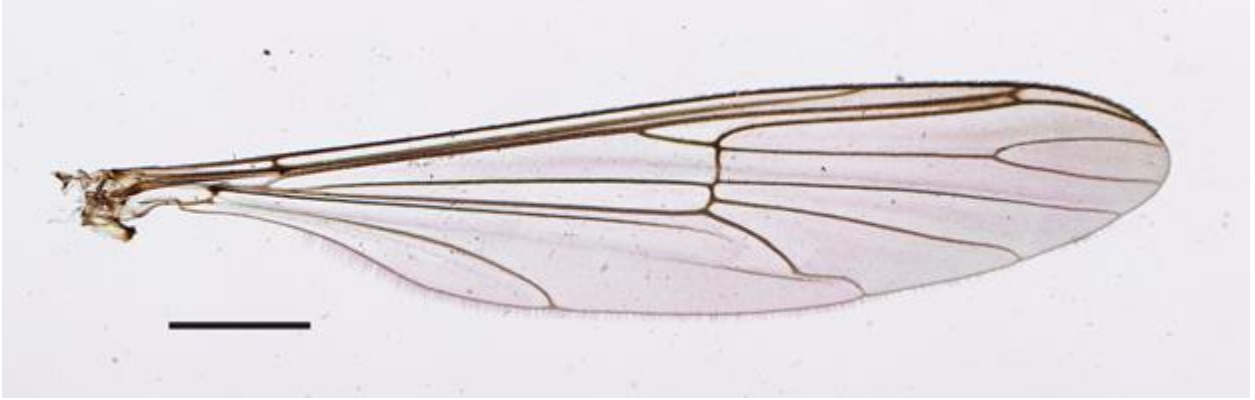


Figure 7.



Figure 8.



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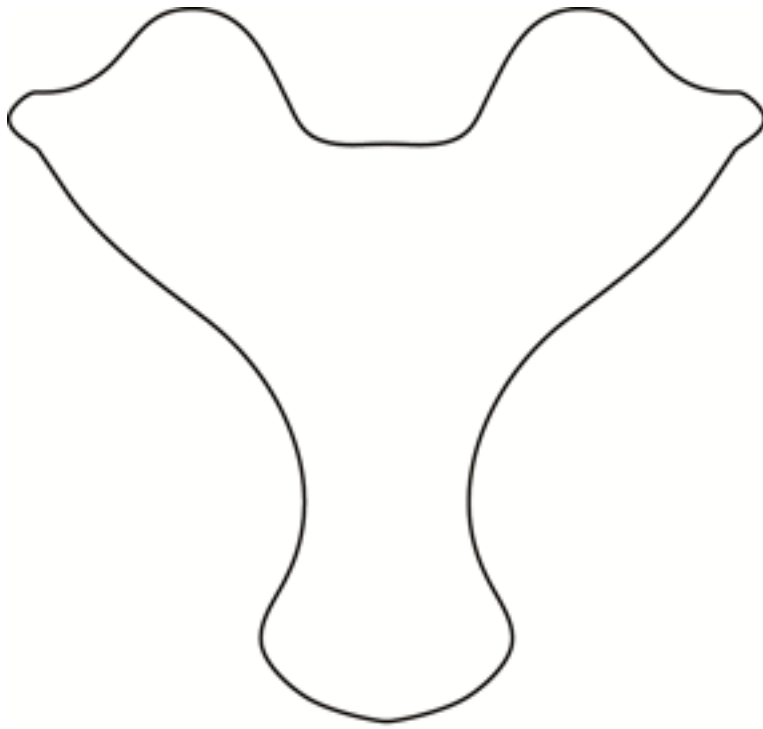


Figure 10.



Figure 11.

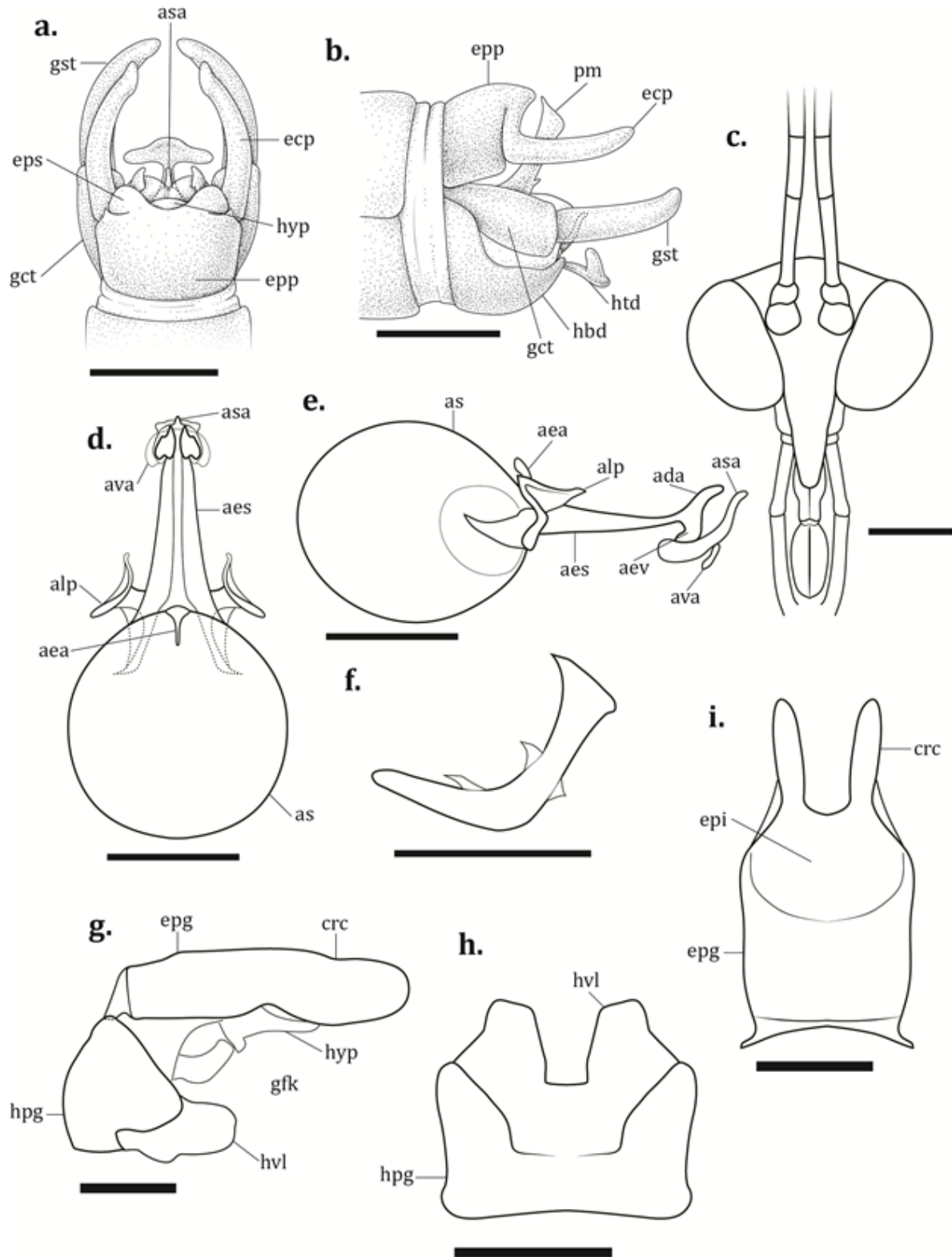


Figure 12.



Figure 13.



Figure 14.

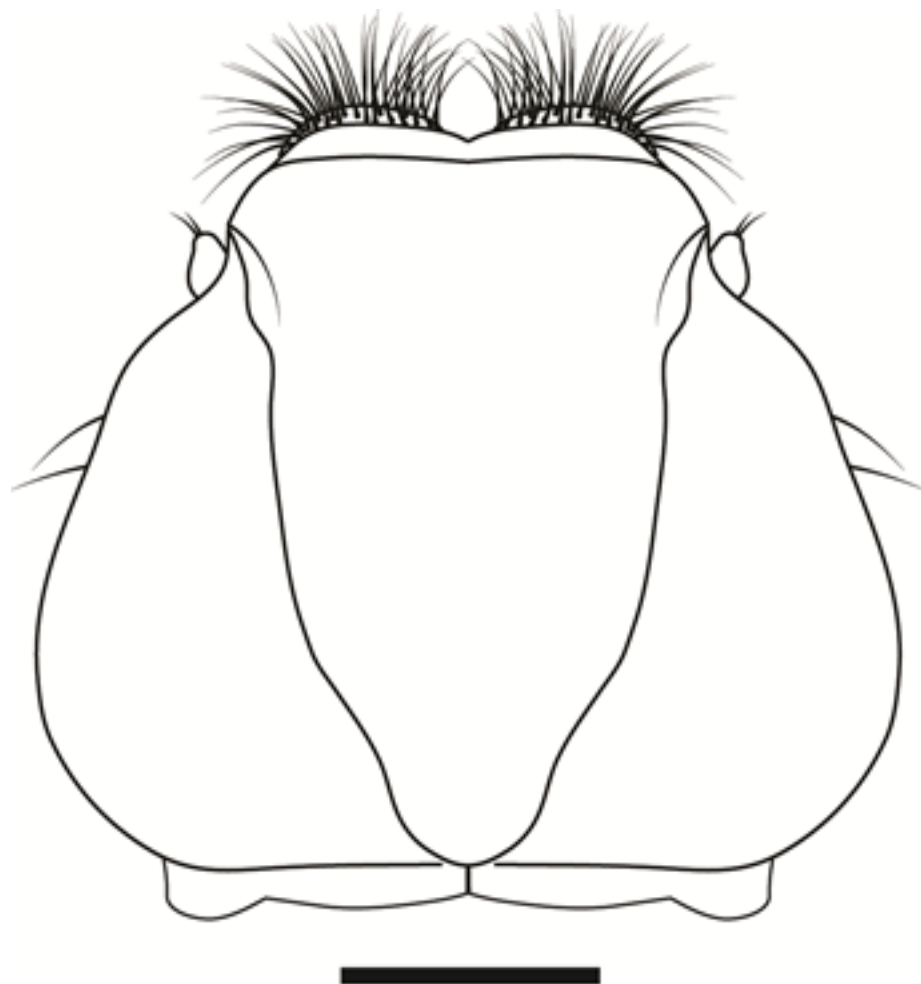


Figure 15.



Figure 16.



Figure 17.

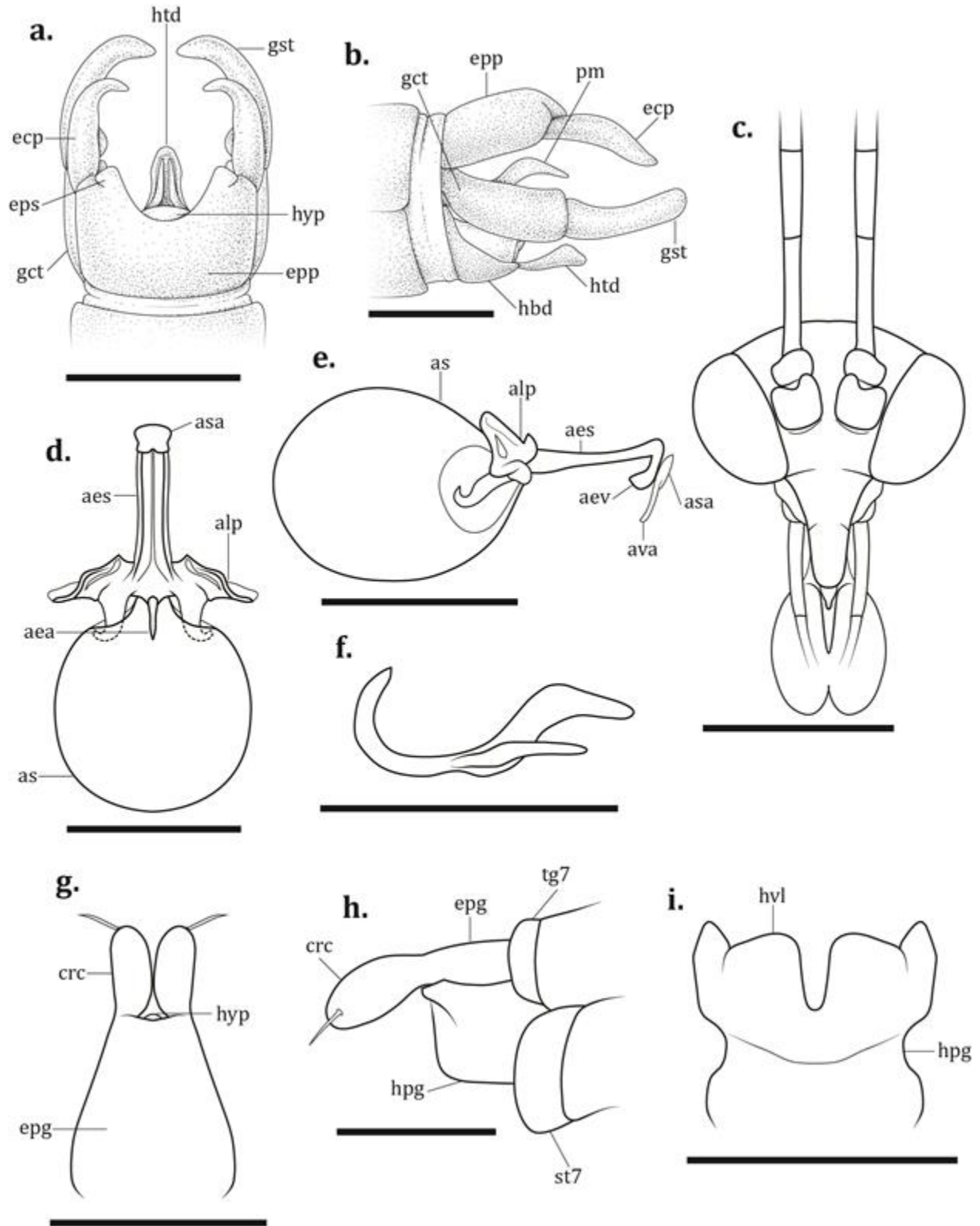


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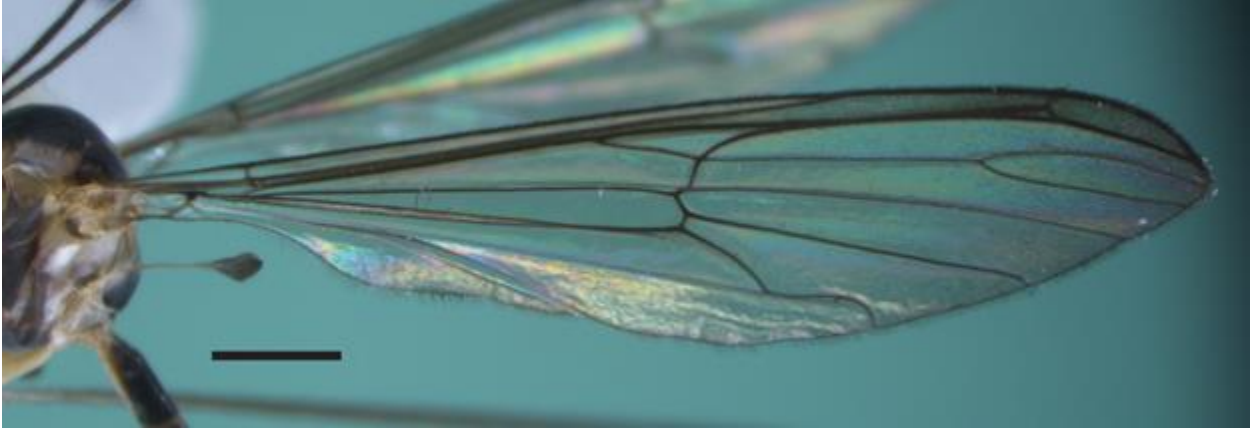


Figure 19.



Figure 20.

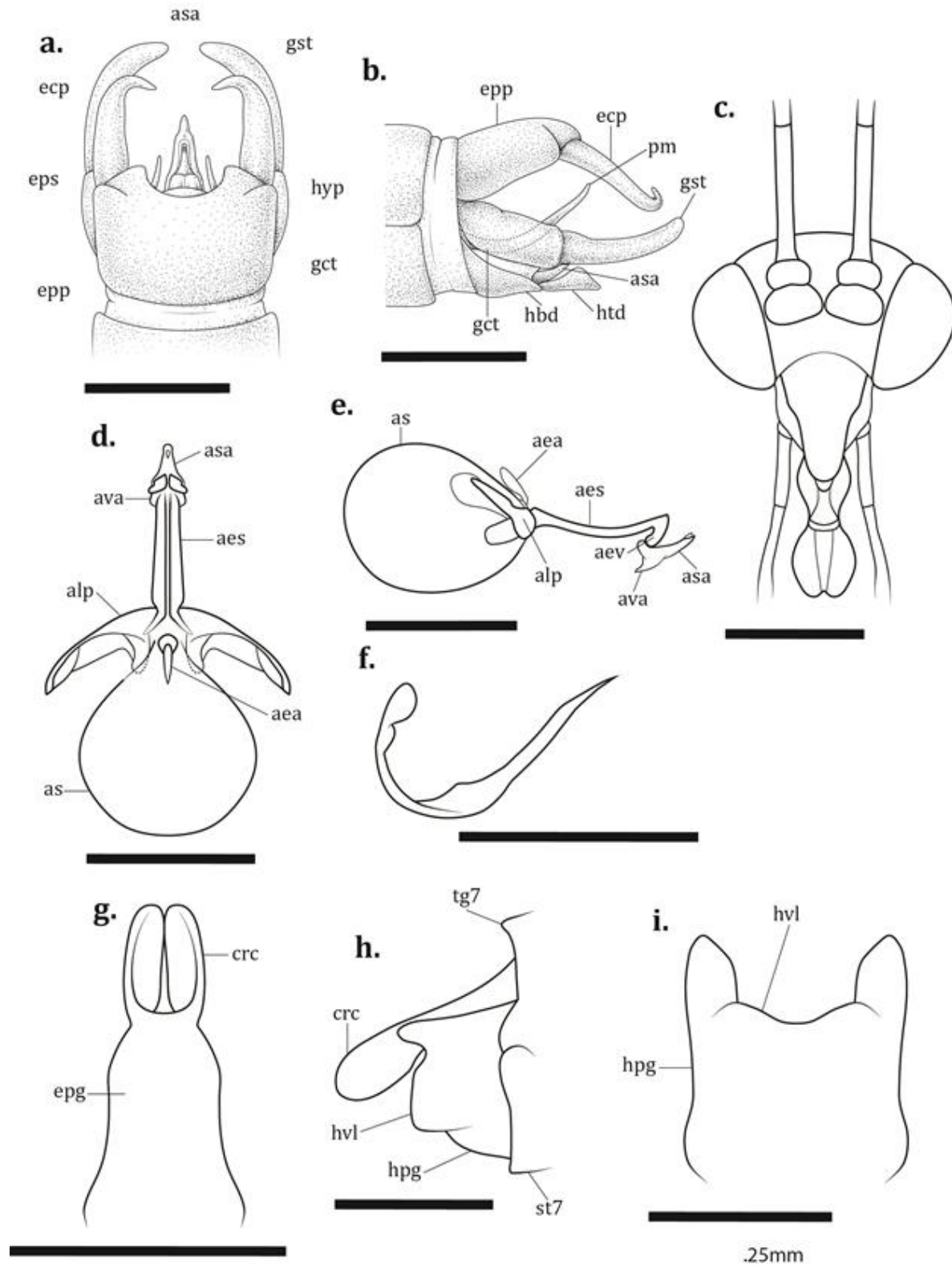


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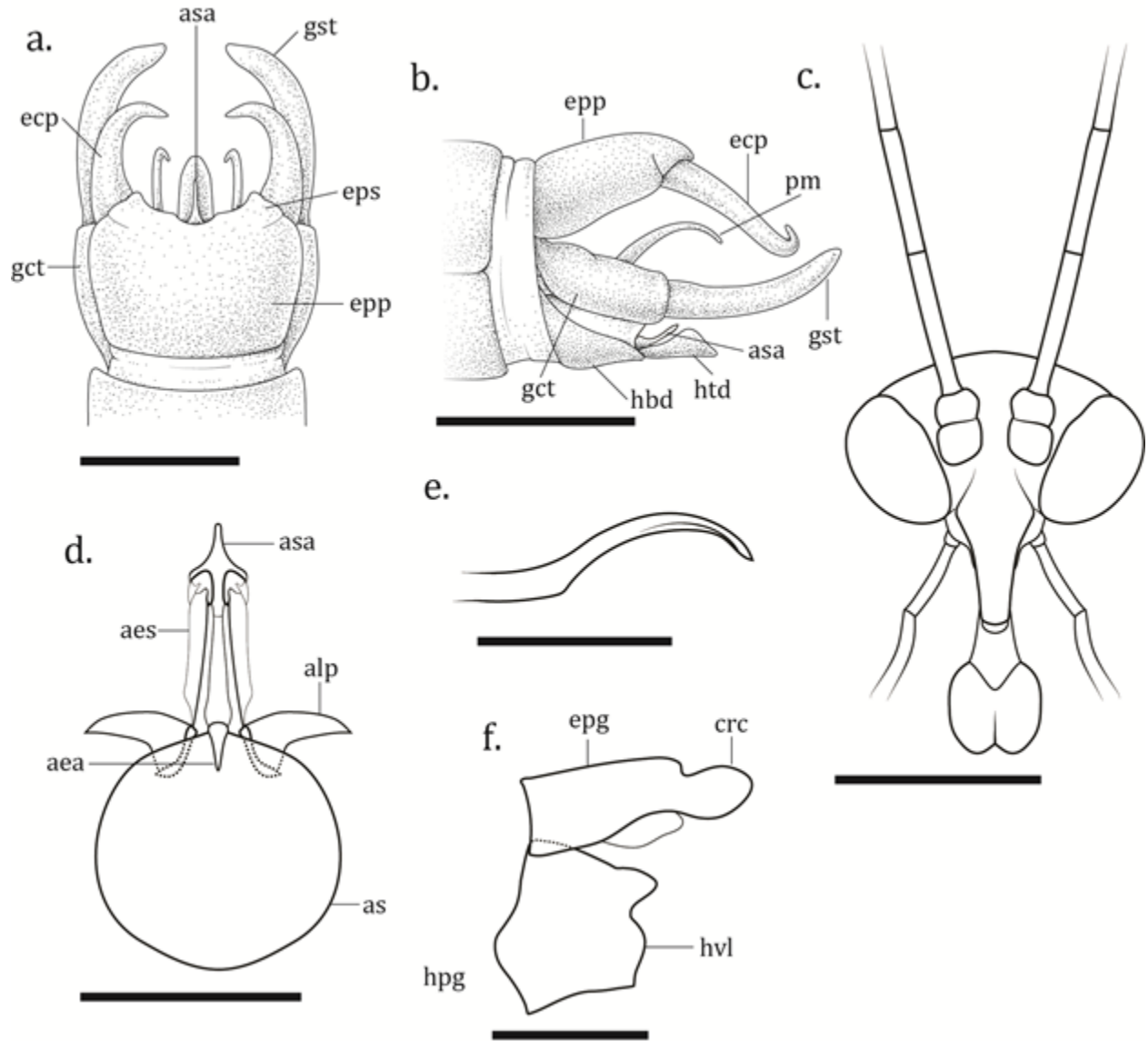


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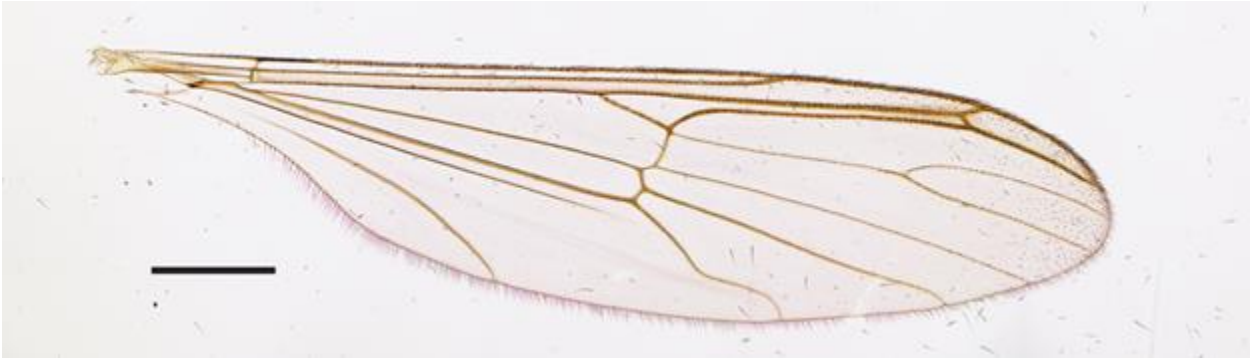


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Figure 26.

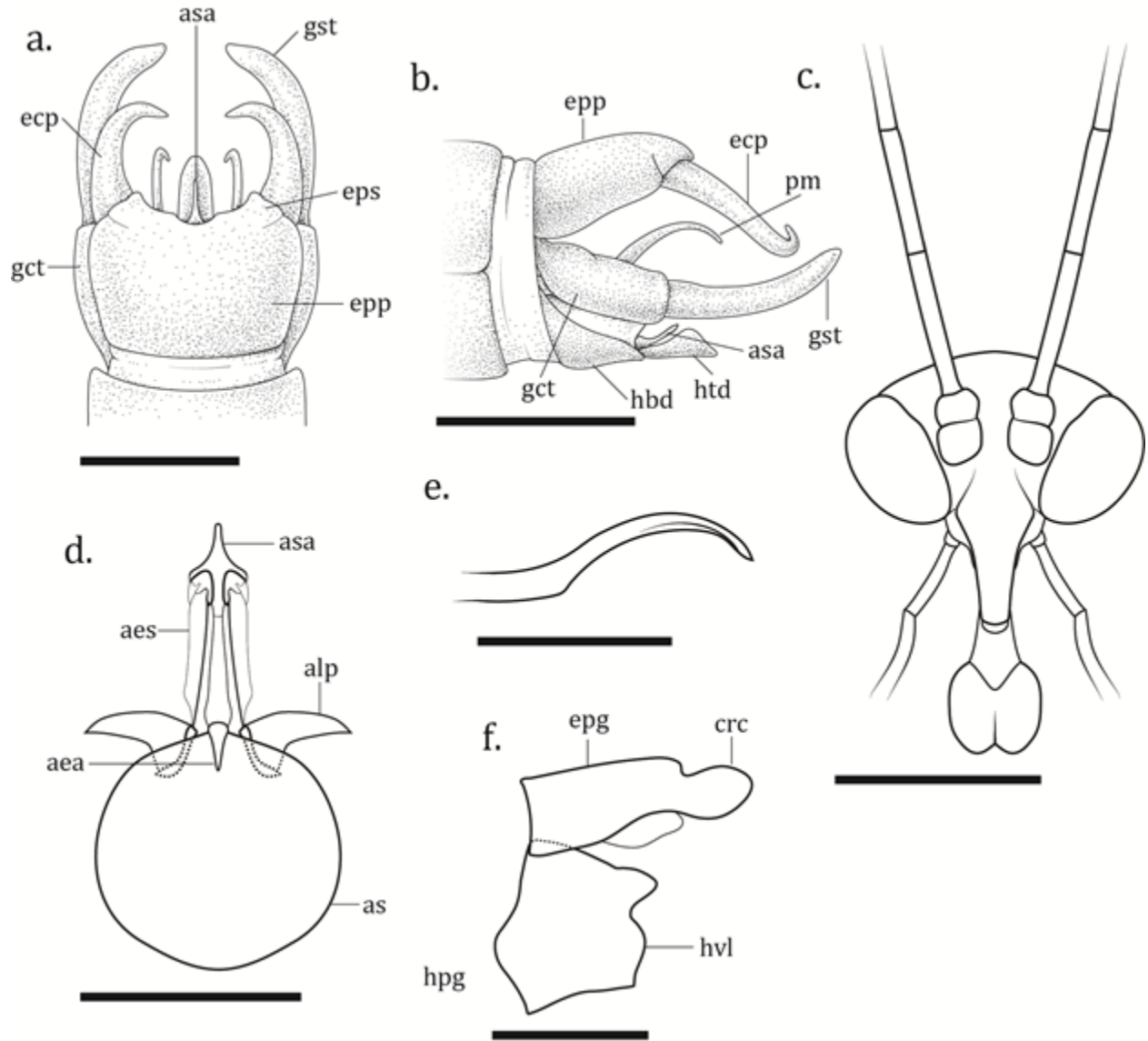


Figure 27.



Figure 28.



Figure 29.

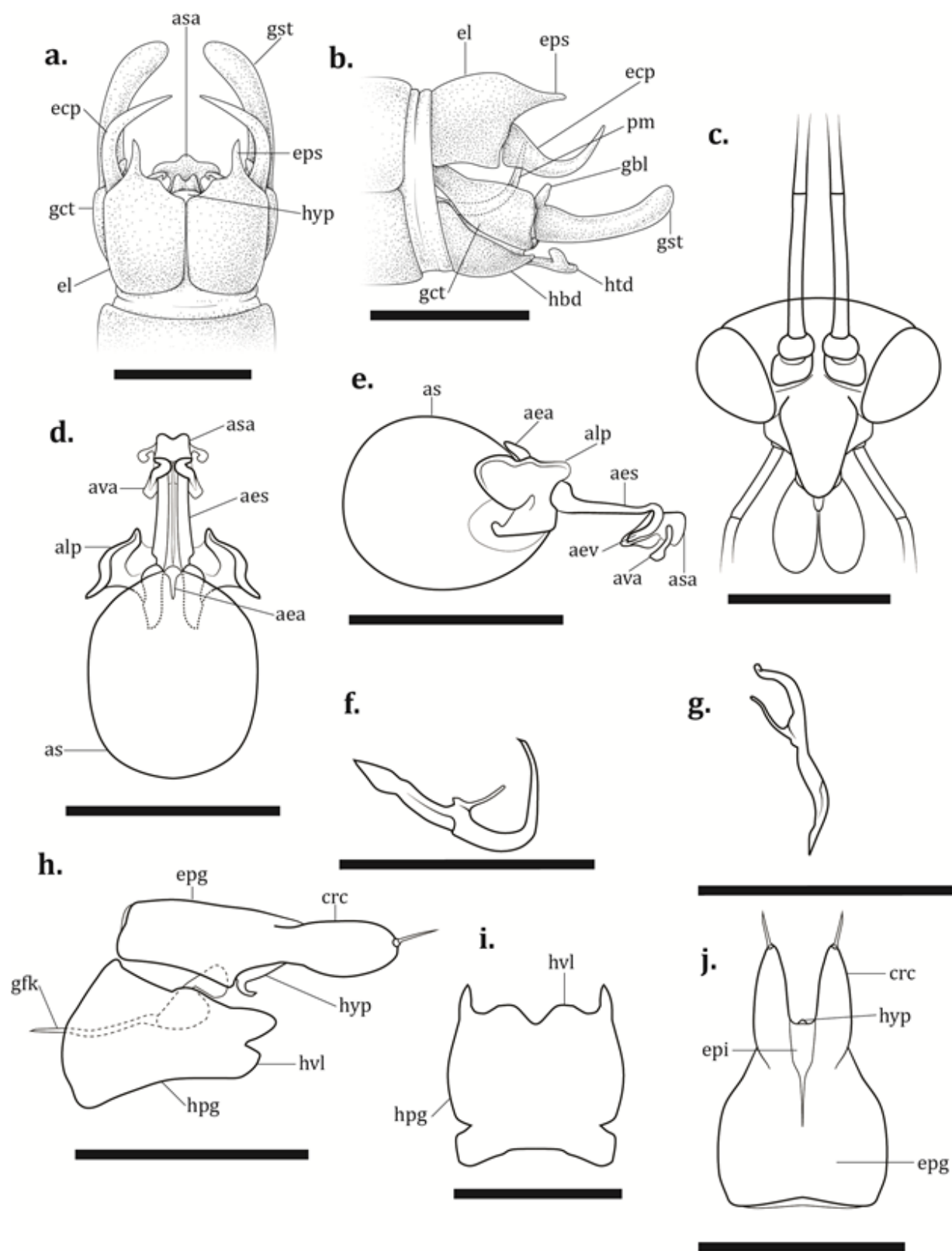


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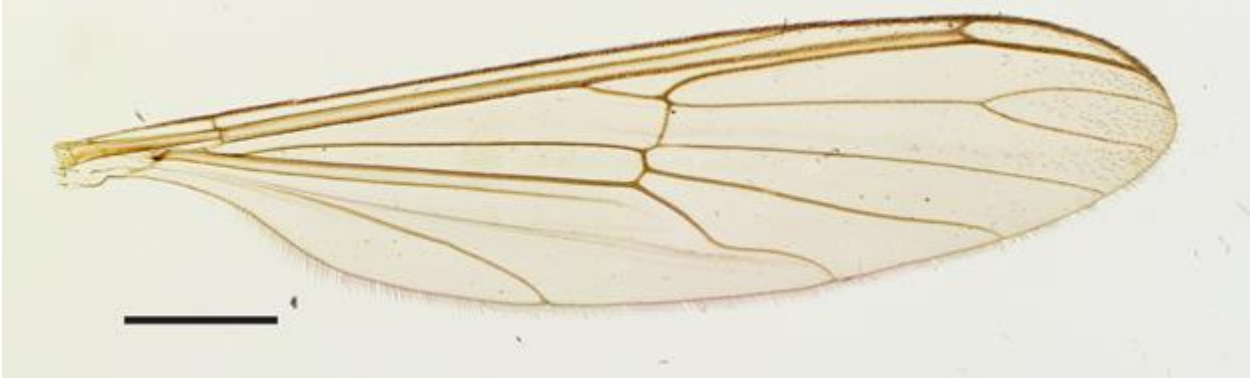


Figure 31.



Figure 32.

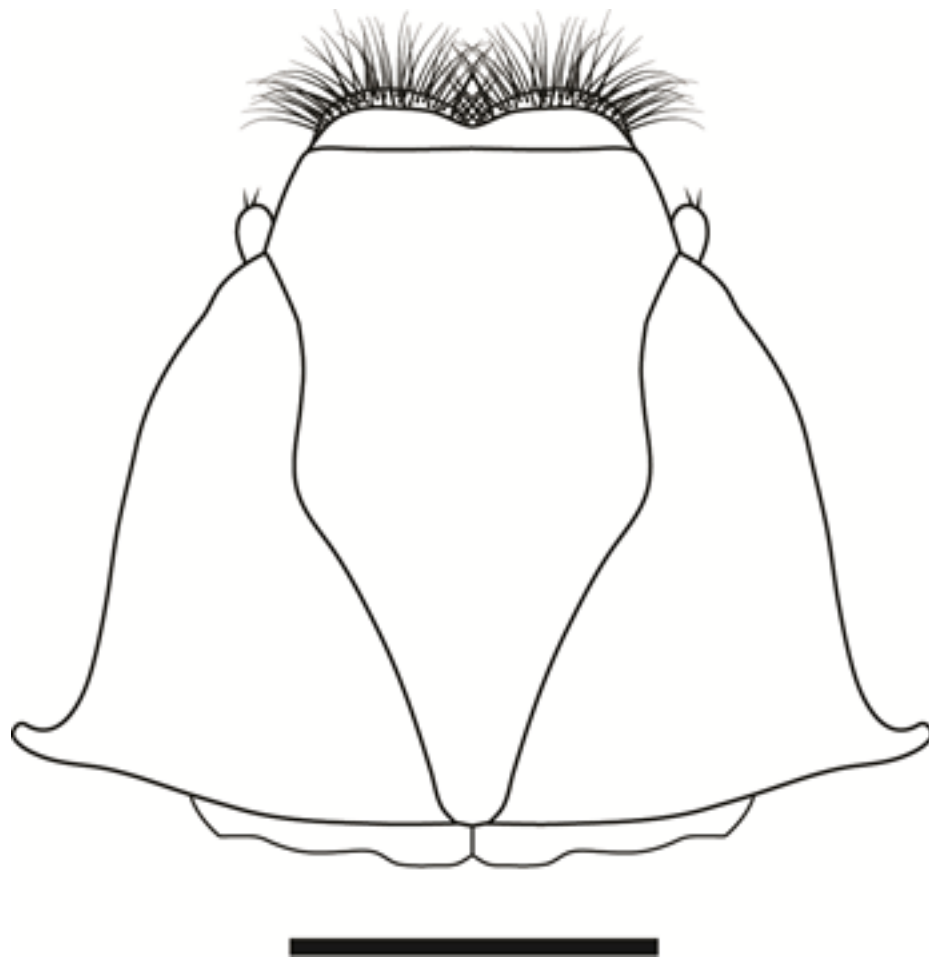


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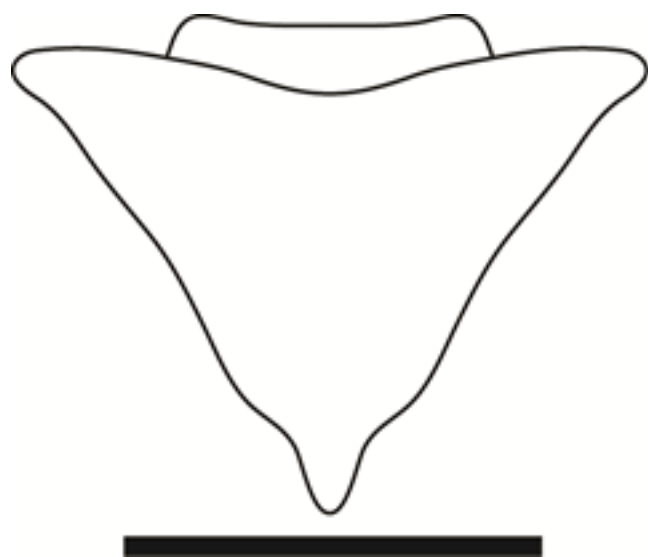


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Figure 35.

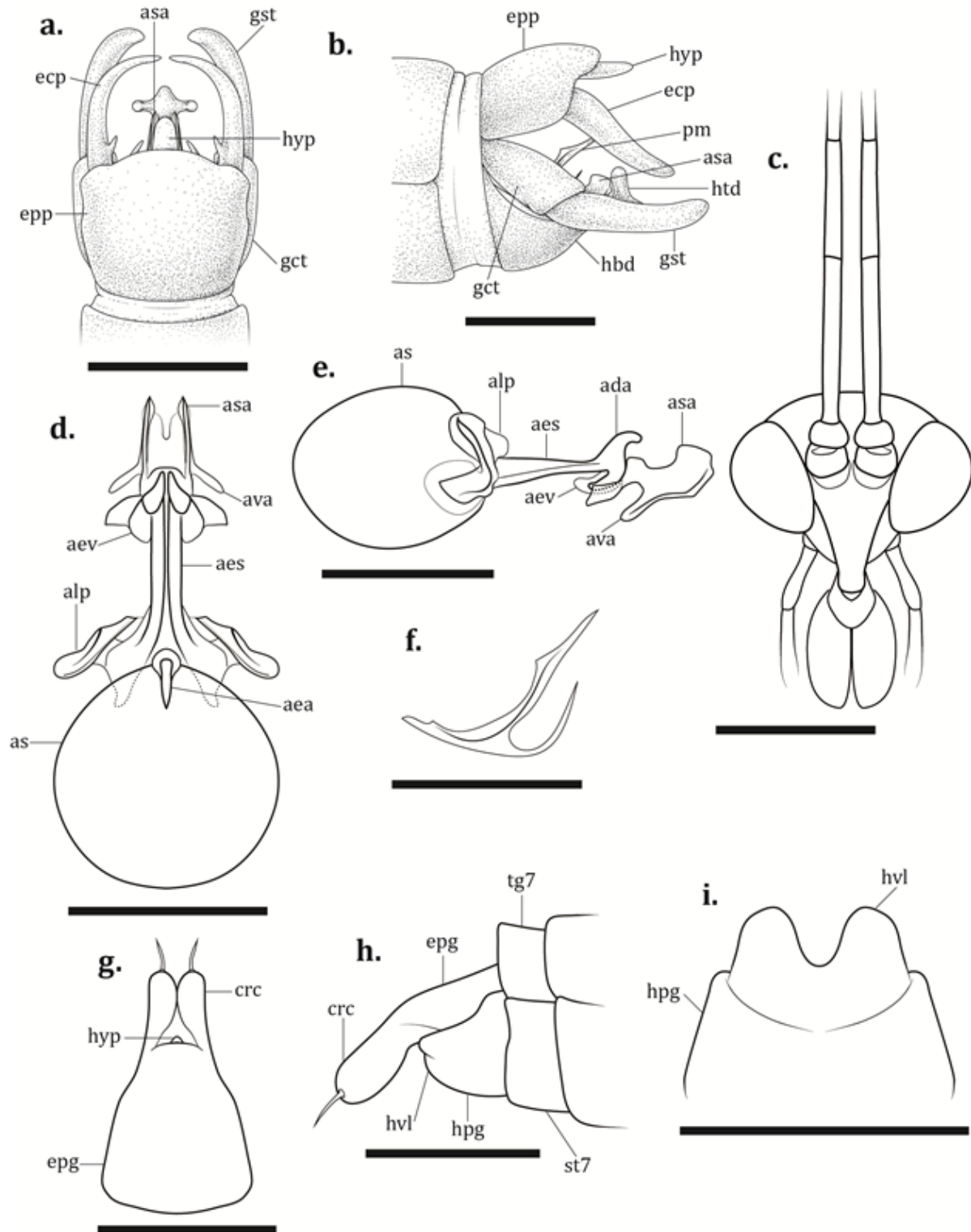


Figure 36.



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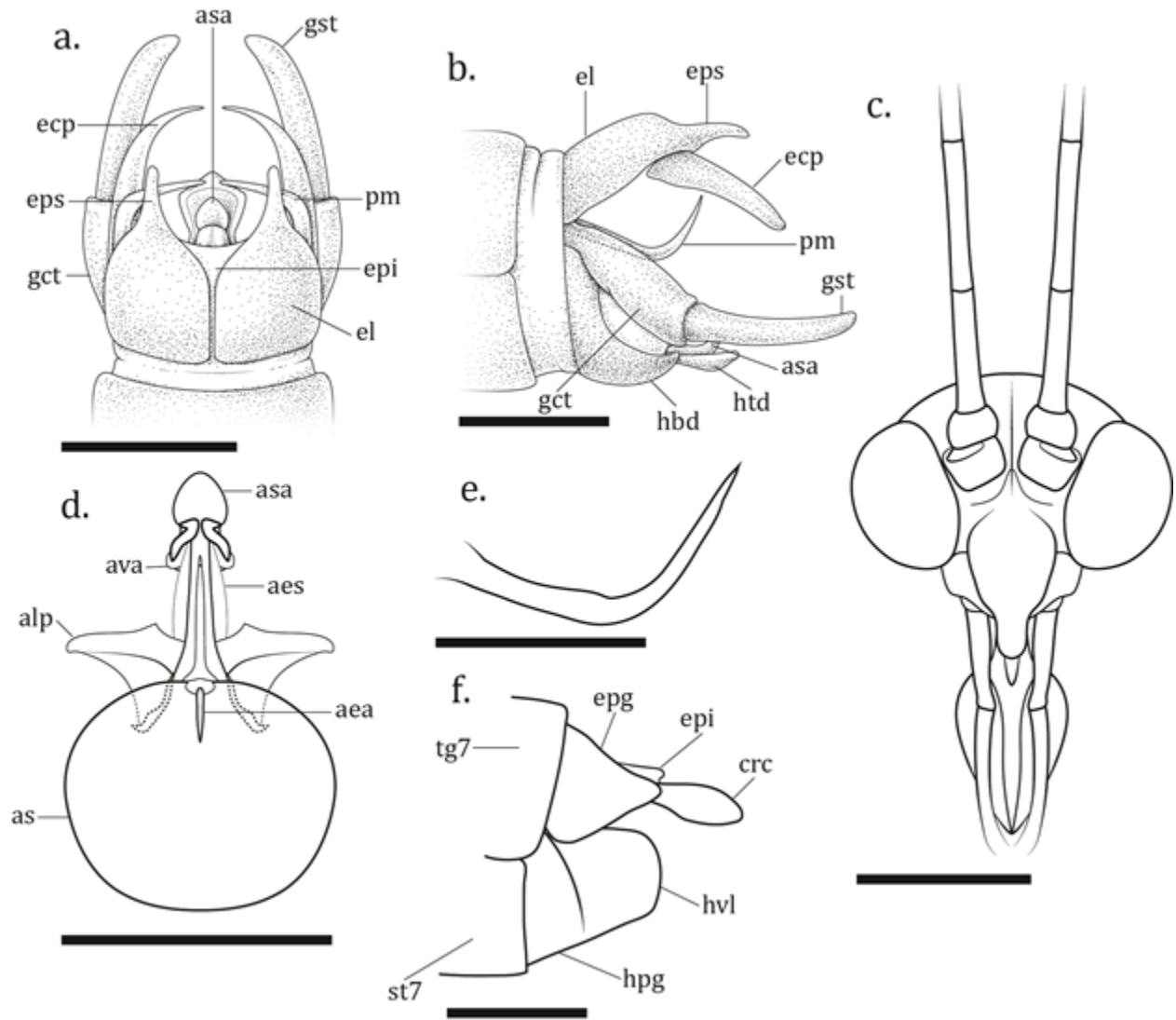


Figure 39.



Figure 40.



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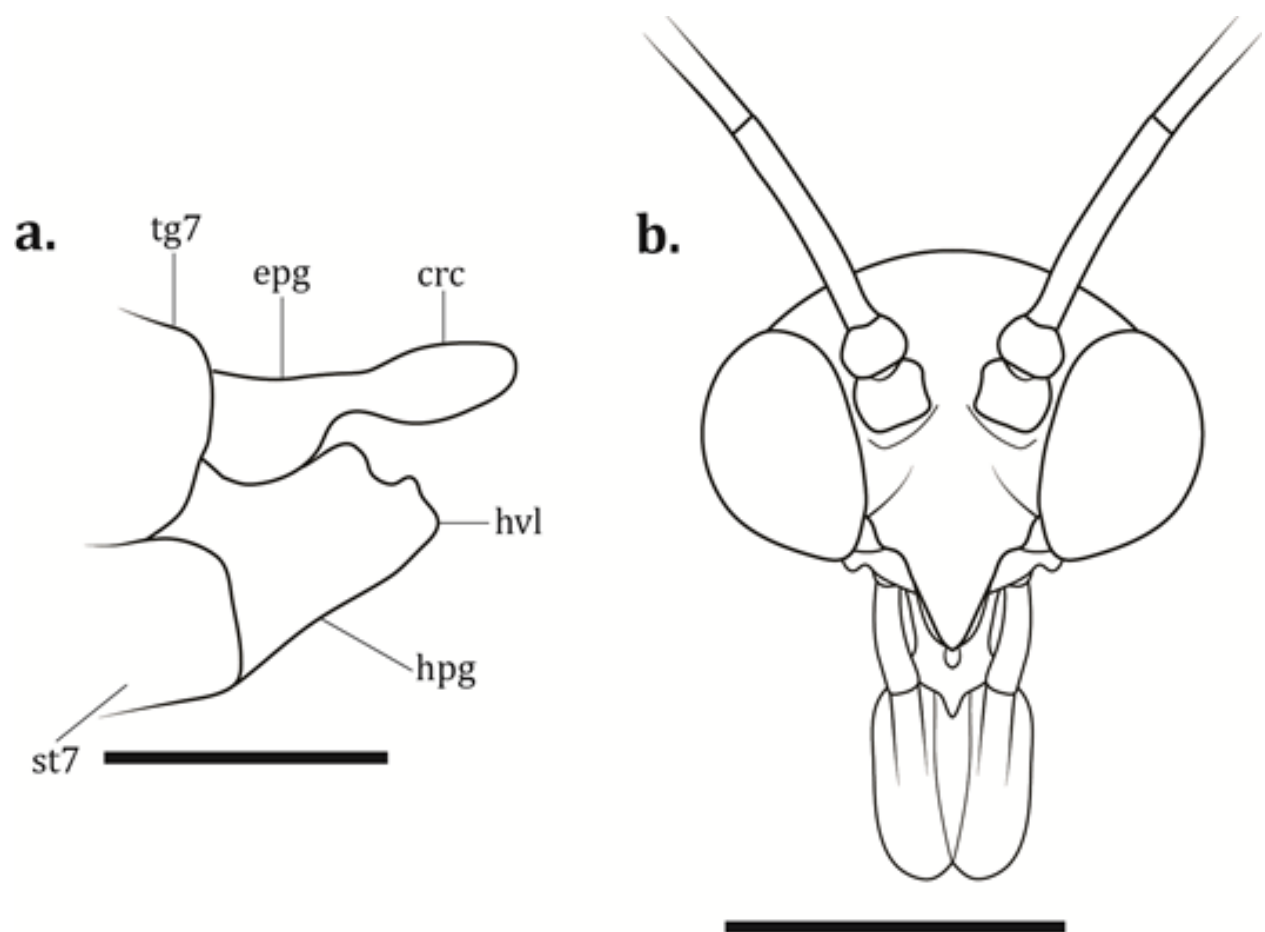


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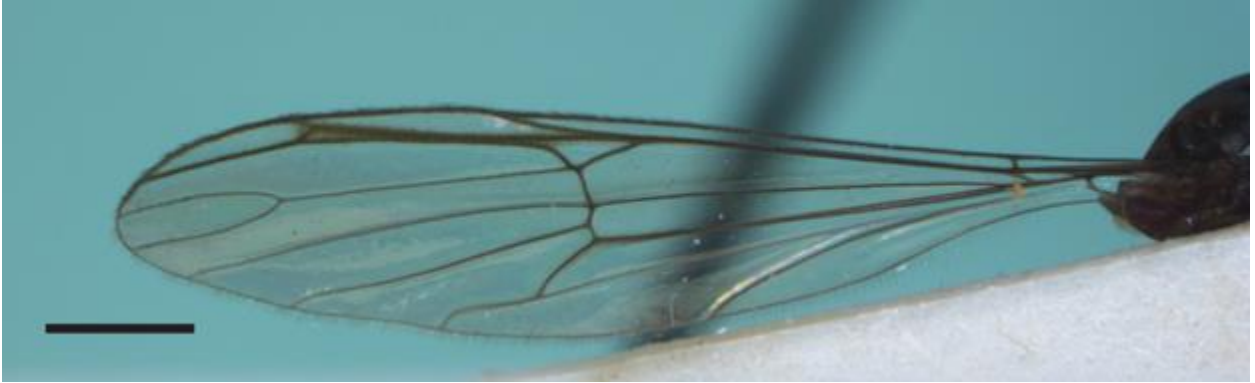


Figure 43.



Figure 44.

CHAPTER SEVEN: A REVISION OF PTYCHOPTERA MEIGEN WITH AN EVALUATION OF SUBGENERIC CONCEPTS, INCLUDING A MOLECULAR PHYLOGENY OF THE NEARCTIC PTYCHOPTERIDAE (DIPTERA)

To be submitted to *Zootaxa*

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Abstract

The extant species in the genus *Ptychoptera* Meigen are revised, including redescrptions and illustrations. *Ptychoptera pseudosimilis* Fasbender **sp. n.** is described. Phylogenetic analyses were performed on a comprehensive morphological dataset and a molecular dataset of the Nearctic taxa. Several monophyletic groups have been identified, and the subgeneric classification of the genus has been revised. *Ptychoptera (Ptychoptera)* Meigen is fully described and more concisely delimited, *Ptychoptera (Parapteroptera)* Tonnoir is demonstrated as a monophyletic taxon, and the subgenera *Ptychoptera (Amblyptycha)* Fasbender **subgen. n.**, *Ptychoptera (Chrysoptycha)* Fasbender **subgen. n.**, *Ptychoptera (Rheoptycha)* Fasbender **subgen. n.**, *Ptychoptera (Tigrimyia)* Fasbender **subgen. n.**, and *Ptychoptera (Unguipitycha)* Fasbender **subgen. n.** are described based on clades recovered in the phylogenetic analyses.

Introduction

The first ptychopterid was described as a species of *Tipula* by Linnaeus in 1758 (Linnaeus, 1785), and much of the first century and a half of research on the group was a trend towards recognizing their distinctness at first the generic and later familial level (Meigen 1803, Osten Sacken 1862, Hart 1895). Comprised of two extant subfamilies (Bittacomorphinae and Ptychopterinae), the group is associated

with their larval habitat of saturated organic sediments, even as adults (Mattingly 1987, Wolf & Zwick 2001). The family is distributed throughout the Holarctic region, as well as the Afrotropics.

The majority of the extant species of Ptychopteridae are members of the subfamily Ptychopterinae, placed in the single genus *Ptychoptera* Meigen, 1803. Most species in the genus were described in the first half of the 20th century, with over half of all extant species described by the prolific crane fly specialist Charles P. Alexander. Descriptions were often rudimentary, lacking illustrations, and larger revisions or regional catalogs were rare. The only faunas that have received systematic examination have been Europe (Peus 1958, Krzeminski & Zwick 1993) and Japan (Nakamura & Saigusa 2009). Even in Europe the species composition and distribution has not been fully resolved (Zwick & Starý 2003, Ujvárosi *et al* 2011). There is currently no comprehensive key to the world fauna, and many species remain undeterminable without examining type specimens.

Taxonomic History of *Ptychoptera*

Initially described as *Liriope* Meigen, 1800, *Ptychoptera* was more widely used due to the wider availability of the later publication (Melville, 1960). In 1963 the International Commission of Zoological Nomenclature suppressed *Liriope* in favor of *Ptychoptera* (ICZN 1963). The only other significant change to the generic composition of Ptychopterinae was the description of the genus *Parapteroptera* Tonnoir, 1919, for a distinctive group of European *Ptychoptera* species delimited by the presence of an auxiliary sexual organ on abdominal Sternite IX. This name was soon synonymized (Alexander, 1927) and largely ignored until Zwick & Starý (2003) resurrected it as a subgenus of *Ptychoptera*, stating:

“The derived condition in *Parapteroptera* is very distinct and monophyly of the group appears certain. However, its recognition as a genus group taxon may turn the remaining *Ptychoptera* into a paraphyletic taxon. To decide on this, a phylogenetic study of *Ptychoptera* on a global scale is required which is presently impractical.”

Only one subsequent publication (Ujvárosi *et al* 2011) has dealt with the European fauna and recognized *P. (Paraptychoptera)*. Other recent publications have focused primarily on describing new taxa from Asia (Kang *et al* 2013, Paramonov 2013) and thus have not had to consider *P. (Paraptychoptera)*. The phylogeny and classification within *Ptychoptera* has thus remained essentially unexplored outside Europe.

The early species taxonomy of Ptychopteridae was based on external morphological features, primarily coloration and wing patterns, with limited consideration of the male genitalia (i.e. Linnaeus 1758, Fabricius 1781, 1787, 1801, Meigen 1804, Say 1824, Osten Sacken 1860, 1877). The understanding of the species diversity of Ptychopteridae was revolutionized by the detailed examination of male genitalia, which allowed the recognition of numerous previously unrecognized species (i.e. Tonnoir 1919, Tjeder 1968), as well as the investigation of previously unexplored faunas (Alexander 1917, 1920b, 1921b, 1936, 1937a, 1937b, 1943, 1946, 1947, 1953, 1955, 1956, 1958 etc.). It was during the early to mid 20th century that the majority of the known ptychopterid fauna was described, and not until the second half of that century that attempts at regional revisions and faunistics were attempted, continuing to the present (Peus 1958, Freeman 1959, Alexander 1967, Draskovits 1983, Krzeminski 1986, Krzeminski & Zwick 1993, Pârvu 2004, Nakamura & Saigusa 2009, Ujvárosi *et al* 2011). To date there has been no comprehensive revision of the world fauna, and outside of Europe faunistic studies have been of limited geographic areas (Alexander 1967, Nakamura & Saigusa 2009) or of limited depth (Freeman 1959).

Though the keys and descriptive literature of Europe are well developed, publications on *Ptychoptera* in the rest of the world have historically focused primarily on diagnostic characters, with little in depth interpretation or discussion of the morphology of individual species. Species were often delineated in original descriptions by comparison to other established species, sometimes even citing

diagnostic characters as “differing in details of (structure)” (i.e. Alexander, 1937). Many of these species were essentially undeterminable without consultation of type specimens. Previous authors also frequently did not update old descriptions when describing similar new taxa, meaning that older names could only be determined in opposition to the new species (i.e. Alexander, 1959). Even more thorough modern publications (Kang *et al* 2013) have not treated previously described species beyond keys. Finally, many species were described based on characters that are not actually diagnostic when examined among larger samples of specimens, with some being too variable within a species and others too static between species (Alexander 1920b, 1937).

Ecological History of *Ptychoptera*

The association of *Ptychoptera* with saturated sediments has been known for over a century (Hart 1895), but attempts at understanding habitat partitioning and phenology did not occur for nearly forty years (Rogers 1933, 1942) and focused ecological study of the group was not undertaken until the second half of the 20th century (Hodkinson 1973, Harris & Carlson 1978, Mattingly 1987, 1988, Stubbs 1993, Wolf *et al* 1997, Wolf & Zwick 2001).

Studies of the phenology and life cycle of *Ptychoptera* find that *Ptychoptera* overwinter as larvae in temperate climates and emerge in the spring and early summer (Rogers 1942, Hodkinson 1973, Wolf & Zwick 2001). Some species are univoltine (Hodkinson 1973, Wolf & Zwick 2001), while others are multivoltine (Rogers 1942). This data is represented from only three species, all of which are known from temperate areas, thus the phenology of the group as a whole remains poorly understood – especially in the tropics.

Other studies have examined the feeding ecology of *Ptychoptera*, though only in two lotic species (Mattingly 1987, 1988, Wolf *et al* 1997). *Ptychoptera* larvae are collector-gatherers, feeding on fine particulate organic matter less than 250 micrometers in diameter (Mattingly 1987).

Rogers (1933, 1942) provided early ecological notes on *Ptychoptera*. Stubbs (1993) provided the most detailed descriptions of habitats for the European fauna, noting the general conformation of habitat (drainage ditch, bog, etc.) and other details such as water flow and presence of vegetation. Harris & Carlson (1978) examined the distribution of the larvae of two ptychopterids, *Bittacomorpha clavipes* Fabricius, 1781 and *Ptychoptera quadrifasciata* Say, 1824 in a stream in North Dakota and found that these species partitioned habitat space within the stream based on the velocity and depth of the water flow.

Extent of the Current Study

This study is an examination of the species diversity and evolutionary structure of *Ptychoptera*, based on material of 64 of 81 valid extant species, with 56 being suitable for morphological assessment and analysis using Maximum Parsimony (Goloboff *et al* 2008) and Bayesian Inference (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003). A group of Nearctic taxa were also sampled for DNA sequences of the COI (mitochondrial) and TUFT (nuclear) genes for a molecular phylogeny. All specimens with material available are redescribed and illustrated, and a new species (*Ptychoptera pseudosimilis* Fasbender sp.n.) was discovered. Based on the results of the phylogenetic analyses five new subgenera: *Ptychoptera (Amblyptycha)* Fasbender subgen.n., *Ptychoptera (Chrysoptycha)* Fasbender subgen.n., *Ptychoptera (Rheoptycha)* Fasbender subgen.n., *Ptychoptera (Tigrimya)* Fasbender subgen.n., and *Ptychoptera (Unguptycha)* Fasbender subgen.n. are erected. *Ptychoptera (Parapteroptera)* Tonnoir is found to represent a monophyletic group, and the subgenus *Ptychoptera (Ptychoptera)* Meigen, 1803 is more stringently defined as a monophyletic group. Ecological aspects of the Nearctic taxa are also discussed.

Materials and Methods

Material used in this study was acquired both through field collections of the authors and loans from research collections. These collections include: Institut Royal des Sciences Naturelles de Belgique (IRNSB), Personal Collection of Art Borkent (BORK), Moravian Museum of Brno (MZMB), Clemson University Arthropod Collection (CUAC), Carnegie Museum of Natural History (CMNH), Gillette Museum of Arthropod Diversity, Colorado State University (CSU), Natural History Museum of Denmark (ZMUC), the Field Museum of Chicago (FMNH), Harvard Museum of Comparative Zoology (MCZ), Hunterian Museum of Glasgow (HMG), Illinois Natural History Survey (INHS), Iowa State Insect Collection (ISIC), University of Kansas Snow Entomological Museum (KU), Natural History Museum, London (BMNH), Michigan State University Arthropod Research Collection (ARC), University of Michigan Museum of Zoology (UMMZ), University of Minnesota Museum of Arthropods (UMSP), North Carolina State University Insect Museum (NCSU), Oberösterreichs Landesmuseum (OOLM), Oregon State University (ORSU), Pacific Northwest Diptera Research Lab (PNDL), Purdue University Entomology Research Collection (PERC), Smithsonian National Museum of Natural History (USNM), Washington State University James Entomological Collection (WSU). In “Material Examined” line breaks are denoted by a “,”, and separate labels on the same specimen are designated using a “/”.

Specimens were examined using Olympus SZX12 and SZX9 stereomicroscopes and a Nikon E800 compound microscope fitted with Differential Interference Contrast optics. Photomicrographs were taken using a Nikon DS-Fi1 camera mounted to a Nikon DS-U3 control unit. Photomicrographs were processed using Adobe Photoshop CS5, and illustrations were rendered from photomicrographs using Adobe Illustrator CS5. Measurements and scales were recorded using an optical micrometer mounted in the SZX12 stereomicroscope. Descriptive terminology is based on Cumming & Wood (2009), supplemented by the ingroup terminology proposed in chapter five.

Specimens were cleared for dissection by first rehydrating for 18-48 hours, then preparing an aqueous KOH solution made by inserting one KOH pellet into a 3/4 full 1dram shell vial. The specimen was then placed in the KOH solution and heated on a warming plate to 60°C. Specimens were checked every five minutes until soft tissue was completely dissolved and external sclerites were partially transparent. Cleared specimens were then rinsed twice in water for five minutes and transferred through a series of alcohol concentrations (30-50-70-95%). Finally specimens were placed in alcohol-diluted glycerin, which was allowed to evaporate, at which time the glycerin suspended specimen was transferred to a microvial pinned with the remainder of the insect.

Phylogenetic Methods

Morphological Phylogenies

Outgroups were selected for morphological analysis based on early divergence in the dipteran phylogeny (Pediidae: *Tricyphona*) or phyletic proximity to Ptychopteridae (Blephariceridae: *Edwardsina*, Ceratopogonidae: *Culicoides*, Dixidae: *Dixa*, Tanyderidae: *Araucoderus*, *Protoplasa*) (Wiegmann *et al* 2011). Ingroup taxa were selected for inclusion based on the availability of substantial male genitalia for scoring (as >75% of informative characters are in the male genitalia), though many species were incomplete. Species known only from females or with especially fragmentary material were excluded from the analysis as their placement would not be resolved. Characters were scored by direct visual observation of specimens under compound and stereomicroscopes, and data was input into a Microsoft Excel 2010 spreadsheet. The completed spreadsheet was then loaded into MacClade 4.08 (Maddison & Maddison 2005) and exported as Nexus and Hennig86 files. Analyses were made using MrBayes 3.01 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003) for Bayesian Inference and TNT (Goloboff *et al* 2008) for Maximum Parsimony.

The parameters used in the Bayesian analysis were: a Markov Chain Monte Carlo analysis was run for 5,000,000 generations in two runs with four chains each, temperature set to 0.2, sample frequency was set at 100, swap frequency was set to one and the number of swaps set to one, burn-in set using burninfrac at 0.15. After the analysis was complete the split frequencies were 0.010124, and the sampled trees were compiled into a consensus tree using the “sumt” function with a burn-in of 8500. The dataset was analyzed in TNT using the “New Technology Search” with the “Sectorial Search” option, “Init. Adseqs.” set at five and “Find min. Length” set at thirty. Bootstrap values were calculated using a “Standard Search” with 100 replicates, Bremer support was calculated using TBR from existing trees.

Character state changes were recovered through MacClade’s character state visualization function (Maddison & Maddison 2005), and were plotted onto the trees using Adobe Illustrator.

Molecular Phylogeny

Outgroups for the molecular phylogeny were selected based on the availability of a complete genome (*Drosophilidae: Drosophila*) or the phyletic proximity to Ptychopteridae (*Blephariceridae: Edwardsina*, *Culicidae: Anopheles*). Ingroup taxa were selected based on the availability of material suitable for molecular analysis. Two genes were selected, the rapidly evolving mitochondrial gene Cytochrome Oxidase I and the more slowly evolving nuclear gene TUFT. This combination was desired to obtain resolution at both the metapopulation/species level as well as higher levels of the phylogeny.

The combined dataset was analyzed using MrBayes 3.01 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003). The analysis was run using the GTR model with a gamma distribution and accounting for invariable sites, with the MCMC analysis running for 2,000,000 generations over two runs with four chains each, with a temperature of .2. The swap frequency was set at one with two

attempted swaps, and parameters were sampled every 100 generation. The burn-in was set using burninfrac at .15. Split frequencies at the conclusion of the analysis were 0.00296, and a consensus tree was generated using a burnin of 5000.

Results

The results of the morphological phylogenetic analyses are presented in Figures 1 and 2. The results of the molecular phylogenetic analysis is presented in Figure 3. The results of the taxonomic study are presented below.

Valid species of *Ptychoptera* Meigen, 1803

Ptychoptera (Ptychoptera) Meigen sensu stricto (Holarctic)

Ptychoptera contaminata Linnaeus, 1758 +
Ptychoptera hugoi Tjeder, 1968
Ptychoptera metallica Walker, 1848
Ptychoptera minuta Tonnoir, 1919
Ptychoptera scutellaris Wiedemann, 1818[^]
Ptychoptera subscutellaris Alexander, 1921
Ptychoptera yankovskiana Alexander, 1945

Ptychoptera (Amblyptycha) Fasbender (Indian Subcontinent)

Ptychoptera garhwalensis Alexander, 1959
Ptychoptera sikkimensis Alexander, 1965
Ptychoptera tibialis Brunetti, 1911 +

Ptychoptera (Chrysoptycha) Fasbender (Nearctic Pacifica Coast)

Ptychoptera sculleni Alexander, 1943 +

Ptychoptera (Parapterychoptera) Tonnoir (Europe, West Asia, North Africa)

Ptychoptera (Parapterychoptera) agnes Krzeminski & Zwick, 1993*
Ptychoptera (Parapterychoptera) delmastroi Zwick & Sary, 2003*
Ptychoptera (Parapterychoptera) handlirschi Cizek, 1919
Ptychoptera (Parapterychoptera) helena Peus, 1958
Ptychoptera (Parapterychoptera) lacustris Meigen, 1830
Ptychoptera (Parapterychoptera) longicauda Tonnoir, 1919
Ptychoptera (Parapterychoptera) paludosa, Meigen 1804 +
Ptychoptera (Parapterychoptera) resseli Theischinger, 1978
Ptychoptera (Parapterychoptera) silvicola, Zwyrtsek & Rozkosny, 1967[^]
Ptychoptera (Parapterychoptera) surcoufi Seguy, 1925*

Ptychoptera (Rheoptycha) Fasbender (Western North America)*Ptychoptera espica* Fasbender*Ptychoptera monoensis* Alexander, 1947*Ptychoptera pendula* Alexander, 1937 +*Ptychoptera townesi* Alexander, 1943***Ptychoptera (Tigrimya) Fasbender*** (Eastern North America)*Ptychoptera abbreviata* Fasbender*Ptychoptera osceola* Alexander, 1959*Ptychoptera quadrifasciata* Say, 1824 +***Ptychoptera (Unguptycha) Fasbender*** (Western North America, Eastern Asia)*Ptychoptera bilobata* Copley & Cannings*Ptychoptera byersi* Alexander, 1966*Ptychoptera coloradensis* Alexander, 1937*Ptychoptera daimio*, Alexander, 1921*Ptychoptera lacrimiformis* Fasbender & Courtney*Ptychoptera lenis* Osten Sacken, 1877 +*Ptychoptera minor* Alexander, 1920*Ptychoptera obscura* Peus, 1958*Ptychoptera uta* Alexander, 1947***Ptychoptera incertae sedis******Ptychoptera near P. (Amblyptycha) & P. (Unguptycha)****Ptychoptera albimana* Fabricius, 1787 (Europe)*Ptychoptera alina* Krzeminski & Zwick, 1993 (Caucasus)***Ptychoptera with plesiomorphic genital features****Ptychoptera alexanderi* Hancock, 2006 (Central America)*Ptychoptera ichitai* Nakamura & Saigusa, 2009 (Japan)*Ptychoptera japonica* Alexander, 1913 (Japan)*Ptychoptera kyushuensis* Nakamura & Saigusa, 2009 (Japan)**Ptychoptera yamato* Nakamura & Saigusa, 2009 (Japan)***Afrotropical Ptychoptera****Ptychoptera africana* Alexander, 1920 +*Ptychoptera camerounensis* Alexander, 1921*Ptychoptera capensis* Alexander, 1917*Ptychoptera kosiensis** Stuckenberg, 1983*Ptychoptera madagascariensis* Alexander, 1937*Ptychoptera matongoensis* Alexander, 1958 (f)*Ptychoptera pauliani* Alexander, 1957^*Ptychoptera robinsoni* Alexander, 1957**Ptychoptera stuckenbergi* Alexander, 1956^ (f)*Ptychoptera uelensis* Alexander, 1928^

East Asian *Ptychoptera*

Ptychoptera annandalei Brunetti, 1918
Ptychoptera bannaensis Kang, Yao & Yang, 2013*
Ptychoptera bellula Alexander, 1937
Ptychoptera chalybeata Alexander, 1956
Ptychoptera clitellaria Alexander 1935 (f)
Ptychoptera distincta Brunetti, 1911 (f)
Ptychoptera formosensis Alexander, 1924
Ptychoptera gutianshana Yang & Chen, 1995
Ptychoptera ichneumonoidea Alexander, 1946*
Ptychoptera javensis Alexander, 1937
Ptychoptera lii Kang, Yao & Yang 2013*
Ptychoptera longwangshana Yang & Chen 1998*
Ptychoptera lushuiensis Kang, Yao & Yang 2013*
Ptychoptera malaisei Alexander, 1946
Ptychoptera noonandani Paramonov, 2013*
Ptychoptera pallidicostalis Nakamura & Saigusa, 2009*
Ptychoptera perbona Alexander, 1946 (Southeast Asia)
Ptychoptera persimilis Alexander, 1947
Ptychoptera praescutellaris Alexander, 1946
Ptychoptera pseudosimilis Fasbender sp. n.
Ptychoptera qinggouensis Kang, Yao & Yang, 2013*
Ptychoptera sumatrensis Alexander, 1936
Ptychoptera takeuchii Tokunaga, 1938*
Ptychoptera wangae Kang, Yao & Yang, 2013*
Ptychoptera xinglongshana Yang, 1996*
Ptychoptera yasumatsui Tokunaga, 1939

West Asian *Ptychoptera*

Ptychoptera peusi Joost, 1974*

+ Type species.

*Material not available for the current study.

^ Only fragmentary material available for the current study.

(f) Species known only from females

Key to the Males of *Ptychoptera* based on Genitalia

1. Epandrium with epandrial claspers (invaginated extension of epandrial lobe)... **2**

- Epandrium lacking epandrial claspers... **48**

2. Hypandrium with spathate lobes (paired lobes on ventral portion of posterior surface of basal division)... **3**

- Hypandrium lacking spathate lobes... **29**

3. Epandrial clasper with ventromesal lobe (large lobe on medial surface directed ventrally)... **4**

- Epandrial clasper lacking ventromesal lobe... **17**

4. Epandrium with elongate, nematoform claspers... *Ptychoptera albimana* Fabricius

- Epandrium with blunt or claw-like claspers... **5**

5. Epandrial clasper blunt, with ventromesal lobe near apex, apex of terminal division of hypandrium round plate. *Ptychoptera (Amblyptycha)*... **15**

- Epandrial clasper claw-like, ventromesal lobe with base subapical, apex of terminal division of hypandrium triangular trough... **6**

6. Basal lobe of gonostylus subdivided, apical stylus flattened in cross section with glabrous dorsal ridge, apex square and posterodorsal corner extended... *Ptychoptera alina* Kzeminski & Zwick

- Basal lobe of gonostylus undivided knob, apical stylus round in cross section with glabrous dorsal ridge, apex rounded. *Ptychoptera (Unguptycha)*... **7.**

7. Epandrium with two spines medial to ventromesal lobe, hypandrial spathate lobes rounded... *P.*

(*Unguptycha*) *daimio* Alexander

- Epandrium with one spine medial to ventromesal lobe, hypandrial spathate lobes with apex pointed...

8

8. Hypandrium with spathate lobes not reaching gonopods, ventromesal lobe with C-shaped apex... *P.*

(*Unguptycha*) *lenis* Osten Sacken

- Hypandrium with spathate lobes extending to gonopods, ventromesal lobe apex undivided... **9**

9. Ventromesal lobe directed anterior... **10**

- Ventromesal lobe directed ventrally... **11**

10. Paramere with lateral lobe subequal to apical portion beyond lateral lobe... *P. (Unguptycha) obscura*

Peus

- Paramere with lateral lobe shorter than apical portion beyond lateral lobe... *P. (Unguptycha)*

coloradensis Alexander

11. Ventromesal lobe stylate, not flattened... **12**

- Ventromesal lobe flattened... **13**

12. Epandrial clasper with lateral lobe at apex... *P. (Unguptycha) bilobata* Copley & Cannings

- Epandrial clasper with simple lateral margin at apex... *P. (Unguptycha) byersi* Alexander

13. Paramere dorsoventrally flattened at apex... *P. (Unguptycha) uta* Alexander

- Paramere laterally compressed at apex... **14**

14. Ventromesal lobe less than 2x length of petiole, apex of paramere recumbent... *P. (Unguptycha)*

minor Alexander

- Ventromesal lobe greater than 2x length of petiole, apex of paramere nearly vertical... *P. (Unguptycha)*

lacrimiformis Fasbender & Courtney

15. Epandrium without dorsolateral spine at epandrial clasper apex, gonostylus with apical stylus bent at sharp angle medially, triangular secondary lobe present... *P. (Amblyptycha) garhwalensis* Alexander

- Epandrium with dorsolateral spine at epandrial clasper apex, gonostylus with apical straight, triangular secondary lobe absent... **16**

16. Apices of paramere narrow, rod-like... *P. (Amblyptycha) tibialis* Brunetti

- Apices of paramere dorsoventrally flattened, semicircular... *P. (Amblyptycha) tibialis* Brunetti

17. Apical stylus and secondary lobe cross at apex of gonostylus... **18**

- Secondary stylus absent, or apical stylus and secondary lobe do not cross at apex of gonostylus... **21**

18. Paramere with apical lobes dorsoventrally flattened, semicircular with spine curved anterior...

Ptychoptera annandalei Brunetti

- Paramere with apical lobes not semicircular, if spines present directed posterior... **19**

19. Paramere with elongate, ribbon-like spines directed posterior, crossing medially... *Ptychoptera*

persimilis Alexander

- Paramere with without spines, or spines short, not extended posterior or crossing... **20**

20. Paramere trapezoidal in dorsal view... *Ptychoptera pseudosimilis* Fasbender

- Paramere bandlike in dorsal view... *Ptychoptera formosensis* Alexander

21. Epandrial clasper shorter than epandrial lobe... **22**

- Epandrial clasper longer than epandrial lobe... **24**

22. Epandrial clasper laterally compressed, basal lobe of gonostylus mushroom shaped... *Ptychoptera*

malaisei Alexander

- Epandrial clasper round in cross section, basal lobe simple knob or flattened paddle... **23**

24. Epandrial lobe tubular, apex of epandrial clasper not expanded, apex of gonostylus simple...

Ptychoptera capensis Alexander

- Epandrial lobe tapering, apex of epandrial clasper bulbous, apex of gonostylus with notch...

Ptychoptera chalybeata Alexander

24. Gonostylus longer than gonocoxite... **25**

- Gonostylus shorter or subequal to gonocoxite... **27**

25. Epandrial clasper with swelling approximately 3/4 length from apex, gonostylus lacking tertiary lobe at apex... *Ptychoptera madagascariensis* Alexander

- Epandrial clasper of uniform tapering length, gonostylus with tertiary lobe at dorsally at apex... **26**

26. Epandrial clasper with apex spatulate, gonostylus with tertiary lobe not extending to epandrial clasper... *Ptychoptera javensis* Alexander

- Epandrial clasper with apex not expanding, gonostylus with tertiary lobe extending dorsally beyond epandrial clasper... *Ptychoptera sumatrensis* Alexander

27. Gonocoxite broader than tall... *Ptychoptera camerounensis* Alexander

- Gonocoxite taller than broad... **27**

28. Apex of epandrial clasper pointed, secondary lobe of apical stylus semicircular... *Ptychoptera africana* Alexander

- Apex of epandrial clasper bulbous, secondary lobe of apical stylus subtrapezoidal... *Ptychoptera praescutellaris* Alexander

29. Terminal division of hypandrium with base divided... **30**

- Terminal division with base undivided... **42**

30. Epandrium nematoform, gonocoxites ovoid... *P. (Chrysoptycha) sculleni* Alexander

- Epandrium with triangular to trapezoidal epandrial lobes with articulated epandrial claspers, gonocoxites not ovoid... **31**

31. Hypoproct inevident, paired subepandrial sclerites present, apical stylus of gonostylus well sclerotized, undivided; abdominal sternite III with setal clusters. *Ptychoptera (Ptychoptera)*... **32**

- Hypoproct readily apparent, paired subepandrial sclerite single, fused to hypoproct, or absent, apical

stylus of gonostylus poorly sclerotized, often divided or reduced; abdominal sternite III with complex auxiliary sexual organ. *Ptychoptera* (*Parapteroptera*)... **37**

32. Epandrial claspers curving, without distinct angle, round in cross section... **33**

- Epandrial claspers with distinct medial angle, flattened in cross section... **34**

33. Gonostylus with secondary lobe of apical stylus placed basally... *P. (Ptychoptera) contaminata*

Linnaeus

- Gonostylus with secondary lobe of apical stylus placed midway along length... *P. (Ptychoptera) hugoi*

Tjeder

34. Gonostylus with secondary lobe located midway along apical stylus... **35**

- Gonostylus with secondary lobe located subapically on apical stylus... **36**

35. Apex of terminal division subquadrate, weakly constricted at base, subapical sclerite of aedeagus with ventral arms having triangular lateral lobe... *P. (Ptychoptera) subscutellaris* Alexander

- Apex of terminal division subtriangular, strongly constricted at base, ventral arms of subapical sclerite lacking lateral lobe... *P. (Ptychoptera) yankovskiana* Alexander

36. Epandrial clasper with subapical ventral surface convex and rounded, apices of paramere with three spines... *P. (Ptychoptera) metallica* Walker

- Epandrial clasper with subapical ventral surface with distinct angle, apices of paramere with two spines... *P. (Ptychoptera) minuta* Tonnoir

37. Apical stylus of gonostylus reduced... *P. (Parapteroptera) resli* Theischinger

- Apical stylus of gonostylus prominent... **38**

38. Epandrial clasper lacking lateral swelling, basal division of hypandrium without basal scale... **39**

- Epandrial clasper with lateral swelling, basal scale present... **40**

39. Posteromedial stylus present at base of epandrial clasper, hypoproct furcate apically, apical stylus and secondary lobe subequal in length... *P.(Parapychoptera) helena* Peus

- Posteromedial stylus absent, hypoproct triangular, secondary lobe shorter than apical stylus...

P.(Parapychoptera) lacustris Meigen

40. Epandrial clasper with semicircular paddle-like posteromedial stylus, apex of epandrial clasper pointed... *P.(Parapychoptera) handlirschi* Czizek

- Epandrial clasper with spine-like posteromedial stylus, apex of epandrial clasper rounded... **41**

41. Apical stylus of gonostylus pendulant, apex of terminal division of hypandrium elongate spine with furcate tip... *P.(Parapychoptera) longicauda* Tonnoir

-Apical stylus of gonostylus not pendulant, apex of terminal division of hypandrium low semicircular plate... *P.(Parapychoptera) paludosa* Meigen

42. Basal division of hypandrium subhemispherical, terminal division broadly fused to basal division... **43**

- Basal division of hypandrium band-like, terminal division narrowly fused to basal division... **46**

43. Dorsal gonocoxal lobe present, basal lobe of gonostylus sickle shaped... *Ptychoptera alexanderi* Hancock

- Dorsal gonocoxal lobe absent, basal lobe of gonostylus peglike... **44**

44. Apex of terminal division of hypandrium subquadrate, subapical sclerite of aedeagus subacute triangular, ventral surface smooth... *Ptychoptera ichitai* Nakamura & Saigusa

- Apex of terminal division of hypandrium spine-like, subapical sclerite of aedeagus acute spine, ventral surface serrated... **45**

45. Apex of parameres directed laterally... *Ptychoptera japonica* Alexander

- Apex of parameres directed medially... *Ptychoptera yamato* Nakamura & Saigusa

46. Apical stylus of gonostylus stylete, apex of terminal division of hypandrium with paired needle-like lateral lobes... *Ptychoptera perbona* Alexander

- Apical stylus of gonostylus paddle-like, apex of terminal division of hypandrium simple medial spine or plate... **47**

47. Gonocoxite ovoid, basal scale of hypandrium absent... *Ptychoptera yasumatsui* Tokunaga

- Gonocoxite quadrate, basal scale of hypandrium present... **47**

48. Dorsal margin of gonostylus sloping... *Ptychoptera bellula* Alexander

- Dorsal margin of gonostylus with large semicircular lobe... *Ptychoptera gutianshana* Yang & Chen

49. Gonostylus simple, knoblike basal lobe and weakly spatulate apical stylus; sperm sac larger than remainder of aedeagus, ejaculatory apodeme scythe-like. *Ptychoptera (Tigrimya)*... **50**

- Gonostylus complex, anteriorly directed basal lobe and poorly sclerotized, pendulant apical stylus with secondary lobe; sperm sac smaller than remainder of aedeagus, ejaculatory apodeme fan-like.

Ptychoptera (Rheoptycha)... **52**

50. Medial gonocoxal lobe fused to paramere, apex of terminal division of hypandrium simple point... *P. (Tigrimya) osceola* Alexander

- Medial gonocoxal lobe free of paramere, apex of terminal division of hypandrium inflated... **51**

51. Apices of epandrial lobes convergent, apices of lateral plates of subapical sclerite of aedeagus divergent... *P. (Tigrimya) quadrifasciata* Say

- Apices of epandrial lobes divergent, apices of lateral plates of subapical sclerite of aedeagus convergent... *P. (Tigrimya) abbreviata* Fasbender

52. Secondary lobe of gonostylus fingerlike, directed medially... **53**

- Secondary lobe of gonostylus paddlelike, semicircular, directed posterior... **54**

53. Subapical spine of epandrial lobe simple point, apex of medial gonocoxal lobe rounded... *P.*

(*Rheoptycha*) *pendula* Alexander

- Subapical spine of epandrial lobe simple clavate, apex of medial gonocoxal lobe hammer shaped... *P.*

(*Rheoptycha*) *monoensis* Alexander

54. Basal lobe of gonostylus with elongate anteriorly directed spine... *P.* (*Rheoptycha*) *townesi* Alexander

- Basal lobe of gonostylus lacking elongate anteriorly directed spine... *P.* (*Rheoptycha*) *espica* Fasbender

***Ptychoptera* Descriptions**

***Ptychoptera* (*Ptychoptera*) Meigen, 1803**

Diagnosis

Adult. Epandrium with triangular epandrial lobes, articulated epandrial claspers well sclerotized with squared basal lobe and complex ventral lobe, hypoproct reduced to paired rectangular plates in subepandrial membrane. Gonostylus with basal lobe divided into scythe-like anterior lobe and paddle-like medial lobe. Cluster of setae on abdominal sternite III, but invagination lacking.

Description

Male Genitalia. Epandrium with triangular epandrial lobes, ventromesal lobe absent. Epandrial clasper well sclerotized and well articulated; stylate, with quadrate basal lobe on medial margin associated with cercus, ventral surface with lobe basally. Epandrial collar distinct; epandrial apodeme broad, tapering to hypandrium, breaks at epandrium and hypandrium. Cerci directed anterior, not evident externally, spine-like with scallop shaped medial lobe. Epiproct prominent, extending nearly to

apex of epandrial lobe, epandrial lobes in contact anteriorly. Hypoproct reduced, forming paired rectangular sclerites in subepandrial membrane.

Parameres fused to bridge, trapezoidal in dorsal view, medioposterior extension present, apex furcate. Paramere apices cluster of dorsoposterior directed spines, with elongate ventrally directed spine.

Gonocoxal apodeme acute, ventral margin straight dorsal margin convex, length approximately 1/4th length of remainder of gonocoxite. Dorsal spur of gonocoxal apodeme merged with external portion of gonocoxite, curved dorsally. Dorsal gonocoxal lobe present, others absent. Gonostylus with basal lobe divided into anterior and medial lob: anterior lobe scythe-shaped, directed anterior, medial lobe paddle-like, directed dorsally; apical stylus subequal to gonocoxite, simple cylinder with rounded apex. Secondary lobe of apical stylus present.

Hypandrium with basal division band-like, lateral margins narrow. Spathate lobes absent. Eversible sac present, windowlike. Terminal division broadly attached to lateral surfaces of basal division, apex variable, lateral extensions of terminal division absent, broken; membranous window basent.

Aedeagal sclerites with lateral apices angled at apex, approximately 1x length of sperm sac; apical apodemes present; subapical sclerite well developed, forming trough medially, ventral arms present forming flattened bars along lateral surface. Sperm sac nearly spherical, subequal than ejaculatory apodeme. Ejaculatory apodeme attached dorsoanteriorly to sperm sac, closely associated with aedeagal sclerites, extending anteriorly into segment VII, arcing ventrally to enlarged rounded terminus; curling around anterior margin of sperm sac. Lateral ejaculatory processes 2x as broad as wide, attached dorsolaterally to sperm pump, directed anterolaterally, dorsal and ventral margins straight, discoid apodeme directed ventrally.

Taxonomic Notes:**Type Species:**

Ptychoptera (Ptychoptera) contaminata Linnaeus

Other Species

Ptychoptera (Ptychoptera) hugoi Tjeder

Ptychoptera (Ptychoptera) metallica Walker

Ptychoptera (Ptychoptera) minuta Tonnoir

Ptychoptera (Ptychoptera) scutellaris Wiedemann

Ptychoptera (Ptychoptera) subscutellaris Alexander

Ptychoptera (Ptychoptera) yankovskiana Alexander

***Ptychoptera (Ptychoptera) contaminata* Linnaeus, 1758**

Diagnosis.

Adult. Male. A large member of the *Ptychoptera (Ptychoptera)*. Male: Epandrial clasper round in cross-section, gonostylus with secondary lobe of apical stylus placed basally, fingerlike.

Description.

Adult. Measurements (n=5). Overall length 8.8mm. **Head.** Width: 1.06mm, Height: 0.94mm, Length: 0.57mm; Antenna flagellum length: 4.48mm. **Thorax.** Length: 2.18mm, Height: 2.29mm; Wing length: 8.0mm, Width: 2.2mm. **Abdomen.** Length: 6.05mm; Male Genitalia Width: 0.8mm, Height: 1.45mm.

Head. Vertex shining black, tapering posteriorly, sparsely set with trichoid sensilla; frons largely inapparent. Occiput bare. Antennae: scape dark brown, cylindrical, with long brown setae projecting dorsally from anterior surface; pedicel globular, dark brown, with anterior patch of trichoid sensilla; flagellomeres brown, fusiform. Facial sclerite black, broadly subquadrate, fused to clypeus, weakly delineated by depression on dorsal margin of clypeus. Clypeus rhomboidal, bulbous, heavily covered in macrotrichia, black. Maxillary palpus with basal segments, 4&5th segments darkening to apex. Labrum short, stylate, yellow, neither epipharynx nor hypopharynx readily apparent. Labellae yellow.

Thorax. Anteprenotum a black, broad, square lobe extending entire width of anteprenotum; row of black trichoid sensilla on anterior margin near forecoxa. Prescutum and scutum shining, glabrous black; medial and prescutal suture with row of clear trichoid sensilla, extending posteriorly from posterior apex of prescutum to scutellum; short, clear prealar sensilla present. Scutellum brownish yellow medially, ovoid, dorsal surface with long, yellow setae, anterior and posterior lateral ridges dark brown. Mediotergite of metanotum shining blue black, anterolateral sensilla patches fused medially, extending to posterior margin. Laterotergite of metanotum glabrous, blue black, with dorsal patch of yellow, trichoid sensilla. Pleural sclerites all velvety black, with weak pollinosity. Anepisternal cleft broad, extending nearly to base of wing, membrane black. Suture between epimeron and metapleurite complete. **Wing.** With three bands and multiple spots, proximal band from h to base of CuA, medial band extending from base of R_{1+2} to CuA_1+CuA_2 fork, distal band from R_{1+2} fork to base of R_5 , spots at apex of Sc, divergence of R_{3+4+5} , apex of R_3 , and at the M_1+M_2 fork; membrane with macrotrichia in cells br, R_1 , R_5 , CuA_2 and apical portions of cells Sc, R_3 , R_4 , M_1 , M_2 , CuA_1 . All veins covered in short stout macrotrichia. Sc: 5.10mm, apex of Sc to apex of R_1 0.86mm, R_{3+4+5} stem 1.41mm, straight; R_{4+5} stem 1.60mm; R_4 after fork 1.78mm, R_5 after fork 1.83mm. r-m 0.30mm; M distal to r-m 2.28mm; M_1 0.74mm, M_2 0.44mm. CuA_1 broken into two nearly straight sections by angle at joint with m-cu, proximal 0.37mm, distal 1.93mm; CuA_2 1.32mm weakly sinuous. A_1 straight for 3.16mm. $R_{3+4+5}:R_{4+5}-$

stem: $R_4 = 1.00 : 1.13 : 1.26$ Mdistal: $M_1 = 1.00 : 0.32$, R_{3+4+5} :Mdistal = $1.00 : 1.61$, R_4 : $M_1 = 1.00 : 0.41$. m-cu joins R_{3+4+5} before r-m. Halter stem yellow, knob darkened. Prehalter dark brown. **Legs.** Coxae yellow with thin black patch at dorsolateral margin. Femur and tibia yellow, darkening to brown near joints. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensilla.

Abdomen. Tergites and sternites shining black, yellow band in middle of segment II and anterior portion of segment III, thickly covered in elongate yellow setae. **Male Genitalia.** Epandrium with domelike epandrial lobes, posterior margin weakly emarginated, forming a small depression on posterior surface, lateral margins rounded and convex, anterolateral margin angled medially, medial margin weakly rounded at posterior apex, otherwise straight. Epiproct prominent, epandrial lobes separate anterior. Epandrial clasper with medially directed basal lobe, subtriangular in dorsal view, expanding to weakly emarginated medial margin, expanding as triangular lobe extending ventrally in lateral view, posterior projection simple, forming blunt style with rounded apex; style of epandrial clasper round in cross section, extending straight posterior, slightly expanding at apex. Hypoproct not apparent, subsumed as part of subepandrial membrane. Subepandrial membrane with two prominent baciliform sclerites extending anterior from base of epandrial clasper, curling ventrally at posterior wall of genital cavity.

Paramere forming fused bridge, basal portion articulating on gonocoxite nearly at joint with gonostyle, extending posterior, loosely associated with gonocoxite; medial portion of paramere bowed posterior, lateral apices with posterior directed triangular tooth, posterolateral lobes present, dorsal lobe weakly hooked at tip, with flattened rectangular lateral lobe; medioposterior extension present, weakly bifurcate at apex.

Gonocoxite with anterior apex directed dorsally, serving as point of articulation for epandrium; gonocoxal lobe triangular, with prominent longitudinal reinforcement rib; posterior portion of gonocoxite expanding to base of gonostyle, dorsal surface with small, thumblike poorly sclerotized dorsal lobule; gonocoxal lobe absent. Gonostylus with primary lobe circular in cross section, extending posterior and weakly curved medially, expanding slightly at apex. Basal lobe divided, medial portion consisting of semicircular expanded base with two prominent spike-like sensilla, finger-like process directed anteriorly, with spikelike sensilla directed dorsally; dorsal portion of basal lobe laterally compressed, anterior portion semicircular, posterior portion tapering to blunt point. Apical lobule located halfway along primary style's length, circular in cross section, extending dorsally, bending posterior, apex expanding to blunt tip.

Hypandrium with basal division forming broad strap across ventral surface of hypopygium, posterior margin with broad triangular emargination medially. Terminal division fused to basal division; eversible sac present at ventral apex, lacrimiform, weakly inflated; apex of terminal division scallop shaped, apex with triangular notch medially, lateral apices broadly triangular. Aedeagus oriented nearly vertical, ejaculatory apodeme broad and fanlike, extending into preceeding abdominal segment, sperm sac broader than long, lateral ejaculatory process without distinct angle, nodules present at base.

Aedeagal sclerites triangular, thin, apex with rounded acute angle. Subapical sclerite with elongate ribbonlike lateral processes, extending ventrally beyond base of lateral ejaculatory process, dorsally to apex of basal projection of subapical sclerite.

Figures. Male Genitalia: 5, Wing: 6, Distribution: 7.

Taxonomic Notes.

Ptychoptera contaminata is a member of the *Ptychoptera contaminata* species group, though it probably represents is placed with *P. hugoi* as sister to the remainder of *P. (Ptychoptera)* based on the weakly bifurcated parameral spur, epandrial clasper rounded in cross-section, and fingerlike apical lobule of the gonostylus.

Material Examined:

Material Examined. Neotype. Dania, Lolland, Saxkøbing, Sómose, 20-5-1966, Bo Vest Pedersen (Pinned: 1 m#, 1 f#) (ZMUC) **Other material.** Amager, 4/9 1954, Worm-H (Pinned: 1 f#) (ZMUC). Dania, Bornholm, Bastemose, 16.juli 1966, leg. Bo Vest Pedersen (Pinned 2 m#) (ZMUC). Dania, Fyn, Arreskov Sø, 19.aug.1964, N.P.K. (Pinned: 1 m#) (ZMUC). Hørsholm, 29-8-1961, Dr. Tuxen (Pinned: 1 f#) (ZMUC). Dania, Langeland, Fredm. Saedballe, 23.juli.1964, Ole Martin (Pinned: 2 m#) (ZMUC). Dania, LFM, Mandemarke, 31.viii-5.ix.2008, O. Karsholt (Pinned: 1 f#) (ZMUC). Dania, Lolland, Saxkøbing, Sómose, 20-5-1966, Bo Vest Pedersen (Pinned: 1 m#, 1 f#) (ZMUC). Skanderberg, DENMARK v-25-61, H.S. Telford (Pinned: 1 f#) (WSU). NEJ: Tranesig I Tofte Skov, 9-18.6.2006 NJ70, J. Pedersen leg. Vinduesfaelde (Pinned: 1 m#, 1 f#) (ZMUC). Nors, Thisted OK, 24-6-1964, Leg. Nils Kolstrup (Pinned: 1 m#) (ZMUC). Berlins Ungeb. A. Bottcher. (Pinned: 1 m#) (WSU). Ber (Pinned: 1 f#) (WSU). Feuerbacher, Hald. b. Stuttg. 27.VII.1947, Lindner leg. (Pinned: 1 m#) (WSU). England – Kent, Brookland, V-19,1962, (R.I. Vane-Wright) (Slide: 1m#) (USNM). Mus. Hausbild, 12-9-1914 (Pinned: 1 m#) (ZMUC). T. uw 1/6 14 (Pinned: 1 m#) (ZMUC).

Ptychoptera (Ptychoptera) sp. near hugoi**Diagnosis**

Adult. Male. Epandrium with epandrial clasper round in cross section; gonostylus with basal lobe posterodorsal corner petiole broader than long, secundary lobe of apical stylus placed midway along length, secondary lobetrianglur.

Description

Adult. Measurements (n=3). Overall length 7.8mm. **Head.** Width: 0.8mm (0.8-0.8), Height: 0.875mm (0.81-0.94), Length: 0.53mm (0.55-0.51); Antenna flagellum length: 3.9mm (3.54-4.4). **Thorax.** Length: 1.80mm (1.72-1.96), Height: 1.76mm (1.6-1.92); Wing length: 6.81mm (6.5-7.25), Width: 1.98mm (1.56-2.8). **Abdomen.** Length: 5.5 (4.8-6.2)mm; Male Genitalia Width: xmm, Height: xmm.

Head. Vertex shining black, tapering posteriorly, moderately set with trichoid sensilla; frons largely inapparent. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: scape dark brown, flattened cylinder with long brown setae projecting dorsally from anterior surface; pedicel globular, dark brown, trichoid sensilla absent; flagellomeres brown, fusiform. Facial sclerite black, fused to clypeus, delineated by pinched band at dorsal surface of clypeus. Clypeus rhomboidal, bulbous, apical portion covered in macrotrichia, black. Maxillary palpus with 1st segment dark, 2nd&3rd segments yellow, 4&5th segments darkening to apex. Labrum spade shaped, yellow, epipharynx not readily apparent, hypopharynx narrow, straight sided, black.

Thorax. Antepronotum metallic black, with transverse fold, broad, square lobe medially; row of black trichoid sensilla on anterior margin near forecoxa. Prescutum and scutum shining, glabrous dark blue; medial and prescutal suture with row of yellow trichoid sensilla, extending posterior from

posterior apex of prescutum to scutellum; long yellow prealar sensilla present. Scutellum yellow medially, ovoid, dorsal surface with long, yellow setae, well defined anterior and posterior ridges extend from wing base to scutellum dark brown. Mediotergite of metanotum shining blue black, anterolateral sensilla patches fused medially, extending to posterior margin. Laterotergite of metanotum glabrous blue black, dorsal patch of trichoid sensilla yellow. Pleural sclerites all velvety black, with weak pollinosity. Anepisternal cleft broad, extending nearly to base of wing, membrane dark brown. Suture between epimeron and metapleurite incomplete and poorly defined. **Wing.** Hyaline, no infuscation; membrane with macrotrichia in apical portions of cells Sc, R₁, R₃, R₄, R₅, M₁, M₂, CuA₁, CuA₂. All veins covered in short stout macrotrichia. Sc: 4.50mm, Apex of Sc to Apex of R₁ 0.75mm, R₃₊₄₊₅ stem 0.60mm, square posterior turn at fork from R₁₊₂; R₄₊₅ stem 1.22mm; R₄ after fork 1.44mm, R₅ after fork 1.38mm; R₃₊₄₊₅:R₄₊₅-stem:R₄ = 1.00 : 2.03 : 2.4. r-m 0.30mm; M distal to r-m 1.80mm; M₁ 0.60mm, M₂ 0.40mm; Mdistal:M₁ = 1.00:0.33, R₃₊₄₊₅:Mdistal = 1.00:3.0, R₄:M₁ = 1.00:0.41. CuA₁ broken into two nearly straight sections by angle at joint with m-cu, proximal 0.16mm, distal 1.64mm; CuA₂ 0.96mm not sinuous, very weak angle. Apex of CuA₂ to A₁ 1.0mm. m-cu joins R₃₊₄₊₅ at r-m. Halter with stem yellow, darkening to apex. Prehalter dark brown. **Legs.** Coxae robust, yellow with dark brown band proximally. Femur and tibia yellow, darkening to brown near joints. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensillae.

Abdomen. Tergites and sternites black, with weakly defined yellow borders along posterior margin, thickly covered in elongate yellow setae. **Male Genitalia.** Epandrial collar complete, epandrial apodemes well developed, extending to lateroanterior apex of hypandrium, extending ribbon-like across gonocoxal apodeme, prominent break between epandrial collar and epandrial apodeme. Epandrial lobes domelike, anterior margin weakly emarginate, posterior sulcus weak, lateral margins rounded and convex, without a distinct angle, medial margin straight, angling to parallel at epandrial lobe contact.

Epiproct prominent, epandrial lobes in contact for $1/5^{\text{th}}$ of length anteriorly. Posteromedial stylus present, external portion flattened in, directed at oblique angle rising posterior, not significantly narrowed basally; internal portion extremely elongate, spine-like and extending anterior, midway along spine a bean shaped lobe pendulant ventrally which is provided heavily with stout spines. Epandrial clasper with flattened square basal lobe at medial anterior margin; ventral lobe broad, directed medially to rounded apex with finger-like lateral lobe at $1/2$ length; stylus round in cross section, weakly tapering towards slightly expanded and flattened apex, epandrial clasper curved medially, apex extending slightly past midline of genitalia at rest. Hypoproct not readily evident, subsumed as part of subepandrial membrane. Subepandrial membrane with prominent baciliform sclerites extending nearly to base of epandrial clasper, posterior portion flattened and platelike, anterior extension narrow, extremely heavily sclerotized.

Parameral bridge broadly affixed to gonocoxite, extending from sclerotized band extending from the ventral surface of the dorsal gonocoxal lobe to the ventral margin of the gonostylus. Apical lobes of paramere directed dorsally, semicircular, with variable number (4-6) of prominent triangular serrations on dorsal margin. Medioposterior extension prominent, bifurcate apices convergent, two small spines located on dorsal surface of paramere anterior to base of medioposterior extension. Ventral surface of paramere with two pairs of hypertrophied spines. Inner pair pendulant ventrally, with moderate divergent curve towards apex. Outer pair directed posterior, not extending beyond anterior margin of parameral bridge, laterally compressed.

Gonocoxal apodeme spine-like, dorsoventrally compressed. Main portion of gonocoxite as per genus, dorsal gonocoxal lobe prominent, extending dorsally to half height of basal lobe of gonostylus. Gonostylus extending approximately the same length of epandrial clasper. Basal lobe of gonostylus subquadrate in lateral view, posterior margin extended dorsoposterior, dorsoposterior corner with

petiolate base to ovoid apex; medial margin with stout, finger-like lobe ventrally, and sclerotized bridge anterior descending ventrally to bean-shaped lobule angled dorsally with stout spine-like sensilla. Apical stylus of gonostylus round in cross section, almost no expansion at apex, secondary lobe located at 2/3 length of apical stylus, base extremely petiolate, apex forming broad, Y shape tilted posterior, posterior arm longer.

Basal division of hypandrium with midpoint of dorsal margin expanded laterally. Eversible sac scallop shaped in posterior view, extending as a narrow slit dorsally into terminal division. Terminal division broadly attached to basal division, apex of terminal division tapering to dorsal apex, medial suture extending to apex.

Aedeagus oriented nearly vertical, ejaculatory apodeme with base expanded laterally; dorsal margin of lateral ejaculatory process convex; subapical sclerite with ventral arms dorsoventrally compressed, fused along contact with medial section, medial section of subapical sclerite subequal in length to aedeageal sclerites.

Figures. Male Genitalia: 8, Wing: 9, Distribution: 10.

Taxonomic Notes.

Tjeder separated *Ptychoptera hugoi* from *Ptychoptera scutellaris* based on characters of the male genitalia. This species is very similar to the illustrations of *P. hugoi*, but differs in certain characters such as the ventral lobe of the epandrial clasper and the anterior lobule of the basal lobe of the gonostylus. As the authors were not able to examine the type material of *Ptychoptera hugoi* they refrain from applying a name to this species at this time.

Material Examined. MONGOLIA: Hove Aimag, Buyant Soum. Buyant Gol., ~4 km SW Hovd Aimag Center, 47.58.35N: 91.35.28E. 1428m, 1 July 2009. Chen Young (Pinned: 2 m#, 1 f#) (CMNH).

MONGOLIA: Hove Aimag, Duut Soum. unnamed springfed, stream. ~2 km NE Dunt, 47.32.08N:

91.58.35E. 2234m, 20 July 2009. Chen Young (Pinned: 1m#) (CMNH). **Questionable Placement.**

KYRGYZSTAN: Chuy, Suusamyr Valley, W. Kichi-Korumdy R. 2291m, 42-12-28N / 73-41-31E, 13 June 1999

C. Young.

***Ptychoptera (Ptychoptera) metallica* Walker, 1848**

Diagnosis.

Adult. Male. Epandrial clasper flattened, subapical ventral angle rounded; posterolateral corner of paramere with three dorsal spines; gonostylus with secondary lobe of apical stylus placed subapically.

Description

Adult. Measurements (n=5). Overall length 7.68mm. **Head.** Width: 0.95mm (0.92-1.0), Height: 0.83mm (0.69-0.96), Length: 0.52mm (0.49-0.55); Antenna flagellum length: 3.72mm (3.37-4.38).

Thorax. Length: 1.85mm (1.65-1.97), Height: 1.76mm (1.53-1.88); Wing length: 6.44mm (6.2-6.8),

Width: 1.79mm (1.7-1.88). **Abdomen.** Length: 4.88 (4.5-5.3)mm; Male Genitalia Width: xmm, Height: xmm.

Head. Vertex shining dark brownish black, moderately set with trichoid sensilla; frons well developed as high portion of cranium behind antennae, shining brownish black. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: scape dark brown, oblong cylinder with long brown setae projecting dorsally from anterior surface; pedicel dark brown, globular, trichoid sensilla present. Flagellomeres brown, fusiform. Facial sclerite shining dark brown, distinct from clypeus, forming square sclerite above clypeus. Clypeus ventrally tapering

subtriangular, bulbous, generally covered in macrotrichia, light brown. Maxillary palpus with segments 1,2&3 yellow, posterior segments dark. Labrum bullet shaped, brown; hypopharynx and epipharynx not externally apparent, labellae yellow.

Thorax. Antepronotum dark yellow medially, brown at lateral margins, medial lobe width of remainder of antepronotum, straight; diffuse patch of yellow trichoid sensilla on anterior margin near forecoxa. Prescutum and scutum shining, glabrous blue black or chocolate brown; medial and prescutal suture with row of yellow trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum; long clear prealar sensilla present. Scutellum yellow, lateral ridges fading to brown dorsal surface with long, clear setae. Mediotergite of metanotum shining blue black or chocolate brown, line of yellow trichoid sensilla medially. Laterotergite of metanotum pollinose, blue black or chocolate brown, dorsal patch of clear trichoid sensilla. Pleural sclerites all dark brown, with medium pollinosity. Anepisternal cleft broad, extending nearly to base of wing, membrane yellow. Suture between epimeron and metapleurite incomplete. **Wing.** Two bands, proximal extending from base of R_{1+2} to CuA_1+CuA_2 fork, distal from R_{1+2} fork to base of R_5 , with an additional spot at the M_1+M_2 fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 4.75mm, Apex of Sc to Apex of R_1 0.76mm, R_{3+4+5} stem 0.62mm, slight posterior turn at fork from R_{1+2} ; R_{4+5} stem 1.23mm; R_4 after fork 1.55mm, R_5 after fork 1.60mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 1.98 : 2.58$. r-m 0.25mm; M distal to r-m 1.98mm; M_1 0.79mm, arcuate, M_2 0.62mm; $M_{\text{distal}}:M_1 = 1.00:0.41$, $R_{3+4+5}:M_{\text{distal}} = 1.00:3.06$, $R_4:M_1 = 1.00:0.50$. CuA_1 proximal 0.12mm, distal 1.8mm; CuA_2 1.36mm sinuous. Apex of CuA_2 to A_1 1.65mm. m-cu joins R_{3+4+5} at r-m. Halter with dark yellow. Prehalter dark yellow. **Legs.** Forecoxae yellow. Femur and tibia yellow. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensillae.

Abdomen. Tergites and sternites chocolate brown, thickly covered in elongate yellow setae.

Male Genitalia. Epandrial collar complete, epandrial apodemes well developed, extending to lateroanterior apex of hypandrium, extending ribbon-like across gonocoxal apodeme, prominent break between epandrial collar and epandrial apodeme. Epandrial lobes domelike, triangular, anterior margin weakly straight, posterior sulcus weak, lateral margins rounded angle anterior, straight posterior, medial margin straight, weakly rounded anterior. Epiproct prominent, epandrial lobes in contact for $1/5^{\text{th}}$ of length anteriorly. Posteromedial stylus with external portion broadly spatulate, angled dorsoposteriorly, with broad petiole basally; internal portion short, directed anterior arcing ventrally as broad lobe. Epandrial clasper without distinct basal lobe forming squared angle directed anteroventrally; ventral lobe simple forming low ridge leading to conical lobe distally; stylus flattened in cross section on horizontal plane, lateral margin expanded as rounded lobe at approximately $1/2$ length of stylus, epandrial clasper weakly curved medially, apex approaching but not crossing midline of genitalia at rest. Hypoproct not readily evident, subsumed as part of subepandrial membrane. Subepandrial membrane with prominent baciliform sclerites with spatulate shape.

Parameral bridge broadly affixed to gonocoxite, attached to sclerotized band extending from the ventral surface of the dorsal gonocoxal lobe to the ventral margin of the gonostylus. Apical lobes of paramere forming low, triangular posteriorly directed spine on posterior margin with two low spines flanking either side, and elongate ventrally directed spine. Medioposterior extension prominent, bifurcate apices moderate length, weakly convergent, two anteriorly directed small curved spines located on dorsal surface of paramere anterior to base of medioposterior extension. Ventral surface of paramere with two laterally directed spines near lateral margins, apex of spine curved sinuously.

Gonocoxal apodeme spine-like, dorsoventrally compressed. Main portion of gonocoxite as per genus, dorsal gonocoxal lobe extremely short, little more than a bump on dorsal surface of gonocoxite.

Gonostylus extending approximately the same length of epandrial clasper. Basal lobe of gonostylus subtriangular in lateral view, expanding dorsoposteriorly, dorsoanterior corner expanded semicircularly, dorsoposterior corner slightly extended; medial margin with stout, heavily sclerotized scythe-like lobule directed medially, provided with irregular number (3-5) of stout spines on dorsal surface. Apical stylus of gonostylus round and narrow basally, expanding apically to rounded apex, secondary lobe located at 3/4 length of apical stylus, petiolate triangle directed dorsoposterior, dorsoanterior corner extended.

Basal division of hypandrium with eversible sac lacrimiform in posterior view, extending 2/3rds length of terminal division. Terminal division broadly attached to basal division, apex of terminal division broad square, angles rounded.

Aedeagus oriented nearly vertical, ejaculatory apodeme with base narrow; dorsal margin of lateral ejaculatory process straight; apex of aedeagal sclerites blunt, subapical sclerite with ventral arms laterally, pointed at anterior apex, brief fusion with medial section, medial section of subapical sclerite figure expanding dorsally, dorsoposterior margin notched, subequal to aedeagal sclerites.

Figures. Male Genitalia: 11, Wing: 12, Distribution: 13.

Taxonomic Notes.

This species is almost identical to *Ptychoptera minuta* of Europe, suggesting a possible transatlantic dispersal event.

Material Examined. Holotype. St. Martin's Falls. Albany River, Hudson's Bay. G. Barnston (Pinned: 1 f#) (BMNH). **Other Material.** Colorado, Platte Canyon, nr. Idlewild, June 10, 1927, (J.M. Aldrich) (Pinned: 1 m#, Slide: 2 m#) (USNM). Park Co. CO, 7 June 1995, R. Durfee, A. Polonsky High Cr. Fen Preserve, 9 mi. S of Fairplay, sweeping (Pinned: 1 m#) (CSUI). USA Iowa, Dickinson Co. Silver Lake Fen May-17-2010, Sweeping nr. Seep, 43.437472N, 96.365009W, GW Courtney (Alcohol: 1 m#, 1 f#)

(ISIC). MINNESOTA: AITKIN CO. 14 mi. w. of Willow River, 46.334 N, 93.069 W, 19.v.1994, col. D.E. Hansen (Pinned: 1 m#, 2 f#) (UMN). Farm Island Lake, Aitkin Co. Minn, July 31, 1964, Jean L. Laffoon (Pinned: 1 f#) (ISIC). U.S.A., Minnesota, Itasca Co. Grand Rapids, North Central Exp. Sta. Malaise Trap, August 15, 1973 (Pinned: 1 m#, 4 f#) (UMN). Itasca Park, Minn. Aug 11 1951/ Collector M.E. Warters (Pinned: 1 f#) (UMN). Mille Lacs Lake, near Vineland, Minn. May 24 1941 (Pinned: 1 m#) (UMN) Vineland, Minn. May 24, 1941, G. Kretzschmar (Pinned: 1 m#) (UMN). U.S.A., Minnesota, Pine Co. Little Sand Ck. 1 mi. E Cloverdale, Malaise Trap, July 5, 1973 (Pinned: 1 f#) (UMN). U.S.A., Minnesota, Pope Co. Glacial Lakes, State Park, Malaise Trap, June 13, 1973 (Pinned: 2 f#) (UMN). Cape Henrietta Maria, Ontario VII-4-48 (Slide: 1 m#) (USNM)

***Ptychoptera (Ptychoptera) minuta* Tonnoir, 1919**

Diagnosis

Adult. Male. Epandrial clasper flattened, subapical ventral angle distinctly angled; posterolateral corner of paramere with two dorsal spines; gonostylus with secondary lobe of apical stylus placed subapically.

Description

Adult. Measurements (n=4). Overall length 7.72mm. **Head.** Width: 0.95mm (0.91-0.97), Height: 0.83mm (0.74-0.88), Length: 0.52mm (0.47-0.56); Antenna flagellum length: 4.58mm (4.4-4.94). **Thorax.** Length: 1.88mm (1.8-2.0), Height: 1.86mm (1.73-2.06); Wing length: 7.02mm (6.8-7.2), Width: 1.83mm (1.8-1.9). **Abdomen.** Length: 5.32 (5.0-5.7)mm; Male Genitalia Width: xmm, Height: xmm. **Head.** Vertex shining dark brownish black, moderately set with trichoid sensilla; frons well developed as high portion of cranium behind antennae, shining brownish black. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: scape dark brown, oblong cylinder

with long brown setae projecting dorsally from anterior surface; pedicel dark brown, globular, trichoid sensilla present. Flagellomeres brown, fusiform. Facial sclerite dark brown, weakly delineated from clypeus. Clypeus ventrally tapering subtriangular, bulbous, generally covered in macrotrichia, light brown. Maxillary palpus with segments 1,2 yellow, posterior segments dark. Labrum D-shaped, yellow; epipharynx and hypopharynx not externally apparent, labellae yellow.

Thorax. Anteprenotum dark yellow medially, brown at lateral margins, medial lobe half width remainder of anteprenotum, small notch medially; diffuse patch of yellow trichoid sensilla on anterior margin near forecoxa. Prescutum and scutum shining, glabrous chocolate brown; medial and prescutal suture with row of yellow trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum; long clear prealar sensilla present. Scutellum yellow, lateral ridges fading to brown dorsal surface with long, clear setae. Mediotergite of metanotum shining chocolate brown, line of yellow trichoid sensilla medially. Laterotergite of metanotum pollinose, blue black or chocolate brown, dorsal patch of clear trichoid sensilla. Pleural sclerites all dark brown, with strong pollinosity. Anepisternal cleft broad, extending nearly to base of wing, membrane yellow. Suture between epimeron and metapleurite incomplete. **Wing.** Two bands, proximal extending from base of R_{1+2} to CuA_1+CuA_2 fork, distal from R_{1+2} fork to base of R_5 , with an additional spot at the M_1+M_2 fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 4.55mm, Apex of Sc to Apex of R_1 0.74mm, R_{3+4+5} stem 0.51mm, slight posterior turn at fork from R_{1+2} ; R_{4+5} stem 1.53mm; R_4 after fork 1.50mm, R_5 after fork 1.587mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 2.07 : 1.97$. r-m 0.25mm; M distal to r-m 1.53mm; M_1 0.64mm, arcuate, M_2 0.49mm; $M_{\text{distal}}:M_1 = 1.00:0.32$, $R_{3+4+5}:M_{\text{distal}} = 1.00:2.81$, $R_4:M_1 = 1.00:0.46$. CuA_1 proximal 0.25mm, distal 1.87mm; CuA_2 1.18mm simple angle. Apex of CuA_2 to A_1 1.75mm. m-cu joins R_{3+4+5} at r-m. Halter with dark yellow. Prehalter dark yellow. **Legs.** Forecoxae yellow, with brown spot on dorsal margin, mid- and hindcoxae yellow. Femur and tibia yellow. First tarsomere yellow proximally, turning

brown distally. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensillae.

Abdomen. Tergites and sternites chocolate brown, thickly covered in elongate yellow setae.

Male Genitalia. Epandrial collar complete, epandrial apodemes well developed, extending to lateroanterior apex of hypandrium, extending ribbon-like across gonocoxal apodeme, prominent break between epandrial collar and epandrial apodeme. Epandrial lobes domelike, triangular, anterior margin weakly straight, posterior sulcus weak, lateral margins rounded angle anterior, straight posterior, medial margin straight, weakly rounded anterior. Epiproct prominent, epandrial lobes in contact for 1/5th of length anteriorly. Posteromedial stylus with external portion broadly spatulate, angled dorsoposteriorly, with broad petiole basally; internal portion short, directed anterior arcing ventrally as broad lobe. Epandrial clasper without distinct basal lobe forming squared angle directed anteroventrally; ventral lobe simple forming low ridge leading to conical lobe distally; stylus flattened in cross section on horizontal plane, lateral margin expanded as rounded lobe at approximately ½ length of stylus, epandrial clasper weakly curved medially, apex approaching but not crossing midline of genitalia at rest. Hypoproct not readily evident, subsumed as part of subepandrial membrane. Subepandrial membrane with prominent baciliform sclerites with spatulate shape.

Parameral bridge broadly affixed to gonocoxite, attached to sclerotized band extending from the ventral surface of the dorsal gonocoxal lobe to the ventral margin of the gonostylus. Apical lobes of paramere forming low, triangular posteriorly directed spine on posterior margin with one low spines flanking medial side, gap and two additional dorsally directed spines laterally, and elongate ventrally directed spine. Medioposterior extension prominent, bifurcate apices moderate length, weakly convergent, two anteriorly directed small curved spines located on dorsal surface of paramere anterior

to base of medioposterior extension. Ventral surface of paramere with two laterally directed spines near lateral margins, apex of spine curved sinuously.

Gonocoxal apodeme spine-like, dorsoventrally compressed. Main portion of gonocoxite as per genus, dorsal gonocoxal lobe extremely short, little more than a bump on dorsal surface of gonocoxite. Gonostylus extending approximately the same length of epandrial clasper. Basal lobe of gonostylus subtriangular in lateral view, expanding dorsoposteriorly, dorsoanterior corner expanded semicircularly, dorsoposterior corner slightly extended; medial margin with stout, heavily sclerotized scythe-like lobule directed medially, provided with irregular number (3-5) of stout spines on dorsal surface. Apical stylus of gonostylus round and narrow basally, expanding apically to rounded apex, secondary lobe located at 3/4 length of apical stylus, petiolate triangle directed dorsoposterior, dorsoanterior corner extended.

Basal division of hypandrium with eversible sac lacrimiform in posterior view, extending 2/3rds length of terminal division. Terminal division broadly attached to basal division, apex of terminal division broad square, angles rounded.

Aedeagus oriented nearly vertical, ejaculatory apodeme with base narrow; dorsal margin of lateral ejaculatory process straight; apex of aedeagal sclerites blunt, subapical sclerite with ventral arms laterally, pointed at anterior apex, brief fusion with medial section, medial section of subapical sclerite figure expanding dorsally, dorsoposterior margin notched, subequal to aedeagal sclerites.

Figures. Male Genitalia: 15, Wing: 16, Distribution: 17.

Taxonomic Notes.

This species is almost identical to *P. metallica* of America, differing only in minor details of the male genitalia, primarily the angle of the ventroapical surface of the epandrial clasper and spines of the apical lobe of the paramere.

Material Examined. Holotype. Auderghem, 5.VIII.00/ Coll. et det. J. Jacobs. (Pinned: 1 m#) (IRNSB). **Other material.** England – MX, Potters Bar, May 4, 1963 (Vane-Wright, Jerrod & Deenling) (Slide: 1 m#) (USNM). Felling, 5-8-18/ ex coll. Esben-Petersen (Pinned: 1 m#) (ZMUC). Grimstrup 18.7.20 (Pinned: 1 m#) (ZMUC). Hansted reservatet, Jyli. Torkaer og, 11.6.1960 Blegsø, leg. Zool. Mus. Exp (Pinned: 1 m#) (ZMUC). DANMARK: SZ, UB14, Munkeskov ved Bjerrede, 30.9.2001, N 55 23.115' E 12 0.768, J. Pedersen leg. ZMUC. (Pinned: 1 m#) (ZMUC). Tønder 20.7.20 (Pinned: 1 m#) (ZMUC). Silkeborg. Mosen, H, 2.8.17 (Pinned: 2 f#) (ZMUC). Lyngod, Silkeborg a, 1.7.1916 (Pinned: 1 m#) (ZMUC). Vedersø, Klit, 8/vi.61 (Pinned: 2 m#, 2 f#, various dates) (ZMUC). Urdringen, Niederrhein, April 23, 1911, M.P. Riedel (Slide: fragmentary 1 m#, misidentified as *P. scutellaris*) USNM. Skarbek Krat, Aulum, 3.6.1962 (Pinned: 1 f#) (ZMUC). Boh. Ljung, Anfasteröd, Bo Tjeder (Pinned: 1 m#) (ZMUC). BoesSkoro, (indecipherable) 25.7.1917 (Pinned: 1 f#) (ZMUC).

***Ptychoptera (Ptychoptera) scutellaris* Wiedemann, 1818**

Diagnosis

Adult. Male. Epandrium with epandrial clasper round in cross section; gonostylus with basal lobe posterodorsal corner with basal petiole longer than broad, with secodany lobe of apical stylus placed midway along length, secondary lobe triangular.

Description

Adult. Measurements (n=1). Head. Width: 0.94mm, Height: 0.81mm, Length: 0.49mm; Antenna flagellum length: 4.5mm. **Thorax.** Length: 1.85mm, Height: 1.68mm; Wing length: 6.7mm, Width: 1.7mm. **Head.** Vertex shining black, moderately set with trichoid sensilla; frons weakly developed indistinguishable from vertex, shining black. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: scape light brown, oblong cylinder with long

brown setae projecting dorsally from anterior surface; pedicel brown, globular, trichoid sensilla present. Flagellomeres brown, fusiform. Facial sclerite dark brown, distinct from clypeus, forming bowed band above clypeus. Clypeus ventrally tapering subtriangular, bulbous, thickly covered in macrotrichia, dark brown. Maxillary palpus with 1st segment orange, 2nd yellow, all distal segments brown. Labrum small, leaf shaped, yellow; epipharynx and hypopharynx not externally apparent, labellae dark yellow.

Thorax. Anteprenotum dark brown, medial lobe absent; diffuse patch of yellow trichoid sensilla on anterior margin near forecoxa. Prescutum and scutum shining, glabrous black; medial and prescutal suture with row of clear trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum; long clear prealar sensilla present. Scutellum yellow medially, lateral ridges brown, dorsal surface with long, clear setae; dorsal and ventral lateral ridges brownish yellow. Mediotergite of metanotum shining reddish-brown, sparse yellow trichoid sensilla medially. Laterotergite of metanotum shining, reddish-brown, dorsal patch of trichoid sensilla yellow, knob rising above halter. Pleural sclerites brownish black, with weak pollinosity. Anepisternal cleft broad, extending nearly to base of wing, membrane brown. Suture between epimeron and metapleurite complete. **Wing.** Largely hyaline, with two weak bands of infuscation, proximal extending from base of R_{1+2} to CuA_1+CuA_2 fork, distal spot at R_{1+2} fork; membrane with macrotrichia in apical portions of cells Sc, R_1 , R_3 , R_4 , R_5 , M_1 , M_2 , CuA_1 , CuA_2 . Sc: 4.5mm, Apex of Sc to Apex of R_1 0.72mm, R_{3+4+5} stem 0.69mm, slight posterior turn at fork from R_{1+2} ; R_{4+5} stem 1.41mm; R_4 after fork 1.47mm, R_5 after fork 1.18mm $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 2.04 : 1.71$. r-m 0.31mm; M distal to r-m 1.94mm; M_1 0.63mm, M_2 0.47mm; $M\text{distal}:M_1 = 1.00 : 0.32$, $R_{3+4+5}:M\text{distal} = 1.00 : 2.81$, $R_4:M_1 = 1.00 : 0.42$. CuA_1 proximal 0.20mm, distal 1.78mm; CuA_2 1.23mm sinuous. Apex of CuA_2 to A_1 1.75mm. m-cu joins R_{3+4+5} before r-m. Halter with yellow stem, brown knob. Prehalter yellow. **Legs.** Coxae yellow. Femur yellow, darkening to brown near tibial joint.

Pre-genital Abdomen. Tergites and sternites shining black, posterior margin with thin yellow band, thickly covered in elongate yellow setae. **Male Genitalia.** Gonopod as per subfamily. Dorsal gonocoxal lobe short, less than $\frac{1}{2}$ height of basal lobe of gonostylus. Gonostylus with basal lobe forming inverse trapezoid in lateral view, dorsoposterior apex extended posterior, inner lobule paddle-like, anteromedial margin emarginate, medial surface with circular row of stout trichoid sensilla. Apical stylus round in cross section, apex rounded, secondary lobe triangular with elongate petiole, dorsal margin straight.

Figures. Wing: 17, Distribution: 18.

Taxonomic Notes.

The only male specimen available during this study had a damaged abdomen, prohibiting description of the male genitalia. For more complete description see Tjeder, 1968.

Material Examined. "Friuds, MI." (indecipherable), 4.VIII-51 (Pinned: 1 m#) (ZMUC). SWEDEN, SK, Abrolla, Osby, 56°26'N 14°08'E, 142m, 14-17.vii.2011, V. Michelsen – ZMUC (Pinned: 1 f#) (ZMUC).

***Ptychoptera (Ptychoptera) subscutellaris* Alexander, 1921**

Diagnosis

Adult. Epandrial clasper flattened, ventral lobe triangular, directed laterally; gonostylus with secondary lobe of apical stylus placed midway along length; hypandrium apex rectangular with emarginate dorsal margin, base not petiolate.

Description

Adult. Measurements (n=1). Overall length ? (genitalia removed) **Head.** Width: 1.11mm, Height: 0.99mm, Length: 0.67mm; Antenna flagellum length: ? (broken) **Thorax.** Length: 2.29mm, Height:

2.33mm; Wing length: 9.9mm, Width: 2.5mm. **Head.** Vertex shining black, moderately set with trichoid sensilla; frons weakly developed indistinguishable from vertex, shining black. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: scape light brown, oblong cylinder with long brown setae projecting dorsally from anterior surface; pedicel yellow, globular, trichoid sensilla present. Flagellomeres brown, fusiform. Facial sclerite dark brown, distinct from clypeus, forming subquadrate plate. Clypeus ventrally tapering subtriangular, bulbous, thickly covered in macrotrichia, brown. Maxillary palpus with all segments yellow. Labrum small, leaf shaped, yellow; epipharynx and hypopharynx not externally apparent, labellae yellow.

Thorax. Antepronotum shining brown, transverse fold weakly developed, medial lobe trapezoidal with minute medial notch; diffuse patch of yellow trichoid sensilla on anterior margin near forecoxa. Prescutum and scutum shining, glabrous black; medial and prescutal suture with row of clear trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum; long clear prealar sensilla present. Scutellum yellow, dorsal surface with long, clear setae; dorsal and ventral lateral ridges brownish yellow. Mediotergite of metanotum shining black, sparse clear trichoid sensilla medially. Laterotergite of metanotum shining, black, dorsal patch of trichoid sensilla yellow, knob rising above halter. Pleural sclerites black, with weak pollinosity. Anepisternal cleft broad, extending nearly to base of wing, membrane yellow. Suture between epimeron and metapleurite complete. **Wing.** Largely hyaline, with two weak bands of infuscation, proximal extending from base of R_{1+2} to CuA_1+CuA_2 fork, distal spot at R_{1+2} fork; membrane with macrotrichia in apical portions of cells Sc, R_1 , R_3 , R_4 , R_5 , M_1 , M_2 , CuA_1 , CuA_2 . Sc: 6.40mm, Apex of Sc to Apex of R_1 1.00mm, R_{3+4+5} stem 0.68mm, slight posterior turn at fork from R_{1+2} ; R_{4+5} stem 2.00mm; R_4 after fork 2.00mm, R_5 after fork 2.08mm; r-m 0.41mm; M distal to r-m 2.88mm; M_1 1.04mm, M_2 0.72mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 2.94 : 3.05$ Mdistal: $M_1 = 1.00 : 0.36$, $R_{3+4+5}:M\text{distal} = 1.00 : 4.23$, $R_4:M_1 = 1.00 : 0.52$. CuA_1 proximal 0.29mm, distal 2.60mm; CuA_2 1.32mm

sinuous. A_1 3.12mm. m-cu joins R_{3+4+5} before r-m. Halter with yellow stem, brown knob. Prehalter yellow. **Legs.** Coxae yellow. Femur yellow, darkening to brown near tibial joint.

Abdomen. Tergites and sternites shining black, posterior margin with thin yellow band, thickly covered in elongate yellow setae.

Male Genitalia. Epandrial collar complete, epandrial apodemes well developed, extending to lateroanterior apex of hypandrium, extending ribbon-like across gonocoxal apodeme, prominent break between epandrial collar and epandrial apodeme. Epandrial lobes domelike, triangular, anterior margin weakly emarginate, posterior sulcus strong, lateral margins with distinct rounded angle anterior, posterior margin straight, medial margin straight, angling weakly at anterior base. Epiproct prominent, epandrial lobes in contact for $1/5^{\text{th}}$ of length anteriorly. Posteromedial style present, external portion flattened in horizontal plane, scallop shaped; internal portion elongate fingerlike glabrous lobe directed ventrally. Epandrial clasper with weakly developed basal lobe forming round angle directed anteroventrally; ventral lobe directed laterally, triangular with ventral margin emarginate, visible dorsally; stylus flattened in cross section, dorsal surface rotated medially, semicircular notch present on anterior medial margin, medial margin tapering heavily towards slightly expanded and round apex, weakly curved medially, apex not approaching midline of genitalia at rest. Hypoproct not readily evident, subsumed as part of subepandrial membrane. Subepandrial membrane with prominent baciliform sclerites extending nearly to base of epandrial clasper, posterior portion flattened and platelike, anterior extension narrow, extremely heavily sclerotized.

Parameral bridge broadly affixed to gonocoxite, extending from sclerotized band extending from the ventral surface of the dorsal gonocoxal lobe to the ventral margin of the gonostylus. Apical lobes of paramere with paired spines directed posterior on posterolateral corner, additional two divergent spines on posterior surface of paramere. Medioposterior extension prominent, bifurcate apices short,

parallel, two anteriorly directed small curved spines located on dorsal surface of paramere anterior to base of medioposterior extension. Ventral surface of paramere with two laterally directed spines at posterolateral corners.

Gonocoxal apodeme spine-like, dorsoventrally compressed. Main portion of gonocoxite as per genus, dorsal gonocoxal lobe short, extending dorsally to half of the height of the basal lobe of gonostylus. Gonostylus extending approximately the same length of epandrial clasper. Basal lobe of gonostylus subtrapezoidal in lateral view, expanding dorsoposteriorly, dorsoanterior corner rounded, dorsoposterior corner slightly extended; medial lobe stout, heavily sclerotized fingerlike lobule directed anterior, covered in stout spines ventral margin. Apical stylus of gonostylus slightly flattened basally, round apically, almost no expansion at apex, secondary lobe located at 2/3 length of apical stylus, petiolate triangle directed dorsoposterior.

Basal division of hypandrium very broad, 1.5x height. Eversible sac lacrimiform in posterior view, extending 2/3rds length of terminal division. Terminal division broadly attached to basal division, apex of terminal division with broad base, subquadrate with emarginate dorsal margin.

Aedeagus oriented nearly vertical, ejaculatory apodeme with base narrow; dorsal margin of lateral ejaculatory process convex; apex of aedeagal sclerites blunt, subapical sclerite with ventral arms dorsoventrally compressed ventrally, laterally compressed dorsally and expanded posterior at apex, brief fusion with medial section lateral margin with large triangular lobe 1/3 at 1/3 height; medial section of subapical sclerite spatulate dorsally and tapering ventrally, dorsoposterior margin notched, 1.33x length of aedeagal sclerites.

Figures. Male Genitalia: 19, Wing: 20, Distribution: 21.

Taxonomic Notes.

Material Examined. Holotype. Sapporo, 28.VIII-09, Col. T. Shiraki/ 6978 (Pinned: 1m#) (USNM)

Ptychoptera (Ptychoptera) yankovskiana* Alexander, 1945*Diagnosis**

Adult. Epandrial clasper flattened, ventral lobe fingerlike, directed ventrally; gonostylus with secondary lobe of apical stylus placed midway along length; hypandrium apex scallop shaped with convex dorsal margin, petiolate at base.

Description

Adult. Measurements (n=4). Overall length 7.72mm. **Head.** Width: 1.09mm, Height: 1.00mm, Length: 0.54mm; Antenna flagellum length: 3.63mm. **Thorax.** Length: 2.03mm, Height: 1.92mm; Wing length: 7.6mm, Width: 2.1mm. **Abdomen.** Length: 5.6 mm; Male Genitalia Width: xmm, Height: xmm.

Head. Vertex shining dark brown, moderately set with trichoid sensilla; frons well developed as high portion of cranium behind antennae, shining brown. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: scape light brown, oblong cylinder with long brown setae projecting dorsally from anterior surface; pedicel yellow, globular, trichoid sensilla present. Flagellomeres brown, fusiform. Facial sclerite dark brown, distinct from clypeus, forming even band above clypeus. Clypeus ventrally tapering rhomboidal, bulbous, generally covered in macrotrichia, black. Maxillary palpus all segments yellow. Labrum broadly blade shaped, yellow; hypopharynx and epipharynx not externally apparent, labellae yellow.

Thorax. Anteprenotum shining tea brown, transverse fold weakly developed, medial lobe trapezoidal with minute medial notch; diffuse patch of yellow trichoid sensilla on anterior margin near

forecoxa. Prescutum and scutum shining, glabrous tea brown; medial and prescutal suture with row of clear trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum; long clear prealar sensilla present. Scutellum uniform orange-brown, dorsal surface with long, clear setae.

Mediotergite of metanotum shining tea brown, sparse clear trichoid sensilla medially. Laterotergite of metanotum shining, tea colored, dorsal patch of trichoid sensilla yellow, knob rising above halter.

Pleural sclerites all velvety chocolate brown, with weak pollinosity. Anepisternal cleft broad, extending nearly to base of wing, membrane dark brown. Suture between epimeron and metapleurite complete.

Wing. Two bands, proximal extending from base of R_{1+2} to CuA_1+CuA_2 fork, distal from R_{1+2} fork to base of R_5 , with an additional spot at the M_1+M_2 fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 5.6mm, Apex of Sc to Apex of R_1 1.11mm, R_{3+4+5} stem 0.86mm, right angle at fork from R_{1+2} ; R_{4+5} stem 1.98mm; R_4 after fork 1.87mm, R_5 after fork 1.96mm; $R_{3+4+5}:R_{4+5}$ stem: R_4 = 1.00 : 2.07 : 1.97. r-m 0.37mm; M distal to r-m 2.60mm; M_1 0.88mm, arcuate, M_2 0.60mm; Mdistal: M_1 = 1.00:0.32, R_{3+4+5} :Mdistal = 1.00:2.81, R_4 : M_1 = 1.00:0.46. CuA_1 proximal 0.27mm, distal 2.40mm; CuA_2 1.48mm sinuous. Apex of CuA_2 to A_1 2.24mm. m-cu joins R_{3+4+5} at r-m. Halter with dark yellow. Prehalter dark yellow. **Legs.** Forecoxae yellow, with dark brown band at dorsoanterior apex, mid- and hindcoxae dark brown. Femur yellow, darkening to brown near tibial joint, tibia yellow. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensillae.

Abdomen. Tergites and sternites chocolate brown, with prominent yellow bands in the middle of segment II and the anterior of segment III, thickly covered in elongate yellow setae. **Male Genitalia.** Epandrial collar complete, epandrial apodemes well developed, extending to lateroanterior apex of hypandrium, extending ribbon-like across gonocoxal apodeme, prominent break between epandrial collar and epandrial apodeme. Epandrial lobes domelike, triangular, anterior margin weakly emarginate,

posterior sulcus strong, lateral margins straight, with distinct rounded angle anterior, medial margin straight, angling weakly at anterior base. Epiproct prominent, epandrial lobes in contact for 1/5th of length anteriorly. Posteromedial style present, external portion flattened in horizontal plane, not significantly narrowed basally; internal portion short, clavate glabrous lobe directed ventrally. Epandrial clasper with weakly developed basal lobe forming squared angle directed anteroventrally; ventral lobe directed ventrally, fingerlike stylus; stylus flattened in cross section, dorsal surface rotated medially, semicircular notch present on anterior medial margin, medial margin tapering heavily towards slightly expanded and round apex, weakly curved medially, apex not approaching midline of genitalia at rest. Hypoproct not readily evident, subsumed as part of subepandrial membrane. Subepandrial membrane with prominent baciliform sclerites extending nearly to base of epandrial clasper, posterior portion flattened and platelike, anterior extension narrow, extremely heavily sclerotized.

Parameral bridge broadly affixed to gonocoxite, extending from sclerotized band extending from the ventral surface of the dorsal gonocoxal lobe to the ventral margin of the gonostylus. Apical lobes of paramere reduced to two divergent spines on posterior surface of paramere, forming lateral margins of rhomboidal plate supporting medioposterior extension. Medioposterior extension prominent, bifurcate apices short, parallel, two anteriorly directed small curved spines located on dorsal surface of paramere anterior to base of medioposterior extension. Ventral surface of paramere with two laterally directed spines near lateral margins.

Gonocoxal apodeme spine-like, dorsoventrally compressed. Main portion of gonocoxite as per genus, dorsal gonocoxal lobe short, extending dorsally to half of the height of the basal lobe of gonostylus. Gonostylus extending approximately the same length of epandrial clasper. Basal lobe of gonostylus subtrapezoidal in lateral view, expanding dorsoposteriorly, dorsoanterior corner rounded, dorsoposterior corner slightly extended; medial margin with stout, heavily sclerotized paddle-like lobule

directed anterior, ventral margin emarginate, dorsal margin convex, with two horizontally directed rows of 4-7 triangular trichoid sensilla. Apical stylus of gonostylus slightly flattened basally, round apically, almost no expansion at apex, secondary lobe located at 2/3 length of apical stylus, petiolate triangle directed dorsoposterior.

Basal division of hypandrium very broad, 1.5x height. Eversible sac lacrimiform in posterior view, extending 2/3rds length of terminal division. Terminal division broadly attached to basal division, apex of terminal division petiolate, scallop shaped with two dorsal lobes.

Aedeagus oriented nearly vertical, ejaculatory apodeme with base narrow; dorsal margin of lateral ejaculatory process convex; apex of aedeagal sclerites blunt, subapical sclerite with ventral arms dorsoventrally compressed ventrally, laterally compressed dorsally and expanded posterior at apex, brief fusion with medial section, medial section of subapical sclerite figure eight shaped, dorsoposterior margin notched, 1.33x length of aedeagal sclerites.

Figures. Male Genitalia: 22, Wing: 23, Distribution: 24.

Taxonomic Notes.

Krzeminski & Zwick (1993) synonymized *Ptychoptera yankovskiana* with *Ptychoptera subscutellaris*, though they noted differences in the paramere and coloration of these species. The current authors feel that these differences warrant consideration as distinct species.

Material Examined. Holotype. North Korea, Kankyo Nando, Puksu Pyaksan/ Alt. 6000ft, VI-25-1939, A. Yankovsky (Pinned: 1 m#) (USNM). **Other material.** Manchuria - Kaolingtzu, Kirin, Prov. VIII-3, 1940, (M. Weymann) (Slide: 1m#) (USNM). No. Korea, Kankyo Nando, Puksu Pyaksan, 6000' – VI-25-39, (A. Yankovsky) (Slide Mounted: 1m#; Pinned: 1m#, 1f#) (USNM). S. Korea: Jirisan, Hamyang, Songieon-li Munsu-sa 400m, 35°24.739N 127°43.818E, 4-19 June 2005 Tripotin (Alcohol: 3m#) (ISIC).

***Ptychoptera (Amblyptycha)* Fasbender, subgen. n.**

Diagnosis

Adult. Epandrium divided into two massive composite epandrial claspers which taper to a distinct point or rounded apex, ventromesal lobe of epandrium present, located at approximately 2/3rds the length of the epandrial lobe/clasper. Female: Hypogynium with small triangular lobes ventrolateral to cerci. Larvae: Labral brushes short, not extending dorsoposteriorly over labrum; incisor lobe of mandible with poorly defined denticulations; postmentum with <14 broad rounded denticulations.

Description

Male Genitalia. Epandrium with massive epandrial lobes fused with composite epandrial claspers, apex blunt, not curved medially; ventromesal lobe present, dorsal portion formed as crenulated ridges on medial margin of epandrial lobe apex, pendulant lobe sometimes present; ventromedial corner with subapical spine as short conical spine, dorsolateral corner of epandrial clasper apex formed to laterally directed conical spine. Epandrial collar poorly developed, evident only laterally at epandrial apodeme; epandrial apodeme broad, tapering to hypandrium, no breaks. Posterolateral stylus forming plate at margin of epiproct, with stylus directed posteromedially. Epiproct forming narrow web at posterior apex of epandrial lobe contact, epandrial lobes in contact anteriorly. Hypoproct with external portion ovoid sclerite, subepandrial membrane fully sclerotized, forming paired bacilliform sclerites divided by a medial suture covering entire ventral surface of epandrium.

Parameres fused, narrow contact medially, broadly attached to gonocoxite on dorsal surface, base with broad lobe directed posterior; apical lobes of paramere prominent, directed posterior,

parallel, nearly in contact on medial margin, broad secondary lobe developed on ventral surface at base, directed ventroposterior.

Gonocoxal apodeme acute, ventral margin straight dorsal margin convex, length approximately 1/3rd length of remainder of gonocoxite. Gonocoxal lobes absent. Gonostylus with basal lobe directed medially, closely associated with medial ridge of apical stylus, apical stylus subequal to gonocoxite, broad triangular medially directed point at rounded apex; dorsal glabrous ridge present, low and not convex; medial ridge developed on apical stylus. Secondary lobe of apical stylus absent.

Hypandrium with basal division band-like, lateral margins narrow. Spathate lobes directed posterior, short. Eversible sac absent. Terminal division narrowly attached medially, apex spatulate, lateral extensions of terminal division present, broken; membranous window narrow, extending to base of hypandrium.

Aedeagal sclerites with lateral apices convex, approximately 1x length of sperm sac; apical apodemes absent; subapical sclerite well developed, not extending beyond phallotrema, ventral arms present. Sperm sac nearly spherical, smaller than ejaculatory apodeme. Ejaculatory apodeme attached dorsoanteriorly to sperm sac, not closely associated with aedeagal sclerites, extending anteriorly into segment VII, arcing ventrally to enlarged rounded terminus; curling around anterior margin of sperm sac. Lateral ejaculatory processes 2x as broad as wide, attached dorsolaterally to sperm pump, directed straight anteroventrally, dorsal and ventral margins arced dorsally, discoid apodeme directed subventrally.

Type Species:

Ptychoptera (Amblyptycha) tibialis Brunetti **comb. nov.**

Other Species

Ptychoptera (Amblyptycha) garhwalensis Alexander **comb. nov.**

Ptychoptera (Amblyptycha) sikkimensis Alexander **comb. nov.**

Etymology:

Amblyptycha refers to the blunted apex of the epandrial claspers.

***Ptychoptera (Amblyptycha) garhwalensis* Alexander, 1959.**

Diagnosis

Adult. Mediotergite of metanotum black, legs without distinct yellow bands **Male.** Paramere apices laterally compressed, apex bluntly square; gonostylus bent medially with distinct angle, triangular secondary lobe present.

Description

Adult. Measurements (n=1). Overall length ? (genitalia dissected). **Head.** Width: 1.18mm, Height: 0.99, Length: 0.67; Antenna flagellum length: 4.95mm. **Thorax.** Length: 2.32mm, Height: 2.19mm; Wing length: 9.0, Width: 2.3mm. **Abdomen.** Length: ? (genitalia dissected); Male Genitalia Width: x, Height: x

Head. Vertex shining black, evenly provided with elongate trichoid sensilla posteriorly; frons extremely narrow strip, black. Occiput and genae with dense elongate yellow trichoid sensilla. Antennae: scape brown, oblong cylinder with ring of long black trichoid sensilla well separated from dorsal apex; pedicel brown basally, brown dorsally, globular, ring of trichoid sensilla on lateral margin. Flagellomeres brown, fusiform. Facial sclerite black, square, flat. Clypeus triangular, inflated, generally covered in yellow sensilla, brown medially, fading to yellow at margin. Maxillary palpus with segments

1&2 dark, posterior segments dark brown. Labrum narrowly spade shaped, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae dull orange.

Thorax. Antepronotum with transverse fold broader than height of anterior ridge, dark brown, medial lobe approximately one fifth width of remainder of antepronotum, highly tapered trapezoid, dorsal surface with medial notch. Prescutum and scutum subobscurely shining black black, microtrichia vestiture present; medial and prescutal suture with row of minute clear trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum as longer yellow sensilla; long clear prealar sensilla present. Scutellum brown. Mediotergite of metanotum subobscurely shining black, with strong pollinosity, lateral corners with short yellow triangular patches. Laterotergite of metanotum pollinose black,. Pleural sclerites all black, except yellow vertical stripe on episternum descending from anepisternal cleft with heavy pollinosity. Anepisternal cleft broad trapezoidal, membrane yellow. Suture between epimeron and metapleurite incomplete, weak. **Wing.** Hyaline, weak infuscation extending from base of R_{1+2} to CuA_1+CuA_2 fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 5.8mm, Apex of Sc to Apex of R_1 0.94mm, R_{3+4+5} stem 0.64mm, slight posterior turn at fork from R_{1+2} ; R_{4+5} stem 1.50mm; R_4 after fork 1.980mm, R_5 after fork 1.93; $R_{3+4+5}:R_{4+5}$ -stem: R_4 = 1.0 : 2.34 : 3.09. r-m 0.35mm; M distal to r-m 2.40mm; M_1 0.84mm, arcuate, M_2 0.49mm; Mdistal: M_1 = 1.0 : 0.35, $R_{3+4+5}:Mdistal$ = 1.0 : 3.75, $R_4:M_1$ = 1.0 : 0.42. CuA_1 proximal 0.22mm, distal 2.10mm; CuA_2 1.50mm sinuous. CuA_2 to A_1 1.90mm. m-cu joins R_{3+4+5} before r-m. Halter yellow. Prehalter yellow. **Legs.** Forecoxa yellow with brown band at base, midcoxa dirty yellow with two sloped line ascending posterior, hindcoxa dark brown with yellow spot at posterior base. Femur and tibia yellow, darkening slightly at shared joint, joint of tibia and first tarsomere brown. First tarsomere light brown proximally, darkening distally. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Tergites and sternites dark brown, posterior margins of all segments posterior to seg. II with yellow band. **Male Genitalia.** Epandrial collar as genus. Epandrial lobes as per genus; subapical and lateral spines as per genus; posteromedial stylus as per genus; ventromesal lobe located at medial apex of epandrial lobe, dorsal portion with ridges weakly developed, ventral portion extending ventrally, apex tapering (difficult to discern in holotype). Epiproct as per genus; hypoproct as per genus.

Parameres with broad base, posterior surface rounded lobe at base, directed posterior with apex shifted laterally; posterior margin semicircular, notch medially; apical lobe slightly shorter than length of base, laterally compressed, directed dorsoposteriorly, apex square, apical margin weakly emarginate, apical corners rounded, dorsal corner slightly extended slightly shorter than width of individual paramere; secondary apical lobes broad, apex squared ovoid, leaning laterally.

Dorsal spur of gonocoxal apodeme present. Gonocoxite rounded, nearly as broad as long, with dorsal margin largely flat anteriorly, straight angle weakly descending posterior, ventral margin heavily rounded, nearly semicircular. Gonostylus with basal lobe poorly differentiated from medial ridge of apical stylus, delineated only by small notch at base; apical stylus with medial ridge extremely short, ending approximately half length of stylus, ending in medially directed broad triangular point, apical stylus with distinct angle, apex directed medially, apex simple and round. Small dorsal triangular lobe at medial bend of apical stylus.

Basal division of hypandrium as per genus. Hypandrial spathate lobes clavate, slightly constricted at base, apex rounded. Terminal division, apex rounded plate, external surface with prominent spine-like sensilla. Membranous window slit-like dorsally, expanding weakly ventrally, forming flattened ovoid pennant.

Aedeagus not readily interpreted on holotype.

Figures. Male Genitalia: 25, Wing: 26, Distribution: 27.

Material Examined. Holotype. India, Pauri Garhwal, Manghu Chatti, 9000-9270', V-20-1958 (F. Schmid) (Pinned & Slide: 1 m#) (USNM)

***Ptychoptera (Amblyptycha) sikkimensis* Alexander, 1965.**

Diagnosis

Adult. Mediotergite of metanotum yellow, legs without distinct yellow bands **Male.** Paramere apices rounded; gonostylus straight, without secondary lobe.

Description

Adult. Measurements (n=1). Overall length 9.54. **Head.** Width: 1.25mm, Height: 1.09mm, Length: 0.69mm; Antenna flagellum length: 4.2mm. **Thorax.** Length: 2.85mm, Height: 2.55mm; Wing length: 10.85mm, Width: 3.05mm. **Abdomen.** Length: 6.0mm; Male Genitalia Width: x, Height: x

Head. Vertex shining black, evenly provided with elongate trichoid sensilla posteriorly; frons extremely narrow strip, black. Occiput and genae with dense elongate yellow trichoid sensilla. Antennae: scape yellow basally, brown distally, oblong cylinder with ring of long black trichoid sensilla well separated from dorsal apex; pedicel brown, globular, ring of trichoid sensilla on lateral margin. Flagellomeres brown, fusiform. Facial sclerite triangular, black, flat. Clypeus rhomboidal, inflated, generally covered in yellow sensilla, yellow. Maxillary palpus with all segments yellow. Labrum narrowly spade shaped, yellow; hypopharynx and epipharynx not yellow, labium and labellae yellow.

Thorax. Antepronotum with transverse fold narrower than height of anterior ridge, yellow, medial lobe approximately half width of remainder of antepronotum, trapezoidal, dorsal surface with weak medial notch. Prescutum and scutum subobscurely shining black, microtrichia vestiture present;

medial and prescutal suture with row of minute clear trichoid sensilla, long clear prealar sensilla present. Scutellum yellow. Mediotergite of metanotum subobscurely yellow, shining. Laterotergite of metanotum dark brown, covered profusely in macrotrichia. Pleural sclerites with complex coloration, base dark brown: except yellow vertical stripe on episternum descending from anepisternal cleft to epimeron, epimeron and metapleuron yellow dorsally, brown ventrally, with heavy pollinosity. Anepisternal cleft broad quadrate, membrane yellow. Suture between epimeron and metapleurite incomplete, weak. **Wing.** Hyaline, weak infuscation extending from base of R_{1+2} to CuA_1+CuA_2 fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 6.9mm, Apex of Sc to Apex of R_1 1.16mm, R_{3+4+5} stem 1.23mm, slight posterior turn at fork from R_{1+2} ; R_{4+5} stem 1.80mm; R_4 after fork 2.42mm, R_5 after fork 2.30; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.0 : 1.46 : 1.96$. r-m 0.37mm; M distal to r-m 2.84mm; M_1 1.16mm, arcuate, M_2 0.80mm; $M\text{distal}:M_1 = 1.0 : 0.40$, $R_{3+4+5}:M\text{distal} = 1.0 : 0.94$, $R_4:M_1 = 1.0 : 0.47$. CuA_1 proximal 0.32mm, distal 2.60mm; CuA_2 1.54mm simple angle. CuA_2 to A_1 2.32mm. m-cu joins R_{3+4+5} before r-m. Halter yellow. Prehalter yellow. **Legs.** Forecoxa and midcoxa muddy yellow, hindcoxa dark brown dorsally, yellow ventrally. Femur brown, expanding at apex, broad yellow band distally 1/2 length distally, tibia brown, expanding at apex, with broad yellow band 1/3 length distally All tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Tergites and sternites light orange brown, tergite V-VII dark brown. **Male Genitalia.** Epandrial collar as genus. Epandrial lobes as per genus; subapical and lateral spines as per genus; posteromedial stylus undeveloped; ventromesal lobe located at medial apex of epandrial lobe, dorsal portion as crenulated ridges, ventral portion not distinguishable on holotype (likely reduced). Epiproct as per genus; posteromedial stylus placed lateral to hypoproct, forming medial hook weakly curved posterior, hypoproct as per genus.

Paramere forming bridge, narrowing medially, base rounded, broadly attached to gonocoxite, broad lobe on anterior margin with tapering rounded apex directed laterally; base of apical lobe with laterally directed dorsoventrally flattened semicircular lobe; apical lobe laterally compressed, with margins parallel, apex expanding, posterior margin weakly emarginate, dorsoposterior weakly extended.

Dorsal spur of gonocoxal apodeme absent. Gonocoxite rounded, nearly as broad as long, with dorsal margin largely flat anteriorly, straight angle weakly descending posterior, ventral margin heavily rounded, nearly semicircular. Gonostylus with basal lobe forming low ridge on dorsomedial surface; apical stylus narrow, with distinct angle medially midway along length at nearly 90 degrees, apex rounded; secondary lobe present at base of angle, right triangle directed medially.

Basal division of hypandrium as per genus. Hypandrial spathate lobes with parallel margins and rounded apex. Terminal division, apex rounded plate, external surface with prominent spine-like sensilla. Membranous window slit-like dorsally, expanding weakly ventrally, forming flattened ovoid pennant.

Aedeagus as per genus; subapical sclerite with ventral arms flattened, expanding to apex; medial portion with apical margin flat, tapering ventroanterior to short stylus, arc slightly dorsoanterior. Ejaculatory apodeme tapering to apex, base broad.

Figures. Male Genitalia: 28, Wing: 29, Distribution: 30.

Taxonomic Notes.

Material Examined. Holotype. Sikkim-Yedang, Rhododendron area, 9680', VI-10, '59 (Schmid) (Pinned & Slide: 1 m#) (USNM). **Paratypes.** Sikkim, Chachu, V-17.'59, F. Schmid (Pinned: 2 m#) (USNM). **Other material.** Sikkim (Slide: 1 m#) (USNM). Sikkim, Chamikemp, 9900' Aug.24.'59 (Schmid) (Slide: 1

m#) (USNM). Sikkim, Phune Kongma, 11,150', VI-30.'59 (Schmid) (Slide: 1 m#) (USNM). Sikkim, Yaotang, 11,600', VI-17.'59, Schmid (Slide: 1 m#) (USNM). Sikkim-Zoma, 8900' V-24.'59, (F. Schmid) (Slide: 1 m#) (USNM).

***Ptychoptera (Amblyptycha) tibialis* Brunetti, 1911.**

Ptychoptera atritarsis Brunetti, 1911

Diagnosis

Adult. Mediotergite of metanotum black, legs with yellow bands on femur and tibia. **Male.**

Paramere apices rod-like; gonostylus straight, without secondary lobe.

Description

Adult. Measurements (n=1). Overall length 8.43mm. **Head.** Width: 1.14mm, Height: 1.06mm, Length:0.67mm; Antenna flagellum length:3.65mm,. **Thorax.** Length:2.76mm, Height:2.48mm; Wing length: 9.4mm, Width: 2.8mm; **Abdomen.** Length: 5.0mm; Male Genitalia Width: x, Height: x

Head. Vertex shining black, glabrous; frons extremely narrow strip, black. Occiput and genae with dense elongate yellow trichoid sensilla. Antennae: scape brown, oblong cylinder with ring of long black trichoid sensilla well separated from dorsal apex; pedicel brown basally, brown dorsally, globular, ring of trichoid sensilla on lateral margin. Flagellomeres brown, fusiform. Facial sclerite inevent. Clypeus rhomboidal, inflated, generally covered in yellow sensilla, yellow. Maxillary palpus with all segments yellow. Labrum narrowly spade shaped, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae yellow.

Thorax. Anteprenotum with transverse fold narrower than height of anterior ridge, dark brown, medial lobe approximately equal to width of remainder of anteprenotum, broad arc, dorsal surface

without medial notch. Prescutum and scutum subobscurely shining brown, microtrichia vestiture present; medial and prescutal suture with row of minute clear trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum as longer yellow sensilla; long clear prealar sensilla present. Scutellum brown. Mediotergite of metanotum subobscurely dull brown, with weak pollinosity, lateral corners with short yellow triangular patches. Laterotergite of metanotum pollinose brown. Pleural sclerites all brown, except yellow vertical stripe on episternum descending from anepisternal cleft with heavy pollinosity. Anepisternal cleft broad trapezoidal, membrane yellow. Suture between epimeron and metapleurite incomplete, weak. **Wing.** Hyaline, weak infuscation extending from base of R_{1+2} to CuA_1+CuA_2 fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 6.07mm, Apex of Sc to Apex of R_1 0.99mm, R_{3+4+5} stem 0.88mm, broadly rounded turn at fork from R_{1+2} ; R_{4+5} stem 1.60mm; R_4 after fork 2.0mm, R_5 after fork 1.98mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.0 : 1.81 : 2.27$. r-m 0.37mm; M distal to r-m 2.56mm; M_1 1.04, arcuate, M_2 0.74mm; $M\text{distal}:M_1 = 1.0 : 0.40$, $R_{3+4+5}:M\text{distal} = 1.0 : 1.18$, $R_4:M_1 = 1.0 : x$. CuA_1 proximal 0.30mm, distal 2.4mm; CuA_2 1.62mm simple angle. CuA_2 to A_1 2.33mm. m-cu joins R_{3+4+5} before r-m. Halter yellow. Prehalter yellow. **Legs.** Forecoxa and midcoxa muddy yellow, hindcoxa dark brown dorsally, yellow ventrally. Femur brown, expanding at apex, broad yellow band distally 1/2 length distally, tibia brown, expanding at apex, with broad yellow band 1/3 length distally All tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Tergites and sternites dark brown, dark orange band across segment II, anterolateral margins of tergites afterward orange. **Male Genitalia.** Epandrial collar and epandrial apodemes as per genus. Epandrial lobes as per genus; subapical and lateral spines as per genus; ventromesal lobe located at medial apex of epandrial lobe, dorsal portion as crenulated ridges, ventral portion with flattened subacute triangular pendulant lobe, reaching beyond ventral margin of epandrial lobe. Epiproct as per genus; posteromedial stylus absent; hypoproct as per genus.

Parameres with basal forming bridge, lateral apex elongate, fused to gonopod; small laterally curved spur on posterior margin near base of apical lobe, apical lobe flattened ovoid, slightly longer than width, dorsal surface with secondary lobule with paired spines, flattened semicircular lobes on anterior margin.

Dorsal spur of gonocoxal apodeme absent. Gonocoxite much longer than broad tapering anterior, with dorsal margin straight posterior, weakly emarginate anterior, ventral margin convex, arc shallower anterior. Gonostylus with basal lobe poorly differentiated from medial ridge of apical stylus, without notch at base; apical stylus with medial ridge extending to apex, rounded posterior and tapering anteriorly, heavily provided with spine-like sensilla.

Basal division of hypandrium as per genus. Hypandrial spathate lobes with parallel margins, apex with apical section of ventral margin directed dorsally to meet dorsal margin. Terminal division, apex pentagonal, external surface with prominent spine-like sensilla forming narrow band at base of plate. Membranous window slit-like dorsally, expanding weakly ventrally, forming flattened ovoid pennant. Aedeagus as per genus; subapical sclerite with ventral arms flattened, expanding to apex; medial portion with apical margin flat, tapering ventroanterior to short stylus, arc slightly dorsoanterior. Ejaculatory apodeme tapering to apex, base broad.

Figures. Male Genitalia: 31, Wing: 32, Distribution: 33.

Material Examined. Cotypes. Brit. India, Darjiling, 7000', X-16, '05, (Brunetti) (Slide: 3 m#) (USNM) **Paratypes.** As cotypes (Pinned: 3 m#) (USNM). Calcutta/ C.F. Baker Collection (Pinned: 2 m#) (USNM).

Ptychoptera (Chrysoptycha) Fasbender* subgen. nov.*Diagnosis**

Adult. Epandrium nematoform, with slipper shaped subapical stylus at $\frac{3}{4}$ length of gonostylus, paramere forming flat bridge floating on supraedeagal membrane, gonopod with gonocoxite massive, ovoid, with medial gonocoxal lobe; apical stylus of gonostylus poorly sclerotized, pendulant. Larvae: Postmentum with >14 broad rounded denticulations, respiratory siphon shorter than remainder of anal division (Currently indistinguishable from *P. (Rheoptycha)*).

Description

Male Genitalia. Epandrium with nematoform epandrial clasper weakly delineated from epandrial lobe; subapical spine developed at $\frac{3}{4}$ th epandrial clasper as ventral knob with weakly petiolate base. Epandrial collar well developed, extending to epandrial apodeme; epandrial apodeme without break, ribbon-like extending to hypandrium. Posterolateral stylus not developed. Epiproct reduced, forming narrow web at apex of epandrial clasper contact. Hypoproct subobtusely triangular, subepandrial membrane heavily sclerotized, forming semicircular plate with rounded anterolateral apices.

Parameres fused to bridge, floating on membrane, well separated from gonocoxite, apical lobe weakly developed on posterior margin.

Gonocoxal apodeme round, extremely broad, length approximately $\frac{1}{5}$ th length of remainder of gonocoxite. Dorsal spur reduced, evident only as internal shelf. Gonocoxite very large, ovoid, with dorsal margin weakly convex, ventral margin broadly arced, becoming straighter posterior. Dorsal gonocoxal lobe placed at $\frac{2}{3}$ rd length of gonocoxite. Gonostylus with basal lobe directed medially,

knoblike; apical stylus flattened, weakly sclerotized, pendulant; secondary lobe of directed medially, hooked anterior, with threadlike dorsal lobe present.

Hypandrium with basal division extremely broad, trapezoidal in ventral view. Eversible sac heavily incising terminal division, forming broad rectangle, lateral margins rounded ventrally, ventral portion weakly lacrimiform. Terminal division broadly affixed to lateroposterior margins of basal division, supported by narrow lateral beam leading to quadrate recumbent apex.

Aedeagal sclerites weakly tapering, approximately 2/3rds length of sperm sac; apical apodemes absent; subapical sclerite well developed, elongate conical medial portion apex directed posterior; lateral plates present: placed at base of aedeagal sclerite, directed posterior, anterior base petiolate, posterior margin emarginate. Sperm sac nearly spherical, smaller than ejaculatory apodeme. Ejaculatory apodeme attached dorsomedially to sperm sac, not closely associated with aedeagal sclerites, not extending into segment VII, arcing heavily anteriorly; curling around anterior margin of sperm sac. Lateral ejaculatory processes attached dorsolaterally to sperm pump, directed straight anteroventrally, dorsal and ventral margins straight, terminal apodeme directed subventrally.

Taxonomic Notes:

Chrysoptycha is closely allied to *Parapterychoptera* and *Rheophiliabased* on the weakly sclerotized, pendulant apical stylus of the gonostylus and paramere floating on the superaedeagal membrane.

Type Species:

Ptychoptera (Chrysoptycha) sculleni Alexander **comb. nov.**

Etymology:

Chrysoptycha refers to the golden-yellow color of this unique species, as well as the distinctive transverse folds in the wing of the family.

Ptychoptera (Chrysoptycha) sculleni* Alexander, 1943*Diagnosis.**

Adult. As per subgenus.

Description

Adult. Measurements (n=1). Overall length 9.5mm. **Head.** Width: 1.18mm, Height: 0.93mm, Length: 0.60mm; Antenna flagellum length: 5.7mm. **Thorax.** Length: 2.5mm, Height: 2.5mm; Wing length: 11.2mm, Width: 2.6mm. **Abdomen.** Length: 6.4mm.

Head. Vertex shining black, sparsely set with trichoid sensilla; frons extremely narrow strip, black. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: scape yellow, oblong cylinder with long black setae, projecting dorsally from anterior surface; pedicel yellow, globular, patch of trichoid sensilla on lateral margin. Proximal flagellomeres yellow, fading to brown distally, bacilliform. Facial sclerite dark brown or black, distinct from clypeus, narrowed considerably above dorsal extent of clypeus. Clypeus ventrally tapering subtriangular, bulbous, generally covered in yellow sensilla, dorsal margin dark brown, remainder yellow. Maxillary palpus yellow. Labrum leaf shaped, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae yellow.

Thorax. Anteprenotum with transverse fold broad, yellow, medial lobe approximately quarter width of remainder of anteprenotum, highly tapered trapezoid, dorsal surface with shallow medial

notch. Prescutum and scutum shining, glabrous black, sutures and margins outlined in yellow, often highly reducing black region, with narrow yellow stripe from posterior apex of prescutum to scutellum; medial and prescutal suture with row of minute clear trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum as longer yellow sensilla; long clear prealar sensilla present, becoming shorter and blacker above wing. Scutellum yellow. Mediotergite of metanotum yellow, ventral margin with black band which is often reduced, patch of short yellow trichoid sensilla medially, medial suture apparent. Laterotergite of metanotum yellow, except for black band ventral extremity, dorsal patch of very elongate yellow trichoid sensilla. Pleural sclerites yellow, often with black dorsal and ventral margins in northern populations, weakly pollinose. Anepisternal cleft broad, membrane yellow. Suture between epimeron and metapleurite strong. **Wing.** Hyaline, weak infuscation extending from base of R_{1+2} to CuA_1+CuA_2 fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 6.01mm, Apex of Sc to Apex of R_1 1.534mm, R_{3+4+5} stem 1.06mm, slight posterior turn at fork from R_{1+2} ; R_{4+5} stem 1.98mm; R_4 after fork 1.98mm, R_5 after fork 2.08mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 1.86 : 1.86$. r-m 0.30mm; M distal to r-m 2.88mm; M_1 0.91mm, arcuate, M_2 0.67mm; $M\text{distal}:M_1 = 1.00:0.31$, $R_{3+4+5}:M\text{distal} = 1.00:2.71$, $R_4:M_1 = 1.00:0.68$. CuA_1 proximal 0.22mm, distal 2.66mm; CuA_2 1.23mm sinuous. CuA_2 to A_1 2.66mm. m-cu joins R_{3+4+5} after r-m. Halter yellow. Prehalter yellow. **Legs.** Coxae yellow. Femur and tibia yellow. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensillae.

Abdomen. Tergites and sternites black, wide bands of yellow on posterior and lateral margins, moderately covered in elongate yellow sensilla. **Male Genitalia.** Epandrial collar complete, developed laterally, epandrial apodemes well developed, extending to lateroanterior apex of hypandrium, tapering across gonocoxal apodeme, no break. Epandrial lobes nematoform, epandrial clasper indistinguishably fused, basal portion quadrate, rapidly tapering to stylate, apex slipper-like tapering to acute point;

clavate lobe located at approximately $\frac{3}{4}$ length of epandrial clasper on ventral surface. Epiproct reduced, developed at thin web at apex near apex of epandrial lobe contact, epandrial lobes in contact for less than $\frac{1}{5}$ th of length anteriorly. Posteromedial stylus not developed. Hypoproct tongue-like expanding anteriorly to delta shaped plate, weak medial suture evident, partially derived from subepandrial membrane.

Parameral bridge floating on medial membrane of gonocoxite. Broad arc, lateral apices obtusely rounded, low bump on anteromedial apex, apical lobes inevident.

Gonocoxal apodeme as broad as gonocoxite, apex broadly rounded, dorsal spur highly reduced, little more than internal plate. Gonocoxite broadly elliptical, dorsal gonocoxal spur located at approximately $\frac{3}{4}$ length of gonocoxite, short, triangular. Medial gonocoxal lobe directed dorsomedially at base, approximately 45 degrees from horizontal, at half-length directed dorsoanterior, apex rounded arc hooking posterior, tip rounded. Gonostylus with basal lobe formed to knob directed dorsomedially expanding at apex, weak sulcus on dorsomedial surface near posterior margin. Apical stylus pendulant directed slightly oblique from vertical, pendulant lobe rounded cross section with flattened medial surface, tapering weakly to apex; secondary lobe located on dorsoposterior margin ventral to basal lobe, broad, forming semicircular arc directed anteromedially, apex expanding slightly to flattened apical surface, dorsal surface with elongate, thread-like lobule directed dorsally, poorly sclerotized. Basal division of hypandrium with paired triangular lobes on posteromedial margin, medioposterior apex of basal division inflated. Eversible sac not prominent, formed as quadrate window ventral to terminal division with two secondary windows ventrally in the inflated posterior apex of the basal division. Terminal division narrowly attached to basal division, subquadrate, forming plate bent slightly posterior, apex curved weakly anterior. Aedeagus oriented approximately 15 degrees from vertical, ejaculatory apodeme with base narrow; dorsal margin of lateral ejaculatory process straight; apex of aedeagal

sclerites rounded. Subapical sclerite broadly stylate, base flattened, split to two short unattached ventral arms, dorsal apex bent posterior. Lateral plates of subapical sclerite associated with base of lateral ejaculatory processes, petiolate anterior, expanding posterior with posterior margin emarginate.

Figures. Male Genitalia: 34, Wing: 35, Distribution: 36.

Material Examined. Holotype. Elbe, Wash. July 13, 1940, H.&M. Townes (Pinned: 1 m#) (USNM). **Paratypes.** Alsea Ore. May 25 1931, H.A. Scullen, Col. (Pinned: 1 m#) (USNM). Cascadia, Ore. 8-11-24/ H.A. Scullen, Collector (Pinned: 1 f#) (USNM). **Other Material.** CALIFORNIA, Siskiyou Co. #3, Mt. Shasta (town), 18 June 1959, G.W. Byers (Pinned: 3 m#, 1 f#) (KU). Oregon, Benton Co. Mary's Peak, 7-5-10/7-17-10, GW Courtney (Pinned: 2 m#) (ISIC). USA, Oregon, Benton Co., Mary's Pk, seeps mid Parker Ck, 44°29.90'N 123°34.12'W 700m, 19 Aug 2014 coll. GW Courtney, near mucky seeps along road (Alcohol: 1 m#, 2 f#) (ISIC). Oregon, Benton Co. Mid Parker Seep, 7-6-10/7-14-10, GW Courtney (Pinned: 1 m#) (ISIC). OREGON – Lane Co. #1, Salt Creek, 24 June 1959, George W. Byers (Pinned: 1 m#) (KU). USA, Oregon, Lane Co. H.J. Andrews Exp. Forest, seeps W of Andersen Creek, 44°13.81'N 122°11.12'W 615m, 23 May 2012 coll. GW Courtney, from sandy/muddy seep (Pinned: 2 m#) (ISIC). USA, Oregon, Benton Co. seeps @ Alder Ck Falls 715m, 44°28.49'N 123°31.61'W, 7.vii.2010 coll. GW Courtney, swept from vegetation (Alcohol: 3 m#, 1 f#) (ISIC). USA, Oregon, Yamhill Co. Peavine Rd, upper Deer Creek, 45°14.38'N 123°23.15'W 400m, 13.vii.2011 coll. G.W. Courtney, on riparian vegetation (Alcohol: 1 m#, 4 f#) (ISIC). USA, Oregon, Yamhill Co. Peavine Rd, upper Deer Creek, 45°14.38'N 123°23.15'W 400m, 18 May 2012 coll. G.W. Courtney, depositional zone/ marginal muck (Alcohol: 3 m#) (ISIC). OREGON, Yamhill County, Peavine Ridge, VI-13 1953, Fender Sta. 3A (Pinned: 1 m#) (UMMZ). WASHINGTON, Olympic N.P. Hoh River, July 18, 1953, K.M. Fender (Pinned: 1 m#) (UMMZ). USA, Washington, Jefferson Co. Olympic National Park, Queets River Valley, 47°34.30'N, 124°08.40'W 50m, 20 July 2011 coll. GW

Courtney, from roadside seep (Alcohol: 1 m#, 1 f#) (ISIC). USA, Washington, Jefferson Co. Olympic National Park, Queets River Valley, 47°34.30'N, 124°08.40'W 50m, 28 May 2012 coll. GW Courtney, from roadside seep (Alcohol: 2 m#, 3 f#) (ISIC).

Ptychoptera (Parptychoptera) Tonnoir, 1919

Diagnosis

Adult. Epandrium with triangular epandrial lobes, articulated epandrial claspers poorly sclerotized without basal lobe, variable ventral lobe, hypoproct tonguelike. Gonostylus with basal lobe divided into knoblike anterior lobe and scythelike medial lobe. Invaginated auxiliary sexual organ on abdominal sternite III.

Description

Male Genitalia. Epandrium with triangular epandrial lobes, ventromesal lobe absent. Epandrial clasper poorly sclerotized and well articulated; stylate, with lacking basal lobe on medial margin, ventral surface often with spine or lobe basally. Epandrial collar distinct; epandrial apodeme broad, tapering to hypandrium, breaks at epandrium and hypandrium. Cerci variably developed. Epiproct prominent, extending nearly to apex of epandrial lobe, epandrial lobes in contact anteriorly. Hypoproct tonguelike, subepandrial sclerite variably developed.

Parameres fused to narrowly medially, forming narrow arc in dorsal view, medioposterior extension absent. Paramere apices laterally compressed dorsally directed paddles.

Gonocoxal apodeme acute, ventral margin straight dorsal margin convex, length approximately 1/4th length of remainder of gonocoxite. Dorsal spur of gonocoxal apodeme directed medially. Dorsal gonocoxal lobe present, medial gonocoxal lobe present, directed posterior. Gonostylus with basal lobe

divided into anterior and medial lobe: anterior lobe knob-like, directed anterior, medial lobe scythe-like, directed medially; apical stylus variable developed, poorly sclerotized.

Hypandrium with basal division band-like, lateral margins narrow. Spathate lobes absent. Eversible sac present, windowlike to leaflike. Basal scale often present Terminal division broadly attached to lateral surfaces of basal division, apex variable, lateral extensions of terminal division absent; membranous window absent.

Aedeagal sclerites with lateral apices angled at apex, approximately 1.5x length of sperm sac; apical apodemes present; subapical sclerite well developed, spine or rod-like with ventral arms developed as lateral plates. Sperm sac nearly ovoid, subequal than ejaculatory apodeme. Ejaculatory apodeme attached dorsoanteriorly to sperm sac, closely associated with aedeagal sclerites, extending anteriorly into segment VII, stretching posterior; not curling around anterior margin of sperm sac. Lateral ejaculatory processes, attached dorsolaterally to sperm pump, directed anterolaterally, dorsal and ventral margins straight, discoid apodeme directed ventrally.

Taxonomic Notes:

Type Species:

Ptychoptera (Parapterychoptera) paludosa Meigen

Other Species

Ptychoptera (Parapterychoptera) anges Krzeminski & Zwick*

Ptychoptera (Parapterychoptera) delmastroi Zwick & Stary*

Ptychoptera (Parapterychoptera) handlirschi Czizek

Ptychoptera (Parapterychoptera) helena Peus

Ptychoptera (Parapterychoptera) lacustris Meigen

Ptychoptera (Parapterychoptera) longicauda Tonnoir

Ptychoptera (Parapterychoptera) resli Theischinger

Ptychoptera (Parapterychoptera) silvicola Zwyrtek & Rozkosny

Ptychoptera (Parapterychoptera) surcoufi Seguy*

* Not examined in this study, assigned by species authors.

***Ptychoptera (Parapterychoptera) handlirschi* Czizek, 1919**

Liriope handlirschi Czizek, Czizek 1919

Diagnosis

Adult. Two bands on wing, no spots. Thoracic pleurites black with yellow dorsal margin, abdominal segments black with narrow yellow posterior margin. **Male.** Epandrial claspers with laterally compressed semicircular lobe at base, apex pointed, hemispherical lobe laterally at base, hypoproct with apex simple; gonopod with gonostylus having anterior lobe of basal lobe hook shaped, medial lobe with apex spatulate, apical stylus directed 45 degrees ventrally from horizontal, secondary lobe subequal in length; hypandrium with terminal division apex with medial portion spoon shaped, lateral margins simple.

Description

Adult. Measurements (n=1). Overall length 10.32mm. **Head.** Width: 1.06mm, Height: 0.88mm, Length: 0.57mm; Antenna flagellum length: 3.35mm. **Thorax.** Length: 2.45mm, Height: 2.35mm; Wing length: 10.3mm, Width: 2.8mm. **Abdomen.** Length: 7.3mm

Head. Vertex shining russet brown, evenly set with trichoid sensilla; frons weakly developed between antennae. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: Scape yellow elongate cylinder; pedicel brown with yellow apex, globular, few trichoid sensilla. Flagellomeres brown, fusiform. Facial sclerite russet brown, distinct from clypeus, roughly pentagonal plate above clypeus. Clypeus elongate rectangle, flattened, generally covered in macrotrichia, yellow. Maxillary palpus with all but final segment yellow, distal segment brown. Labrum D-shaped, dark yellow; epipharynx and hypopharynx not externally apparent, labium and labellae yellow.

Thorax. Antepronotum yellow, transverse fold narrow, medial lobe quarter width of antepronotum, trapezoidal, medial notch present. Prescutum and scutum obscurely shining russet brown; microtrichia vestiture present, medial and prescutal suture with row of clear trichoid sensilla, short yellow prealar sensilla present. Scutellum yellow; lateral ridges with dark highlights. Mediotergite of metanotum shining chestnut brown. Laterotergite of metanotum shining, chestnut brown, dorsal patch of trichoid sensilla yellow. Pleural sclerites all chestnut brown, with weak pollinosity, dorsal apices yellow. Anepisternal cleft broad, trapezoidal, not extending nearly to base of wing, membrane brown. Suture between epimeron and metapleurite prominent.

Wing. Two broad bands, proximal extending from base of R_5 to M, distal from R_{1+2} fork to base of R_5 , spot on R_1 below apex of Sc; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 6.9mm, Apex of Sc to Apex of R_1 1.41mm, R_{3+4+5} stem 0.44mm, with severe medial angle; R_{4+5} stem 2.15mm; R_4 after fork 2.35mm, R_5 after fork 2.4mm; R_{3+4+5} : R_{4+5} -stem: R_4 , 1.0 : 4.88mm : 5.34. r-m 0.37mm; M distal to r-m 2.85mm; M_1 1.3mm, arcuate, M_2 0.95mm; Mdistal: M_1 , 1.0:0.45, R_{3+4+5} :Mdistal, 1.0:6.47, R_4 : M_1 , 1.0:0.60. CuA_1 proximal 0.37mm, distal 2.85mm; CuA_2 2.35mm with anterior angle well developed, posterior angle absent. CuA_2 to A_1 2.47mm. R_3 branching at r-m. Halter

yellow. Prehalter yellow. **Legs.** Coxae yellow. Femur yellow, darkening to brown near tibial joint, tibia yellow. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere cannot fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensilla.

Abdomen. Tergites and sternites chocolate brown, with prominent yellow bands at the middle of segment II and the anterior of segment III, thickly covered in elongate yellow setae. Third segment with accessory copulatory organ, posterior margin with paired rounded lobes, low U-shaped ridge between the lobes, medial sclerotized strip present. **Male Genitalia.** Epandrial collar complete, epandrial apodemes well developed, extending to lateroanterior apex of hypandrium, extending flatly across gonocoxal apodeme, prominent break between epandrial collar and epandrial apodeme. Epandrial lobes flattened, elongate over twice as long as wide, apex indistinct, lateral margins straight and weakly convergent. Epandrial clasper with two lobules at base; lateral lobule hemispherical, on lateral surface at base; ventral lobule flattened scallop shape directed posterior; primary stylus of epandrial clasper round in cross section, apex rounded, convergent. Epiproct prominent, epandrial lobes with point contact anteriorly. Posteromedial stylus present, forming prominent hemispherical bulge on medial surface directly anterior to epiproct. Hypoproct broad, nearly as wide as epandrial lobe, tongue-like. Subepandrial membrane without sclerites.

Parameral bridge narrowly affixed to gonocoxite. Apical lobes of paramere subquadrate, directed dorsoanteriorly, lateral margin squared, medial margin extended dorsally, ending in weakly furcate apex.

Gonocoxal apodeme and gonocoxite as per genus. Dorsal gonocoxal lobe directed posterior, forming finger-like lobe nearly reaching epandrium. Medial gonocoxal lobe bifurcate, directed dorsally, fingerlike to rounded apex. Gonostylus extending beyond the apex of the epandrial clasper. Basal lobe

with dorsal lobe having slightly petiolate base leading to flattened spatulate knob with finger shaped apex directed posteromedially; medial lobe scythe shaped, apex spatulate. Apical stylus directed 45 degrees from horizontal, round in cross section with rounded apex, secondary lobe subequal, directed posterior, round in cross section.

Hypandrium basal division with eversible sac inverse T-shape, expanding above basal scale; basal scale undivided, generally triangular, lateral apices pointed triangular, medial apex rounded. Terminal division broadly attached to basal division; apex of terminal division subquadrate plate with rounded projection medially, two pairs of brushes on lateral margin.

Aedeagus oriented 15 degrees from vertical, apex of aedeagal sclerites angled; dorsal margin of lateral ejaculatory process weakly curved ventrally at apex. Ejaculatory apodeme fan-like with base narrow, larger than sperm sac, not closely paralleling anterior margin, sperm sac spherical. Subapical sclerite with medial portion parallel sided stylus, apex bluntly rounded, becoming trapezoidal below aedeagal sclerites; apex extending beyond apex of terminal division of hypandrium; lateral plates L-shaped in posterior view, dorsomedial apex flat and slanted.

Female Genitalia. Tergite VII brown with yellow posterior margin. Cerci orange, lateral ridge weakly defined, dorsal furrow poorly developed. Cercus length:width, 4:1. Hypogynium yellow, rotated dorsally approximately 40 degrees from vertical; straight-sided. Apical margin triangular, lateral corner rounded. Lateral margin hidden.

Figures. Male Genitalia: 37, Wing: 38, Distribution: 39.

Material examined. Bulgaria – Rilski, Monastir, 26.06.1982, leg. W. Krzeminski (Pinned: 1 m#) (USNM). Czechoslovakia, Tatranská Kotlina. 21.vi.1932. Bela Kalk Alpen, 3000ft./ D. Aubertin, E. Trewavas. B.M. 1932-310 (Pinned: 1 m#) (BMNH). 10-VI-66, Vihorlat, (indecipherable)/ Leg. R. Rozkošný,

1973 (Pinned: 1 f#) (BMNH). Poland, Zakopane, Byskej Vally. 7.vii.1932. Tatra Mts. 3300ft. D. Aubertin, E. Trewavas. B.M. 1932-310 (Pinned: 1 m#, 1 f#) (BMNH).

***Ptychoptera (Parptychoptera) helena* Peus, 1958**

Diagnosis

Adult. Wing with three bands, one at base, two spots on anterior margin. **Male.** Epandrial claspers with two spines at base, apex expanded, hypoproct with apex bifurcate; gonopod with gonostylus having anterior lobe of basal lobe quadrate spatulate, with single blunt medially directed spine, medial lobe with apex pointed, apical stylus directed posterior, secondarily lobe subequal in length; hypandrium with terminal division apex with medial portion spoon shaped, lateral margins formed to acute spines.

Description

Adult. Measurements (n=1). Overall length ? (abdomen dissected). **Head.** Width: 1.0mm, Height: 0.88mm, Length: 0.54mm; Antenna flagellum length: 3.65mm. **Thorax.** Length: 1.9mm, Height: 1.95mm; Wing length: 7.6mm, Width: 2.0mm. **Abdomen.** Length: ? (dissected).

Head. Vertex shining black, evenly set with trichoid sensilla; frons weakly developed between antennae. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: Scape black elongate cylinder; pedicel brown, globular, few trichoid sensilla. Flagellomeres brown, fusiform. Facial sclerite black, distinct from clypeus, roughly pentagonal plate above clypeus. Clypeus elongate rectangle, flattened, generally covered in macrotrichia, yellow. Maxillary palpus with all but final segment yellow, distal segment brown. Labrum D-shaped, dark yellow; epipharynx and hypopharynx not externally apparent, labium and labellae yellow.

Thorax. Antepronotum black medially, brown laterally, transverse fold narrow, medial lobe quarter width of antepronotum, trapezoidal, medial notch absent. Prescutum and scutum obscurely shining black; microtrichia vestiture present, medial and prescutal suture with row of clear trichoid sensilla, short yellow prealar sensilla present. Scutellum yellow; lateral ridges with dark highlights. Mediotergite of metanotum shining black. Laterotergite of metanotum shining, black, dorsal patch of trichoid sensilla yellow. Pleural sclerites all black, with strong pollinosity. Anepisternal cleft broad, trapezoidal, not extending nearly to base of wing, membrane brown. Suture between epimeron and metapleurite prominent.

Wing. Three broad bands, proximal at h, traversing halfway across wing, medial extending from base of R_5 to angle of CuA_2 , distal from R_{1+2} fork to base of R_5 , spots on R_1 below apex of Sc and M fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 5.0mm, Apex of Sc to Apex of R_1 1.06mm, R_{3+4+5} stem 0.35mm, with severe medial angle; R_{4+5} stem 1.73mm; R_4 after fork 1.6mm, R_5 after fork 1.93mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4$, 1.0 : 4.94 : 4.57. r-m 0.22mm; M distal to r-m 2.15mm; M_1 0.86mm, arcuate, M_2 0.64mm; Mdistal: M_1 , 1.0:0.4mm, $R_{3+4+5}:M_{\text{distal}}$, 1.0:6.14, $R_4:M_1$, 1.0:0.53. CuA_1 proximal 0.25mm, distal 2.05mm; CuA_2 1.36mm with anterior angle well developed, posterior angle absent. CuA_2 to A_1 1.78mm. R_3 branching before r-m. Halter yellow. Prehalter yellow.

Legs. Coxae orange. Femur yellow, darkening to brown near tibial joint, tibia yellow. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere cannot fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensilla.

Abdomen. Tergites and sternites chocolate brown, with prominent yellow bands at the middle of segment II and the anterior of segment III, thickly covered in elongate yellow setae. Third segment

with accessory copulatory organ, posterior margin with paired rounded lobes, low U-shaped ridge between the lobes, medial sclerotized strip present.

Male Genitalia. Epandrial collar complete, epandrial apodemes well developed, extending to lateroanterior apex of hypandrium, extending flatly across gonocoxal apodeme, prominent break between epandrial collar and epandrial apodeme. Epandrial lobes flattened, short, less than twice as long as wide, apex distinct, lateral margins straight and weakly parallel. Epandrial clasper simple, directed straight posterior, weak expanding to cylindrical bulb at apex, lateral lobe formed to ventrally directed spine. Epiproct prominent, posterior margin simple, nearly straight, epandrial lobes with point contact anteriorly. Posteromedial stylus present, narrow blunt spine on ventral surface at junction of epandrial lobe and epandrial clasper, minute hook on medial surface. Hypoproct broad basally, tapering to bifurcate apex, nearly as wide as epandrial lobe. Internal portion fused to single rectangular subepandrial sclerite.

Parameral bridge narrowly affixed to gonocoxite, base directed anterior, bending ventroposterior and straightening apically. Apical lobes of directed dorsoposterior, hatchet shaped with broad base.

Gonocoxal apodeme and as per genus, gonocoxite expanding to rounded apex, dorsal and ventral margins straight. Dorsal gonocoxal lobe near posterior margin, forming finger-like lobe shorter than basal lobe of gonostylus. Medial gonocoxal lobe bifurcate, directed posterior, lateral branch narrowly spinelike with clavate apex, medial fused at apex to apical lobe of paramere. Gonostylus shorter than epandrial clasper. Basal lobe with anterior lobe ovoid with paired blunt spines directed medially; medial lobe scythe shaped, apex rounded. Apical stylus directed posterior, round in cross section with rounded apex, secondary lobe subequal, directed posterior, round in cross section.

Hypandrium basal division with eversible sac acutely triangular, widest ventrally; basal scale undivided, semicircular, lateral margins curved dorsally. Terminal division broadly attached to basal division; apex expanded to lateral bars terminating in dorsal spines along dorsal margin of basal division, medial portion of apex acute spine with broad bulging base.

Aedeagus and hypandrium nearly horizontal, apex of aedeagal sclerites angled, lateral margins straight; dorsal margin of lateral ejaculatory process with low bump on dorsal surface. Ejaculatory apodeme fan-like with base narrow, larger than sperm sac, not closely paralleling anterior margin, sperm sac spherical. Subapical sclerite with medial portion triangular base with rod-like blunt apex, apex extending beyond apex of terminal division of hypandrium; lateral plates L-shaped in posterior view, dorsomedial apex flat and slanted.

Female Genitalia. Tergite VII brown with yellow posterior margin. Cerci orange, lateral ridge weakly defined, dorsal furrow poorly developed. Cercus length:width, 5:1. Hypogynium yellow, rotated dorsally approximately 40 degrees from vertical; straight-sided. Apical margin triangular, lateral corner emarginate. Lateral margin hidden.

Figures. Male Genitalia: 40, Wing: 41, Distribution: 42.

Material examined. Paratypes. Oiti-Geb., Graecia, Gorgopotamos, 350m, 27.v.1956, F. Peus (Pinned: 1 m#, 1 f#) (USNM).

***Ptychoptera (Parptychoptera) lacustris* Meigen, 1830**

Diagnosis

Adult. Wing with two broken bands and spot at base. **Male.** Epandrial claspers without lobes or spines at base, apex rounded, hypoproct with apex simple; gonopod with gonostylus having anterior

lobe of basal lobe quadrate hook like dorsally, flattened ventrolaterally, medial lobe with apex pointed, apical stylus directed posterior, secondarily lobe less than half length; hypandrium with terminal division apex with medial portion spine shaped, tip inflated, lateral margins simple.

Description

Adult. Measurements (n=1). Overall length 7.78mm. **Head.** Width: 1.03mm, Height: 0.93mm, Length: 0.58mm; Antenna flagellum length: 3.55mm. **Thorax.** Length: 2.6mm, Height: 2.5mm; Wing length: 10.3mm, Width: 3.1mm. **Abdomen.** Length: 4.6mm

Head. Vertex shining black, evenly set with trichoid sensilla; frons weakly developed between antennae. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: Scape black elongate cylinder; pedicel brown, globular, few trichoid sensilla. Flagellomeres brown, fusiform. Facial sclerite black, distinct from clypeus, roughly pentagonal plate above clypeus. Clypeus elongate rectangle, flattened, generally covered in macrotrichia, yellow. Maxillary palpus with all but final segment yellow, distal segment brown. Labrum D-shaped, dark yellow; epipharynx and hypopharynx not externally apparent, labium and labellae yellow.

Thorax. Anteprenotum black medially, brown laterally, transverse fold narrow, medial lobe quarter width of anteprenotum, trapezoidal, medial notch absent. Prescutum and scutum obscurely shining black; microtrichia vestiture present, medial and prescutal suture with row of clear trichoid sensilla, short yellow prealar sensilla present. Scutellum yellow; lateral ridges with dark highlights. Mediotergite of metanotum shining black. Laterotergite of metanotum shining, black, dorsal patch of trichoid sensilla yellow. Pleural sclerites all black, with weak pollinosity. Anepisternal cleft broad, trapezoidal, not extending nearly to base of wing, membrane brown. Suture between epimeron and metapleurite prominent. **Wing.** Three broad bands, proximal at h, traversing halfway across wing, medial extending from base of R_s to angle of CuA_2 , distal from R_{1+2} fork to base of CuA_1 ; membrane with

macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 5.5mm, Apex of Sc to Apex of R_1 1.36mm, R_{3+4+5} stem 0.5mm, with severe medial angle; R_{4+5} stem 1.83mm; R_4 after fork 2.0mm, R_5 after fork 1.93mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4$, 1.0 : x : x. r-m 0.30mm; M distal to r-m 2.35mm; M_1 1.13mm, arcuate, M_2 0.85mm; Mdistal: M_1 , 1.0:x, R_{3+4+5} :Mdistal, 1.0:x, $R_4:M_1$, 1.0:x. CuA_1 proximal 0.27mm, distal 2.25mm; CuA_2 1.5mm with anterior angle well developed, posterior angle absent. CuA_2 to A_1 2.15mm. R_3 branching before r-m. Halter yellow. Prehalter yellow. **Legs.** Coxae yellow. Femur yellow, darkening to brown near tibial joint, tibia yellow. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere cannot fold back on penultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensilla.

Abdomen. Tergites and sternites chocolate brown, with prominent yellow bands at the middle of segment II and the anterior of segment III, thickly covered in elongate yellow setae. Third segment with accessory copulatory organ, posterior margin with paired rounded lobes, low U-shaped ridge between the lobes, medial sclerotized strip present. **Male Genitalia.** Epandrial collar complete, epandrial apodemes well developed, extending to lateroanterior apex of hypandrium, extending flatly across gonocoxal apodeme, prominent break between epandrial collar and epandrial apodeme. Epandrial lobes flattened, triangular, slightly broader than wide, apex rounded, lateral margins straight and weakly convergent, anterior angle nearly 90 degrees, medial margin straight posterior to medial contact, diverging at 90 degree angle. Epiproct prominent, epandrial lobes in contact for 1/4th of length anteriorly. Posteromedial style absent. Epandrial clasper simple, weakly flattened in cross section, curving weakly medially, subequal to epandrial lobe, apex rounded. Hypoproct broad, nearly as wide as epandrial lobe, tongue-like. Subepandrial membrane without sclerites. Parameral bridge narrowly affixed to gonocoxite. Apical lobes of paramere subquadrate, directed dorsoanteriorly, corners heavily rounded. Gonocoxal apodeme and gonocoxite as per genus. Dorsal gonocoxal lobe directed posterior, forming finger-like lobe. Gonostylus extending beyond the apex of the epandrial clasper. Basal lobe with

dorsal lobe with slightly petiolate base expanding to broad spatulate lobe with figure-8 shaped apex directed posteromedially; posterior lobe scythe shaped, apex acute point. Apical stylus directed posterior, round in cross section with rounded apex, with posterior directed finger-like secondary lobe at base, extending $1/3^{\text{rd}}$ length of apical stylus. Basal division with eversible sac lacrimiform, slit-like dorsally, traversing much of terminal division. Terminal division broadly attached to basal division, apex of terminal division spine-like. Basal scale absent. Aedeagus oriented 35-45 degrees beyond horizontal, ejaculatory apodeme with base narrow; dorsal margin of lateral ejaculatory process straight; apex of aedeagal sclerites subacute. Subapical sclerite medial portion stylate, base broad, ventral notch present subapically, extending beyond apex of terminal division of hypandrium; lateral plates with rounded medially directed dorsal apex, expanding to broad, straight margin ventrally, lateroventral apex extended laterally.

Female Genitalia. Tergite VII brown with yellow posterior margin. Cerci orange, lateral ridge weakly defined, dorsal furrow poorly developed. Cercus length:width, 3:1. Hypogynium yellow, rotated dorsally approximately 40 degrees from vertical; constricted at base. Apical margin quadrate, lateral corner rounded. Lateral margin hidden.

Figures. Male Genitalia: 43, Wing: 44, Distribution: 45.

Material examined. Bulgaria – Lakatnik, near Sofia, 18.06.1982, leg. W. Krzeminski (Pinned: 1 f#) (USNM). Dania, Bornholm, Bastemose, 16.juli 1966, leg. Bo Vest Pedersen (Pinned 2 m#) (ZMUC). Dania, Jylland, Grejsdalen, 29.juli 1964, Ole Martin (Pinned: 1 m#) (ZMUC). DK. Sønderjyll. Hønsnap skov, 28.6.1960, leg. Lyneborg (Pinned: 2 f#) (ZMUC). Strandby, 15.7.16/ V. Olson (Pinned: 1 m#) (ZMUC). Denmark – Zealand, 5km NW of Hillerød, 31 July 1969, G.W. Byers #3 (Pinned, 1 m#, 2 f#). Denmark – Zealand, 7km NW of Frederiksvaert, 30 July 1969, G.W. Byers #1 (Pinned, 2 m#, 2 f#). Poland-dol.

Bedkowska, near Krakow, 2.06.1983, leg. W. Krzeminski (Pinned: 1 m#) (USNM). ENGLAND – Cambridge-shire, Gog-magog, Hills, 24 July 1960, G.W. Byers #2 (Pinned: 1 f#) (ZMUC). Jugoslavia, Trebevic, 1000m, Vii-15.55, Schmid (Pinned: 1 m#) (USNM).

***Ptychoptera (Parptychoptera) longicauda* Tonnoir, 1919**

Diagnosis

Adult. Two bands on wing, distal band broken, spots at base of wing and between band. **Male.** Epandrial claspers with single spine on base, subhemispherical lateral swelling present at base, apex rounded, hypoproct with apex simple; gonopod with gonostylus having anterior lobe of basal lobe massively quadrate, medial lobe with apex spatulate, apical stylus directed pendulant, secondary lobe much shorter, directed posterior; hypandrium with terminal division apex with spine-like with weakly furcate apex, lateral margins simple.

Description

Adult. Measurements (n=1). Overall length 8.33mm. **Head.** Width: 0.83mm, Height: 0.80mm, Length: 0.53mm; Antenna flagellum length: 4.13mm. **Thorax.** Length: 2.1mm, Height: 2.0mm; Wing length: 8.7mm, Width: 2.2mm. **Abdomen.** Length: 5.7mm.

Head. Vertex shining chestnut brown, sparsely set with trichoid sensilla; frons weakly developed between antennae, black. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: scape yellow basally, brown at distal apex, oblong fusiform cylinder; pedicel brown at base, yellow distally, globular, few trichoid sensilla. Flagellomeres brown, fusiform. Facial sclerite dark brown, distinct from clypeus, forming even band above clypeus. Clypeus ventrally tapering rhomboidal, bulbous, generally covered in macrotrichia, brown at dorsal margin,

ventral portion yellow. Maxillary palpus with basal segments yellow, 5th segment brown. Labrum bullet shaped, yellow; epipharynx and hypopharynx not externally apparent, labium black, labellae yellow.

Thorax. Anteprenotum with yellow transverse band, anterior and ventral sections chestnut brown, transverse fold weakly developed, medial lobe trapezoidal with minute medial notch; diffuse patch of yellow trichoid sensilla on anterior margin near forecoxa. Prescutum and scutum covered in microscopic punctures, glabrous chestnut brown; medial and prescutal suture with row of clear trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum; short yellow prealar sensilla present. Scutellum uniform light brown, dorsal surface with long, clear setae. Mediotergite of metanotum shining reddish-brown, glabrous. Laterotergite of metanotum shining, reddish-brown, dorsal patch of trichoid sensilla yellow. Pleural sclerites all reddish-brown, with weak pollinosity. Anepisternal cleft narrow, extending nearly to base of wing, membrane yellow. Suture between epimeron and metapleurite prominent. **Wing.** Two bands, proximal extending from base of R_{1+2} to CuA_1+CuA_2 fork, distal from R_{1+2} fork to base of R_5 , with an additional spot at the h crossvein; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 5.31mm, Apex of Sc to Apex of R_1 1.28mm, R_{3+4+5} stem 0.49mm, nearly right angle near r-m; R_{4+5} stem 1.73mm; R_4 after fork 1.71mm, R_5 after fork 1.78mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 3.53 : 3.48$. r-m 0.25mm; M distal to r-m 2.24mm; M_1 1.01mm, arcuate, M_2 0.84mm; $M\text{distal}:M_1 = 1.00 : 0.45$, $R_{3+4+5}:M\text{distal} = 1.00 : 2.06$, $R_4:M_1 = 1.00 : 0.57$. CuA_1 proximal 0.30mm, distal 2.27mm; CuA_2 1.18mm sinuous. CuA_2 to 1.90mm. m-cu joins R_{3+4+5} at r-m. Halter with dark yellow. Prehalter dark yellow. **Legs.** Forecoxae yellow. Femur yellow, darkening to brown near tibial joint, tibia yellow. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere cannot fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensilla.

Abdomen. Tergites and sternites chocolate brown, with prominent yellow bands in the at the anterior and middle of segment II and the anterior of segment III, thickly covered in elongate yellow setae. Third segment with accessory copulatory organ, posteriorly with square lobe with margins folded inward into two triangular lobes, medial sclerotized strip present.

Male Genitalia. Epandrial collar complete, epandrial apodemes well developed, extending to lateroanterior apex of hypandrium, extending flatly across gonocoxal apodeme, prominent break between epandrial collar and epandrial apodeme. Epandrial lobes flattened, triangular, apex extended with margins nearly parallel, lateral margins straight and parallel, anterior angle nearly 90 degrees, medial margin straight posterior to medial contact, diverging at 90 degree angle. Epiproct prominent, epandrial lobes in contact for 1/4th of length anteriorly. Posteromedial style present as ventrally directed tapering spine curved posterior at apex. Epandrial clasper simple, round in cross section, curving ventrally, longer than epandrial lobe, apex rounded; lateral lobe knob-like semicircular at base of clasper. Hypoproct broad, nearly as wide as epandrial lobe, tongue-like. Subepandrial membrane without sclerites.

Parameral bridge narrowly affixed to gonocoxite. Apical lobes of paramere subquadrate, directed dorsoanteriorly, corners heavily rounded.

Gonocoxal apodeme and gonocoxite as per genus. Dorsal gonocoxal lobe directed anterior, forming subacute triangle. Gonostylus extending approximately the same length of epandrial clasper. Basal lobe with dorsal lobe knob-like with short subacute triangular lobe on ventromedial margin, medial margin with two elongate trichoid sensillae directed posteriorly; posterior lobe scythe shaped, apex flattened and spatulate. Apical stylus pendulant, round in cross section, with posterior directed finger-like lobe at base, pendulant section of stylus extending to base of hypandrium, curving posteriorly near apex, small notch on ventral apex.

Basal division of hypandrium very broad, 1.5x height. Eversible sac slit-like, traversing much of terminal division, extending to dorsal extent of basal division. Terminal division broadly attached to basal division, apex of terminal division spine-like. Basal scale present, scallop shaped.

Aedeagus oriented 35-45 degrees beyond horizontal, ejaculatory apodeme with base narrow; dorsal margin of lateral ejaculatory process straight; apex of aedeagal sclerites subacute, subapical sclerite medial section spine-like, with medial fold forming funnel, closely associated with terminal division of hypandrium; lateral plates with rounded laterally directed dorsal apex, expanding to broad, straight margin ventrally, lateroventral apex extended laterally.

Figures. Male Genitalia: 46, Wing: 47, Distribution: 48.

Material examined. Holotype. Linkebeek, 3 Sept. 1918, A. Tonnoir (Pinned: 1 m#) (IRNSB). **Other**

Material. Aaremyre, 22.7.32/ e. coll. Peder Nielsen (Pinned: 1 m#) (ZMUC). Raarup, Aug. 31/ Skat Hoft. Meyer leg. (Pinned: 1 m#) (ZMUC). England – Oxford, Wytham Wood, V-12. 1963 (Pont, Ackland & Vane-Wright) (Slide: 1 m#) (USNM).

***Ptychoptera (Parptychoptera) paludosa* Meigen, 1804**

Diagnosis

Adult. Two bands on wing, distal band broken, spots at base of wing and between band. **Male.** Epandrial claspers with single spine on base, subhemispherical lateral swelling present at base, apex rounded, hypoproct with apex simple; gonopod with gonostylus having anterior lobe of basal lobe rounded with single spine directed medially, medial lobe with apex rounded, apical stylus directed posterior, secondary lobe much shorter, directed posteriorly; hypandrium with terminal division apex broad crescent with convex apical margin directed dorsally.

Description

Adult. Measurements (n=1). Overall length ? (abdomen dissected). **Head.** Width: 1.0mm, Height: 0.95mm, Length: 0.5mm; Antenna flagellum length: 2.75mm. **Thorax.** Length: 2.1mm, Height: 2.1mm; Wing length: 8.8mm, Width: 2.2mm. **Abdomen.** Length: ? (dissected).

Head. Vertex shining chocolate brown, evenly set with trichoid sensilla; frons weakly developed between antennae. Occiput with patch of short chocolate brown trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: Scape chocolate brown elongate cylinder; pedicel brown, globular, few trichoid sensilla. Flagellomeres brown, fusiform. Facial sclerite chocolate brown, distinct from clypeus, roughly pentagonal plate above clypeus. Clypeus rounded triangle, flattened, generally covered in macrotrichia, brown. Maxillary palpus with all but final segment yellow, distal segment brown. Labrum D-shaped, dark yellow; epipharynx and hypopharynx not externally apparent, labium and labellae yellow.

Thorax. Anteprenotum chocolate brown medially, brown laterally, transverse fold narrow, medial lobe quarter width of anteprenotum, trapezoidal, medial notch absent. Prescutum and scutum obscurely shining chocolate brown; microtrichia vestiture present, medial and prescutal suture with row of clear trichoid sensilla, short yellow prealar sensilla present. Scutellum brown. Mediotergite of metanotum shining chocolate brown. Laterotergite of metanotum shining, chocolate brown, dorsal patch of trichoid sensilla yellow. Pleural sclerites all chocolate brown, with weak pollinosity. Anepisternal cleft broad, trapezoidal, not extending nearly to base of wing, membrane brown. Suture between epimeron and metapleurite prominent.

Wing. Two broad bands, proximal extending from base of R_s to angle of CuA_2 , distal from R_{1+2} fork to M fork; membrane with macrotrichia in all cells; spots at h and apex of CuA_1 . All veins covered in short stout macrotrichia. Sc: 1.23mm, Apex of Sc to Apex of R_1 1.23mm, R_{3+4+5} stem 0.44mm, with severe

medial angle; R_{4+5} stem 1.8mm; R_4 after fork 1.85mm, R_5 after fork 1.9mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4$, 1.0 : 4.09 : 4.2. r-m 0.35mm; M distal to r-m 2.3mm; M_1 1.05mm, arcuate, M_2 0.80mm; Mdistal: M_1 , 1.0:0.45, $R_{3+4+5}:M\text{distal}$, 1.0:5.22, $R_4:M_1$, 1.0:0.56. CuA_1 proximal 0.25mm, distal 2.3mm; CuA_2 1.35mm with anterior angle well developed, posterior angle absent. CuA_2 to A_1 2.2mm. R_3 branching before r-m. Halter yellow. Prehalter yellow. **Legs.** Coxae yellow. Femur yellow, darkening to brown near tibial joint, tibia yellow. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere cannot fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensilla.

Abdomen. Tergites and sternites chocolate brown, with prominent yellow bands at the middle of segment II and the anterior of segment III, thickly covered in elongate yellow setae. Third segment with accessory copulatory organ, posterior margin with paired rounded lobes, low U-shaped ridge between the lobes, medial sclerotized strip present.

Male Genitalia. Epandrial collar complete, epandrial apodemes well developed, extending to lateroanterior apex of hypandrium, extending flatly across gonocoxal apodeme, prominent break between epandrial collar and epandrial apodeme. Epandrial lobes weakly domed, rounded triangular, elongate over twice as long as wide, apex indistinct, lateral margins rounded and weakly convergent at apex. Lateral lobule of epandrial clasper at base hemispherical; primary stylus of epandrial clasper round in cross section, apex rounded, parallel. Epiproct prominent, posterior margin simple broad arc, epandrial lobes with point contact anteriorly. Posteromedial stylus present, formed to spine directed ventromedial at base of epandrial clasper. Hypoproct narrow, half as wide as epiproct, tongue-like. Subepandrial sclerite elongate rectangle, fused to base of hypoproct.

Parameral bridge narrowly affixed to gonocoxite. Apical lobes of paramere shaped like a bent hatchet head with straight apical margin, dorsoposterior corner extended dorsally, directed dorsoposterior.

Gonocoxal apodeme and gonocoxite as per genus. Dorsal gonocoxal lobe directed posterior, forming finger-like lobe nearly reaching epandrium. Medial gonocoxal lobe bifurcate, directed posterior, both blade-like, medial branch with squared apex, lateral branch expanding to birdshead shape with apex pointed. Gonostylus extending subequal to epandrial clasper. Basal lobe with dorsal lobe scallop shaped directed posteromedially, medial corner extended to stylus; medial lobe scythe shaped, apex rounded. Apical stylus directed posterior, round in cross section with rounded apex, secondary lobe absent.

Hypandrium basal division with eversible sac tapering triangle, expanding above basal scale; basal scale undivided, generally triangular, lateral apices pointed triangular, medial apex pointed. Terminal division broadly attached to basal division; apex of terminal division scallop shaped, lacking brushes.

Aedeagus oriented 35 degrees from vertical, apex of aedeagal sclerites angled; dorsal margin of lateral ejaculatory process weakly curved ventrally at apex. Ejaculatory apodeme fan-like with base narrow, larger than sperm sac, not closely paralleling anterior margin, sperm sac spherical. Subapical sclerite with medial portion having triangular base expanding to parallel sided stylus, apex squared; apex extending beyond apex of terminal division of hypandrium; lateral plates L-shaped in posterior view, dorsomedial apex flat and slanted.

Female Genitalia. Tergite VII brown with yellow posterior margin. Cerci orange, lateral ridge weakly defined, dorsal furrow poorly developed. Cercus length:width, 4:1. Hypogynium brown basally,

yellow posterior, rotated dorsally approximately 40 degrees from vertical; constricted midway along length. Apical margin triangular, lateral corner rounded. Lateral margin hidden.

Figures. Male Genitalia: 49, Wing: 50, Distribution: 51.

Taxonomic Notes.

Material examined. RiseBak, Aabenraa, 29.5.36 E-P. (Pinned: 1 m#) (ZMUC). Poland-Bresie, n. Krakow 14.05.1983, leg. W. Krzeminski (Pinned: 1 m#) (USNM). Biykobbe (indecipherable), 28.5.31. (Pinned: 1 f#) (ZMUC). N. Forest, 12/1/10, F.C. Adams (Pinned: 1 f#) (USNM).

***Ptychoptera (Parptychoptera) ressl* Theischinger, 1978**

Diagnosis

Adult. Male. Epandrial claspers with single spine and no swelling at base, apex pointed, hypoproct with apex simple; gonopod with gonostylus having anterior lobe of basal lobe laterally compressed semicircular paddle, medial lobe with apex rounded, apical stylus reduced; hypandrium with terminal division apex with spoon shaped with two setose lobes basally, lateral margins simple.

Description

Head. Vertex shining russet brown, evenly set with trichoid sensilla; frons weakly developed between antennae. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: Scape brown elongate cylinder; pedicel brown, globular, few trichoid sensilla. Flagellomeres brown, fusiform. Facial sclerite russet brown, indistinct from clypeus. Clypeus rhomboidal, bulbous, generally covered in macrotrichia, brown. Maxillary palpus with all but final segment yellow, distal segment brown. Labrum D-shaped, dark yellow; epipharynx and hypopharynx not externally apparent, labium and labellae yellow.

Thorax. Antepronotum yellow, transverse fold narrow, medial lobe quarter width of antepronotum, trapezoidal, medial notch present. Prescutum and scutum obscurely shining russet brown; microtrichia vestiture present, medial and prescutal suture with row of clear trichoid sensilla, short yellow prealar sensilla present. Scutellum yellow; lateral ridges with dark highlights. Mediotergite of metanotum shining chestnut brown. Laterotergite of metanotum shining, chestnut brown, dorsal patch of trichoid sensilla yellow. Pleural sclerites all tan, with weak pollinosity, ventral margins dark brown. Anepisternal cleft broad, trapezoidal, extending nearly to base of wing, membrane brown. Suture between epimeron and metapleurite prominent.

Abdomen. Tergites and sternites chocolate brown, with prominent yellow bands anterior on segment II and the anterior of segment III, thickly covered in elongate yellow setae. Third segment with accessory copulatory organ, posterior margin with paired rounded lobes, low U-shaped ridge between the lobes, medial sclerotized strip present.

Male Genitalia. Epandrial collar complete, epandrial apodemes well developed, extending to lateroanterior apex of hypandrium, extending flatly across gonocoxal apodeme, prominent break between epandrial collar and epandrial apodeme. Epandrial lobes weakly domed, less than 1.5 times as wide as long, apex distinct, lateral margins rounded and heavily convergent. Epandrial clasper without lobules; primary stylus of epandrial clasper round in cross section, apex with acute point, convergent. Epiproct prominent, posterior margin simple arc, epandrial lobes with point contact anteriorly. Posteromedial stylus present, acute spine directed sublaterally at base of epandrial clasper. Hypoproct half as wide as epandrial lobe, tongue-like. Subepandrial sclerite narrow rectangle fused to base of hypoproct.

Parameral bridge narrowly affixed to gonocoxite. Apical lobes of paramere subquadrate curved dorsoanteriorly on arc, anterior margin square.

Gonocoxal apodeme and gonocoxite as per genus. Dorsal gonocoxal lobe directed posterior, massive heavily sclerotized triangle. Medial gonocoxal lobe simple dorsally directed curving spine, extending beyond paramere apex. Gonostylus extending beyond the apex of the epandrial clasper. Basal lobe with anterior portion scallop shaped, directed posterior; medial portion scythe-like, apex rounded, weakly curved ventrally. Apical stylus reduced, small bump on base of basal lobe.

Hypandrium basal division with eversible sac extended rhombus, expanding above basal scale; basal scale divided, lateral apices pointed rounded. Terminal division broadly attached to basal division; apex of terminal division spoon shaped, with two flattened setose lobes at base.

Aedeagus oriented 45 degrees from vertical, apex of aedeagal sclerites angled; dorsal margin of lateral ejaculatory process straight. Ejaculatory apodeme fan-like with base narrow, larger than sperm sac, not closely paralleling anterior margin, sperm sac spherical. Subapical sclerite with medial portion rounded spine with potbellied furcate apex, becoming trapezoidal below aedeagal sclerites; apex extending beyond apex of terminal division of hypandrium; lateral plates with subtrapezoidal base, dorsally directed spinelike apex extended from lateral margin.

Female Genitalia. Tergite VII brown with yellow posterior margin. Cerci orange, lateral ridge readily apparent, dorsal furrow poorly developed. Cercus length:width, 3:1. Hypogynium yellow, rotated dorsally approximately 20 degrees from vertical; constricted at base, bulging apically. Apical margin triangular, medial portion acute, lateral portions less severe angle, lateral corner rounded. Lateral margin hidden.

Figures. Male Genitalia: 52, Distribution: 53.

Material examined. Holotype. Iran, Weisar, 350 Norshar 1400m, 1-14.6.1977, C. Holzschuh & F. Ressler leg. (Alcohol: 1 m#) (OOLM). **Paratype.** As holotype specimen (Alcohol: 1 f#) (OOLM).

***Ptychoptera (Parptychoptera) silvicola* Zwyrtek & Rozkošný, 1971**

Diagnosis

Adult. Insufficient Material.

Description

Adult. Measurements (n=1). Overall length ? (abdomen dissected). **Head.** Width: 1.09mm, Height: 0.91mm, Length: 0.57mm; Antenna flagellum length: 3.75mm. **Thorax.** Length: 2.25mm, Height: 2.25mm; Wing length: 9.6mm, Width: 2.4mm. **Abdomen.** Length: ? (dissected).

Head. Vertex shining black, evenly set with trichoid sensilla; frons weakly developed between antennae. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: Scape brown elongate cylinder; pedicel black, globular, few trichoid sensilla. Flagellomeres black, fusiform. Facial sclerite black, distinct from clypeus, scallop shaped band above clypeus. Clypeus elongate triangle, flattened, generally covered in macrotrichia, yellow. Maxillary palpus with all first two segments yellow, proximal two segments brown. Labrum D-shaped, dark yellow; epipharynx and hypopharynx not externally apparent, labium and labellae yellow.

Thorax. Anteprenotum yellow, medial lobe dark brown, transverse fold narrow, medial lobe fifth width of anteprenotum, trapezoidal, medial notch present. Prescutum and scutum obscurely shining black; microtrichia vestiture present, medial and prescutal suture with row of clear trichoid sensilla, short yellow prealar sensilla present. Scutellum dark orange; lateral ridges with sulci black. Mediotergite of metanotum shining black. Laterotergite of metanotum shining, black, dorsal patch of trichoid sensilla yellow. Pleural sclerites black with dorsal margins yellow, with no pollinosity.

Anepisternal cleft broad, trapezoidal, extending nearly to base of wing, membrane brown. Suture between epimeron and metapleurite prominent.

Wing. Two broad bands, proximal extending from base of R_5 to angle of CuA_2 , distal from R_{1+2} fork to base of R_5 ; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 6.3mm, Apex of Sc to Apex of R_1 1.35mm, R_{3+4+5} stem 0.27mm, with severe medial angle; R_{4+5} stem 1.98mm; R_4 after fork 2.1mm, R_5 after fork 2.1mm; $R_{3+4+5}:R_{4+5}$ -stem: R_4 , 1.0mm : x : x. r-m 0.37mm; M distal to r-m 2.6mm; M_1 1.25mm, arcuate, M_2 1.0mm; Mdistal: M_1 , 1.0mm:x, R_{3+4+5} :Mdistal, 1.0mm:x, $R_4:M_1$, 1.0mm:x. CuA_1 proximal 0.32mm, distal 2.6mm; CuA_2 1.4mm with anterior angle well developed, posterior angle absent. CuA_2 to A_1 2.3mm. R_3 branching at r-m. Halter yellow. Prehalter yellow. **Legs.** Coxae yellow orange. Femur yellow, darkening to brown near tibial joint, tibia yellow. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere cannot fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensilla. **Abdomen.** Segments black, with posterior margins with narrow yellow band.

Figures. Wing: 54, Distribution: 55.

Taxonomic Notes. Male genitalia damaged, female genitalia missing.

Material examined. Holotype. Vihorlat – Morske oko, 7.VI.1966, leg. Zwyrtek. (Pinned: 1 m#) (MZMB). **Paratype.** As holotype specimen (Pinned: 1 f#) (MZMB).

***Ptychoptera (Rheoptycha) Fasbender* subgen. nov.**

Diagnosis

Adult. Epandrium with epandrial claspers reduced, subepandrial sclerite divided, covering entire ventral surface; paramere floating on supraedeagal membrane, arched dorsally; gonocoxite cylindrical,

gonostylus with apical stylus poorly sclerotized, pendant. **Larvae:** Postmentum with >14 broad rounded denticulations, respiratory siphon shorter than remainder of anal division (Currently indistinguishable from *P. (Chrysotypcha)*).

Description

Male Genitalia. Epandrium with flattened triangular epandrial lobes lacking epandrial claspers, subapical spine present or absent. Epandrial collar well developed, extending to epandrial apodeme; epandrial apodeme with distinct break from epandrial collar, ribbon-like extending to hypandrium. Posterolateral stylus developed on medial margin of epandrial lobe. Epiproct with simple posterior margin; tapering toward anterior margin of epandrial complex, epandrial lobes in contact anteriorly. Hypoproct with external portion ovoid sclerite, subepandrial membrane fully sclerotized, forming paired bacilliform sclerites divided by a medial suture covering entire ventral surface of epandrium.

Parameres fused to bridge, floating on membrane, extending from ventral surface of gonocoxite, forming flattened bow directed dorsally. Lateral margins with acute anteriorly directed spur.

Gonocoxal apodeme triangular, ventral margin convex in some species, length approximately 1/5th length of remainder of gonocoxite. Dorsal spur of gonocoxite developed as short triangle. Gonocoxite tapering anterior, with dorsal margin straight, anterior portion of ventral margin forming shallow arc, median section of ventral margin weakly emarginate. Dorsal gonocoxal lobe placed at 2/3rds length of gonocoxite. Gonostylus with basal lobe directed dorsoanterior, apical stylus flattened, weakly sclerotized, pendant. Secondary lobe of apical stylus present, variable in form; tertiary lobe of apical stylus present, placed near secondary lobe.

Hypandrium with basal division band-like, lateral margins broad. Posterior margin of lateral apices having small triangular lobe. Eversible sac heavily incising terminal division, forming an inflated narrow

rectangle dorsally, ventral portion weakly lacrimiform. Terminal division broadly affixed to lateroposterior margins of basal division, dorsal apex triangular to rhomboidal, slightly inflated.

Aedeagal sclerites heavily tapering, flattened, approximately 1.25x length of sperm sac; apical apodemes absent; subapical sclerite well developed, conical medial portion with flattened dorsoanterior surface, lateral plates present: broad basally, tapering dorsally. Sperm sac nearly spherical, smaller than ejaculatory apodeme. Ejaculatory apodeme attached dorsomedially to sperm sac, not closely associated with aedeagal sclerites, extending anteriorly into segment VII, arcing ventrally to enlarged rounded terminus; curling around anterior margin of sperm sac. Lateral ejaculatory processes attached dorsolaterally to sperm pump, directed straight anteroventrally, dorsal and ventral margins straight, terminal apodeme directed subventrally.

Taxonomic Notes:

Rheoptycha is known only from the western Nearctic, though further sampling of East Asia is needed to fully assess the range of this group.

Type Species:

Rheoptycha pendula Alexander **comb. nov.**

Other Species

Rheoptycha espica Fasbender & Courtney **comb. nov.**

Rheoptycha monoensis Alexander **comb. nov.**

Rheoptycha townesi Alexander **comb. nov.**

Etymology: *Rheoptycha* refers to the habitat preference of this genus, which is found in lotic systems of the western Nearctic. *Rheoptycha* was selected over *Rheophila* to avoid confusion with a genus of fungus in the botanical nomenclature.

***Ptychoptera (Rheoptycha) espica* Fasbender & Courtney**

Diagnosis.

Adult. Epandrial lobe with ventral spine absent; gonostylus with basal lobe without spine, apical stylus laterally compressed, apex rounded, secondary lobe located midway along length, rounded, laterally compressed, with tertiary lobe semicircular.

Description

Adult. Measurements (n=1). Overall length 8.28mm. **Head.** Width: 0.75mm, Height: 0.91mm, Length: 0.58mm; Antenna flagellum length: 4.2mm. **Thorax.** Length: 2.1mm, Height: 2.1mm; Wing length: 9.5mm, Width: 2.2mm. **Abdomen.** Length: 5.6mm

Complete description in Chapter 5.

Figures. Male Genitalia: 56, Wing: 57, Distribution: 58.

Material Examined. Holotype. USA, Washington, Jefferson Co. Olympic National Park, Queets River Valley, 47°34.30'N, 124°08.40'W 50m, 20 July 2011 coll. GW Courtney, from roadside seep (Alcohol: m#, 1 f#) (ISIC). USA, Washington, Jefferson Co. Olympic National Park, Queets River Valley, 47°34.30'N, 124°08.40'W 50m, 28 May 2012 coll. GW Courtney, from "Skunk cabbage" seep (Alcohol: 1 m#, 6 f#) (ISIC) **Paratype.** Same as holotype specimen (Alcohol 2 f#) (ISIC). WASHINGTON Lewis & Clark, St. Pk. Lewis Co. July 12, 1953, K.M Fender (Pinned: 1 m#) (UMMZ). WASHINGTON Olympic N.P. Hoh River, July 19, 1953, K.M. Fender (Pinned: 2 m#, 2 f#) (UMMZ).

Ptychoptera (Rheoptycha) monoensis* Alexander, 1947*Diagnosis.**

Adult. Epandrial lobe with ventral spine present, clavate; gonopod with medial gonocoxal lobe apex hammer shaped; gonostylus basal lobe with posteriorly directed spine, apical stylus scythe-like, secondary lobe located basally, secondary lobe fingerlike, tertiary lobe a small triangle on lateral margin near basal lobe.

Description

Adult. Measurements (n=1). Overall length 8.0mm. **Head.** Width: 0.88mm, Height: 0.7mm, Length: 0.40mm; Antenna flagellum length: 3.68mm. **Thorax.** Length: 2.1mm, Height: 2.0mm; Wing length: 8.1mm, Width: 1.8mm. **Abdomen.** Length: 5.5

Head. Vertex shining purplish black, very sparsely set with trichoid sensilla; frons extremely narrow strip, black. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: scape dark yellow, oblong cylinder with long black setae, projecting dorsally from anterior surface; base of pedicel light brown, distal portion yellow, globular, trichoid sensilla ringlike. Flagellomeres brown, fusiform. Facial sclerite purplish black, distinct from clypeus, forming bowed sclerite above clypeus. Clypeus ventrally tapering subtriangular, bulbous, generally covered in yellow macrotrichia, yellow. Maxillary palpus with proximal segments yellow, apex of 5th segment dark. Labrum bullet shaped, orange; hypopharynx and epipharynx not externally apparent, labium and labellae yellow.

Thorax. Anteprenotum yellow medially, brown at lateroventral margins, medial lobe half width of remainder of anteprenotum, dorsal surface with small distinct medial notch; diffuse patch of yellow trichoid sensilla on anterior margin near forecoxa. Prescutum and scutum shining, glabrous purplish

black, with narrow yellow stripe from posterior apex of prescutum to scutellum; medial and prescutal suture with row of minute clear trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum as longer yellow sensilla; short black prealar sensilla present. Scutellum yellow.

Mediotergite of metanotum lightly pollinose purplish black, patch of short yellow trichoid sensilla medially, medial suture present. Laterotergite of metanotum pollinose purplish black, except for yellow patch near wing base, dorsal patch of yellow trichoid sensilla. Pleural sclerites all ruddy black, with medium pollinosity. Anepisternal cleft broad, membrane yellow. Suture between epimeron and metapleurite complete. **Wing.** Hyaline, weak infuscation extending from base of R_{1+2} to CuA_1+CuA_2 fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 5.31mm, Apex of Sc to Apex of R_1 0.99mm, R_{3+4+5} stem 0.86mm, slight posterior turn at fork from R_{1+2} ; R_{4+5} stem 1.58mm; R_4 after fork 1.73mm, R_5 after fork 1.75mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 2.07 : 1.97$. r-m 0.22mm; M distal to r-m 2.08mm; M_1 0.86mm, arcuate, M_2 0.65mm; $M\text{distal}:M_1 = 1.00:0.32$, $R_{3+4+5}:M\text{distal} = 1.00:2.81$, $R_4:M_1 = 1.00:0.46$. CuA_1 proximal 0.20mm, distal 2.05mm; CuA_2 1.28mm sinuous. CuA_2 to A_1 1.85mm. m-cu joins R_{3+4+5} before r-m. Halter yellow. Prehalter yellow. **Legs.** Coxae yellow, hindcoxae with dark brown band dorsally. Femur and tibia yellow. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensillae.

Abdomen. Tergites and sternites black, posterior and posterior portion of lateral margins yellow except segment I which is uniform color, moderately covered in elongate yellow setae.

Male Genitalia. Epandrial collar incomplete, not extending completely to epandrial margin epandrial apodemes well developed, extending to lateroanterior apex of hypandrium, extending threadlike across gonocoxal apodeme, prominent break between epandrial collar and epandrial apodeme. Epandrial lobes subtriangular, posterior portion curving ventrally, anterior margin largely

straight, curved posterior near lateral margins; lateral margin rounded, continuous curve to convergence; medial margin parallel at contact of epandrial lobes, divergent at nearly 90 degree angle posteriorly; anterior apex with lateral triangular point, flat margin leading to posteromedial stylus. Epiproct prominent, posterior margin strongly emarginate, epandrial lobes in contact for 1/4th of length anteriorly. Posteromedial stylus flattened knob-like, located apically of epandrial lobe. Ventral surface of epandrial lobe apex with clavate lobe covered in stout sensilla at apex. Hypoproct small ovoid sclerite tucked under epiproct. Subepandrial membrane heavily sclerotized over nearly the entire surface, divided into paired baciliform sclerites roughly corresponding to ventral surface of each epandrial lobe.

Parameral bridge floating on medial membrane of gonocoxite. Lateral apices spine-like, bridge rectangular, dorsal angles 90 degrees, small medial spur present.

Gonocoxal apodeme with dorsal spur reduced, bifid. General shape of gonocoxite as per genus. Dorsal gonocoxal lobe low bump on dorsal surface. Medial gonocoxal lobe broad and straplike, descending ventrally before arcing dorsally, weakly tapering before rectangular point, subapical anterior margin serrated. Gonostylus with basal division with broad base quadrate in cross section, directed anteromedially, tapering to acute point, dorsal surface with three stout black sensilla basally, row of shorter clear sensilla leading to stout black sensillum directed dorsoanterior at apex. Apical stylus pendulant, forming blade broadening in middle, tapering to apex directed perpendicular to gonocoxite, additional short round lobe on medial margin near base of secondary stylus. Secondary stylus of apical lobe directed medially, round in cross section, expanding significantly at apex with apex rounded.

Basal division of hypandrium with paired triangular lobes on posteromedial margin. eversible sac rectangular in posterior view, swollen ventrally, to dorsal margin of terminal division. Terminal division broadly attached to basal division, acutely triangular, lateral apices rounded lobes with patches of heavily sclerotized sensilla at base, dorsal apex bent posterior at tip.

Aedeagus oriented vertical, ejaculatory apodeme with base narrow; dorsal margin of lateral ejaculatory process straight; apex of aedeagal sclerites blunt, flattened, subapical sclerite having medial portion trowel-shaped with extremely prominent ventral keel, as deep as medial portion is wide. Lateral plates elongate, extending to apex of subapical sclerite, base with subobtuse point on lateral margin, dorsal portion of lateral margin emarginate, apex acute, directed dorsally.

Figures. Male Genitalia: 59, Wing: 60, Distribution: 61.

Material Examined. Holotype. Calif. Mono Co. Coleville, Slinker Can. V-28.39, Cazier & Aitken (Pinned & Slide: 1 m#) (USNM). **Other Material.** California, Yosemite – Bridalveil VI-30-1957 (Alexander) (Slide: 1 m#) (USNM). Nevada Co., CA, 24 June 2009, B. Kondratieff, R. Baumann, Prosser Cr., Hwy 89 (Pinned: 2 m#) (CSU). USA, CA, Sierra Co. Tahoe Nat. Frst. Cottonwood Crk 39. 5434°N 120.3185°W, 17.vi.2007 alt. 5600', coll.: JD Davis, MJ Petersen (Alcohol: 6 m#) (ISIC). USA California, Tahoe Nat. For Cottonwood Crk nr. CA89, Slow stream w/riparian veg, 39.54802N, 120.317524W, A Fasbender June-14-2012 (Alcohol: 2 m#, 1 f#) (ISIC).

***Ptychoptera (Rheoptycha) pendula* Alexander, 1937**

Diagnosis.

Adult. Epandrial lobe with ventral spine present, simple, tapering; gonopod with medial gonocoxal lobe apex rounded; gonostylus basal lobe with posteriorly directed spine, apical stylus scythe-like, secondary lobe located basally, secondary lobe fingerlike, tertiary lobe small triangle on lateral margin near basal lobe.

Description

Adult. Measurements (n=1). Overall length 8.05mm. **Head.** Width: 1.04mm, Height: 0.86mm, Length: 0.55mm; Antenna flagellum length: 3.08mm. **Thorax.** Length: 2.3mm, Height: 5.2mm; Wing length: 7.8mm, Width: 2.0mm. **Abdomen.** Length: 2.0mm.

Head. Vertex shining black, sparsely set with trichoid sensilla; frons extremely narrow strip, black. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: scape dark yellow, oblong cylinder with long black setae, projecting dorsally from anterior surface; base of pedicel light brown, distal portion yellow, globular, trichoid sensilla ringlike. Flagellomeres brown, fusiform. Facial sclerite black, distinct from clypeus, forming square sclerite above clypeus. Clypeus ventrally tapering subtriangular, bulbous, generally covered in yellow macrotrichia, light brown medially, lateral margins yellow. Maxillary palpus with all segments yellow. Labrum bullet shaped, orange; hypopharynx and epipharynx not externally apparent, labium and labellae yellow.

Thorax. Anteprenotum yellow medially, brown at lateroventral margins, medial lobe same width of remainder of anteprenotum, dorsal surface with small median bump; diffuse patch of yellow trichoid sensilla on anterior margin near forecoxa. Prescutum and scutum shining, glabrous black, with narrow yellow stripe from posterior apex of prescutum to scutellum; medial and prescutal suture with row of minute clear trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum as longer yellow sensilla; short black prealar sensilla present. Scutellum yellow. Mediotergite of metanotum lightly pollinose black, line of short yellow trichoid sensilla medially. Laterotergite of metanotum pollinose black, except for yellow patch near wing base, dorsal patch of yellow trichoid sensilla. Pleural sclerites all black, with medium pollinosity. Anepisternal cleft narrow, membrane yellow. Suture between epimeron and metapleurite incomplete, weak. **Wing.** Hyaline, weak infuscation

extending from base of R_{1+2} to CuA_1+CuA_2 fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 5.63mm, Apex of Sc to Apex of R_1 0.99mm, R_{3+4+5} stem 0.92mm, short posterior turn at fork from R_{1+2} ; R_{4+5} stem 1.36mm; R_4 after fork 1.50mm, R_5 after fork 1.83mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 1.47 : 1.63$. r-m 0.30mm; M distal to r-m 2.15mm; M_1 0.76mm, arcuate, M_2 0.62mm; $M\text{distal}:M_1 = 1.00 : 0.35$, $R_{3+4+5}:M\text{distal} = 1.00:2.33$, $R_4:M_1 = 1.00:0.50$. CuA_1 proximal 0.22mm, distal 1.93mm; CuA_2 1.21mm sinuous. CuA_2 to A_1 1.85mm. m-cu joins R_{3+4+5} before r-m. Halter yellow. Prehalter yellow. **Legs.** Coxae yellow with dark brown bands dorsally. Femur and tibia yellow. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensillae.

Abdomen. Tergites and sternites black, posterior and posterior portion of lateral margins yellow except segment I which is uniform color, moderately covered in elongate yellow setae. **Male Genitalia.** Epandrial collar complete, epandrial apodemes well developed, extending to lateroanterior apex of hypandrium, extending threadlike across gonocoxal apodeme, prominent break between epandrial collar and epandrial apodeme. Epandrial lobes triangular, posterior portion curving ventrally, anterior margin largely straight, curved posterior near lateral margins; lateral margin rounded, straightening posterior, convergent; medial margin parallel at contact of epandrial lobes, divergent at nearly 90 degree angle posteriorly; anterior apex triangular, forming nearly right angle. Epiproct prominent, posterior margin weakly emarginate, epandrial lobes in contact for 1/3rd of length anteriorly. Posteromedial stylus triangular base tapering to stylate point, directed medially. Ventral surface of epandrial lobe apex with cone-like point. Hypoproct small ovoid sclerite tucked under epiproct. Subepandrial membrane heavily sclerotized over nearly the entire surface, divided into paired baciliform sclerites roughly corresponding to ventral surface of each epandrial lobe. Parameral bridge floating on medial membrane of gonocoxite. Lateral apices spine-like, bridge directed posteromedially, then

dorsomedially, arc tightening to square-like medial apex. Medial gonocoxal lobes fused to paramere. Gonocoxal apodeme as per genus. General shape of gonocoxite as per genus. Dorsal gonocoxal lobe low bump on dorsal surface. Medial gonocoxal lobe narrow and straplike, descending ventrally before arcing dorsally, tapering before expanding to rounded subcircular apex. Gonostylus with basal division with broad base clothed in stout, heavily sclerotized black trichoid sensilla, quadrate cross section, directed anteromedially, tapering to acute point. Apical stylus pendulant, forming broad spathe-like blade tapering to apex directed perpendicular to gonocoxite, additional short triangular lobe on medial margin near base of secondary stylus. Secondary stylus of apical lobe directed medially, round in cross section, expanding slightly at apex with dorsal portion of apex formed to blunt triangle. Basal division of hypandrium with paired triangular lobes on posteromedial margin. eversible sac rectangular in posterior view, swollen ventrally, to dorsal margin of terminal division. Terminal division broadly attached to basal division, broadly triangular pendant-like, lateral apices forming acute points with patches of heavily sclerotized sensilla at base, dorsal apex directed slightly anterior, bent posterior at tip. Aedeagus oriented vertical, ejaculatory apodeme with base narrow; dorsal margin of lateral ejaculatory process straight; apex of aedeagal sclerites blunt, flattened, subapical sclerite having medial portion trowel-shaped with ventral keel. Lateral plates small, not extending beyond apex of subapical sclerite, broad base, lateral margin emarginate, apex directed laterally.

Figures. Male Genitalia: 62, Wing: 63, Distribution: 64.

Material Examined. Holotype. Green Mt Falls, Colo VI.27-34, C.P. Alex. (Pinned: 1 m#) (USNM).

Paratype. Colorado, Monarch Pass, alt. 10,500', VII-1-1934', (C.P. Alexander) (Slide: 1 m#) (USNM).

Material Examined. ARIZONA Apache Co. #3, Alpine Divide, 4 mi. NW. Alpine, 8480 ft. 13 June 1979, George W. Byers (Pinned: 9 m#, 2 f#) (KU). ARIZONA Apache Co. #4, Alpine Divide, 4 mi. NW Alpine, 8480 ft. 14 June 1979, George W. Byers & J. Gelhaus (Pinned: 19 m#, 3 f#) (KU). COLORADO Chaffee, Co.

#6, Cottonwood, Lake, 10mi. W. Buena, Vista 18 Aug. 1965, 9600' G.W. Byers (Pinned: 1 m#) (KU).

COLORADO Costilla Co. #1, North LaVeta Pass, Sangre de Cristo Crk. 27 June 1981. 9150', George W. Byers (Pinned: 1 m#) (KU). COLORADO Fremont Co. #1, Hayden Creek, 4, mi. SW. Coal Dale, 13 July 1974 7200', G.W. Byers C.W. Young (Pinned: 10 m#) (KU). Garfield Co. CO, 26 June 1997, S. Fitzgerald & B Kondratieff, Coffee Pot Springs (Pinned: 16 m#, 2 f#) (CSU). COLORADO: Teller County, Florissant Fossil Beds, R71W T13S Sec 13 8350, Grape Creek (Pinned: 1 m#) (KU). IDAHO: Strychnine Crk. 15 mi. ENE Potlatch, Latah Co., 2900 ft. 2 July 1981, W.J. Turner (Pinned: 9 m#, 2 f#) (WSU). NEW MEXICO Taos Co. Capulin Campground, 10 mi. E. of Taos, 22 June 1981 7650 ft. S.A. Teale & G.W. Byers (Pinned: 3 m#) (KU). NEW MEXICO Taos Co. LaJara Canyon Palo, Flechado Pass, 8950', 21 June 1981, S. A. Teale (Pinned: 5 m#, 1 f#) (KU). NEW MEXICO Taos Co. #2, La Jara Canyon, 0.8mi. SW. Palo Flechado Pass, 17 June 1979. 8960ft. George W. Byers (Pinned: 18 m#, 3 f#) (KU). NEW MEXICO Taos Co. #3, LaJara Canyon Palo, Flechado Pass, 8950', 21 June 1981, G.W. Byers, E.M. May (Pinned: 12 m#, 2 f#) (KU). NEW MEXICO Taos Co. #4, Carson Nat'l Forest, La, Jara Canyon, 0.8mi. SW. Palo Flechado Pass 8960', 17 June 1979. 8960ft. J.K. Gelhaus (Pinned: 14 m#, 2 f#) (KU). NEW MEXICO Taos Co. 1.3 mi SE Tres Ritos, 25 June 1981. 8500', G.W. Byers & S.A. Teale (Pinned: 5 m#) (KU). NEW MEXICO Taos Co. Agua Piedra Cpgr., Rio, Pueblo, 1 mi. NW. Tres, Ritos, 25 June 1981, 8400' E. May, S. Teale (Pinned: 3 m#, 1 f#) (KU). OREGON: L. Goose Crk., 36, mi. SE Union, Baker Co. Wallowa-Whitman NF, 4000, ft., 9-VI-1976, W. Turner, sweeping. (Pinned: 2 m#) (WSU). OR, Clatsop Co, Ecola St. Park, 1 June 2011, em 21 June, GW Courtney (Alcohol: 1 m#) (ISIC). USA, Oregon, Yamhill Co., Peavine Rd, upper Deer Creek, 45°14.38'N 123°23.15'W 400m, 19 May 2012 coll. GW Courtney, on riparian vegetation (Alcohol: 1 m#) (ISIC). USA. Utah, Wasatch Co. Little, Deer Ck below Cascade Springs, 40°27.33'N 111°32.91'W 1880m, 9 June 2011 coll. GW Courtney, on riparian vegetation (Alcohol: 7 m#, 1 f#) (ISIC). USA Utah, Uinta National Forest, Deer Creek Below Cascade- Springs, Old Beaver Dam, 40.455966N, 111.548599W, A Fasbender June-7-2012 (Pinned: 5 m#, 2 m# June-20-2012) (ISIC). WASHINGTON: 12 mi. NE Goldendale, Hwy. 97, Brooks Mem. SP, Klick. Co., 2-

VI-73/ Malaise trap, with dry ice/ W.B. Garnett, collector (Pinned: 3m#, 3 f#) (WSU). WASHINGTON: Brooks, Mem. SP, 12 mi. NE, Goldendale, Klickitat, Co., 2700-3000 ft. 27-VI-1975/ W.J. Turner (Pinned: 1 f#) (WSU). WASHINGTON: Yakima, Co., 8 mi. SW Tieton, RS, Snoqualmie NF, Bear Crk. VI-(11-12)-73/ Malaise trap, with dry ice/ W.J. Turner collection (Pinned: 3m#, 3 f#) (WSU). WASHINGTON: Bear Crk., 8 mi. SW Tieton RS, nr, Rimrock Lk., Yakima Co. VI-(24-25)-1974 3000ft. W.J. Turner Malaise/CO₂ (Pinned: 28 m#, 34 f#) (WSU). USA Wyoming, Medicine Bow, Nat. For. Nash Fork nr. WY130, Beaver Dam Complex, 41.348236N, 106.219477W, A Fasbender June-21-2012 (Alcohol: 3 m#) (ISIC). Arrowhead Lodge, Bighorn Mtns. Wyo. VII.21.53, PB Lawson (Pinned: 5 m#, 1 f#) (KU). WYOMING Sheridan, Co. No.3 Granite, Pass 8600 ft. 7 July 1959, George W. Byers (Pinned: 7 m#, 2 f#) (KU). WYOMING Teton Co. No.4 Grand Teton, Nat. Park, 15 July 1957, George W. Byers (Pinned: 7 m#) (KU).

***Ptychoptera (Rheoptycha) townesi* Alexander, 1943**

Diagnosis.

Adult. Epandrial lobe with ventral spine absent; gonostylus with basal lobe with elongate, spine-like trichoid sensilla, apical stylus laterally compressed, apex rounded, secondary lobe located midway along length, rounded, laterally compressed, with tertiary lobe semicircular.

Description

Adult. Measurements (n=1). Overall length 8.5mm. **Head.** Width: 0.95mm, Height: 0.93mm, Length: 0.5mm; Antenna flagellum length: 4.03mm. **Thorax.** Length: 2.1mm, Height: 2.1mm; Wing length: 9.3mm, Width: 2.2mm. **Abdomen.** Length: 5.9mm

Head. Vertex shining black, sparsely set with trichoid sensilla; frons extremely narrow strip, black. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: scape dark yellow, oblong cylinder with long black setae, projecting dorsally

from anterior surface; base of pedicel light brown, distal portion yellow, globular, line of trichoid sensilla on lateral margin. Flagellomeres brown, fusiform. Facial sclerite black, distinct from clypeus, forming bent square sclerite above clypeus. Clypeus ventrally tapering subtriangular, bulbous, generally covered in yellow sensilla, dark brown. Maxillary palpus with proximal segments yellow, 5th segment brown. Labrum leaf shaped, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae yellow.

Thorax. Anteprenotum with central crease broad, yellow medially, brown at lateroventral extremity, medial lobe approximately half width of remainder of anteprenotum, highly tapered trapezoid, dorsal surface with medial notch. Prescutum and scutum shining, glabrous black, with narrow yellow stripe from posterior apex of prescutum to scutellum; medial and prescutal suture with row of minute clear trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum as longer yellow sensilla; long clear prealar sensilla present. Scutellum yellow. Mediotergite of metanotum lightly pollinose black, patch of short yellow trichoid sensilla medially, medial suture apparent. Laterotergite of metanotum pollinose black, except for yellow patch near wing base, dorsal patch of very elongate yellow trichoid sensilla. Pleural sclerites all black, with heavily pollinose. Anepisternal cleft broad, membrane yellow. Suture between epimeron and metapleurite weak, formed primarily depressed. **Wing.** Hyaline, weak infuscation extending from base of R_{1+2} to CuA_1+CuA_2 fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 6.25mm, Apex of Sc to Apex of R_1 1.36mm, R_{3+4+5} stem 1.36mm, slight posterior turn at fork from R_{1+2} ; R_{4+5} stem 1.73mm; R_4 after fork 1.83mm, R_5 after fork 1.80mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 1.27 : 0.95$. r-m 0.32mm; M distal to r-m 2.66mm; M_1 0.78mm, arcuate, M_2 0.60mm; $M\text{distal}:M_1 = 1.00:0.29$, $R_{3+4+5}:M\text{distal} = 1.00:1.95$, $R_4:M_1 = 1.00:0.42$. CuA_1 proximal 0.19mm, distal 2.50mm; CuA_2 1.53mm sinuous. CuA_2 to A_1 2.09mm. m-cu joins R_{3+4+5} before r-m. Halter yellow. Prehalter yellow. **Legs.** Fore- and midcoxae yellow with dark band on dorsal margin, hindcoxae black. Femur and tibia yellow. First tarsomere yellow proximally, turning

brown distally. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensillae.

Abdomen. Tergites and sternites black, posterior and posterior portion of lateral margins yellow except segment I which is uniform color, moderately covered in elongate yellow sensilla. **Male Genitalia.** Epandrial collar incomplete, developed laterally, epandrial apodemes well developed, extending to lateroanterior apex of hypandrium, extending threadlike across gonocoxal apodeme, prominent break between epandrial collar and epandrial apodeme. Epandrial lobes triangular, posterior portion curving ventrally, anterior margin largely straight, curved posterior near lateral margins; lateral margin straight, rounded angle anterior, convergent; medial margin parallel at contact of epandrial lobes, curving laterally, straightening to nearly parallel posterior; in some populations anterior apex triangular, forming nearly right angle, in other populations apex extended, flattened, square. Epiproct prominent, posterior margin weakly emarginate with low lateral lobes, epandrial lobes in contact for over ½ of length anteriorly. Posteromedial stylus flattened knob-like, directed medially, placed nearly at apex of epandrial lobe. Ventral surface of epandrial lobe apex flat. Hypoproct small ovoid sclerite tucked under epiproct. Subepandrial membrane heavily sclerotized over nearly the entire surface, divided into paired baciliform sclerites roughly corresponding to ventral surface of each epandrial lobe.

Parameral bridge floating on medial membrane of gonocoxite. Lateral apices spine-like, bridge directed posteromedially, then dorsomedially, forming trapezoidal arc. Lateral margins of paramere with subtrapezoidal lobe.

Gonocoxal apodeme as per genus. General shape of gonocoxite as per genus. Dorsal gonocoxal lobe high, triangular, nearly touching epandrium. Medial gonocoxal lobe narrow and straplike, directed at right angle medially from gonocoxite before turning dorsally at a right angle, expanding to bean-shaped apex with numerous stout cylindrical sensilla on anterior surface. Gonostylus with basal lobe

formed to finger-like lobe directed dorsoanterior with elongate moveable spine. Apical stylus pendulant directed at approximately 45 degree ventral angle, forming broad laterally compressed paddle-like lobe, apex poorly sclerotized, secondary lobe forming semicircular lobule on dorsal surface, with tertiary lobule located directly posterior, both moderately sclerotized and with patches of elongate trichoid sensilla on the medial surface.

Basal division of hypandrium with paired triangular lobes on posteromedial margin. eversible sac rectangular in posterior view, swollen ventrally, to dorsal margin of terminal division. Terminal division broadly attached to basal division, pentagonal, inflated, lateral apices forming acute points with patches of heavily sclerotized sensilla at base, dorsal apex broadly triangular.

Aedeagus oriented vertical, ejaculatory apodeme with base narrow; dorsal margin of lateral ejaculatory process straight; apex of aedeagal sclerites blunt, flattened, subapical sclerite having medial portion trowel-shaped with ventral keel. Lateral plates small, not extending beyond apex of subapical sclerite, ovoid with ventral margin emarginate.

Figures. Male Genitalia: 65, Wing: 66, Distribution: 67.

Taxonomic Notes.

Material Examined. Holotype. Elbe, Wash. July 13, 1940, H&M Townes (Pinned & Slide m#) (USNM). **Paratype.** As type specimen (Pinned: 1 m#) (USNM) **Other Material.** OREGON Benton Co. No.2 4.6mi. SW, of Philomath, 26 June 1959, George W. Byers (Pinned: 2 m#, 1 f#) (KU). USA, Oregon, Benton Co. S. Alsea River above Alsea Falls, 44°18.85'N 123°28.39'W 255m, 22 May 2012, coll. GW Courtney, from depositional zone (Alcohol: 2 m#, 1 f#) (ISIC). OREGON, Yamhill County, Peavine Ridge, June 24 1953, Fender Sta. 1 (Pinned: 12 m#, 3 f#, dates from May 5 – July 8) (UMMZ). USA, Oregon, Yamhill Co.

Peavine Rd, Little Deer Creek, 45°14.40'N 123°22.34'W 390m, 13.vii.2011 coll. G.W. Courtney,
 depositional zone / marginal muck (Alcohol: 14 m#, 33 f#) (ISIC). SwuakCreekWN, 28 June 1924, A.L.
 Melander (Pinned: 1 f#) (USNM).

***Ptychoptera (Tigrimya) Fasbender* subgen. n.**

Diagnosis

Adult. Epandrium divided into two massive composite epandrial claspers which taper to a distinct point or rounded apex, ventromesal lobe of epandrium present, located at approximately 2/3rds the length of the epandrial lobe/clasper. Female: Hypogynium with small triangular lobes ventrolateral to cerci. Larvae: Postmentum with >14 broad rounded denticulations, respiratory siphon longer than remainder of anal division.

Description

Male Genitalia. Epandrium with flattened subtrapezoidal to triangular epandrial lobes, curving medially, subapical spine absent. Epandrial collar well developed, extending to epandrial apodeme; epandrial apodeme with distinct break from epandrial collar, ribbon-like extending to hypandrium. Posterolateral stylus absent. Epiproct with simple posterior margin; tapering toward anterior margin of epandrial complex, epandrial lobes with at most point contact anterior. Hypoproct with external portion tonguelike, subepandrial membrane with heavily sclerotized plate associated with external portion of hypoproct, ovoid, expanded laterally.

Parameres fused into bridge, flattened, attached to inner division of dorsal surface of gonocoxite, base directed anterior, curving medially at nearly right angle. Apical lobes present on dorsal surface medial to angles.

Gonocoxal apodeme triangular, length approximately 1/5th length of remainder of gonocoxite. Dorsal spur of gonocoxite developed as short triangle, set away from anterior margin of external surface of gonocoxite. Gonocoxite tapering anterior, with dorsal margin weakly convex, anterior portion of ventral margin with shallow angle to anterior apex, posterior section of paralleling dorsal margin. Dorsal gonocoxal lobe placed at posterior margin gonocoxite, low and recumbent triangular. Medial gonocoxal lobe flattened, ribbon-like, directed dorsally, sometimes recumbent. Gonostylus with basal lobe having cylindrical base directed posterior, angled slightly ventomedial, apex expanded to knob with numerous stout trichoid sensilla; apical stylus directed posterior flattened, apex spatulate, weakly curving medially. Secondary lobe of apical stylus absent.

Hypandrium with basal division subhemispherical, without secondary lobes. Eversible sac heavily incising terminal division, forming an inflated narrow rectangle dorsally, ventral portion weakly lacrimiform. Terminal division affixed to dorsal division at medial point of dorsal margin, base bow-like, with medial spine directed dorsally.

Aedeagal sclerites tapering, subequal to sperm sac; apical apodemes present, extending far anterior; subapical sclerite well developed, conical triangular medial portion with internal keel on dorsoanterior surface, lateral plates present: broad basally, tapering dorsally. Sperm sac somewhat oblong, much larger than ejaculatory apodeme, extending into preceeding abdominal segment. Ejaculatory apodeme attached dorsoposteriorly to sperm sac, not closely associated with aedeagal sclerites, scythe-like, arcing dorsally to pointed terminus; curling around dorsal margin of sperm sac. Lateral ejaculatory processes triangular in outline attached posterolaterally to sperm pump, directed straight laterally, dorsal and ventral margins straight, terminal apodeme directed subventrally.

Taxonomic Notes:

Tigrimyia is known only from the eastern Nearctic.

Type Species:

Ptychoptera (Tigrimya) quadrifasciata Say **comb. nov.**

Other Species

Ptychoptera (Tigrimya) abbreviata Fasbender & Courtney **comb. nov.**

Ptychoptera (Tigrimya) osceola Alexander **comb. nov.**

Etymology:

Tigrimya refers to the orange and black banding on the abdomen of these flies.

***Ptychoptera (Tigrimya) abbreviata* Fasbender & Courtney**

Diagnosis

Adult. Male. Apices of epandrial lobes not convergent; hypandrium with leaf-like eversible sac not extending to ventral margin; medial gonocoxal lobe free of paramere; aedeagus with apices of lateral plates of subapical sclerite convergent.

Description

Adult. Measurements (n=1). Overall length 6.25mm. **Head.** Width: 0.85mm, Height: 0.73mm, Length: 0.55mm; Antenna flagellum length: 3.25mm. **Thorax.** Length: 1.9mm, Height: 1.9mm; Wing length: 6.3mm, Width: 1.6mm **Abdomen.** Length: 3.8mm

Figures. Male Genitalia: 68, Wing: 69, Distribution: 70.

Complete description in Chapter 5.

Material Examined. Holotype. Valentine, Nebraska, June 9 1950, Hicks, Slater, Laffoon (Pinned: 1m#) (USNM) **Paratypes.** Valentine, Nebraska, June 9 1950, Hicks, Slater, Laffoon (Pinned: 11 m#, 3 f#)

(ISIC). **Other Material.** Boulder Co., CO, 16 Aug 2010, B. Kondratieff & D. Rees, Stazio Ball Fields, Boulder (Pinned: 2 m#, 2 f#) (CSU). Larimer Co., CO, 6 June 2010, R. Stoak & A. Blevins, B. Kondratieff, Soapstone Prairie Natural Area, Graves Creek (Pinned: 1 m#, 1 f#) (CSU). Larimer Co., CO, 6 June 2010, R. Stoak & A. Blevins, B. Kondratieff, Soapstone Prairie Natural Area, Spottlewood Cr. Area (Pinned: 1 m#, 3 f#) (CSU). Larimer Co., CO, 3 July 2006, D. Leatherman, Fort Collins, Running Deer NA, Poudre R, S. Prospect (Pinned: 1 f#) (CSU). Weld Co., CO, 6 June 2010, R.S. & K. Stoaks, Meadow Springs, Sweep Net (Pinned: 1 m#, 1f#) (CSU). Iowa Lakeside Lab., Dickinson Co., Iowa, July 18, 1959, Jean L. Laffoon (pinned: 1 m#) (ISIC). USA Iowa, Dickinson Co. Iowa Lakeside Lab, sampling in Seep May-17-10, 43.383374N, 95.179974W, GW Courtney + A Fasbender (Pinned: 1 m#) (ISIC). USA Iowa, Dickinson Co. Silver Lake Fen May-17-2010, Hillside Seep nr. Marsh, 43.437472N, 95.365009W, GW Courtney + A Fasbender (Pinned: 1 f#) (ISIC). Sioux City, IOWA, June 11, 1949, Slater & Laffoon (Pinned: 8 m#, 3 f#) (ISIC). 3 m S Afton, Minn. May 19 1956 (Pinned: 1 m#) (ISIC). Itasca State, Park, Minn. IX-2 1950, Jean Laffoon (Pinned: 1 m#) (ISIC). Itasca Park, Minn. Aug 11 1951 (Pinned: 1 f#) (ISIC). Minnehaha Park, Hennepin Co., Minn. June 23 1956 (Pinned: 1 m#, 1 f#) (ISIC). Mora, Minnesota, June24-30, 1934, C.R. Yeager (Pinned: 2 f#) (ISIC). Mississippi Bluff, 1-2 m N State Line, Houston Co. Minn. June 19_ (Pinned: 1 m#) (ISIC). John Latsch St. Pk., S Minneiska, Minn. May 25 1956 (Pinned: 8 m#, 1 f#) (ISIC). MINNESOTA: WASHINGTON CO. Falls Creek State Natural Area, 10 miles N. of Stillwater, 6.vii.1994, col. Daniel E. Hansen (Pinned: 1 m#) (ISIC). Winona Co., Minn. May 25 1940 (Pinned: 1 m#) (ISIC). Extreme nw. corner, Brown Co., Nebraska, June 10, 1950, Hicks, Slater, Laffoon (Pinned: 5 m#) (ISIC). Garden Co., NE, 22 May 1998, B. Kondratieff, N. Platte R. Rd. 199 (Pinned: 1 m#) (CSU).

Ptychoptera (Tigrimya) osceola* Alexander, 1959*Diagnosis.**

Adult. Male. Apices of epandrial lobes not convergent; hypandrium with leaf-like eversible sac extending beyond ventral margin; medial gonocoxal lobe fused to paramere; aedeagus with apices of lateral plates of subapical sclerite divergent.

Description

Adult. Measurements (n=1). Overall length 5.88mm. **Head.** Width: 1.03mm, Height: 0.8mm, Length: 0.58mm; Antenna flagellum length: 4.5mm. **Thorax.** Length: 1.9mm, Height: 1.9mm; Wing length: 6.4mm, Width: 1.8mm. **Abdomen.** Length: 3.4mm

Head. Vertex shining black, sparsely set with trichoid sensilla; frons extremely narrow strip, black. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: scape yellow, oblong cylinder with long black setae, projecting dorsally from anterior surface; pedicel yellow, globular, line of trichoid sensilla on lateral margin. Flagellomeres brown, fusiform. Facial sclerite black, divided by clypeus, forming paired triangular sclerites laterally and above clypeus. Clypeus rhomboidal, bulbous, generally covered in yellow sensilla, dorsal quarter black, remainder yellow. Maxillary palpus yellow, apex of 5th segment brown. Labrum leaf shaped, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae yellow.

Thorax. Anteprenotum with central crease narrow, anterior corners yellow, remainder fading to brown, medial lobe approximately half width of remainder of anteprenotum, highly tapered trapezoid, dorsal surface with medial notch. Prescutum and scutum greasy black, surface with numerous minute punctures;; medial and prescutal suture with row of minute clear trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum as longer yellow sensilla; long clear prealar sensilla

present as line extending nearly to anterior margin. Scutellum brown. Mediotergite of metanotum greasy black, covered in minute punctures, patch of short yellow trichoid sensilla medially poorly developed. Laterotergite of metanotum greasy black, with minute punctures, dorsal patch of very elongate yellow trichoid sensilla. Pleural sclerites orange medially, fading to brown at margins, glabrous. Anepisternal cleft broad, membrane yellow. Suture between epimeron and metapleurite complete.

Wing. Two broad bands, proximal extending from base of R_5 to CuA_1+CuA_2 fork, distal from R_{1+2} fork to base of R_5 ; membrane with macrotrichia in all cells except br & bm. All veins covered in short stout macrotrichia. Sc: 4.35mm, Apex of Sc to Apex of R_1 1.04mm, R_{3+4+5} stem 0.56mm, distinct angle medially, nearly traverse; R_{4+5} stem 1.13mm; R_4 after fork 1.36mm, R_5 after fork 1.43mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.0 : 2.01 : 2.42$. r-m 0.20mm; M distal to r-m 1.65mm; M_1 0.84mm, arcuate, M_2 0.64mm; $M\text{distal}:M_1 = 1.0 : 0.50$, $R_{3+4+5}:M\text{distal} = 1.0 : 2.94$, $R_4:M_1 = 1.0:x$. CuA_1 proximal 0.27mm, distal 1.83mm; CuA_2 1.28mm with anterior angle well developed, posterior angle absent. CuA_2 to A_1 1.75mm. r-m joins R_{3+4+5} at well before R_3 divergence. Halter yellow. **Legs.** Coxae yellow. Femur and tibia yellow. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensillae.

Abdomen. Base of segments I-V orange, posterior portion brown, posterior segments brown, moderately covered in elongate brown sensilla. **Male Genitalia.** Epandrial collar complete, epandrial apodemes well developed, extending to lateroanterior apex of hypandrium, extending threadlike across gonocoxal apodeme, prominent break between epandrial collar and epandrial apodeme. Epandrial lobes triangular, anterior margin largely straight, only weak curve near lateral apex; lateral margin weakly convex, parallel apically; medial margin curved laterally at base, parallel apically; anterior apex broadly triangular; epandrial lobe apices do not reach apex of terminal division. Epiproct prominent, posterior margin straight, epandrial lobes with point contact at anterior apex of epiproct. Posteromedial stylus

absent. Ventral surface of epandrial lobe flat. Hypoproct with external portion tongue-like, internal portion plate-like, extended laterally beyond base of external portion; subepandrial membrane otherwise membranous.

Parameral bridge nearly straight, narrow. Apices of paramere directed dorsally, triangular with subacute point. Posterior margin paramere fused to medial gonocoxal lobes

Gonocoxal apodeme as per genus. General shape of gonocoxite as per genus. Dorsal gonocoxal lobe located near base of gonostylus, short, recumbent triangular. Medial gonocoxal lobe narrow and straplike, forming broad arc at base, directed dorsomedially, apical portion directed straight dorsally, slightly recumbent. Gonostylus with basal lobe low knob tilted slightly posterior from vertical, cylindrically petiolate at base, rounded apex with stout trichoid sensilla. Apical stylus subspatulate, flattened, expanding to rounded apex, secondary lobe absent.

Basal division of hypandrium about 1.5 times as tall as wide, eversible sac elliptical leaf-like, adhered at dorsal margin, extended ventroposterior, not approaching either dorsal margin of basal division, extending beyond ventral margin. Terminal division narrow, broadly attached to basal division as dorsally directed C-shape with lateral apices acute, medially with elongate medial stylus, extending nearly to epandrial lobes, apex simple, rounded.

Aedeagus with sperm pump as per genus; dorsal margin of lateral ejaculatory process straight; apex of aedeagal sclerites rounded, ventral apical apodeme prominent, subapical sclerite having medial portion trowel-shaped with medial internal keel. Lateral plates prominent, extending beyond apex of medial portion, base rounded, extended laterally, dorsomedial apex directed nearly dorsally, apex directed laterally.

Figures. Male Genitalia: 71, Wing: 72, Distribution: 73.

Material Examined. Holotype. Alachua Co., Fla. Gainesville, V-2-1930, J.S. Rogers (Pinned: 1 m#) (USNM) **Paratypes.** Same as holotype specimen (Pinned: 1 m#, 1 f#; Slide: 1 f#) (USNM). **Other Material.** Jackson Co. Fla. Marianna, iii.31.1929, J.S. Rogers (Pinned: 1 m#) (USNM). Putnam Co Fla, Apr. 11 – 1947, Resback (Slide: 1 m#) (USNM). Suwannee Co. Fla, T.35 R.15E, IV-28-1924, J.S. Rogers (Pinned: 1 m#) (USNM). Libb Co. Georgia, Macon, IV-6-1924, J.S. Rogers (Pinned: 1 m#) (USNM).

***Ptychoptera (Tigrimya) quadrifasciata* Say, 1824**

Ptychoptera quadrifasciata Say, 1824: 359 (original description)

Ptychoptera rufocincta Osten Sacken 1860: 252 (description)

Ptychoptera rufocincta Osten Sacken, Alexander 1920: 775-779 (description of larva and pupa)

Ptychoptera quadrifasciata Say, Alexander 1927: 7 (catalog)

Ptychoptera rufocincta Osten Sacken, Alexander 1927: 7 (catalog)

Ptychoptera quadrifasciata Say, Alexander 1965: 97 (catalog)

Ptychoptera rufocincta Osten Sacken, Alexander 1965: 97 (catalog, synonymy)

Diagnosis

Adult. Male. Apices of epandrial lobes convergent; hypandrium with leaf-like eversible sac not extending to ventral margin; medial gonocoxal lobe free of paramere; aedeagus with apices of lateral plates of subapical sclerite divergent.

Description

Adult. Measurements (n=1). Overall length 5.83mm. **Head.** Width: 0.98mm, Height: 0.78mm, Length: 0.53mm; Antenna flagellum length: 3.83mm. **Thorax.** Length: 1.9mm, Height: 1.9mm; Wing length: 5.5mm, Width: 1.2mm. **Abdomen.** Length: 3.4mm

Figures. Male Genitalia: 74, Wing: 75, Distribution: 76.

Complete description in Chapter 5.

Material Examined. Neotype. USA, PA, Centre County, Moshannon State Forest, Smays Run @ N Run Rd, 40°53.88'N 81°01.19'W, 580m 27.iii.2012 coll. GW, Courtney, depo. zone (Pinned: 1 m#) (ANSP) **Other Material.** Same as neotype specimen (Pinned: 3 m#, 2 f#; Alcohol: 6 m#, 10 f#, 1 larva, 2 pupa) (ISIC). FLORIDA, Leon County, III-18-1939, J.S. Rogers (Pinned: 1 m#) (ISIC). GEORGIA: Oconee Co. 2mi. N. Watkinsville, 3 October 1977, George W. Byers #1 (Pinned: 2 m#, 2 f#) (KU). KENTUCKY: Whitley Co. Cumberland Falls, St. Pk. 6 June 1960, George W. Byers #2 (Pinned: 1 m#) (KU). MARYLAND Garrett Co. #8. New Germany St. Park, 2300', 8 June, 1977. Byers, May, Young (Pinned: 2 m#) (KU). Montcalm Co. Mich, 8-14.48, R.R. Deisbach (Pinned: 1 m#) (KU). Fayetteville NC, 14 May 59, DL Wray (Pinned: 1 f#) (NCSU). PENNSYLVANIA: Alle-gheny Co. Schenly Park, Pittsburgh. 40-26-17N, 79-56-44W/ 320m., 22-23 June 2001, PITTSBURGH BIOBLITZ, 2001 staff Carnegie, Museum Natural History (Pinned: 2 m#, 4 f#) (CMNH). PENNSYLVANIA, Franklin Co. No.1, Caledonia St. Park, 2 July 1960, Byers and Party (Pinned: 1 m#) (KU).

***Ptychoptera (Unguptycha)* Fasbender subgen. n.**

Diagnosis

Larva. Labral brushes short, not extending dorsoposteriorly over labrum; incisor lobe of mandible with poorly defined denticulations; postmentum with <14 broad rounded denticulations. **Adult.** Epandrium divided into two massive composite epandrial claspers which taper to a distinct point or rounded apex, ventromesal lobe of epandrium present, located at approximately 2/3rds the length of the epandrial lobe/clasper. Female: Hypogynium with small triangular lobes ventrolateral to cerci.

Description

Male Genitalia. Epandrium with medially opposed clawlike epandrial claspers dominant structure, epandrium rising well above surface of tergite VII, with subapical spine closely associated with ventral surface of apex. Medial margin with pendulous ventromesal lobe projecting ventrally, divided into discous base with inverse lacrimiform blade narrowing ventrally, slightly emarginate anteriorly. Medial surface of blade nodulated, with sparse setae, anterior margin concave, posterior margin convex. Posteriolateral style medio-ventrally positioned near lateral margin of epiproct, pendant bladelike, tip obtusely rounded, lateral edge slightly concave, glabrous. Epiproct with U-shaped medial notch; tapering toward anterior margin of epandrial complex. Hypoproct platelike basally, tapering to slightly flattened, tonguelike, rounded apex extending well beyond epiproct. Apical portion moderately set with setae ~0.03mm in length. Subepandrial sclerite very reduced, divided, forming lightly sclerotized strips in sub-epandrial membrane anterolaterally to hypoproct.

Parameres not fused, basal portion extending medially to dorsally ascendant blade. Basal portion glabrous, poorly sclerotized except for longitudinal ridge. Ascendant blade highly sclerotized, foliform, posterior margin concave, anterior margin convex. Anterodorsal edge of blade and apex slightly divergent laterally, coming to obtuse point. Lateral ridge of blade absent.

Gonocoxite tapers anteriorly to gonocoxal apodeme; apodeme rounded in dorsal view, acutely triangular laterally. Anterior part of gonocoxite bulbous, rounded knoblike ventral gonocoxal lobe under gonostylus. Dorsomedial margin of gonocoxite forming flat plate fused with basal portion of paramere, medial anterior margin with small lobule provided with small cluster of elongate trichoid sensillae.

Gonostyle with knoblike basal lobe and simple apical stylus. Apical portion knob like, widening anteriorly to flat plane, surface nodulated and covered in setae. Stylus with prominent glabrous ridge, flexed sub-obtusely medially.

Hypandrium with basal division consisting of broad band extending dorsolaterally to epandrium, tapering dorsally, emarginate medially. Lateral apices of emarginated region developed to spathate lobes,. Terminal division of hypandrium joined at emarginated region of basal division. Base often with two knoblike structures, narrowing to a narrow sclerotized septum flanked by circular openings to the lateral canals of the terminal division. Lateral canals largely concealed by the hypandrial spathae. Above the septum heavily sclerotized pendant; lacrimiform membranous window set dorsal to pendant. Apex of terminal division triangular, arrow-like, forming subobtuse angle in dorsal view. Lower 2/3rds of terminal division laterally attached to remaining hypopygium with membranous tissue, forming walls of lateral canals.

Aedeagal sclerites blunt, approximately 2/3rds length of sperm sac, sclerites expanding ventro-basally; apical apodemes absent; subapical sclerite well developed, narrow flat rod extending over twice the length of the aedeagal sclerites, divided basally with medial membranous portion and sclerotized prongs extending ventroanterior to lateral base of aedeagus, narrowing to parallel sided rod apically, apex with variable shape; dorsal surface of subapical sclerite with distinct broad triangular spine at phallotreme, tip bent slightly dorsoposterior. Sperm sac nearly spherical, smaller than ejaculatory apodeme. Ejaculatory apodeme attached dorsomedially to sperm sac, not closely associated with aedeagus, larger than sperm sac, extending anteriorly into segment VII, arcing ventrally to enlarged rounded terminus; curling around anterior margin of sperm sac. Lateral apodemes attached dorsolaterally to sperm pump, similar in shape to ejaculatory apodeme but approximately quarter size, extending anteroventrally, paralleling ejaculatory apodeme. Entire aedeagal complex directed dorsoposteriorly, as in other Ptychopterinae.

Taxonomic Notes:

The taxonomy of the *Unguipitycha* has been problematic, with many descriptions relying on variable characters such as the configuration of the subapical spine of the epandrial clasper. The configuration of the parameres and ventromesal lobe of the epandrium represent the best diagnostic characters of the group.

Type Species:

Ptychoptera (Unguipitycha) lenis Osten Sacken **comb. nov.**

Other Species

Ptychoptera (Unguipitycha) bilobata Copley & Cannings **comb. nov.**

Ptychoptera (Unguipitycha) byersi Alexander **comb. nov.**

Ptychoptera (Unguipitycha) coloradensis Alexander **comb. nov.**

Ptychoptera (Unguipitycha) daimio Alexander **comb. nov.**

Ptychoptera (Unguipitycha) lacrimiformis Fasbender & Courtney **comb. nov.**

Ptychoptera (Unguipitycha) minor Alexander **comb. nov.**

Ptychoptera (Unguipitycha) obscura Peus **comb. nov.**

Ptychoptera (Unguipitycha) uta Alexander **comb. nov.**

Etymology:

Ungue refers to the distinctive claw-like shape of the epandrial claspers.

Ptychoptera (Unguptycha) bilobata* Copley & Cannings*Diagnosis**

Adult. Fore- and midcoxae with brown dot on anterodorsal surface, hindcoxae with upper portion of lateral surface brown. Male genitalia with hypandrial spathate lobes extending beyond ventral margin of gonopods, epandrial lobe with accessory subapical spine laterally at apex.

Female and immature stages unknown.

Description

Adult. Measurements (n=1). Overall length 9.58mm. **Head.** Width: 1.13mm, Height: 1.00mm, Length: 0.58mm; Antenna flagellum length: 4.75mm. **Thorax.** Length: 2.6mm, Height: 1.6mm; Wing length: 10.2mm, Width: 2.1. **Abdomen.** Length: 6.4mm.

Complete Description in Chapter 5.

Figures. Male Genitalia: 77, Wing: 78, Distribution: 79.

Material Examined. Paratype. Seattle, WASH. U.W. Campus, IV-28 1956, RW Sleeper (Pinned: 1 m#) (ORSU).

Ptychoptera (Unguptycha) byersi* Alexander 1966.*Diagnosis**

Adult. Fore- and midcoxae yellow anterodorsal surface, hindcoxae with upper portion of lateral surface brown. Male genitalia with hypandrial spathate lobes extending beyond ventral margin of gonopods, epandrial lobe without accessory subapical spine laterally at apex.

Description

Adult. Measurements (n=1). Overall length 7.83mm. **Head.** Width: 0.98mm, Height: 0.95mm, Length: 0.53mm; Antenna flagellum length: 4.1mm. **Thorax.** Length: 2.2mm, Height: 2.2mm; Wing length: 8.2mm, Width: 2.2mm. **Abdomen.** Length: 5.1mm

Head. Vertex shining black, sparsely set with trichoid sensilla; frons weakly developed between antennae, black. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: dark orange, oblong fusiform cylinder; pedicel dark orange, globular, few trichoid sensilla. Flagellomeres brown, fusiform. Facial sclerite orange brown, distinct from clypeus, forming even band above clypeus. Clypeus elongate blunt triangle, bulbous, generally covered in macrotrichia, dark brown. Maxillary palpus with 1st segment dark brown, 2nd segment yellow, distal segments yellow brown. Labrum D-shaped, dark yellow; epipharynx and hypopharynx not externally apparent, labium and labellae orange-yellow.

Thorax. Anteprenotum dark brown, medial lobe narrow trapezoidal with dorsal angles slightly extended; diffuse patch of yellow trichoid sensilla on anterior margin near forecoxa. Prescutum and scutum covered in microscopic punctures, black; medial and prescutal suture with row of yellow trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum; short yellow prealar sensilla present. Scutellum uniform dark brown, dorsal surface with long, clear setae; lateral ridges dark yellow. Mediotergite of metanotum shining chestnut brown, weakly pollinose, yellow sensilla along dorsal margin extending along medial portion to posterior margin. Laterotergite of metanotum shining, chestnut brown, dorsal patch of trichoid sensilla yellow. Pleural sclerites all chestnut brown, with weak pollinosity. Anepisternal cleft very narrow, not extending nearly to base of wing, membrane brown. Suture between epimeron and metapleurite prominent.

Wing. Two bands, proximal extending from base of R_{1+2} to CuA_1+CuA_2 fork, distal from R_{1+2} fork to base of R_5 , with an additional spots at the h crossvein, apex of Sc, apex of R_3 and M_1+M_2 fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 6.0mm, Apex of Sc to Apex of R_1 1.04mm, R_{3+4+5} stem 0.74mm, slight posterior turn at fork from R_{1+2} ; R_{4+5} stem 1.78mm; R_4 after fork 2.0mm, R_5 after fork 1.73mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 2.4 : 2.7$. r-m 0.35mm; M distal to r-m 2.24mm; M_1 0.95mm, arcuate, M_2 0.94mm; Mdistal: $M_1 = 1.00:0.42$, $R_{3+4+5}:M\text{distal} = 1.00:3.02$, $R_4:M_1 = 1.00:0.47$. CuA_1 proximal 0.25mm, distal 2.10mm; CuA_2 0.96mm sinuous. CuA_2 to A_1 straight for 1.56mm. m-cu joins R_{3+4+5} at r-m. Halter yellow. Prehalter dark yellow. **Legs.** Coxae yellow. Femur yellow, darkening to brown near tibial joint, tibia yellow. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere cannot fold back on penultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensilla.

Abdomen. Tergites and sternites black, posterior and posterior portion of lateral margins yellow except segment I which is uniform color, moderately covered in elongate yellow sensilla. Sternite VII forming plate under genitalia, with medial triangular notch prominent and directed posterior. **Male Genitalia.** Epandrial collar complete, narrow, epandrial apodemes broad and triangular, extending flat across gonocoxal apodeme to hypandrium, break at epandrium absent. Epandrial lobes fused to composite claspers: massive, clawlike, medial curve moderately-developed fingerlike to apex; subapical spine placed subapically, finger-like with rounded apex, ; ventromesal lobe located $\frac{3}{4}$ length of epandrial lobe, ovoid in cross section basally, not petiolate, directed ventromedially, tapering acutely to rounded point, nodulated on dorsoanterior surface near apex, nodules spaced less than individual width apart; medial stylus rounded and flattened, weakly curved medially. Epiproct prominent, posterior with U-shaped notch medially; posteromedial stylus poorly distinguished; hypoproct as per genus. Parameres paired, sclerotized portion separate and held together anterior with parameral membrane, medial spur present; lateral spur present, directed straight lateral, less than $\frac{1}{4}$ th length of apical lobe, apex

rounded; apex of paramere blade-like, laterally compressed, dorsal margin convex, ventral margin straight. Apex of paramere nearly vertical. Gonopods as per genus, dorsal glabrous ridge low, apex of gonostylus extended posterior as tapering rounded lobe beyond apex of dorsal glabrous ridge. Basal division of hypandrium with medial paired knobs prominent, subspherical, directed laterally; spathate lobes elongate, directed dorsally, extending beyond ventral margin of gonocoxite, triangular with rounded apex, posterior margin convex, anterior margin concave, posterior margin of lobes in contact medially. Terminal division with lateral canals at base prominent, membranous window lacrimiform, extending from base to 2/3rds height of terminal division, membranous window flat. Apex of terminal division as per genus, angle of trough 75 degrees. Aedeagus as per genus, subapical sclerite tapering heavily at apex of aedeagal sclerites to parallel sided rod, apex of subapical sclerite rounded, flattened like a knife's edge.

Female Genitalia. Tergite VII brown, lightening posteromedially. Cerci orange, with lateral margins darkened, lateral ridge well defined, dorsal furrow well developed, dark orange. Cercus length:width, 2.8:1. Hypogynium dull orange, rotated dorsally approximately 30 degrees from vertical; weakly bulbous, prow-like, widening ventrally, dorsal apex slightly widening to form near equilateral triangle. Apex marginally with small triangular, tongue-like lobes nestled laterally under cerci.

Figures. Male Genitalia: 80, Wing: 81, Distribution: 82.

Material Examined. Holotype. CALIFORNIA, Siskiyou Co. #3, Mt. Shasta (town), 18 June 1959, Byers & party (Pinned & Slide: 1 m#) (KU & USNM). **Other Material.** CALIFORNIA: Siskiyou Co., Mt. Shasta, 24 August 1959, Ellen Ordway (Pinned: 1 m#) (KU). OREGON – Klamath, Co. #1, Crater L. Nat. Park area, 23 June 1959, George W. Byers (Pinned: 2 m#) (KU). USA Oregon, Fremont Nat. For. Buckboard Spring at NF3360, Spring Creek w/ emergent veg. 42.413132N, 120.749178W, A Fasbender June-11-2012 (Alcohol: 2 m#, 1 f#) (ISIC). USA Oregon, Fremont Nat. For. Gilbert Spring at NF3360,

Hillside seeps with vegetation, 42.42599N, 120.755315W, A Fasbender June-11-2012 (Pinned: 9 m#, 1 f#; Alcohol: 3 m#) (ISIC). USA, Oregon, Harney Co. Blitzen R above Page Springs CG, 42°47.61'N 118°52.23'W 1295, 18 May 2012 coll. GW Courtney, seep ~0.5 mi above trailhead (Alcohol: 2 m#, 12 f#) (ISIC). USA, NV, Elko Co. Ruby Mnts, Angel Lake, 41.0266°N 115.0833°W, 16.vi.2007 alt 8300', coll.: JD Davis, MJ Petersen (Alcohol: 6 m#, 1f#; Pinned: 1 m#) (ISIC). UTAH, Box Elder Co. Clear Cr. Can Cmpg. 19-July-1984, M.F. Whiting (Pinned: 4 m#) (BYU).

***Ptychoptera (Unguptycha) coloradensis* Alexander, 1937.**

Ptychoptera lenis coloradensis Alexander, Alexander 1937

Diagnosis

Adult. Ventromesal lobe directed posterior, lateral lobe of paramere smaller than apical lobe.

Description

Adult. Measurements (n=1). Overall length 6.73mm. **Head.** Width: 1.08mm, Height: 0.93mm, Length: 0.58mm; Antenna flagellum length: 3.38mm. **Thorax.** Length: 2.1mm, Height: 2.0mm; Wing length: 6.7mm, Width: 1.9mm. **Abdomen.** Length: 4.05mm.

Head. Vertex shining black, sparsely set with trichoid sensilla; frons weakly developed between antennae, black. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: dark orange, oblong fusiform cylinder; pedicel dark orange, globular, few trichoid sensilla. Flagellomeres brown, fusiform. Facial sclerite orange brown, distinct from clypeus, forming even band above clypeus. Clypeus elongate blunt triangle, bulbous, generally covered in macrotrichia, dark brown. Maxillary palpus with 1st segment dark brown, 2nd segment yellow, distal segments yellow brown. Labrum D-shaped, dark yellow; epipharynx and hypopharynx not externally apparent, labium and labellae orange-yellow.

Thorax. Antepronotum dark brown, medial lobe narrow trapezoidal with dorsal angles slightly extended; diffuse patch of yellow trichoid sensilla on anterior margin near forecoxa. Prescutum and scutum covered in microscopic punctures, black; medial and prescutal suture with row of yellow trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum; short yellow prealar sensilla present. Scutellum uniform dark brown, dorsal surface with long, clear setae; lateral ridges dark yellow. Mediotergite of metanotum shining chestnut brown, weakly pollinose, yellow sensilla along dorsal margin extending along medial portion to posterior margin. Laterotergite of metanotum shining, chestnut brown, dorsal patch of trichoid sensilla yellow. Pleural sclerites all chestnut brown, with weak pollinosity. Anepisternal cleft very narrow, not extending nearly to base of wing, membrane brown. Suture between epimeron and metapleurite prominent.

Wing. Two bands, proximal extending from base of R_{1+2} to CuA_1+CuA_2 fork, distal from R_{1+2} fork to base of R_5 , with an additional spots at the h crossvein, apex of Sc, apex of R_3 and M_1+M_2 fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 5.25mm, Apex of Sc to Apex of R_1 1.34mm, R_{3+4+5} stem 0.95mm, distinct angle at fork from R_{1+2} ; R_{4+5} stem 1.58mm; R_4 after fork 2.0mm, R_5 after fork 1.96mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 1.67 : 2.10$. r-m 0.32mm; M distal to r-m 2.42mm; M_1 0.81mm, arcuate, M_2 0.51mm; $M\text{distal}:M_1 = 1.00:0.33$, $R_{3+4+5}:M\text{distal} = 1.00:2.54$, $R_4:M_1 = 1.00:0.40$. CuA_1 proximal 0.25mm, distal 2.17mm; CuA_2 1.41mm sinuous. CuA_2 to A_1 1.93mm. m-cu joins R_{3+4+5} at r-m. Halter yellow. Prehalter dark yellow. **Legs.** Coxae yellow. Femur yellow, darkening to brown near tibial joint, tibia yellow. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere cannot fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensilla.

Abdomen. Tergites and sternites black, posterior and posterior portion of lateral margins yellow except segment I which is uniform color, moderately covered in elongate yellow sensilla. Sternite VII

forming plate under genitalia, with medial triangular notch prominent and directed posterior. **Male**

Genitalia. Epandrial collar incomplete, developed medially and at epandrial apodemes, epandrial apodemes broad and triangular, extending flat across gonocoxal apodeme to hypandrium, break at epandrium absent. Epandrial lobes fused to composite claspers: massive, clawlike, curving medially to rounded apex; subapical spine variable; ventomesal lobe located $\frac{3}{4}$ length of epandrial lobe, round in cross section basally, directed ventromedially, before turning with distinct angle towards posterior, apex variable from rounded tapering to flattened. Epiproct prominent, posterior with U-shaped notch; posteromedial style present, formed as low ridge on lateral margins of epiproct; hypoproct as per genus. Parameres paired, medial margin with minute spur often fused with opposing paramere to form bridge, lateral margin with spur approximately $\frac{1}{2}$ size of apical blade, shape variable. Paramere slightly recumbent. Gonopods as per genus. Basal division of hypandrium with medial paired knobs low and subrectangular; hypandrial spathate lobes triangular and directed dorsally, apex slightly inflated and round extending to gonocoxite, posterior margin of lobes not in contact medially. Terminal division with lateral canals at base prominent, membranous window variably lacrimiform, often with ventral or dorsal extensions along medial axis. Apex of terminal division as per genus, angle of trough variable. Aedeagus as per genus, apex of subapical sclerite variable. **Female Genitalia.** Tergite VII brown, lightening posteromedially. Cerci orange, with lateral margins darkened, lateral ridge well defined, dorsal furrow well developed, dark orange. Cercus length:width, 2.66:1. Hypogynium orange, rotated dorsally approximately 30 degrees from vertical; weakly bulbous, prow-like, widening ventrally, dorsal apex slightly widening to form near equilateral triangle. Apex marginally with small triangular, tongue-like lobes nestled laterally under cerci.

Figures. Male Genitalia: 83, Wing: 84, Distribution: 85.

Taxonomic Notes.

Though described as a subspecies of *Ptychoptera lenis*, *Ptychoptera coloradensis* is distinct from that species and all other species in the *Ptychoptera lenis* group. The morphology of this species is highly variable, and this morphological variability combined with the molecular evidence suggests that *Ptychoptera coloradensis* represents a cryptic species complex. It is currently not feasible to separate species from this complex due to limited molecular sampling and a poor understanding of populations in the southern portion of the range.

Material Examined. Holotype. Mt. Avery, Gothic, Col. 10,000', VII-5.'34, Hallahan (Pinned: 1 m#) (USNM). **Allotype.** Same as holotype specimen (Pinned: 1 f#). **Paratype.** Gothic, Col. 10,000' VII-12.39, Alex. (Pinned: 1 m#) (USNM). **Other Material.** ARIZONA Apache Co. #1, 3.7 mi. N. of Alpine, 3 August 1965 8200', George W. Byers (Pinned: 5 m#) (KU). ARIZONA Apache Co. #3, Alpine Divide, 4 mi. NW Alpine, 8480 ft. 13 June 1979, George W. Byers (Pinned: 1 m#) (KU). ARIZONA Greenlee Co. #2, Hannagan Creek, 4.5 mi. NE. Hannagan, Meadow. 8280 ft. 14 June 1979. G.W. Byers & J. Gelhaus (Pinned: 15 m#) (KU). ARIZONA Greenlee Co. #1, Hannagan, Meadow, For. Svc. campgrd. 8280 ft. 14 June 1979. G.W. Byers & J. Gelhaus (Pinned: 1 m#) (KU). CRANBROOK B.C. 27.VI.21, C. Garrett (Pinned: 6 m#) (UMMZ). FERNIE 4 VI BC/ C. Garrett, Collector (Pinned: 1 m#) (UMMZ). COLORADO Boulder Co. #11, Camp Dick, 6mi. N. of Ward, 8600ft. 8 July 1974, G.W. Byers, C.W. Young (Pinned: 6 m#) (KU). Chaffee Co. CO, 20 May 1986, Kondratieff, Mushroom Gulch (Pinned: 1 m#) (CSU). Eagle Co., CO, 22 June 1996, beaver pond at, Fulford Cave cmpgrnd. S. Fitzgerald, A. Foley (Pinned: 1 m#, 1 f#) (CSU). COLORADO Fremont Co. #1, Hayden Creek, 4, mi. SW. Coaldale, 13 July 1974 7200', G.W. Byers C.W. Young (Pinned: 2 m#) (KU). Garfield Co. CO, 26 June 1997, S. Fitzgerald & B Kondratieff, Coffee Pot Springs (Pinned: 2 m#) (CSU). Larimer Co., CO, 20 June 1998, 9600', S. Fitzgerald & A. Foley, Rawah Wild. Blue L. Trail, nr. Fall Cr. (Pinned: 1 f#) (CSU). Larimer Co., CO, 6 June 2010, R. Stoak & A. Blevins, B. Kondratieff, Soapstone

Prairie Natural Area, Graves Creek (Pinned: 5 m#, 4 f#) (CSU). Larimer Co., CO, 6 June 2010, R. Stoak & A. Blevins, B. Kondratieff, Soapstone Prairie Natural Area, Spring, Ranch House (Pinned: 2 m#) (CSU). Larimer Co., CO, 6 June 2010, R. Stoak & A. Blevins, B. Kondratieff, Soapstone Prairie Natural Area, Spottletwood Cr. Area (Pinned: 1 m#) (CSU). Larimer Co., CO, 6 June 2010, R. Stoak & A. Blevins, B. Kondratieff, Soapstone Prairie Natural Area, Jack Springs (Pinned: 1 m#, 1 f#) (CSU). Larimer Co., Colo, 8-11-49, R.R. Dreisbach, R.K. Schwab (Pinned: 3 m#) (UMMZ). Park Co., CO, 7 June 1995, R. Durfee, A. Polonsky, High Cr. Fen Preserve, 9 mi. S of Fairplay, sweeping (Pinned: 1 m#, 2 f#) (CSU). Summit Co., CO, 19 July 1998, S. Fitzgerald & A. Foley, Copper, Mtn Resort (Pinned: 1 f#) (CSU). COLORADO: Teller County, Florissant Fossil Beds, R71W T13S Sec 13 8350, Grape Creek (Pinned: 3 m#) (KU). USA, ID, Custer Co. Boise NF, Stanley Lk Crk, 44.25339°N 115.0074°W, 5.vii.2008 6896', coll.: J.D. Petersen (Pinned: 4 m#) (ISIC). USA, ID, Custer Co. Boise NF, Vader Creek, 44.3469°N 115.1206°W, 5.vii.2008 6746', coll.: J.D. Petersen (Pinned: 3 m#) (ISIC). MONTANA Granite, Co. No.1, 22 mi. WNW of Anaconda, 3 July 1959, George W. Byers (Pinned: 2 m#) (KU). NEW MEXICO Santa Fe, Co. #5, Aspen Basin, 15 mi. NE. Sante Fe, 16 June 1979, 10300', G.W. Byers & J. Gelhaus (Pinned: 10 m#, 1 f#) (KU). NEW MEXICO Santa Fe, Co. #9, Aspen Basin, 17 mi. NE. Sante Fe, 16 June 1979, 10500', G.W. Byers & S.A. Teale (Pinned: 2 m#) (KU). NEW MEXICO Taos Co. #2, La Jara Canyon, 0.8mi. SW. Palo Flechado Pass, 17 June 1979. 8960ft. George W. Byers (Pinned: 12 m#, 2 f#) (KU). NEW MEXICO Taos Co. #4, Carson Nat'l Forest, La, Jara Canyon, 0.8mi. SW. Palo Flechado Pass 8960', 17 June 1979. 8960ft. J.K. Gelhaus (Pinned: 2 m#, 1 f#) (KU). OREGON: Jordan Crk., 28, mi. SSW La Grande, Union, Co., 4840ft., E.J. Davis, VI-(15-18)-1977, Malaise baited with CO₂ (Pinned: 3 m#, 2 f#) (WSU). SOUTH DAKOTA, Harney Nat. For. #2 Harney Trail, VII-12-1950, GW Byers (Pinned: 7 m#) (UMMZ). Clarkston Ut. April 27, 1938 (Pinned: 2 m#) (USNM, BYU). UTAH Grand Co., Bear, Creek above Hidden, Lake, 10 June 1988, Baumann, Nelson, Tibbetts. (Pinned: 1 m) (BYU). Heber, Utah, 7-27-53, R.R. Dreisbach (Pinned: 1 m#) (MSU). UTAH: Summit Co. Kamas, 11 June, 1956 G. Knowlton (Pinned: 2 m#) (KU). WASHINGTON: 6 mi. W. Asotin, along Asotin, Creek, Asotin Co., 5

August 1985, W.J. Turner sweep (Pinned: 13 m#) (WSU). WASH: Asot. Co. Fields' Spr. State, Prk. VII-31-1971/ W.J. Turner, Malaise Trap, dry ice (Pinned: 1 #) (WSU). WASHINGTON: Pullman, Whitman Co., 2000-2500ft., March 1985/ E. Myhre, Collector (Pinned: 1 m#, 1 f#) (WSU). Pampa Pond nr. Lacrosse WASH. May 4, 1969/ Coll. by, M.T. James (Pinned: 6 m#, 1 f#) (WSU). Wash: Whit. Co. Pullman, 21-IV-1977 (Pinned: 2 m#) (WSU). Pullman, Wash. V-11 1965, Roger D. Akre (Pinned: 1 f#, 1 f# May 14 1965) (WSU). Pullman Wash, 23 April 03 (Pinned: 1 f#, 2 m# 28 April 03) (WSU). WASHINGTON: 1 mi. N. Almota, Whitman Co. 840-900 ft., 8-III-75, W.J. Turner, conspecific swarms (Pinned: 1 m#) (WSU). WASHINGTON: Yakawawa, Cyn. 7 mi. NW Colton, Whitman Co. 2500ft. VI-(11-12)-1977, Malaise W.J. Turner (Pinned: 6 m#) (WSU). FieldSpgs. St. Pk. nr. Anatone, WN. June 12, 1949, M.T. James (Pinned: 1 m#) (WSU). USA Wyoming, Medicine Bow, Nat. For. North Laramie River, at Sand Lk. Rd. Beaver Dam Complex, 41.351557N, 106.166511W, A Fasbender June-21-2012 (Alcohol: 5 m#) (ISIC). USA Wyoming, Medicine Bow, Nat. For. Nash Fork nr. WY130, Beaver Dam Complex, 41.348236N, 106.219477W, A Fasbender June-21-2012 (Alcohol: 8 m#) (ISIC). USA Wyoming, Medicine Bow, Nat. For. North Laramie River, at Sand Lk. Rd. Beaver Dam Complex, 41.351557N, 106.166511W, A Fasbender June-21-2012 (Alcohol: 8 m#) (ISIC). Big Horn, Wyo. 8000ft. VII.9.53, PB Lawson (Pinned: 2 m#) (KU). WYOMING Park Co. No.1 27 mi. W. Cody, 6100 ft. 6 July 1959, George W. Byers (Pinned: 1 m#) (KU). WYOMING Sheridan, Co. No.2 Granite, Pass 7500 ft. 6 July 1959, George W. Byers (Pinned: 3 m#, 1 f#) (KU). WYOMING, Sheridan Co #2, VII-13-1950, GW Byers (Pinned: 11 m#, 2 f#) (UMMZ). WYOMING Sheridan, Co. No.3 Granite, Pass 8600 ft. 7 July 1959, George W. Byers (Pinned: 2 m#, 1 f#) (KU). Wyoming Bighorn Nat. Forest, Below Sibley Lk. Seepage below dam, 44.76090N107.44035W, A Fasbender July 1-2010 (Alcohol: 15 m#, 7 larvae, 1 pupa) (ISIC). Wyoming, Teton Nat. Forest, Twogwotee Pass, 9650', VII-9.42, (C.P. Alexander) (Slide: 2 m#) (USNM). WYO. Yellowstone Pk. Bridge Bay of Yellowstone Lake 7800ft. 18.vi.52 E.B. Hayden, H52-163. (Pinned: 1 m#) (KU). Yellowstone, Wyo. V-28-30, J.S. Alexander #18a (Pinned: 25m#, 6f#, various dates) (UMMZ).

Ptychoptera (Unguiptycha) daimio* Alexander 1921.*Diagnosis**

Adult. Subapical spine placed laterally, paddlelike, and laterally compressed.

Female and immature stages unknown.

Description

Adult. Measurements (n=1). Overall length x. **Head.** Width: 1.34mm, Height: 1.13mm, Length: 0.62mm; Antenna flagellum length: 5.0mm. **Thorax.** Length: 3.05mm, Height: 2.75mm; Wing length: 12.43, Width: 2.86mm. **Abdomen.** Length: ? (dissected).

Head. Vertex shining black, sparsely set with trichoid sensilla; frons weakly developed between antennae, black. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: dark orange, oblong fusiform cylinder; pedicel dark orange, globular, few trichoid sensilla. Flagellomeres brown, fusiform. Facial sclerite orange brown, distinct from clypeus, forming even band above clypeus. Clypeus elongate blunt triangle, bulbous, generally covered in macrotrichia, dark brown. Maxillary palpus with 1st segment dark brown, 2nd segment yellow, distal segments yellow brown. Labrum D-shaped, dark yellow; epipharynx and hypopharynx not externally apparent, labium and labellae orange-yellow.

Thorax. Antepronotum dark brown, medial lobe narrow trapezoidal with dorsal angles slightly extended; diffuse patch of yellow trichoid sensilla on anterior margin near forecoxa. Prescutum and scutum covered in microscopic punctures, black; medial and prescutal suture with row of yellow trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum; short yellow prealar sensilla present. Scutellum uniform dark brown, dorsal surface with long, clear setae; lateral ridges dark yellow.

Mediotergite of metanotum shining chestnut brown, weakly pollinose, yellow sensilla along dorsal margin extending along medial portion to posterior margin. Laterotergite of metanotum shining, chestnut brown, dorsal patch of trichoid sensilla yellow. Pleural sclerites all chestnut brown, with weak pollinosity. Anepisternal cleft very narrow, not extending nearly to base of wing, membrane brown. Suture between epimeron and metapleurite prominent. **Wing.** Two bands, proximal extending from base of R_{1+2} to CuA_1+CuA_2 fork, distal from R_{1+2} fork to base of R_5 , with an additional spots at the h crossvein, apex of Sc, apex of R_3 and M_1+M_2 fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 9.0mm, Apex of Sc to Apex of R_1 1.48mm, R_{3+4+5} stem 1.30mm, slight posterior turn at fork from R_{1+2} ; R_{4+5} stem 2.76mm; R_4 after fork 3.16mm, R_5 after fork 3.35mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 2.12 : 2.38$. r-m 0.48mm; M distal to r-m 3.72mm; M_1 2.68mm, arcuate, M_2 2.68mm; $M\text{distal}:M_1 = 1.00:0.18$, $R_{3+4+5}:M\text{distal} = 1.00:2.9$, $R_4:M_1 = 1.00:0.84$. CuA_1 proximal 0.44mm, distal 3.18mm; CuA_2 2.0mm sinuous. CuA_2 to A_1 3.0mm. m-cu joins R_{3+4+5} at r-m. Halter yellow. Prehalter dark yellow. **Legs.** Coxae yellow. Femur yellow, darkening to brown near tibial joint, tibia yellow. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere cannot fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensilla.

Abdomen. Tergites and sternites black, posterior and posterior portion of lateral margins yellow except segment I which is uniform color, moderately covered in elongate yellow sensilla. Sternite VII forming plate under genitalia, with medial triangular notch prominent and directed posterior. **Male Genitalia.** Epandrial collar complete, broad, epandrial apodemes broad and triangular, extending flat across gonocoxal apodeme to hypandrium, break at epandrium absent. Epandrial lobes fused to composite claspers: massive, clawlike, narrower more than 3x as long as wide, medial curve weakly developed anteriorly, straightening posteriorly; apex of epandrial lobe smaller than subapical spines, tapering, ventral surface flattened at apex; subapical spine placed laterally, compressed paddle-like

with rounded apex, extending dorsoposterior beyond epandrial lobe apex; secondary subapical spine present directed straight posterior, round in cross section, apex tapered, extending nearly as long as primary subapical spine; ventromesal lobe located $\frac{3}{4}$ length of epandrial lobe, round in cross section basally, weakly petiolate, directed ventrally, spear shaped, medial surface with sparse nodules; medial stylus round, small, barely longer than wide. Epiproct prominent, posterior margin M-shaped, apices rounded; posteromedial stylus poorly distinguished; hypoproct as per genus.

Parameres paired, sclerotized portion separate and held together anterior with parameral membrane, medial spur absent; lateral spur absent, apex of paramere flattened, triangular, apex curved ventrally, ventral surface buldgin subapically. Apex of paramere nearly completely horizontal. Gonopods as per genus, dorsal glabrous ridge low anterior, taller posterior; apex of gonostylus rounded, extending slightly ventroposterior. Basal division of hypandrium with medial paired knobs prominent, subspherical, directed laterally; spathate lobes short, base petiolate, expanding to scallop shaped apex, posterior margin of lobes not in contact medially. Terminal division with lateral canals at base weakly developed, membranous window slitlike, inflated posterior, extending from base to apical trough of terminal division. Apex of terminal division with triangular lateral notches located laterally, with subacute point dorsally, medial portion of posterior surface with low bar-like lobe, angle of trough 75 degrees. Aedeagus as per genus, subapical sclerite evenly to apex, apex of subapical sclerite ovoid, dorsal margin emarginate.

Figures. Male Genitalia: 86, Wing: 87, Distribution: 88.

Material Examined. Holotype. Teshio, 14-7-1916, T. Isshiki

Ptychoptera (Unguiptycha) lacrimiformis* Fasbender & Courtney*Diagnosis.**

Larvae. Labral brushes short, not extending dorsoposteriorly over labrum; incisor lobe of mandible with poorly defined denticulations; postmentum with broad rounded denticulations (applies all *Ptychoptera lenis* group).

Pupae. Four anteromedial setae present in quadrate formation, not raised on lobe; male genital lobule with obvious blunt pseudoclasper lobes not convergent, female genital lobule with apex of hypogynum with short apical suture.

Adult. Male. Ventromesal lobule of epandrium forms a pendulant inverse teardrop-shaped blade tapering ventrally.

Complete description in Chapter 5.

Figures. Male Genitalia: 89, Wing: 90, Distribution: 91.

Material Examined. Holotype. USA, Washington, Skagit Co., seeps along Hwy 530, Sauk Riv, 48°20.06'N 121°32.99'W, 30.VI.2010 coll. GW Courtney, on vegetation / flying over seep (GWC) (GLAHM). **Other Material.** Hagensborg, B.C. 12-VII-1992 A. Borkent CD1428 (GLAHM). Salmon Arm B.C. 8-VI-1990 A. Borkent CD 1210 (GLAHM). Brit.Columbia, Robson, V.2.1937, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, V.17.1937, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, V.23.1937, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, V.15.1938, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, V.3.1939, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, VII.16.1939, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, VII.23.1939, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, VII.30.1939, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, VIII.6.1939, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, VIII.23.1939, H.H.

Foxlee (UMMZ). Brit.Columbia, Robson, IV.13.1940, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, IV.24.1940, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, V.12.1940, H.H. Foxlee (UMMZ). Brit.Columbia, Robson, VII.16.1940, H.H. Foxlee (UMMZ). British Columbia, Vancouver Island, April 30, 1951, R. Guppy #2 (UMMZ). British Columbia, Vancouver Island, April 26, 1951, R. Guppy #2 (UMMZ). British Columbia, Vancouver Island, May 3, 1951, R. Guppy #1 (UMMZ). British Columbia, Vancouver Island, May 5, 1951, R. Guppy #1 (UMMZ). British Columbia, Vancouver Island, May 9, 1951, R. Guppy #1 (UMMZ). British Columbia, Vancouver Island, May 12, 1951, R. Guppy #2 (UMMZ). British Columbia, Vancouver Island, V-13, 1951, R. Guppy # (UMMZ). British Columbia, Vancouver Island, V-14, 1951 2, Richard Guppy (UMMZ). British Columbia, Vancouver Island, May 16, 1951, R. Guppy #2 (UMMZ). British Columbia, Vancouver Island, May 24, 1951, R. Guppy #4 (UMMZ). British Columbia, Vancouver Island, Hennedy Lake, 1951 R. Guppy #11 VI-15 (UMMZ). OREGON: Benton Co., Corvallis, Sulphur Springs, 44°36'N 123°24'W 100M, 15 May 1999 sweeping, ieg. AVZ Brower (ORSU). MALTBY, WASH, 18-IV-64, D. MILNE (ORSU). Olympia, Wash, 4 10 94 (WSU). Seattle, Wash. (ORSU). WASHINGTON: Bear Crk., nr. Rimrock Lk., 8mi, SW Tieton R5, 3000ft, 27-30 May 1986, W. J. Turner Sweep (WSU). Washington,, Mt. Rainier,,2700'-VIII-13.'40,(H.+M. Townes) (USNM). WASHINGTON, Olympic Nat. Pk., Olympic HtSpgs., July 20, 1953, K. M. Fender (UMMZ). WASHINGTON, Olympic Nat. Pk., Dosewallips R., July 24, 1953, K. M. Fender (UMMZ). WASHINGTON: Whatcom Co., Silver Fir Cmpgr., 14 mi. E Glacier RS, No. Frk. Nooksack R., 2000ft., VIII-(8-11)-74 W. J. Turner Collector (WSU). USA, Washington, Jefferson Co., Olympic National Park, Queets River Valley,, mile 3.2, 47°33.52'N 124°10.97'W 35m, 20.vii. 2012 coll. GW Courtney, from roadside seepage (ISIC). USA, Washington, Jefferson Co., Olympic National Park, Queets River Valley,, mile 3.2, 47°33.52'N 124°10.97'W 35m, 28 May 2012 coll. GW Courtney, from roadside seepage (ISIC).

Ptychoptera (Unguiptycha) lenis* Osten Sacken 1877.*Diagnosis**

Adult. Ventromesal lobe closely appressed to epandrial lobe, apical margin broad and emarginate.

Description

Adult. Measurements (n=1). Overall length 8.88mm. **Head.** Width: 1.2mm, Height: 1.03mm, Length: 0.58mm; Antenna flagellum length: 4.25mm. **Thorax.** Length: 2.4mm, Height: 2.4mm; Wing length: 8.9mm, Width: 2.1mm. **Abdomen.** Length: 5.9mm.

Head. Vertex shining black, sparsely set with trichoid sensilla; frons weakly developed between antennae, black. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: dark orange, oblong fusiform cylinder; pedicel dark orange, globular, few trichoid sensilla. Flagellomeres brown, fusiform. Facial sclerite orange brown, distinct from clypeus, forming even band above clypeus. Clypeus elongate blunt triangle, bulbous, generally covered in macrotrichia, dark brown. Maxillary palpus with 1st segment dark brown, 2nd segment yellow, distal segments yellow brown. Labrum D-shaped, dark yellow; epipharynx and hypopharynx not externally apparent, labium and labellae orange-yellow.

Thorax. Anteprenotum dark brown, medial lobe narrow trapezoidal with dorsal angles slightly extended; diffuse patch of yellow trichoid sensilla on anterior margin near forecoxa. Prescutum and scutum covered in microscopic punctures, black; medial and prescutal suture with row of yellow trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum; short yellow prealar sensilla present. Scutellum uniform dark brown, dorsal surface with long, clear setae; lateral ridges dark yellow. Mediotergite of metanotum shining chestnut brown, weakly pollinose, yellow sensilla along dorsal

margin extending along medial portion to posterior margin. Laterotergite of metanotum shining, chestnut brown, dorsal patch of trichoid sensilla yellow. Pleural sclerites all chestnut brown, with weak pollinosity. Anepisternal cleft very narrow, not extending nearly to base of wing, membrane brown. Suture between epimeron and metapleurite prominent.

Wing. Two bands, proximal extending from base of R_{1+2} to CuA_1+CuA_2 fork, distal from R_{1+2} fork to base of R_5 , with an additional spots at the h crossvein, apex of Sc, apex of R_3 and M_1+M_2 fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 6.5mm, Apex of Sc to Apex of R_1 1.36mm, R_{3+4+5} stem 0.99mm, slight posterior turn at fork from R_{1+2} ; R_{4+5} stem 2.22mm; R_4 after fork 1.98mm, R_5 after fork 2.08mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 2.07 : 1.97$. r-m 0.0.30mm; M distal to r-m 2.95mm; M_1 0.95mm, arcuate, M_2 0.70mm; Mdistal: $M_1 = 1.00:0.32$, $R_{3+4+5}:Mdistal = 1.00:2.81$, $R_4:M_1 = 1.00:0.46$. CuA_1 proximal 0.30mm, distal 2.5mm; CuA_2 1.50mm sinuous. CuA_2 to A_1 2.2mm. m-cu joins R_{3+4+5} at r-m. Halter yellow. Prehalter dark yellow. **Legs.** Coxae yellow. Femur yellow, darkening to brown near tibial joint, tibia yellow. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere cannot fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensilla.

Abdomen. Tergites and sternites black, posterior and posterior portion of lateral margins yellow except segment I which is uniform color, moderately covered in elongate yellow sensilla. Sternite VII forming plate under genitalia, with medial triangular notch prominent and directed posterior.

Male Genitalia. Epandrial collar incomplete, developed medially and at epandrial apodemes, epandrial apodemes broad and triangular, extending flat across gonocoxal apodeme to hypandrium, break at epandrium absent. Epandrial lobes fused to composite claspers: massive, clawlike, medial curve poorly developed to short conical apex; subapical spine placed subapically, conical with rounded apex; ventromesal lobe located $\frac{3}{4}$ length of epandrial lobe, ovoid in cross section basally, weakly petiolate,

directed ventroposterior, flattened broad C-shaped pad with ventral margin heavily emarginate; nodulated across surface, nodules with spaces between greater than width anterior, closer spaced posterior; medial stylus thumb-like with rounded apex, weakly curved anterior. Epiproct prominent, posterior with U-shaped notch medially; posteromedial stylus poorly distinguished; hypoproct as per genus.

Parameres paired, sclerotized portion separate and held together anterior with parameral membrane, medial spur absent; apex of paramere blade-like, laterally compressed, dorsal margin convex, ventral margin straight. Paramere 45 degrees recumbent from vertical.

Gonopods as per genus, except apex of gonostylus extended posterior as round lobe beyond apex of dorsal glabrous ridge.

Basal division of hypandrium with medial paired knobs low and subrectangular; spathate lobes truncate with rounded apex and directed posterior, apex curving weakly dorsally, posterior margin of lobes not in contact medially. Terminal division with lateral canals at base prominent, membranous window lacrimiform, extending from base to 2/3rds height of terminal division, membranous section extending posterolaterally beyond lateral margins, forming ovoid flattened pennant. Apex of terminal division as per genus, angle of trough variable.

Aedeagus as per genus, subapical sclerite tapering evenly to apex, apex of subapical sclerite flattened, spoon-shaped.

Figures. Male Genitalia: 92, Wing: 93, Distribution: 94.

Material Examined. Lectotype. Yosemite, Cal. June 5, O Sack/ O. Sacken West Dipt. **Other Material.** CALIFORNIA, Tehama Co. #3, nr. Lassen N.P., 16 June 1959, G.W. Byers (Pinned: 2 m#) (KU). CALIFORNIA El Dorado, Co. #3, American Riv. 11.4 mi. W. of Kyburz, 6 June 1976 3040ft. G.W. Byers,

C.W. Young (Pinned: 17 m#, 1 f#) (KU). California, Sierra Co. 4.8 mi SE of, Sierraville, VI-1-1959 (Slide: 1 m#) (USNM). USA, California, Eldorado Nat, For. Grass Lake at CA89, 38.793601N 119.95755W, A Fasbender June-15-2012 (Alcohol: 6 m#) (ISIC). Sierra Co., CA, B. Kondratieff, R. Baumann, Dog Valley Cpgd (1 m#) (CSU). USA California, Inyo Nat. For, Roadside seep above, Lundy Lake nr. Marshes, 38.02413N, 119.260243W, A Fasbender June-17-2012 (Alcohol: 3 m#, Pinned: 2 m#) (ISIC). USA, CA, Plumas Co. Lassen Nat Frst, Humbug, 40.107°N, 121.373°W, 19.vi.2007 alt 2007m, coll.: JD Davis, MJ Petersen (Pinned: 1 m#) (ISIC). USA, CA, El Dorado Co. El Dorado Nat Frst, Grass L. 38.7937°N 119.9588°W, 18.vi.2007, alt 7700', coll.: JD Davis, MJ Petersen.

***Ptychoptera (Unguptycha) minor* Alexander 1920.**

Ptychoptera minor Alexander, 1920

Ptychoptera lenis Alexander, Alexander 1967

Diagnosis

Adult. Epandrium with claw-like epandrial clasper, ventromesal lobe directed ventrally, less than 2x length of petiole. Paramere laterally complex, apex recumbent.

Description

Adult. Measurements (n=1). Overall length ? (abdomen dissected). **Head.** Width: 1.25mm, Height: 1.13mm, Length: 0.67mm; Antenna flagellum length: 5.25mm. **Thorax.** Length: 2.90mm, Height: 2.75mm; Wing length: 10.42mm, Width: 2.57mm. **Abdomen.** Length: ? (dissected)

Head. Vertex shining black, evenly provided with elongate trichoid sensilla posteriorly; frons extremely narrow strip, black. Occiput and genae with dense elongate yellow trichoid sensilla. Antennae: scape bright yellow, oblong cylinder with ring of long black trichoid sensilla well separated from dorsal apex; pedicel yellow basally, brown dorsally, globular, ring of trichoid sensilla on lateral

margin. Flagellomeres brown, fusiform. Facial sclerite black, indistinct from clypeus, weakly inflated. Clypeus rhomboidal, inflated, generally covered in yellow sensilla, dark yellow with brown spot at ventral apex. Maxillary palpus with segments 1&2 yellow, segment 3 muddy yellow fading to brown, distal segments brown. Labrum narrowly spade shaped, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae bright yellow.

Thorax. Anteprenotum with transverse fold broader than height of anterior ridge, yellow medially, brown at lateroventral extremity, with elongate yellow trichoid sensilla at lateroventral apex, medial lobe approximately one third width of remainder of anteprenotum, highly tapered trapezoid, dorsal surface with medial notch. Prescutum and scutum greasy black, with numerous microscopic punctures with broad yellow stripe from posterior apex of prescutum to scutellum; medial and prescutal suture with row of minute clear trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum as longer yellow sensilla; long clear prealar sensilla present. Scutellum yellow. Mediotergite of metanotum greasy black, with light pollinosity, medially with elongate tapering yellow stripe extending less than $\frac{1}{2}$ length, lateral corners with short yellow triangular patches. Laterotergite of metanotum pollinose black, except for yellow patch near wing base, dorsal patch of very elongate yellow trichoid sensilla. Pleural sclerites all black, with heavy pollinosity. Anepisternal cleft narrow, membrane yellow. Suture between epimeron and metapleurite incomplete, weak. **Wing.** Hyaline, weak infuscation extending from base of R_{1+2} to CuA_1+CuA_2 fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. . Sc: 7.35mm, Apex of Sc to Apex of R_1 1.31mm, R_{3+4+5} stem 0.97mm, straight, approaching transverse; R_{4+5} stem 2.05; R_4 after fork 1.96mm, R_5 after fork 1.96mm; $R_{3+4+5}:R_{4+5}$ stem: R_4 , 1.0 : 2.11 : 2.02. r-m 0.35mm; M distal to r-m 2.65mm; M_1 1.05mm, M_2 0.80mm; Mdistal: M_1 , 1.0:0.39, R_{3+4+5} :Mdistal, 1.0:0.36, $R_4:M_1$, 1.0:0.53. CuA_1 proximal 0.27mm, distal 2.35mm; CuA_2 1.40mm with anterior angle well developed, posterior angle absent. CuA_2 to A_1 1.95mm. R_3 branch at r-m. Halter yellow. Prehalter yellow. **Legs.** Forecoxa yellow dorsoanterior margin with dark brown spot and ventral

margin with broad brown band sloping anterior, midcoxa yellow with dark brown spot on dorsoanterior apex and ventral margin with broad brown band sloping anterior, hindcoxa dark brown with yellow spot dorsally on posterior surface. Femur and tibia yellow, darkening slightly at shared joint, joint of tibia and first tarsomere brown. First tarsomere light brown proximally, darkening distally. All other tarsi brown. 5th tarsomere can fold back on penultimate tarsomere. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Tergites and sternites black, posterior and posterior portion of lateral margins yellow except segment I which is uniform color, moderately covered in elongate yellow sensilla. Sternite VII forming plate under genitalia, with medial triangular notch prominent and directed posterior. **Male Genitalia.** Epandrial collar incomplete, developed medially and at epandrial apodemes, epandrial apodemes broad and triangular, extending flat across gonocoxal apodeme to hypandrium, break at epandrium absent. Epandrial lobes with medial curve well-developed to pointed apex; subapical spine placed ventrally, conical with rounded apex; ventromesal lobe located $\frac{3}{4}$ length of epandrial lobe, ovoid in cross section basally, strongly petiolate, directed ventrally, flattened oval pad with small emargination on ventroanterior margin, pad less than 2x length of petiole; nodulated across surface; medial stylus thumb-like with rounded apex, weakly curved anterior. Epiproct prominent, posterior with U-shaped notch medially; posteromedial stylus poorly distinguished; hypoproct as per genus. Parameres separate, sclerotized portion separate and held together anterior with parameral membrane, medial spur absent; apex of paramere blade-like, laterally compressed, dorsal margin convex, ventral margin straight. Paramere over 45 degrees recumbent from vertical. Gonopods as per genus. Basal division of hypandrium with medial paired knobs rounded; spathate lobes triangular, directed dorsally, reaching base of gonopods. Terminal division with lateral canals at base prominent, membranous window lacrimiform, extending from base to $\frac{2}{3}$ height of terminal division, membranous section extending posterolaterally beyond lateral margins, forming ovoid flattened pennant. Apex of terminal division as

per genus, angle of trough variable. Aedeagus as per genus, subapical sclerite tapering evenly to apex, apex of subapical sclerite flattened, spoon-shaped.

Figures. Male Genitalia: 95, Wing: 96, Distribution: 97.

Material Examined. *Holotype*. Monterey, Co., Cal. July 22 '96/ HOLOTYPE, *Ptychoptera, minor*, C.P. Alexander (Pinned, 1 m#, USNM); **Other Material.** San Francisco, Cal. IV-11-20 (Pinned, 1m#, USNM)

Taxonomic Notes

The holotype specimen is extremely fragmentary, consisting of the thorax, head, wing bases, and one foreleg. The San Francisco specimen placed as this species was determined by the color pattern on the head and close geographic association with the holotype. This species is extremely similar to *U. lacrimiformis*, being differentiated by the color pattern of the clypeus and abbreviated ventromesal lobe of the epandrium. Due to the vague nature of the original description *U. lenis* has been widely misidentified as this species (i.e. Alexander 1967), though the known ranges of both species are allopatric.

Ecological Notes. The ecology of this species is extremely poorly known. It appears to be associated with the Coast Ranges of California, although the northern and southern limits of the range have not been satisfactorily examined. The species is absent in the inland mountain ranges such as the Cascade and Sierra Nevada Mountains, and is replaced in the Coast Range of Oregon by *U. lacrimiformis*. Whether this species is present in the Central Valley or Southern California is currently unknown, as these regions are essentially unsampled for Ptychopteridae.

Ptychoptera (Unguptycha) obscura* Peus 1958.*Diagnosis**

Adult. Ventromesal lobe directed posterior, paramere with lateral lobe subequal or larger than apical lobe.

Description

Adult. Measurements (n=1). Overall length 8.45mm. **Head.** Width: 0.95mm, Height: 1.20mm, Length: 0.55mm; Antenna flagellum length: 4.48mm. **Thorax.** Length: 2.5mm, Height: 2.3mm; Wing length: 8.3mm, Width: 2.3mm. **Abdomen.** Length: 5.4mm.

Head. Vertex shining black, sparsely set with trichoid sensilla; frons weakly developed between antennae, black. Occiput with patch of short black trichoid sensilla projecting posteriorly behind posterior extremity of eye. Antennae: dark orange, oblong fusiform cylinder; pedicel dark orange, globular, few trichoid sensilla. Flagellomeres brown, fusiform. Facial sclerite orange brown, distinct from clypeus, forming even band above clypeus. Clypeus elongate blunt triangle, bulbous, generally covered in macrotrichia, dark brown. Maxillary palpus with 1st segment dark brown, 2nd segment yellow, distal segments yellow brown. Labrum D-shaped, dark yellow; epipharynx and hypopharynx not externally apparent, labium and labellae orange-yellow.

Thorax. Anteprenotum dark brown, medial lobe narrow trapezoidal with dorsal angles slightly extended; diffuse patch of yellow trichoid sensilla on anterior margin near forecoxa. Prescutum and scutum covered in microscopic punctures, black; medial and prescutal suture with row of yellow trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum; short yellow prealar sensilla present. Scutellum uniform dark brown, dorsal surface with long, clear setae; lateral ridges dark yellow. Mediotergite of metanotum shining chestnut brown, weakly pollinose, yellow sensilla along dorsal

margin extending along medial portion to posterior margin. Laterotergite of metanotum shining, chestnut brown, dorsal patch of trichoid sensilla yellow. Pleural sclerites all chestnut brown, with weak pollinosity. Anepisternal cleft very narrow, not extending nearly to base of wing, membrane brown. Suture between epimeron and metapleurite prominent.

Wing. Two bands, proximal extending from base of R_{1+2} to CuA_1+CuA_2 fork, distal from R_{1+2} fork to base of R_5 , with an additional spots at the h crossvein, apex of Sc, apex of R_3 and M_1+M_2 fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 6.0mm, Apex of Sc to Apex of R_1 1.11mm, R_{3+4+5} stem 0.30mm, slight posterior turn at fork from R_{1+2} ; R_{4+5} stem 1.73mmmm; R_4 after fork 1.98mm, R_5 after fork 1.87mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 2.07 : 1.97$. r-m 0.35mm; M distal to r-m 2.60mm; M_1 0.60mm, arcuate, M_2 0.50mm; $M\text{distal}:M_1 = 1.00:0.32$, $R_{3+4+5}:M\text{distal} = 1.00:2.81$, $R_4:M_1 = 1.00:0.46$. CuA_1 proximal 0.25mm, distal 2.15mm; CuA_2 1.30mm sinuous. CuA_2 to A_1 1.75mm. m-cu joins R_{3+4+5} at r-m. Halter yellow. Prehalter dark yellow. **Legs.** Coxae yellow. Femur yellow, darkening to brown near tibial joint, tibia yellow. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere cannot fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensilla.

Abdomen. Tergites and sternites black, posterior and posterior portion of lateral margins yellow except segment I which is uniform color, moderately covered in elongate yellow sensilla. Sternite VII forming plate under genitalia, with medial triangular notch prominent and directed posterior. **Male Genitalia.** Epandrial collar complete, moderately broad, epandrial apodemes broad and triangular, extending flat across gonocoxal apodeme to hypandrium, break at epandrium absent. Epandrial lobes fused to composite claspers: massive, clawlike, medial curve, moderately-developed weakly tapering cone with rounded apex, curved medially; subapical spine placed apically, small, rounded knob; ventromesal lobe located 2/3rds length of epandrial lobe, round in cross section basally, cylindrical, not

petiolate, apical section bent posterior, ventroanterior margin concave, dorsoanterior margin convex, apex blunt, broadly rounded, apical portion with dorsal surface covered in nodules spaced greater than individual width; medial stylus round in cross section, tapering to apex, posterior margin slightly inflated, weakly angled medially. Epiproct prominent, posterior margin largely straight, with U-shaped notch medially; posteromedial stylus poorly distinguished; hypoproct as per genus. Parameres paired, sclerotized portion separate and held together anterior with parameral membrane, medial spur present; lateral spur present, directed straight lateral, less than longer than length of apical lobe, entire lobe rounded; apex of paramere blade-like, laterally compressed, dorsal margin convex, ventral margin straight. Apex of paramere nearly vertical. Gonopods as per genus, apex of gonostylus extended posterior as tapering rounded lobe beyond apex of dorsal glabrous ridge. Basal division of hypandrium with medial paired knobs prominent, rounded triangular, directed laterally; spathate lobes elongate, directed dorsally, extending nearly to ventral margin of gonocoxite, triangular with rounded apex, posterior margin straight, anterior margin straight at angle, posterior margin of lobes not in contact medially. Terminal division with lateral canals at base prominent, membranous window lacrimiform, with ventral slit at base, extending from base to 3/4ths height of terminal division, membranous window flat. Apex of terminal division as per genus, angle of trough 45 degrees. Aedeagus as per genus, subapical sclerite tapering heavily at apex of aedeagal sclerites to parallel sided rod, apex of subapical sclerite subtrapezoidal, dorsal margin broadest, lateral corners rounded. **Female Genitalia.** Tergite VII brown, lightening posteromedially. Cerci orange, with lateral margins darkened, lateral ridge well defined, dorsal furrow well developed, dark orange. Cercus length:width, 2.25:1. Hypogynium orange, rotated dorsally approximately 30 degrees from vertical; weakly bulbous, prow-like, widening ventrally, dorsal apex slightly widening to form near equilateral triangle. Apex marginally with small triangular, tongue-like lobes nestled laterally under cerci.

Figures. Male Genitalia: 98, Wing: 99, Distribution: 100.

Material Examined. Paratype. Berlin Prof. F. Karsch leg. (teste Enderlein) (F. Peus) (Pinned: 1 m#) (USNM). **Other Material.** Colo./ Collection, C.V. Riley (Pinned: 2 m#) (WSU). COLORADO Park Co. #6, Wagon Tongue Cmpgrd. 5.2 mi. SW Lk. George, 22 July 1981. 8350', G.W. Byers & S.A. Teale (Pinned: 3 m#) (KU).

***Ptychoptera (Unguptycha) uta* Alexander, 1947.**

Ptychoptera uta Alexander, 1947

Ptychoptera uta Alexander, Alexander 1967

Diagnosis

Adult. Fore- and midcoxae with brown dot on anterodorsal surface, hindcoxae with upper portion of lateral surface brown. Male genitalia with hypandrial spathate lobes extending beyond ventral margin of gonopods, epandrial lobe with accessory subapical spine laterally at apex.

Female and immature stages unknown.

Description

Adult. Measurements (n=1). Overall length 7.4mm. **Head.** Width: 1.13mm, Height: 0.93mm, Length: 0.60mm; Antenna flagellum length: 4.1mm. **Thorax.** Length: 2.5mm, Height: 2.4mm; Wing length: 8.0mm, Width: 2.1. **Abdomen.** Length: 4.3mm.

Head. Vertex shining black, evenly provided with elongate trichoid sensilla posteriorly; frons extremely narrow strip, black. Occiput and genae with dense elongate yellow trichoid sensilla. Antennae: scape bright yellow, oblong cylinder with ring of long black trichoid sensilla well separated from dorsal apex; pedicel yellow basally, brown dorsally, globular, ring of trichoid sensilla on lateral margin. Flagellomeres brown, fusiform. Facial sclerite black, indistinct from clypeus, weakly inflated.

Clypeus rhomboidal, inflated, generally covered in yellow sensilla, dark yellow with brown spot at ventral apex. Maxillary palpus with segments 1&2 yellow, segment three and four muddy yellow, terminal segment brown. Labrum narrowly spade shaped, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae muddy yellow.

Thorax. Anteprenotum with transverse fold broader than height of anterior ridge, yellow medially, brown at lateroventral extremity, with elongate yellow trichoid sensilla at lateroventral apex, medial lobe approximately one third width of remainder of anteprenotum, highly tapered trapezoid, dorsal surface with medial notch. Prescutum and scutum greasy black, with numerous microscopic punctures with broad yellow stripe from posterior apex of prescutum to scutellum; medial and prescutal suture with row of minute clear trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum as longer yellow sensilla; long clear prealar sensilla present. Scutellum yellow. Mediotergite of metanotum greasy black, with light pollinosity, medially with elongate tapering yellow stripe extending less than $\frac{1}{2}$ length, lateral corners with short yellow triangular patches. Laterotergite of metanotum pollinose black, except for yellow patch near wing base, dorsal patch of very elongate yellow trichoid sensilla. Pleural sclerites all black, with heavy pollinosity. Anepisternal cleft narrow, membrane yellow. Suture between epimeron and metapleurite incomplete, weak. **Wing.** Hyaline, weak infuscation extending from base of R_{1+2} to CuA_1+CuA_2 fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 5.69mm, Apex of Sc to Apex of R_1 1.31mm, R_{3+4+5} stem 0.57mm, slight posterior turn at fork from R_{1+2} ; R_{4+5} stem 1.80mm; R_4 after fork 1.65mm, R_5 after fork 1.75mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 2.07 : 1.97$. r-m 0.35mm; M distal to r-m 2.53mm; M_1 0.79mm, not arcuate, M_2 0.54mm; $M\text{distal}:M_1 = 1.00:0.32$, $R_{3+4+5}:M\text{distal} = 1.00:2.81$, $R_4:M_1 = 1.00:0.46$. CuA_1 proximal 0.32mm, distal 2.05mm; CuA_2 1.23mm weak simple angle. CuA_2 to A_1 1.85mm. m-cu joins R_{3+4+5} before r-m. Halter yellow. Prehalter yellow. **Legs.** Forecoxa yellow dorsoanterior margin with dark brown spot and ventral margin with broad brown band sloping anterior, midcoxa yellow with dark brown spot on

dorsoanterior apex and ventral margin with broad brown band sloping anterior, hindcoxa dark brown with yellow spot dorsally on posterior surface. Femur and tibia yellow, darkening slightly at shared joint, joint of tibia and first tarsomere brown. First tarsomere light brown proximally, darkening distally. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Tergites and sternites black, posterior and posterior portion of lateral margins yellow except segment I which is uniform color, moderately covered in elongate yellow sensilla. Sternite VII forming plate under genitalia, with medial triangular notch prominent and directed posterior. **Male Genitalia.** Epandrial collar incomplete, developed medially and at epandrial apodemes, epandrial apodemes broad and triangular, extending flat across gonocoxal apodeme to hypandrium, break at epandrium absent. Epandrial lobes fused to composite claspers: massive, clawlike, medial curve poorly developed to triangular apex; subapical spine placed subapically, elongate acute spine; ventromesal lobe located $\frac{3}{4}$ length of epandrial lobe, round in cross section basally, petiolate, directed ventromedially, flattened subcircular pad with anterior margin emarginate; nodulated across surface, nodules with spaces between greater than width. Epiproct prominent, posterior with U-shaped notch medially; posteromedial stylus present, formed as low ridge on lateral margins of epiproct; hypoproct as per genus. Parameres paired, sclerotized portion separate and held together anterior with parameral membrane, medial spur absent; lateral margin with rounded spur approximately $\frac{1}{2}$ size of apical blade; apex of paramere flattened, paddle-like, broadly rounded triangle. Paramere recumbent. Gonopods as per genus, except apex of gonostylus extended posterior as triangular lobe beyond apex of dorsal glabrous ridge. Basal division of hypandrium with medial paired knobs low and subrectangular; spathate lobes triangular and directed dorsally, apex slightly inflated and round extending to gonocoxite, posterior margin of lobes not in contact medially. Terminal division with lateral canals at base prominent, membranous window elongate, extending from base nearly $\frac{2}{3}$ height of terminal

division. Apex of terminal division as per genus, angle of trough variable. Aedeagus as per genus, apex of subapical sclerite expanding weakly, anterior margin weakly emarginate, posterior margin convex.

Figures. Male Genitalia: 101, Wing: 102, Distribution: 103.

Material Examined. Holotype. Willard, Utah, Apr 29 1939/ G.F. Knowlton, F.C. Harmston, Collectors/ HOLOTYPE, *Ptychoptera, uta*, C.P. Alexander (Pinned & Slide, 1 m#, USNM); *Paratypes.* Willard, Utah, Apr 29 1939/ G.F. Knowlton, F.C. Harmston, Collectors (Pinned, 1m#, USNM); Utah, - Portage, May 7 – 1939, (Knowlton &, Harmston) (Slide, 1m#, USNM)

Taxonomic Notes

This species is known only from two collection events, both occurring in 1939. Based on the structure of the ventromesal lobe this species may be sister to *U. lacrimiformis* + *U. minor* as the structure in all of these species is pendulant, flattened and rounded. Unfortunately, there are not enough other morphological characters in the current dataset to fully resolve this relationship. The parameres are also unusual for *Unguptycha*, being dorsoventrally flattened as exhibited by *U. daimio* and *U. lenis*.

Ecological Notes. Collecting trips in 2011 and 2012 failed to find individuals of this species. The distribution of the species appears to be highly localized to the northern shore of the Great Salt Lake, extending towards the Idaho border. *Unguptycha coloradensis* complex populations have been recorded south, east, and northwest of the collecting localities of *U. uta*, again suggesting a high degree of endemism. Further collecting attempts for this species are warranted, although the significant landscape changes from agriculture and other human impacts in the region may have pushed the species to extinction.

Ptychoptera* incertae sedis**Ptychoptera* near *P. (Amblyptycha)* and *P. (Unguptycha)******Ptychoptera albimana* Fabricius, 1787.****Diagnosis**

Adult. Male. Epandrial clasper nematoform with thickened base, ventromesal lobe present. Gonostylus with knoblike basal lobe, apical stylus cylindrical with secondary lobe flattened and ovoid, directed medially.

Description

Adult. Measurements (n=1). Overall length 8.65mm. **Head.** Width: 1.0mm, Height: 1.03mm, Length: 0.65mm; Antenna flagellum length: 4.16mm. **Thorax.** Length: 2.8mm, Height: 2.6mm; Wing length: 9.2mm, Width: 2.4mm. **Abdomen.** Length: 5.2mm.

Head. Vertex shining black, weakly pollinose sparsely set with trichoid sensilla; frons as knifelike strip between antennae, black. Occiput with evenly spaced elongate yellow trichoid sensilla. Antennae: scape dark orange fading to brown at dorsal apex, oblong fusiform cylinder; pedicel brown, globular, few trichoid sensilla. Flagellomeres brown, fusiform, paddle-like 14th flagellomere present. Facial sclerite dark brown, very narrow and not well distinguished from clypeus, heavily incised. Clypeus elongate rhombus, bulbous, covered in macrotrichia ventrally, orange yellow. Maxillary palpus yellow turning light brown distally, ultimate segment extended nearly as long as remainder of palpus. Labrum rounded subtriangular, light yellow; epipharynx and hypopharynx not externally apparent, labium and labella light yellow.

Thorax. Antepronotum yellow medially, lateroventral apices turning chocolate brown, medial lobe narrow trapezoidal with medial notch absent; medial fold of antepronotum narrow. Prescutum and scutum covered in microtrichia, black with narrow yellow stripe above wing base; medial and prescutal suture with row of yellow trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum. Scutellum uniform bright yellow, dorsal surface with long, clear setae; lateral ridges dark yellow. Mediotergite of metanotum black with triangular yellow markings on dorsal margin, one on each dorsolateral corner; weakly pollinose, yellow sensilla along dorsal margin extending along medial portion to posterior margin. Laterotergite of metanotum shining, black-brown with yellow patch near wing base, dorsal patch of trichoid sensilla yellow. Pleural sclerites all black-brown, with weak pollinosity. Anepisternal cleft square, yellow, stripe extending ventrally halfway down episternum. Suture between epimeron and metapleurite weak, becoming obscure midway along length.

Wing. Two spots, proximal at rm , with secondary infuscation near base of R_{3+4+5} , larger distal spot at R_{4+5} fork. All veins covered in short stout macrotrichia, all wing cells with macrotrichia. Sc: 5.82mm, Apex of Sc to Apex of R_1 1.21mm, R_{3+4+5} stem 1.04mm, slight bend at fork from R_{1+2} ; R_{4+5} stem 1.60mm; R_4 after fork 2.0mm, R_5 after fork 1.93mm; $R_{3+4+5}:R_{4+5}$ -stem: R_4 x : x : x. r-m 0.27mm; M distal to r-m 2.66mm; M_1 0.99mm, squared, M_2 0.64mm; Mdistal: M_1 x:x, R_{3+4+5} :Mdistal x:x, R_4 : M_1 x:x. CuA_1 proximal 0.25mm, distal 2.37mm; CuA_2 1.28mm sinuous. CuA_2 to A_1 1.83mm. m-cu joins R_{3+4+5} before R_3 diverges. Halter yellow. Prehalter dark yellow. **Legs.** Coxae yellow with narrow brown band on dorsal margin. Femur yellow, darkening to brown near tibial joint, tibia brown. First tarsomere brown proximally, turning yellow distally on hindleg. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. All legs with Tibia 1st tarsomere with widely spaced double row of minute, spine-like trichoid sensilla.

Abdomen. Segment I black, Segment II-IV dark orange with brown band on posterior margin, posterior abdominal segments brown, posterior margin of segment VII orange yellow. **Male Genitalia.** Epandrial collar incomplete, developed at epiproct and at epandrial apodemes, epandrial apodemes broad and ribbonlike, extending flat across gonocoxal apodeme to hypandrium, break at epandrium absent. Epandrial lobes nematoform, with base considerably thickened approaching composite condition, narrow apex extending greater than length of basem, apex rounded; subapical spine present, located 2/3rds length of epandrial lobe, directed medioventrally, fingerlike; ventomesal lobe located 1/3 length of epandrial lobe, flattened, broad basally, expanding to heavily emarginate apex, anterior apex elongate, directed ventromedially. Epiproct prominent, posterior with U-shaped notch, lateral nodes well developed, posterior margin reaching epandrial collar; posteromedial stylus present, formed as low ridge on lateral margins of epiproct; hypoproct tonguelike.

Paramere forming broad bridge, lateral margins broad and rounded, anterior margin convex, posterior margin concave, posterior apices not readily apparent, distinct medial lobe present with apex notched, two narrow ventral triangular lobes, dorsal and ventral surface without lobes or spines.

Gonopods with gonocoxal apodeme pointed, dorsal spur broadly triangular, shifted to dorsal surface of gonocoxite, gonocoxite weakly expanding to apex; gonocoxal lobes absent; gonostylus with basal lobe directed medially, knob-like, somewhat dorsoventrally flattened; apical stylus elongate, round in cross section, apex rounded, glabrous dorsal ridge running on anterior surface, continuing on secondary lobe; secondary stylus paddle-like, medial apex rounded, directed somewhat posterior.

Basal division of hypandrium bandlike, semicircular in posterior view, lateral extensions to terminal division present, spathate lobes present near base of terminal division, compressed semicircular, basal scale absent. Terminal division of hypandrium with base constricted, lateral margins

extremely narrow, membranous window present from base of terminal division to apical position, apical portion triangular, with paired brushes of trichoid sensillae on laterally.

Aedeagus with sperm ejaculatory apodeme fan-like, larger than sperm sac, closely associated with aedeagal sclerites; sperm sac round; lateral ejaculatory processes directed anterior, dorsal margin heavily convex, nearly as broad as long; aedeagal sclerites very short, constricted at base, apex rounded; subapical sclerite forming paired wings extending near apex of lateral extension of terminal division, expanding to lateral apex. **Female Genitalia.** Cercal ratio width:height 1:3.5. Hypogynium rectangular with hypogynial valves essentially indistinguishable, lateral lobes absent, medial constriction weakly developed.

Figures. Male Genitalia: 104, Wing: 105, Distribution: 106.

Taxonomic Notes.

This widely distributed European species likely represents a species complex (Ujvarosi *et al*, 2011). The presence of a ventromesal lobe places this species as part of a well-supported clade containing (*P.*) *Amblyptycha* and (*P.*) *Unguptycha*.

Material Examined. Aebelø, 14 August 1946, Worm-Hansen (pinned: 1 f#) (ZMUC). Dania, Jylland, Rørbaek Sø, 28.juli 1964, Ole Martin (Pinned: 1 m#) (ZMUC). England (Pinned: 2 m#) (WSU). England – Oxford, Wytham Wood, May 12, 1963 (Pont, Ackland & Vane-Wright) (Slide: 1m#, 1f#) (USNM). Graz, 4 97 (1 m#, 1 f#) (WSU). Sierra Guadarrama, b. Escorial lg. Franz (Pinned: 1 m#) (ZMUC).

***Ptychoptera alina* Krzeminski & Zwick, 1993.**

Ptychoptera alina Krzeminski & Zwick, 1993: 70-73 (original description)

Diagnosis

Adult. Epandrium with clawlike composite epandrial claspers, ventromesal lobe present, base broad and ventral margin emarginate. Gonostylus with apical stylus laterally compressed, dorsoposterior corner extended. Hypandrium with spathate lobes semicircular, concealing majority of terminal division.

Description

Adult. Measurements (n=1). Overall length 10.14. **Head.** Width: 1.13mm, Height: 1.06mm, Length: 0.64mm; Antenna flagellum length: 3.5mm. **Thorax.** Length: 2.50mm, Height: 2.35mm; Wing length: 10.0mm, Width: 2.6mm. **Abdomen.** Length: 7.0mm.

Head. Vertex shining black, shining, sparsely set with trichoid sensilla; frons not reaching face, knifelike, black. Occiput with evenly spaced elongate yellow trichoid sensilla. Antennae: scape yellow, oblong fusiform cylinder; pedicel yellow, globular, ring of trichoid sensilla. Flagellomeres brown, fusiform. Facial sclerite dark brown, well developed subtriangular plate not incised by clypeus. Clypeus elongate triangle, bulbous, covered in macrotrichia generally, orange yellow with brown strip dorsally. Maxillary palpus yellow, ultimate segment brown, extended nearly as long as remainder of palpus. Labrum rounded trowel-shaped, light yellow; epipharynx and hypopharynx not externally apparent, labium and labella light yellow.

Thorax. Anteprenotum dark brown, anterolateral corners yellow, medial lobe broad, rectangular, with medial notch absent; medial fold of anteprenotum narrow. Prescutum and scutum covered in microtrichia, dark brown with narrow yellow stripe above wing base; medial and prescutal

suture with row of yellow trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum. Scutellum uniform bright yellow, dorsal surface with long, clear setae; lateral ridges light yellow. Mediotergite of metanotum black with triangular yellow markings on dorsal margin, one on each dorsolateral corner; shining, yellow sensilla along dorsal margin extending along medial portion to posterior margin. Laterotergite of metanotum shining, black-brown, dorsal patch of trichoid sensilla yellow. Pleural sclerites all black-brown, with weak pollinosity. Anepisternal cleft subtrapezoidal, muddy yellow. Suture between epimeron and metapleurite almost inevident.

Wing. Two broad bands, proximal extending from base of R_5 to CuA_1+CuA_2 fork, distal from R_{1+2} fork to base of R_5 ; membrane with macrotrichia in all cells except br & bm. All veins covered in short stout macrotrichia. Sc: 6.8mm, Apex of Sc to Apex of R_1 1.38mm, R_{3+4+5} stem 1.04mm, weakly bowed along length, nearly traverse; R_{4+5} stem 1.6mm; R_4 after fork 2.22, R_5 after fork 2.20mm; $R_{3+4+5}:R_{4+5}$ -stem: R_4 = 1.0 : 1.53 : 2.13. r-m 0.40mm; M distal to r-m 3.1mm; M_1 1.1mm, arcuate, M_2 0.7mm; Mdistal: M_1 = 1.0:0.35, R_{3+4+5} :Mdistal = 1.0:2.98, $R_4:M_1$ = 1.0:0.49. CuA_1 proximal 0.25, distal 3.65mm; CuA_2 1.55mm with anterior angle well developed, posterior angle absent. CuA_2 to A_1 2.10mm. r-m joins R_{3+4+5} at well before R_3 divergence. Halter yellow. Prehalter dark yellow. **Legs.** Fore- and midcoxae yellow, hindcoxa black. Femur yellow, darkening to brown near tibial joint, tibia brown at proximal joint, yellow medially, apex dark. All tarsi dark brown. 5th tarsomere can fold back on penultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensilla.

Abdomen. Tergites and sternites black, posterior and posterior portion of lateral margins yellow except segment I which is uniform color, moderately covered in elongate yellow sensilla. **Male Genitalia.** Epandrium with composite epandrial claspers, claspers narrow, longer than width of epandrium, weakly curving medially, fully divided by epiproct. Ventromesal lobe placed 3/4 length of epandrium, base broad, not petiolate, lateral margins straight, ventral margin heavily emarginate. Epiproct with lateral

apices well developed, medial notch distinctly round. Gonocoxite expanding to gonostylus, gonocoxal lobes absent. Gonostylus with basal lobe subdivided, anterior lobe setose flattened knob, dorsal lobe flattened, apical margin emarginate, forming two distinct rounded apices; apical stylus laterally compressed, curved medially, not tapering until apex with dorsoposterior corner extended to fingerlike point. Hypandrium with basal division band-like, spathate lobes flattened semicircular, extremely large obscuring almost entire length of terminal division; apex of terminal division forming acute spine.

Figures. Male Genitalia: 107, Wing: 108, Distribution: 109.

Taxonomic Notes. This species belongs to a well-supported clade containing *P. albimana*, (*P.*) *Amblyptycha* and (*P.*) *Unguptycha*, though its position within the clade has not been well resolved. A more extensive description and illustrations can be found in Krzeminski & Zwick, 1993.

Material Examined. ARMENIA, 10 km from Megri, 15.V.1957, L. Zimina (Pinned: 1 m#) (USNM).

***Ptychoptera* with plesiomorphic genital features**

***Ptychoptera alexanderi* Hancock, 2006.**

Diagnosis.

Adult. Epandrium nematoform. Paramere apices semicircular. Gonostylus simple, with scythe-like anterior directed basal lobe. Hypandrium with terminal division weakly delineated from basal division, apex spine-shaped.

Description

Adult. Measurements (n=1). Overall length 6.46mm. **Head.** Width: 0.93mm, Height: 0.95mm, Length: 0.76mm; Antenna flagellum length: 5.58mm. **Thorax.** Length: 1.8mm, Height: 1.8mm; Wing length: 7.4mm, Width: 2.2mm. **Abdomen.** Length: 3.9mm.

Head. Vertex shining dark brown, sparsely provided with elongate trichoid sensilla posteriorly; frons inevident. Occiput and genae with dense elongate yellow trichoid sensilla. Antennae: scape yellow, oblong cylinder with ring of long black trichoid sensilla well separated from dorsal apex; pedicel yellow, globular, ring of trichoid sensilla on lateral margin. Flagellomeres yellow, bacilliform. Facial sclerite brown, lunate, indistinct from clypeus. Clypeus quadrate, inflated, brown sensilla ventrally, yellow. Maxillary palpus yellow. Labrum reduced, yellow; hypopharynx and epipharynx not yellow, labium and labellae yellow.

Thorax. Antepronotum with transverse fold broader than height of anterior ridge, yellow, medial lobe approximately one third width of remainder of antepronotum, strong trapezoid, dorsal surface with medial notch. Prescutum and scutum obscurely shining metallic blue black, microtrichia vestiture present; medial and prescutal suture with row of minute clear trichoid sensilla; shortclear prealar sensilla present. Scutellum yellow medially, lateral ridges brown. Mediotergite of metanotum metallic yellow dorsomedially, brown ventrolaterally, shining. Laterotergite of metanotum shining yellow, brown posterodorsally. Pleural sclerites yellow, shining, except episternum brown. Anepisternal cleft narrow triangular, membrane yellow. Suture between epimeron and metapleurite well developed, weak. **Wing.** Three broad bands, proximal starting $\frac{2}{3}$ length R, extending to CuA, second extending from base of R_5 to angle of CuA₂, spot at R_{4+5} fork, distal from R_{4+5} fork to M fork; membrane with macrotrichia in all cells except br, bm, A. All veins covered in short stout macrotrichia. Sc: 5.2mm, Apex of Sc to Apex of R_1 1.36mm, R_{3+4+5} stem 0.54mm, straight, approaching transverse; R_{4+5} stem 1.43mm; R_4 after fork 1.92mm, R_5 after fork 1.8mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4$, 1.0 : 2.64mm : 3.55. r-m 0.39mm; M distal to r-m 2.15mm; M_1 1.09mm, M_2 0.76mm; Mdistal: M_1 , 1.0:0.50, $R_{3+4+5}:M\text{distal}$, 1.0:3.98, $R_4:M_1$, 1.0:0.56. CuA₁ proximal 0.49mm, distal 2.08mm; CuA₂ 1.43mm with anterior angle well developed, posterior angle absent. CuA₂ to A₁ 1.98mm. R_3 branch at r-m. Halter yellow. **Legs.** Coxae yellow. Femur and tibia yellow, darkening slightly at shared joint, joint of tibia and first tarsomere brown. First tarsomere light

brown proximally, darkening distally. All other tarsi brown. 5th tarsomere cannot fold back on pentultimate tarsomere. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Segments with anterior brown, posterior yellow. **Male Genitalia.** Epandrial collar complete, closely appressed to epandrial lobes; epandrial apodemes well developed, ribbon-like across gonocoxal apodeme to hypandrium, breaks present at epandrium and hypandrium. Epandrial lobes nematoform, elongate, narrow; epandrial clasper indistinguishable from epandrial lobe, apex rounded, epandrial lobes moderately curved ventrally without distinct angle. Epiproct readily apparent, small, lateral apices present, highly arctuate, medial notch well developed U shape, completely separating epandrial lobes. Posteromedial stylus absent. Hypoproct tongue-like, fused to quadrate subepandrial sclerite.

Parameral bridge attached broadly to gonocoxite, arcing dorsally, straight; apical lobes triangular, anteroposteriorly compressed.

Gonocoxal apodeme narrow, weakly tapering, apex pointed, dorsal spur weakly developed, not extending beyond dorsal margin of gonocoxite. Gonocoxite short, scarcely twice as long as tall, expanding posterior, dorsal margin straight, ventral margin bulging anterior. Dorsal gonocoxal lobe present, short, membranous finger-like lobe at 1/3 length of external portion of gonocoxite. Gonostylus with basal lobe sickle-shaped, directed anterior over dorsal surface of gonocoxite. Apical stylus round in cross section, over twice the length of gonocoxite, longer than epandrial claspers, apex spatulate. Secondary and tertiary lobes absent.

Hypandrium with basal division subhemispherically; spathate lobes absent; basal scale absent. Terminal division with broad base indistinguishably fused to basal division, triangular, directed dorsally. Membranous window absent.

Aedeagus approximately 45 degrees from vertical. Aedeagal sclerites with apex angled, simple, base broad, extending over sperm sac with posterior apex rounded, directed laterally. Lateral ejaculatory processes poorly developed, base straight, narrow, extended straight laterally; discoid apodemes truncate, directed subventral. Sperm sac oblong, with prominent transverse constriction approximately 2/3 length; larger than remainder of aedeagus, extending into abdominal segment VII. Ejaculatory apodeme narrow scythe-like, closely associated with aedeagal sclerites, smaller than sperm sac, paralleling dorsal margin of sperm sac. . Subapical sclerite wide basally, narrowing towards apex of aedeagal sclerites, apex forming potbellied spine, ventral surface serrated.

Female Genitalia. Tergite VII yellow. Cerci light orange, lateral ridge poorly defined, dorsal furrow poorly developed. Cercus length:width, 3:1. Hypogynium yellow, rotated dorsally approximately 30 degrees from vertical; base convex constricted weakly subapically. Apical margin triangular, medial apex extended posterior, lateral corner simple. Lateral margin concealed.

Figures. Male Genitalia: 110, Wing: 111, Distribution: 112.

Material Examined. Holotype. Mexico: Chiapas, El Triunfo, 1900m, 15°39'26"N 92°48'32"W, 28-30.vii.2003, *leg.* EG Hancock (Pinned: 1 m#) (GLAHM) **Paratype.** As type specimen (Pinned: 1 f#) (GLAHM) **Other Material.** COSTA RICA: Puntarenas, Estación Biol. Las Alturas, 8.95°N, 82.83°W, el. 1600, 26.ii.1993, col. D.E. Hansen (Pinned: 2 m#) (UMN)

***Ptychoptera ichitai* Nakamura & Saigusa, 2009**

Diagnosis

Adult. Epandrium nematoform. Paramere apices scythe-shaped, directed posteroventrally. Gonostylus simple, with peg like basal lobe. Hypandrium with terminal division weakly delineated from basal division, apex quadrate.

Description

Adult. Measurements (n=1). Overall length ? (dissected). **Head.** Width: 0.99mm, Height: 0.86mm, Length: 0.54mm; Antenna flagellum length: ? (damaged). **Thorax.** Length: 2.08, Height: 1.98mm; Wing length: 8.2mm, Width: 2.2mm. **Abdomen.** Length: ? (dissected).

Head. Vertex shining black, sparsely provided with elongate trichoid sensilla posteriorly; frons inevident. Occiput and genae with dense elongate yellow trichoid sensilla. Antennae: scape brown, oblong cylinder with ring of long black trichoid sensilla well separated from dorsal apex; pedicel brown with orange apex, globular, ring of trichoid sensilla on lateral margin. Flagellomere 1 yellow, remaining brown brown, bacilliform. Facial sclerite yellow, triangular, indistinct from clypeus, weakly flattened. Clypeus rhomboidal, inflated, brown sensilla ventrally, shining black. Maxillary palpus with proximal segments yellow, ultimate segment brown, extended. Labrum broadly spade shaped, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae orange yellow.

Thorax. Anteprenotum with transverse fold broader than height of anterior ridge, black, medial lobe approximately one quarter width of remainder of anteprenotum, strong trapezoid, dorsal surface with medial notch. Prescutum and scutum obscurely shining dark brown, microtrichia vestiture present; medial and prescutal suture with row of minute clear trichoid sensilla; shortclear prealar sensilla present. Scutellum brown. Mediotergite of metanotum black, shining, Laterotergite of metanotum shining black. Pleural sclerites black, shining. Anepisternal cleft narrow, membrane yellow. Suture between epimeron and metapleurite incomplete, weak. **Wing.** Single broad band extending from base of R_5 to angle of CuA_2 , spot at R_{4+5} fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 5.5mm, Apex of Sc to Apex of R_1 1.23mm, R_{3+4+5} stem 0.37mm, straight; R_{4+5} stem 1.73mm; R_4 after fork 1.78mm, R_5 after fork 1.85mm; $R_{3+4+5}:R_{4+5}$ -stem: R_4 , 1.0 : 4.67 : 4.81. r-m 0.32mm; M distal to r-m 2.35mm; M_1 1.01mm, M_2 0.69mm; Mdistal: M_1 , 1.0:0.42, R_{3+4+5} :Mdistal,

1.0:0.15, R₄:M₁, 1.0:0.56. CuA₁ proximal 0.37mm, distal 2.2mm; CuA₂ 1.36mm with anterior angle well developed, posterior angle absent. A₁ straight for x. R₃ with point contact at r-m. Halter yellow. **Legs.** Forecoxa and midcoxa yellow, hindcoxa brown. Femur and tibia yellow, darkening slightly at shared joint, joint of tibia and first tarsomere brown. First tarsomere light brown proximally, darkening distally. All other tarsi brown. 5th tarsomere cannot fold back on pentultimate tarsomere. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Segments black. **Male Genitalia.** Epandrial collar complete, closely appressed to epandrial lobes; epandrial apodemes well developed, ribbon-like across gonocoxal apodeme to hypandrium, breaks present at epandrium and hypandrium. Epandrial lobes nematoform, elongate, narrow; epandrial clasper much narrower than epandrial lobe, apex rounded, epandrial lobes moderately curved ventrally without distinct angle. Epiproct readily apparent, small, lateral apices present, medial notch well developed V shape; completely separating epandrial lobes forming broad arcs. Posteromedial stylus absent. Hypoproct tongue-like, fused to broadly T-shaped subepandrial sclerite.

Parameral bridge with narrow attachment to gonocoxite, arcing dorsally, medial portion formed into conical structure directed posterior, hollow anterior; apical lobes moderate length, not extending to apex of terminal division, laterally compressed spine spine, weakly curved ventrally without twisting.

Gonocoxal apodeme narrow, weakly tapering, apex pointed, dorsal spur weakly developed, not extending beyond dorsal margin of gonocoxite. Gonocoxite short, scarcely twice as long as tall, tapering posterior, dorsal margin bulging anterior, ventral margin straight. Gonocoxal lobes absent. Gonostylus with basal lobe forming minute peg at posteomedial margin. Apical stylus round in cross section, over twice the length of gonocoxite, longer than epandrial clasper, apex pointed and curved dorsally. Secondary and tertiary lobes absent.

Hypandrium with basal division subhemispherical; spathate lobes absent; basal scale absent. Terminal division with broad base indistinguishably fused to basal division, apex subquadrate, lateral margins weakly folded anterior. Membranous window absent.

Aedeagus approximately 45 degrees from vertical. Aedeagal sclerites with apex angled, simple, base broad, extending over sperm sac with posterior apex rounded, directed laterally. Lateral ejaculatory processes poorly developed, base straight, narrow, extended straight laterally; discoid apodemes scythe-like, directed dorsal. Sperm sac oblong; larger than remainder of aedeagus, extending into abdominal segment VII. Ejaculatory apodeme narrow scythe-like, closely associated with aedeagal sclerites, smaller than sperm sac, paralleling dorsal margin of sperm sac. Subapical sclerite wide basally, narrowing towards apex of aedeagal sclerites, apex broadly triangular, truncate apically, ventral surface smooth.

Figures. Male Genitalia: 113, Wing: 114.

Material Examined. Japan. (Pinned: 1 m#) (BMNH).

***Ptychoptera japonica* Alexander, 1913**

Diagnosis

Adult. Epandrium nematoform. Paramere apices L-shaped, directed laterally. Gonostylus simple, with peg like basal lobe. Hypandrium with terminal division weakly delineated from basal division, apex spine like.

Description

Head. Vertex shining russet brown, sparsely provided with elongate trichoid sensilla posteriorly; frons inevident. Occiput and genae with dense elongate yellow trichoid sensilla. Antennae: scape brown,

oblong cylinder with ring of long black trichoid sensilla well separated from dorsal apex; pedicel brown with orange apex, globular, ring of trichoid sensilla on lateral margin. Flagellomere 1 yellow, remaining brown brown, bacilliform. Facial sclerite yellow, triangular, indistinct from clypeus, weakly flattened. Clypeus rhomboidal, inflated, brown sensilla ventrally, shining russet brown. Maxillary palpus with proximal segments yellow, ultimate segment brown, extended. Labrum broadly spade shaped, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae orange yellow.

Thorax. Anteprenotum with transverse fold broader than height of anterior ridge, russet brown, medial lobe approximately one quarter width of remainder of anteprenotum, strong trapezoid, dorsal surface with medial notch. Prescutum and scutum obscurely shining dark brown, microtrichia vestiture present; medial and prescutal suture with row of minute clear trichoid sensilla; shortclear prealar sensilla present. Scutellum brown. Mediotergite of metanotum russet brown, shining, Laterotergite of metanotum shining russet brown. Pleural sclerites russet brown, shining. Anepisternal cleft narrow, membrane yellow. Suture between epimeron and metapleurite incomplete, weak. **Legs.** Forecoxa yellow, posterior coxae brown. Femur and tibia yellow, darkening slightly at shared joint, joint of tibia and first tarsomere brown. First tarsomere light brown proximally, darkening distally. All other tarsi brown. 5th tarsomere cannot fold back on pentultimate tarsomere. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Segments russet brown. **Male Genitalia.** Epandrial collar complete, closely appressed to epandrial lobes; epandrial apodemes well developed, ribbon-like across gonocoxal apodeme to hypandrium, breaks present at epandrium and hypandrium. Epandrial lobes nematoform, elongate, narrow; epandrial clasper much narrower than epandrial lobe, apex rounded and weakly bulbous, epandrial lobes moderately curved ventrally without distinct angle. Epiproct readily apparent, small,

lateral apices present, medial notch well developed U shape; completely separating epandrial lobes.

Posteromedial stylus absent. Hypoproct tongue-like, fused to broadly T-shaped subepandrial sclerite.

Parameral bridge with narrow attachment to gonocoxite, arcing dorsally, medial portion formed into conical structure directed posterior, hollow anterior; apical lobes elongate, extending beyond apex of terminal division, elongate flattened spine twisting flat, apices directed laterally.

Gonocoxal apodeme narrow, weakly tapering, apex pointed, dorsal spur weakly developed, not extending beyond dorsal margin of gonocoxite. Gonocoxite short, scarcely twice as long as tall, tapering posterior, dorsal margin bulging anterior, ventral margin straight. Gonocoxal lobes absent. Gonostylus with basal lobe forming minute peg at posteomedial margin. Apical stylus round in cross section, over twice the length of gonocoxite, longer than epandrial clasper, apex pointed and curved dorsally. Secondary and tertiary lobes absent.

Hypandrium with basal division subhemispherically; spathate lobes absent; basal scale absent. Terminal division with broad base indistinguishably fused to basal division, triangular, directed dorsally. Membranous window absent.

Aedeagus approximately 45 degrees from vertical. Aedeagal sclerites with apex angled, simple, base broad, extending over sperm sac with posterior apex rounded, directed laterally. Lateral ejaculatory processes poorly developed, base straight, narrow, extended straight laterally; discoid apodemes scythe-like, directed dorsal. Sperm sac oblong; larger than remainder of aedeagus, extending into abdominal segment VII. Ejaculatory apodeme narrow scythe-like, closely associated with aedeagal sclerites, smaller than sperm sac, paralleling dorsal margin of sperm sac. Subapical sclerite wide basally, narrowing towards apex of aedeagal sclerites, apex forming potbellied spine, ventral surface serrated.

Female Genitalia. Tergite VII brown. Cerci yellow, lateral ridge well defined, dorsal furrow poorly

developed. Cercus length:width, 2.5:1. brown, rotated dorsally approximately 30 degrees from vertical; base subhemispherical. Apical margin triangular, medial apex with projecting posterior, lateral corner expanded. Lateral margin hidden.

Figures. Male Genitalia: 115, Distribution: 116.

Material Examined. Holotype. Tokyo, Japan; May 7, 1912 (Alcohol: 1 m#) (USNM). **Paratype.** Same as holotype specimen (Alcohol: 1 f#) (USNM).

***Ptychoptera yamato* Nakamura & Saigusa, 2009**

Diagnosis.

Adult. Epandrium nematoform. Paramere apices corkscrew shaped, directed posterior. Gonostylus simple, with peg like basal lobe. Hypandrium with terminal division weakly delineated from basal division, apex spine like.

Description

Adult. Measurements (n=1). Overall length x. **Head.** Width: 1.09mm, Height: 0.94mm, Length: 0.60mm; Antenna flagellum length: 8.25mm. **Thorax.** Length: 2.35mm, Height: 2.30; Wing length: 9.98mm, Width: 3.71mm. **Abdomen.** Length: 5.7mm.

Head. Vertex shining russet brown, sparsely provided with elongate trichoid sensilla posteriorly; frons inevident. Occiput and genae with dense elongate yellow trichoid sensilla. Antennae: scape brown, oblong cylinder with ring of long black trichoid sensilla well separated from dorsal apex; pedicel brown with orange apex, globular, ring of trichoid sensilla on lateral margin. Flagellomere 1 yellow, remaining brown brown, bacilliform. Facial sclerite yellow, triangular, indistinct from clypeus, weakly flattened. Clypeus rhomboidal, inflated, brown sensilla ventrally, shining russet brown. Maxillary palpus with

proximal segments yellow, ultimate segment brown, extended. Labrum broadly spade shaped, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae orange yellow.

Thorax. Anteprenotum with transverse fold broader than height of anterior ridge, russet brown, medial lobe approximately one quarter width of remainder of anteprenotum, strong trapezoid, dorsal surface with medial notch. Prescutum and scutum obscurely shining dark brown, microtrichia vestiture present; medial and prescutal suture with row of minute clear trichoid sensilla; shortclear prealar sensilla present. Scutellum brown. Mediotergite of metanotum russet brown, shining, Laterotergite of metanotum shining russet brown. Pleural sclerites russet brown, shining. Anepisternal cleft narrow, membrane yellow. Suture between epimeron and metapleurite incomplete, weak. **Wing.** Single broad band extending from base of R_5 to angle of CuA_2 , spot at R_{4+5} fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 6.2mm, Apex of Sc to Apex of R_1 1.60mm, R_{3+4+5} stem 0.39mm, straight; R_{4+5} stem 2.47mm; R_4 after fork 2.15, R_5 after fork 2.2mm; R_{3+4+5} : R_{4+5} -stem: R_4 , 1.0 : 6.33 : 5.51. r-m 0.39mm; M distal to r-m 3.10; M_1 1.15, M_2 0.75mm; Mdistal: M_1 , 1.0:0.37, R_{3+4+5} :Mdistal, 1.0:0.12, R_4 : M_1 , 1.0:0.53. CuA_1 proximal 0.39mm, distal 2.75mm; CuA_2 1.55mm with anterior angle well developed, posterior angle absent. CuA_2 to A_1 2.3mm. R_3 branching at r-m. Halter yellow. **Legs.** Forecoxa yellow, posterior coxae brown. Femur and tibia yellow, darkening slightly at shared joint, joint of tibia and first tarsomere brown. First tarsomere light brown proximally, darkening distally. All other tarsi brown. 5th tarsomere cannot fold back on pentultimate tarsomere. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Segments russet brown. **Male Genitalia.** Epandrial collar complete, closely appressed to epandrial lobes; epandrial apodemes well developed, ribbon-like across gonocoxal apodeme to hypandrium, breaks present at epandrium and hypandrium. Epandrial lobes nematoform, elongate, narrow; epandrial clasper much narrower than epandrial lobe, apex rounded, epandrial lobes

moderately curved ventrally without distinct angle. Epiproct readily apparent, small, lateral apices present, medial notch well developed U shape; completely separating epandrial lobes. Posteromedial stylus absent. Hypoproct tongue-like, fused to broadly T-shaped subepandrial sclerite.

Parameral bridge with narrow attachment to gonocoxite, arcing dorsally, medial portion formed into conical structure directed posterior, hollow anterior; apical lobes elongate, extending beyond apex of terminal division, elongate flattened spine twisting along length, apices directed medially.

Gonocoxal apodeme narrow, weakly tapering, apex pointed, dorsal spur weakly developed, not extending beyond dorsal margin of gonocoxite. Gonocoxite short, scarcely twice as long as tall, tapering posterior, dorsal margin bulging anterior, ventral margin straight. Gonocoxal lobes absent. Gonostylus with basal lobe forming minute peg at posteomedial margin. Apical stylus round in cross section, over twice the length of gonocoxite, longer than epandrial clasper, apex pointed and curved dorsally. Secondary and tertiary lobes absent.

Hypandrium with basal division subhemispherically; spathate lobes absent; basal scale absent. Terminal division with broad base indistinguishably fused to basal division, triangular, directed dorsally. Membranous window absent.

Aedeagus approximately 45 degrees from vertical. Aedeagal sclerites with apex angled, simple, base broad, extending over sperm sac with posterior apex rounded, directed laterally. Lateral ejaculatory processes poorly developed, base straight, narrow, extended straight laterally; discoid apodemes scythe-like, directed dorsal. Sperm sac oblong; larger than remainder of aedeagus, extending into abdominal segment VII. Ejaculatory apodeme narrow scythe-like, closely associated with aedeagal sclerites, smaller than sperm sac, paralleling dorsal margin of sperm sac. Subapical sclerite wide basally, narrowing towards apex of aedeagal sclerites, apex forming potbellied spine, ventral surface serrated.

Figures. Male Genitalia: 117, Wing: 118, Distribution: 119.

Material Examined. Japan, Kamikochi, 5000', VI-13-39, Swenson (Pinned: 3 m#) (USNM).

Afrotropical *Ptychoptera*

***Ptychoptera africana* Alexander, 1920**

Diagnosis

Adult. Wing with three bands, and anterior margin infuscated. Male genitalia with gonostylus having semicircular secondary lobe and spine-like apical stylus with rounded apex.

Description

Adult. Measurements (n=1). Overall length x. **Head.** Width: 0.99mm, Height: 0.85mm, Length: 0.57mm; Antenna flagellum length: ? (damaged). **Thorax.** Length: 1.9mm, Height: 2.0mm; Wing length: 7.6mm, Width: 2.0mm. **Abdomen.** Length: ? (dissected).

Head. Vertex shining black, evenly provided with elongate trichoid sensilla posteriorly; frons extremely narrow strip, black. Occiput and genae glabrous. Antennae: dark brown, oblong cylinder with ring of long black trichoid sensilla well separated from dorsal apex; pedicel dark brown, globular, ring of trichoid sensilla on lateral margin. Flagellomeres brown, fusiform. Facial sclerite black, indistinct from clypeus, weakly inflated. Clypeus rectangular, inflated, generally covered in clear sensilla, dark brown. Maxillary palpus with all segments brown, ultimate segment extended. Labrum narrowly semicircular, brown; hypopharynx and epipharynx not externally apparent, labium dark orange, labella dark brown.

Thorax. Anteprenotum with transverse fold broader than height of anterior ridge, yellow except medial lobe brown, with elongate yellow trichoid sensilla at lateroventral apex, medial lobe approximately one third width of remainder of anteprenotum, highly tapered trapezoid, dorsal surface

with medial notch. Prescutum and scutum dark brown obscurely shining, with macrotrichia vestiture; medial and prescutal suture with row of minute clear trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum as longer yellow sensilla; long clear prealar sensilla present. Scutellum brown. Mediotergite of metanotum dark brown, with light pollinosity. Laterotergite of metanotum yellow, except for dorsal patch of very elongate yellow trichoid sensilla. Pleural sclerites all muddy yellow, with heavy pollinosity. Anepisternal cleft broad subquadrate, membrane yellow. Suture between epimeron and metapleurite complete. **Wing.** Three bands, basal band proximal to h, medial band extending from base of R_{1+2} to CuA_2 bend, apical band extending proximal to R_{4+5} and M fork to apex of CuA_1 , anterior margin of wing with cells C and Sc infuscated; membrane with macrotrichia in all cells except br and bm. All veins covered in short stout macrotrichia. Sc: 4.06mm, Apex of Sc to Apex of R_1 1.11mm, R_{3+4+5} stem 0.32mm, straight; R_{4+5} stem 1.41mm; R_4 after fork 1.38mm, R_5 after fork 1.43mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.0 : 4.40 : 4.31$. r-m 0.27mm; M distal to r-m 1.73mm; M_1 1.04mm, nearly flat, M_2 0.81mm; $M\text{distal}:M_1 = 1.0 : 0.60$, $R_{3+4+5}:M\text{distal} = 1.0 : 5.4$, $R_4:M_1 = 1.0 : 0.73$. CuA_1 proximal 0.20mm, distal 1.85mm; CuA_2 1.11mm sinuous. CuA_2 to 1.90mm. R_3 branches at r-m. Halter yellow basally, brown apically. Prehalter yellow. **Legs.** Forecoxa yellow dorsoanterior margin with dark brown spot and ventral margin with broad brown band sloping anterior, midcoxa yellow with dark brown spot on dorsoanterior apex and ventral margin with broad brown band sloping anterior, hindcoxa dark brown with yellow spot dorsally on posterior surface. Femur and tibia yellow, darkening slightly at shared joint, joint of tibia and first tarsomere brown. First tarsomere light brown proximally, darkening distally. All other tarsi brown. 5th tarsomere cannot fold back on pentultimate tarsomere. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Tergites and sternites brown, base of segment II with yellow band, segment VII yellow. **Male Genitalia.** Epandrial collar complete, distinct from epandrial lobes; epandrial apodemes well developed, ribbon-like across gonocoxal apodeme to hypandrium, breaks present at epandrium and

hypandrium. Epandrial lobes nematoform, extending beyond apex of gonostylus, very narrow, apex acutely pointed; epandrial clasper not distinguishable from epandrial lobe. Epiproct readily apparent, posterior margin largely straight with minute notch medially, low ridge on either side of notch, epandrial lobes not in contact. Posteromedial stylus absent. Hypoproct tonguelike, subepandrial sclerite present, single, broadly arrow shaped pointing anterior. Parameral bridge attached narrowly to gonocoxite, directed medially, joining with U-shaped medial structure, posterolateral apices of medial structure extending beyond union with paramere dae, apex flattened rounded, expanding weakly. Apical lobes directed dorsally, located at 2/3rds length of medial structure, quadrate in lateral view, extended rounded posteromedial directed lobe in dorsal view, anterolateral corner with elongate spine with base directed lateral, angling anterior to elongate acute point. Gonocoxal apodeme elongate semicircular, 1/3rd length of remainder of gonocoxite. Dorsal spur of gonocoxal apodeme short, recumbent anterior, less than 1/4th length of remainder of gonocoxal apodeme. Gonocoxite tapering to gonostylus, expanding immediately at joint, dorsal margin weakly emarginate. Gonocoxal lobes absent. Gonostylus with basal lobe directed dorsally, somewhat clavate, with extensive semicircular webbing extending from posterior margin along apical stylus, larger and more distinctive than remainder of basal lobe, dorsal margin with stout trichoid sensilla. Apical stylus very short, thin, curved medially, portion distal of basal lobe approximately 1.25x length of basal lobe, round in cross section, expanding rounded apex, secondary lobe absent. Hypandrium with basal division broad laterally, narrowing considerably medially, with ventral margin forming a point. Spathate lobes present, massive, similar in size to gonocoxite, sebrhomboidal with ventral corner extended, base petiolate, located approximately 1/3rd of height dorsally on lateral margin. Terminal division weakly developed medially, lateral strips not contacting medial portion of basal division, lateral extensions well developed, supporting apex; apex bulging posterior, ventral margin convex and dorsal margin concave, with distinctive laterally compressed semicircular lobes on lateral margins. Aedeagus orientation vertical. Aedeagal sclerites with apex

pointed, simple. Subapical sclerite with base broad, subcircular, narrowing to extremely acute spine beyond apex of aedeagal sclerites. Sperm sac oblong. Ejaculatory apodeme flag-like, closely associated with aedeagal sclerites, much larger than sperm sac, weakly paralleling anterior margin of sperm sac. Lateral ejaculatory processes directed anterolaterally, discoid apodeme extremely large, extending both dorsally and ventrally beyond base of lateral ejaculatory process. **Female Genitalia.** Tergite VII yellow. Cerci orange basally, apex yellow, lateral ridge poorly defined, dorsal furrow well developed. Cercus length:width, 3.5:1. Hypogynium yellow, rotated dorsally approximately 30 degrees from vertical; constricted basally, expanding medially, distinct keel along length. Apical margin triangular. Lateral margin concealed.

Figures. Male Genitalia: 120, Wing: 121, Distribution: 122.

Material Examined. Holotype. Pres. by, Ent. Res. Committee, 1911.4.22/ Ilyesha, S. Nigeria, Capt. R.E.R. Humfrey (Pinned: 1 f#) (BMNH). **Other Material.** Nigeria – Wen. State, Ile-Ife, Mar. 9, '75, (J.T. Mealer) (Slide: 1 m#, Pinned: 1 m# 11-21.'74) (USNM). **Questionable specimen.** Angola, Dunda, Forest, Luachimo, X-2-'60, Machado (Pinned: 1 f#) (USNM).

***Ptychoptera camerounensis* Alexander, 1921**

Diagnosis

Adult. Head with shining blue-black coloration. Pleural sclerites and abdomen orange. Two bands on wing. Male genitalia with gonocoxite wider than tall.

Description

Adult. Measurements (n=1). Overall length 7.57mm. **Head.** Width: 1.0mm, Height: 0.84mm, Length: 0.57mm; Antenna flagellum length: ? (missing). **Thorax.** Length: 1.8mm, Height: 1.78mm; Wing length: 7.3mm, Width: 1.9mm. **Abdomen.** Length: 5.2mm.

Head. Vertex shining blue-black, evenly provided with elongate trichoid sensilla posteriorly; frons extremely narrow strip, blue-black. Occiput and genae nearly bare. Antennae unknown. Facial sclerite black, indistinct from clypeus, weakly inflated. Clypeus rhomboidal, inflated, generally covered in yellow sensilla, dark blue black. Maxillary palpus with segment 1 brown, segments 2-4 dark yellow, final segment brown. Labrum narrowly semicircular brown; hypopharynx and epipharynx not externally apparent, labium and labellae orange.

Thorax. Antepronotum with transverse fold narrower than height of anterior ridge, dark brown, with elongate yellow trichoid sensilla at lateroventral apex, medial lobe approximately one quarter width of remainder of antepronotum, highly tapered trapezoid, dorsal surface with medial notch. Prescutum and scutum dark brown subobscurely shining, with microtrichia vestiture; medial and prescutal suture with row of minute clear trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum as longer yellow sensilla; short clear prealar sensilla present. Scutellum orange brown. Mediotergite of metanotum orange brown, with light pollinosity,. Laterotergite of metanotum shining orange brown, dorsal patch of very elongate yellow trichoid sensilla. Pleural sclerites dark brown dorsally, orange ventrally, with weak pollinosity. Anepisternal cleft broadly triangular, membrane yellow. Suture between epimeron and metapleurite complete. **Wing.** Two bands, proximal extending from base of R_{1+2} to CuA_1+CuA_2 fork, posterior from R_2 to the M fork, small spot at apical margin of cell CuA_1 ; membrane with macrotrichia in all cells except bm and a. All veins covered in short stout macrotrichia. Sc: 4.5mm, Apex of Sc to Apex of R_1 1.11mm, R_{3+4+5} stem 0.17mm, straight, oblique; R_{4+5}

stem 1.5mm; R_4 after fork 1.60mm, R_5 after fork 1.48mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.0 : 8.82 : 8.70$. r-m 0.3mm; M distal to r-m 1.93mm; M_1 0.91mm, arcuate, M_2 0.72mm; $M\text{distal}:M_1 = 1.0 : 0.47$, $R_{3+4+5}:M\text{distal} = 1.0 : 11.35$, $R_4:M_1 = 1.0 : 0.56$. CuA_1 proximal 0.22mm, distal 2.08mm; CuA_2 1.18mm sinuous. CuA_2 to A_1 2.03mm. r-m joins R_3 only point contact with r-m. Halter yellow. Prehalter yellow.

Legs. All coxae yellow. Femur yellow, darkening slightly at tibial joint, remaining segments brown. First tarsomere light brown proximally, darkening distally. All other tarsi brown. 1st tarsomere and tibia on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Segments orange, posterior margin of tergites II-VI with brown band on posterior margin, tergites V & VI brown, VII orange. **Male Genitalia.** Epandrial lobes nematoform, extending to apex of gonostylus, very narrow, apex pointed; epandrial clasper not distinguishable from epandrial lobe. Epiproct readily apparent, posterior margin with lateral margins broadly rounded, medial notch V-shaped. Posteromedial stylus absent. Hypoproct tongue-like.

Gonocoxite ovoid, wider than tall. Gonocoxal lobes absent. Gonostylus with basal lobe directed mediodorsally, round in cross section, fingerlike. Apical stylus subequal in length to gonocoxite, round in cross section, fingerlike, curved dorsally.

Hypandrium with bandlike basal division broad laterally; spathate lobes present, massive, similar in size to gonocoxite, semicircular, base tapering, located approximately 1/3rd of height dorsally on lateral margin. Basal scale present, divided, apical margin rounded. Terminal division with base constricted, articulated, apex parallel sided stylate process with rounded tip.

Figures. Male Genitalia: 123, Wing: 124, Distribution: 125.

Material Examined. Holotype. Lolodorf, Kamerun, A.I. Good. (Pinned: 1 m#) (CMNH)

Ptychoptera capensis* Alexander, 1917*Diagnosis**

Adult. Orange yellow, with brown banded abdomen. Wing with one band and pair of apical spots. Male genitalia with gonostylus having semicircular basal lobe, apical stylus truncate with rounded apex. Female genitalia with hypogyium constricted transversely.

Description

Adult. Measurements (n=1). Overall length? (head missing).. **Thorax.** Length: 2.25mm, Height: 2.45mm; Wing length: 7.5mm, Width: 3.0mm. **Abdomen.** Length: 8.3mm.

Head. Vertex shining light brown, sparsely provided with elongate trichoid sensilla posteriorly; frons extremely narrow strip, yellow. Occiput and genae with dense short yellow trichoid sensilla. Antennae: scape bright yellow, subconical cylinder with limited sensilla; pedicel yellow globular, ring of trichoid sensilla on weakly developed. Flagellomeres dark yellow, fusiform. Facial sclerite yellow, indistinct from clypeus. Clypeus rhomboidal, inflated, generally covered in yellow sensilla, bright yellow. Maxillary palpus with segments yellow, final segment extended. Labrum narrowly spade shaped, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae muddy yellow.

Thorax. Antepronotum with transverse fold broader than height of anterior ridge, yellow with elongate yellow trichoid sensilla at lateroventral apex, medial lobe approximately one quarter width of remainder of antepronotum, weakly tapered trapezoid, dorsal surface without medial notch. Prescutum and scutum shining yellow, brown medially, with microtrichia vestiture; medial and prescutal suture with row of minute clear trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum as longer yellow sensilla; long short prealar sensilla present. Scutellum yellow. Mediotergite of yellow, shining. Laterotergite of yellow, dorsal patch of stout black trichoid sensilla. Pleural sclerites all

yellow, with heavy pollinosity. Anepisternal cleft narrow, membrane yellow. Suture between epimeron and metapleurite complete. **Wing.** With band extending from apex of Sc, R_5 and angle of R_3 to CuA_2 apex, spots at R_2 and R_{4+5} fork. Macrotrichia in all cells except br, bm, CuA, and A. All veins covered in short stout macrotrichia. Sc: 5.37mm, Apex of Sc to Apex of R_1 1.48mm, R_{3+4+5} stem 0.32mm, weakly bowed anterior; R_{4+5} stem 1.71mm; R_4 after fork 2.03mm, R_5 after fork 2.03; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.0 : 5.34 : 6.34$. r-m 0.37mm; M distal to r-m 2.27mm; M_1 1.02mm, arcuate, M_2 1.04mm; $M\text{distal}:M_1 = 1.0 : 0.44$, $R_{3+4+5}:M\text{distal} = 1.0 : 7.09$, $R_4:M_1 = 1.0 : 0.50$. CuA_1 proximal 0.30mm, distal 2.40mm; CuA_2 1.28mm sinuous. CuA_2 to A_1 2.35mm. R_3 branches at r-m. Halter yellow. Prehalter yellow. **Legs.** All coxae yellow. Femur and tibia yellow, darkening slightly at shared joint, joint of tibia and first tarsomere brown. First tarsomere light brown proximally, darkening distally. All other tarsi brown. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Tergites and sternites yellow, segments II-V, segment VI brown basally, yellow apically, posterior segments yellow. **Male Genitalia.** Epandrial collar incomplete, gap medially, closely appressed to epandrial lobes; epandrial apodemes well developed, ribbon-like across gonocoxal apodeme to hypandrium, breaks present at epandrium and hypandrium. Epandrial lobes nematoform, short, subconical; epandrial clasper weakly delineated as taper from epandrial lobe, truncated apex, half-length of epandrial lobe. Epiproct readily apparent, posterior margin straight, epandrial lobes not in contact. Posteromedial stylus absent. Hypoproct and subepandrial membrane not apparent in specimens examined. Parameral bridge attached narrowly to gonocoxite, directed medially, zig-zag in dorsal view with two anterior apices and three posterior apices. Apical lobe placed posteriorly on lateral posterior apices, flattened, base directed posterior, apical portion directed medially at right angle, with posterior margin with serrate notches. Gonocoxal apodeme strongly tapering, apex rounded, greater than half length of gonocoxite,. Dorsal spur of gonocoxal apodeme present, very narrow, closely associated with posterior margin of gonocoxite. Gonocoxite tapering to gonostylus. Gonocoxal lobes

absent. Gonostylus with basal lobe directed medially hatch shaped in dorsal view, covered in trichoid sensilla. Apical stylus very short, subequal in length to basal lobe, cylindrical with rounded apex. Hypandrium damaged on specimen examined. Basal division with spathate lobes present, located approximately 1/3rd of height dorsally on lateral margin, base petiolate, apex heavily expanded, scallop shaped, anteroventral margin heavily incised. Terminal division funnel shaped, otherwise obscured in specimens examined. Aedeagus orientation vertical. Aedeagal sclerites with apex pointed, simple. Subapical with base broad, subcircular, narrowing to extremely acute spine beyond apex of aedeagal sclerites. Sperm sac oblong. Ejaculatory apodeme flag-like, closely associated with aedeagal sclerites, much larger than sperm sac, weakly paralleling anterior margin of sperm sac. Lateral ejaculatory processes directed anterolaterally, discoid apodeme extremely large, extending both dorsally and ventrally beyond base of lateral ejaculatory process. **Female Genitalia.** Tergite VII yellow. Cerci orange basally, apex yellow, lateral ridge poorly defined, dorsal furrow poorly developed. Cercus length:width, 3.5:1. Hypogynium yellow, rotated dorsally approximately 30 degrees from vertical; with subquadrate lateral plateaus, constricted transversely. Apical margin triangular, lateral margins expanded. Lateral margin concealed.

Figures. Male Genitalia: 126, Wing: 127, Distribution: 128.

Material Examined. Natal, Zululand, Eohome, 1650', Jan. 57, Knauss (Pinned, 1 f#) (USNM).

South Africa – Natal, Ngome Forest, Vryheid-Nongoma, Apr. 11-12 1960, Brian and Pamela Stuckenberg (Slide: 1 m#) (USNM). Kaapmuiden, E. Transvaal, Oct. 1919, (H.K. Munro) (Slide: 1 m#) (USNM).

Ptychoptera madagascariensis* Alexander, 1937*Diagnosis**

Adult. Epandrium nematoform with medial swelling at 2/3rds length of epandrial clasper, gonostyli longer than epandrial clasper.

Description

Male Genitalia. Epandrial collar complete, closely appressed to epandrial lobes; epandrial apodemes well developed, thread-like across gonocoxal apodeme to hypandrium, breaks present at epandrium and hypandrium. Epandrial lobes nematoform, elongate, narrow; epandrial clasper weakly delineated from epandrial lobe, apex rounded, prominent medial swelling at 3/4 length of epandrial lobe complex, epandrial lobes moderately curved ventrally without distinct angle. Epiproct readily apparent, small, lateral apices present, low and broad, medial , completely separating epandrial lobes. Posteromedial stylus absent. Hypoproct fused to subepandrial sclerite, quadrate, paired posterior lobes present.

Parameral bridge attached broadly to gonocoxite, arcing dorsally, flexed posterior; apical lobes triangular, laterally compressed.

Gonocoxal apodeme narrow, weakly tapering, apex rounded, dorsal spur subobtuse, over half length of apodeme, ventral margin simple, weakly angled. Gonocoxite elongate, weakly expanding medially, tapering toward gonostylus, dorsal and ventral margins forming loose arc. Gonocoxal lobes absent. Gonostylus with basal lobe having two subdivisions, anterior lobe low rounded dome, medial lobe semiovoid. Apical stylus fingerlike, round in cross section, apex curved dorsally, weakly expanding, over twice length of external portion of gonocoxite. Secondary lobe directed dorsomedially at 1/5 length

of apical stylus, fingerlike, tapering at apex. Tertiary lobe present, fingerlike, 1/3 along length of apical stylus.

Basal division band-like, sloping dorsally; spathate lobes present at base of terminal division, semicircular; basal scale present, divided, petiolate base with spoon shaped apex. Terminal division recumbent, with constricted, articulated base, lateral sclerites broad; apex with prominent lateral extensions fused to basal division, dorsal apex spine-like. Membranous window wide oval, stretching nearly entire length of terminal division.

Aedeagus within approximately 20 degrees of vertical. Aedeagal sclerites with apex pointed, with ventral tooth visible in lateral view, base broad. Lateral ejaculatory processes with base straight, narrow, extended straight lateroanterior; discoid apodemes with elongate ovoid dorsal extension. Sperm sac subspherical. Ejaculatory apodeme flag-like, closely associated with aedeagal sclerites, larger than sperm sac, paralleling anterior margin of sperm sac. . Subapical sclerite cylindrical, apex tapering and weakly bent posterior.

Figures. Male Genitalia: 129, Distribution: 130.

Material Examined. Holotype. Madagascar, Nanisana, 1932 (G. Olsoufieff) (Alcohol: 1 m#) (USNM). **Paratype.** As holotype specimen (Alcohol & Slide: 1 m#) (USNM).

***Ptychoptera matongoensis* Alexander, 1958**

Diagnosis

Adult. Orange yellow, with brown banded abdomen. Wing with one band and pair of apical spots. Female genitalia with hypogyium straight sided.

Description

Adult. Measurements (n=1). Overall length 11.13mm. **Head.** Width: 1.23mm, Height: 1.04mm, Length: 0.62mm; Antenna flagellum length: 3.7mm. **Thorax.** Length: 2.65mm, Height: 2.9mm; Wing length: 12.71mm, Width: 2.2mm. **Abdomen.** Length: 7.86mm.

Head. Vertex shining light brown, sparsely provided with elongate trichoid sensilla posteriorly; frons extremely narrow strip, yellow. Occiput and genae with dense short yellow trichoid sensilla. Antennae: scape bright yellow, subconical cylinder with limited sensilla; pedicel yellow globular, ring of trichoid sensilla on weakly developed. Flagellomeres dark yellow, fusiform. Facial sclerite yellow, indistinct from clypeus. Clypeus rhomboidal, inflated, generally covered in yellow sensilla, bright yellow. Maxillary palpus with segments yellow, final segment extended. Labrum narrowly spade shaped, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae muddy yellow.

Thorax. Antepronotum with transverse fold broader than height of anterior ridge, yellow with elongate yellow trichoid sensilla at lateroventral apex, medial lobe approximately one quarter width of remainder of antepronotum, weakly tapered trapezoid, dorsal surface without medial notch. Prescutum and scutum shining yellow, brown medially, with microtrichia vestiture; medial and prescutal suture with row of minute clear trichoid sensilla, extending posterior from posterior apex of prescutum to scutellum as longer yellow sensilla; long short prealar sensilla present. Scutellum yellow. Mediotergite of yellow, shining. Laterotergite of yellow, dorsal patch of stout black trichoid sensilla. Pleural sclerites all yellow, with heavy pollinosity. Anepisternal cleft narrow, membrane yellow. Suture between epimeron and metapleurite complete. **Wing.** With band extending from apex of Sc, R_5 and angle of R_3 to CuA_2 apex, spots at R_2 and R_{4+5} fork. Macrotrichia in all cells except br, bm, CuA , and A. All veins covered in short stout macrotrichia. Sc: 7.5mm, Apex of Sc to Apex of R_1 2.10mm, R_{3+4+5} stem 1.04mm, weakly bowed anterior; R_{4+5} stem 2.25mm; R_4 after fork 2.10mm, R_5 after fork 2.1mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.0 :$

2.16 : 2.01. r-m 0.5mm; M distal to r-m 3.0; M_1 1.15mm, arcuate, M_2 1.05mm; Mdistal: M_1 = 1.0 : 0.38mm, R_{3+4+5} :Mdistal = 1.0 : 0.34, R_4 : M_1 = 1.0 : 0.54. CuA_1 proximal -0.35, distal 3.0mm; CuA_2 1.55mm sinuous. CuA_2 to A_1 2.75mm. R_3 branches at r-m. Halter yellow. Prehalter yellow. **Legs.** All coxae yellow. Femur and tibia yellow, darkening slightly at shared joint, joint of tibia and first tarsomere brown. First tarsomere light brown proximally, darkening distally. All other tarsi brown. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Tergites and sternites yellow, segments II-IV with brown bands along lateral and posterior margins, segments V and VI brown, posterior segments yellow. **Female Genitalia.** Tergite VII yellow. Cerci orange basally, apex yellow, lateral ridge poorly defined, dorsal furrow poorly developed. Cercus length:width, 3.5:1. Hypogynium yellow, rotated dorsally approximately 30 degrees from vertical; lateral surface with minute inflation, otherwise straight sided. Apical margin triangular, simple. Lateral margin concealed.

Figures. Wing: 131, Distribution: 132.

Material Examined. Ugano, 15-1700m/ Tanganyika-Terr. Matongo Hochland, wsw. v. Songea, 28.IX.37 – F. Zimmer. (Pinned: 1 f#) (USNM). Tanganyika-Terr., Songea, 1100m, 28.IV-2.V.'36.Zerny (Pinned: 1 f#) (USNM).

***Ptychoptera pauliani* Alexander, 1957**

Diagnosis

Adult. Gonostylus with basal lobe simple, secondary lobe 2/3rd length of apical stylus.

Description

Adult. Head. Antennae partial on slide examined, flagellomeres fusiform, not significantly shortening to apex.

Abdomen. Male Genitalia. Epandrial apodeme present, ribbon-like, extending across gonocoxite. Gonocoxal apodeme tapering basally, becoming parallel sided near anterior apex, anterior apex blunt and partially squared off, half length of remainder of gonocoxite. Dorsal spur of gonocoxal apodeme present, broad basally, tapering to rounded apex. Gonocoxite ovoid, nearly subcircular. Gonocoxal lobes absent. Gonostylus approximately 3/4ths length of external portion of gonocoxite; basal lobe directed dorsally, short, thumblike, with base very weakly constricted, with trichoid sensilla at apex. Apical stylus round in cross section, simple, weakly curving dorsally; secondary lobe present, directed dorsoposterior, apex curved dorsally, slightly shorter than apical stylus posterior to base, with numerous elongate trichoid sensilla.

Figures. Male Gonopod: 133, Distribution: 134.

Taxonomic Notes.

Material Examined. Holotype. Madagascar – Ambohimanakana, Mauambato (anove), XI-1955 (Robinson) (Slide: 1 m#) (USNM)

***Ptychoptera stuckenbergi* Alexander, 1956**

Diagnosis

Adult. Wing with proximal band at cord, veins at margin of wing highlighted with infuscation.

Description

Measurements: Wing Length 7.7mm, Wing Width 2.3mm.

Thorax. Wing. Proximal band of infuscation extending from apex of Sc, R₅ and angle of R₃ to CuA fork, continuing along CuA₂, not approaching wing margin; apical portion of R₁, R₂, R₄ and R₅ and their fork, M₁ and M₂ and their fork, and apical portion of CuA₁ outlined with infuscation; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 5.00mm, Apex of Sc to Apex of R₁ 1.60, R₃₊₄₊₅ stem 0.37mm, straight; R₄₊₅ stem 1.73mm; R₄ after fork 1.78mm, R₅ after fork 1.75mm; R₃₊₄₊₅:R₄₊₅-stem:R₄ = x : x : x. r-m 0.37mm; M distal to r-m 2.30mm; M₁ 1.11mm, flattened, M₂ 0.94mm; Mdistal:M₁ = 1.0 : x, R₃₊₄₊₅:Mdistal = 1.0 : x, R₄:M₁ = 1.0 : x. CuA₁ proximal 0.30mm, distal 2.40mm; CuA₂ 1.43mm sinuous. CuA₂ to A₁ straight for 2.17mm. R₃ branches at r-m.

Figures. Wing: 135, Distribution: 136.

Material Examined. Holotype. So. Rhodesia – Rhodes-Inyanga, Nat. Park nr. Inyanga – Jan.14.55 (Stuckenberg – Graham) (Slide: fragmentary 1 f#) (USNM).

Ptychoptera uelensis Alexander, 1928

Diagnosis

Adult. Habitus dark brown, wing with narrow proximal band and broad weak band apically.

Description

Adult. Measurements (n=1). Overall length x. **Head.** Width: 1.23mm, Height: 1.0, Length: 0.69mm; Antenna flagellum length: 2.44mm. **Thorax.** Length: 2.6mm, Height: 2.6mm; Wing length: 9.7mm, Width: 2.9mm. **Abdomen.** Length: 7.2mm.

Head. Vertex shining black, trichoid sensilla nearly absent; frons extremely narrow strip, black. Occiput and genae with dense elongate clear trichoid sensilla. Antennae: scape dark brown, subconical cylinder with ring of long black trichoid sensilla well separated from dorsal apex; pedicel brown basally, yellow dorsally, weakly compressed globular, ring of trichoid sensilla poorly developed. Flagellomeres brown, fusiform. Facial sclerite dark brown, indistinct from clypeus, weakly inflated. Clypeus rhomboidal, inflated, generally covered in clear sensilla. Maxillary palpus with segment 1 brown, 2 & 3 yellow, posterior segments brown, terminal segment extended. Labrum not apparent; hypopharynx and epipharynx not externally apparent, labium dark yellow, and labella brown.

Thorax. Anteprenotum with transverse fold narrower than height of anterior ridge, dark brown, with elongate yellow trichoid sensilla at lateroventral apex, medial lobe approximately one third width of remainder of anteprenotum, highly tapered trapezoid, dorsal surface without medial notch. Prescutum and scutum dark brown, obscurely shining, with microtrichia vestiture; medial and prescutal suture lacking row of minute clear trichoid sensilla; short clear prealar sensilla present. Scutellum dark brown. Mediotergite uniform dark brown. Laterotergite of metanotum uniform dark brown, dorsal patch of sensilla absent. Pleural sclerites all dark brown, weakly pollinose. Anepisternal cleft narrow rectangle, membrane yellow. Suture between epimeron and metapleurite strong. **Wing.** Two bands present, proximal narrow, extending from apex of Sc, R_s and angle of R₃ to CuA₂ apex, apical band very light, extending from R₂ through R₄₊₅ and M proximal to forks, extending to wing apex. All cns with macrotrichia except br and bm. All veins covered in short stout macrotrichia. Sc: 4.75mm, Apex of Sc to Apex of R₁ 1.53mm, R₃₊₄₊₅ stem 0.30, slightly convex dorsally along length; R₄₊₅ stem 2.05mm; R₄ after fork 1.48mm, R₅ after fork 1.46mm; R₃₊₄₊₅:R₄₊₅-stem:R₄ = 1.0 : 6.8 : 4.93. r-m 0.27mm; M distal to r-m 2.33mm; M₁ 0.88mm, arcuate, M₂ 0.72mm; Mdistal:M₁ = 1.0 : 0.37, R₃₊₄₊₅:Mdistal = 1.0 : 0.12, R₄:M₁ = 1.0 : x. CuA₁ proximal 0.25mm, distal 2.27mm; CuA₂ 1.36mm sinuous. CuA₂ to A₁ 2.17mm. R₃ branches after r-m. Halter light brown. Light brown. **Legs.** All coxae dark brown. All legs brown.

Abdomen. Tergites and sternites dark brown, sometimes with yellow band on segment II, segment VII yellow. **Female Genitalia.** Tergite VII yellow. Cerci yellow, lateral ridge poorly defined, dorsal furrow poorly developed. Cercus length:width, 4.5:1. Hypogynium yellow, rotated dorsally approximately 20 degrees from vertical; somewhat surface weakly convex, widening medially. Apical margin rounded, simple. Lateral margin concealed.

Figures. Wing: 137, Distribution: 138.

Material Examined. Urundi, Bururi – 1800-2000m, Mar. 5-12-1953, (P. Basilewski) (Slide: fragmentary 1 f#, *Ptychoptera basilewskyi* Alexander, 1955 Holotype) (USNM). Belg. Congo, Volc. Karissimbi, Nya Muzinga, Jan. 1926, (H. Schouteden) (Slide: fragmentary 1 m#, *Ptychoptera schoutedeni* Alexander 1956 Holotype) (USNM). Congo – Belge, Eala XI 1934, J. Ghesquière (Pinned: 1 f#, *Liriope ghesquiere* Collart, 1936 Holotype) (IRNSB).

Southeast Asian *Ptychoptera*

Ptychoptera annandalei Brunetti, 1918

Diagnosis.

Adult. Male genitalia with paramere dorsoventrally flattened, apical lobes semicircular with spine directed anteromedially. Gonostylus with apices of apical stylus and secondary lobe crossing.

Description

Thorax. Wing. Length 7.2mm, width 2.0mm Two bands, proximal extending from base of R_{1+2} to CuA_1+CuA_2 fork, posterior from R_2 to the M fork; membrane with macrotrichia in all cells except C, Sc, br, bm. All veins covered in short stout macrotrichia. Sc: 4.69mm, Apex of Sc to Apex of R_1 1.43mm, R_{3+4+5} stem 0.25mm, straight R_{1+2} ; R_{4+5} stem 1.60mm; R_4 after fork 1.48mm, R_5 after fork 1.48mm;

$R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.0 : 6.4 : 5.92\text{mm}$. r-m 0.37mm; M distal to r-m 2.08mm; M_1 0.97mm, arcuate, M_2 0.64mm; $M\text{distal}:M_1 = 1.0 : 0.46$, $R_{3+4+5}:M\text{distal} = 1.0 : 8.32$, $R_4:M_1 = 1.0 : 0.65$. CuA_1 proximal 0.35mm, distal 1.98mm; CuA_2 1.18mm sinuous. CuA_2 to A_1 2.15mm. R_3 branches only point contact with r-m.

Abdomen. Male Genitalia. Epandrial complete, epandrial apodemes well developed, triangular, breaks not observable on specimens examined. Epandrial lobes nematoform, curving heavily ventrally, not expanding significantly at base, apex bluntly rounded, brush of trichoid sensilla on ventroanterior surface; epandrial clasper indistinguishable from epandrial lobe. Epiproct prominent, posterior margin simple U-shape, epandrial lobes not in contact. Posteromedial stylus not present. Hypoproct tonguelike. Subepandrial membrane H-shaped, apices rounded.

Parameral bridge attached narrowly to dorsal portion of anterior ring-like; base directed posterior, near right angle directed medially. Apical lobe with narrow base and secondary lateral spine, expanding to flattened plate basally curving medially to distinct hooked, claw-like point directed anterolateral.

Gonocoxal apodeme triangular, subacute. Dorsal spur of gonocoxite present, nearly equilateral. Gonocoxite lozenge shaped, dorsal and ventral margins curved, ventral margin more acutely curved. Gonocoxal lobes absent, nodule provided with elongate trichoid sensilla on dorsomedial margin near base of gonostylus. Gonostylus with basal lobe directed medially, subdivided, anterior branch tapering, distal portion slightly arced dorsally, apex finger-like, surface covered in trichoid sensilla; posterior branch hatchet shaped, trichoid sensilla on posterior margin. Apical stylus broad, broadly trapezoidal weakly arced dorsally, apical corner curved medially, medial surface covered in stout trichoid sensilla; secondary lobe present, located subapically, finger-like, expanding to apex, crossing ventrally under apex of apical stylus.

Basal division of hypandrium band-like, somewhat broad, . Eversible sac absent. Spathate lobes present, base subquadrate, dorsoposterior corner extended to finger-like lobe, gently curved posterior. Terminal division narrowly attached to medial portion of basal division, lateral margins of attachment semicircular; main portion of terminal division very narrow, lateral sclerotized regions very narrow; apex T-shaped, medial base formed to rhomboidal pennant, lateral apices curved dorsally. Membranous window present, extending as thin slit from nearly the apex of terminal division to the base, open ventrally. Aedeagus orientation not readily apparent in specimens examined. Ejaculatory apodeme similar in size to sperm sac, placed far back on dorsoanterior margin, well separated from aedeagal sclerites, curved ventrally and weakly paralleling curvature of sperm sac. Apex of aedeagal sclerites pointed, dorsal margin with small emargination subapically. Lateral ejaculatory processes with discoid apodeme directed ventrally, otherwise difficult to interpret in specimens examined. Subapical sclerite spine-like, extending far beyond apex of aedeagal sclerites, apex directed somewhat posterior, with weak serrations present on ventral surface.

Figures. Male Genitalia: 139, Wing: 140, Distribution: 141.

Material Examined. Burma, So. Shan States, 40km E of Taunggyi, IX-25-X-13. '34 (Rene Malaise)
(Slide: 2 m#) (USNM)

***Ptychoptera bellula* Alexander, 1937.**

Ptychoptera bellula Alexander, 1937: 367-368 (original description)

Ptychoptera bellula Alexander, Krzeminski & Zwick 1993: 78-80 (redescription & illustrations)

Diagnosis.

Adult. Epandrium nematoform, with triangular lobe on medial surface with associated point of articulation. Parameres separate, , spine with distinct dorsal bend. Gonopod with gonocoxite quadrate,

gonostylus having triangular apical stylus without dorsal lobe. Hypandrium lacking spathate lobes, divided basal scale present.

Description

Adult. Measurements (n=1). Overall length ? (dissected). **Head.** Width: 0.88mm, Height: 0.72mm, Length: 0.49mm; Antenna flagellum length: 2.70mm. **Thorax.** Length: 1.65mm, Height: 1.70mm; Wing length: 6.4mm, Width: 1.8mm. **Abdomen.** Length: ? (dissected).

Head. Vertex shining black, sparsely provided with elongate trichoid sensilla posteriorly; frons extremely narrow strip, black. Occiput and genae glabrous. Antennae: scape black, oblong cylinder with ring of long black trichoid sensilla well separated from dorsal apex; pedicel black, globular, ring of trichoid sensilla on lateral margin. Flagellomeres brown, fusiform. Facial sclerite black, indistinct from clypeus, weakly inflated. Clypeus rhomboidal, inflated, generally covered in clear sensilla, pollinose black. Maxillary palpus with segments 1-3 brown, posterior segments dark orange, terminal segment extended. Labrum narrowly spade shaped, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae dark yellow.

Thorax. Antepronotum with transverse fold broader than height of anterior ridge, black with yellow anteriolateral corner, medial lobe approximately one quarter width of remainder of antepronotum, highly tapered trapezoid, dorsal surface with medial notch. Prescutum and scutum shining black, with microtrichia vestiture; medial and prescutal lacking sensilla, short clear prealar sensilla present. Scutellum dark brown. Mediotergite of metanotum black, with heavy pollinosity,. Laterotergite of metanotum pollinose black, dorsal patch of short orange trichoid sensilla. Pleural sclerites all black, with heavy pollinosity. Anepisternal cleft narrow, triangular with membrane dark brown. Suture between epimeron and metapleurite complete. **Wing.** Two broad bands and a large spot, proximal extending from base of R_s to beyond r-m, not extending below M, distal band extending from

R₂ through R₄₊₅ fork to the M fork, spot oval on CuA₁; membrane with macrotrichia in all cells except br & bm. All veins covered in short stout macrotrichia. Sc: 4.3mm, Apex of Sc to Apex of R₁ 1.16mm, R₃₊₄₊₅ stem 1.00mm, elongate, with angle at base; R₄₊₅ stem 1.36mm; R₄ after fork 1.28mm, R₅ after fork 1.36mm; R₃₊₄₊₅:R₄₊₅-stem:R₄ = 1.0 : 1.36 : 1.28. r-m 0.25mm; M distal to r-m 1.68mm; M₁ 0.86mm, arcuate, M₂ 0.67; Mdistal:M₁ = 1.0:0.51, R₃₊₄₊₅:Mdistal = 1.0:1.68, R₄:M₁ = 1.0:0.67. CuA₁ proximal 0.25mm, distal 1.62mm; CuA₂ 1.0mm with anterior angle well developed, posterior angle absent. CuA₂ to A₁ 1.6mm. R₃ branches at r-m. Halter yellow. **Legs.** Coxae dark orange, black spot on lateral surface of hind coxa. Femur and tibia yellow, darkening slightly at shared joint, joint of tibia and first tarsomere brown. First tarsomere light brown proximally, darkening distally. All other tarsi brown. 5th tarsomere cannot fold back on pentultimate tarsomere. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Segments brown, with yellow band on segment II, segment VII yellow. **Male Genitalia.** Epandrial lobes nematoform, elongate, narrow; epandrial clasper distinguished from epandrial lobe, distinct triangular lobe directed medially along 1/3 of length with associated point of weak articulation, epandrial clasper apex rounded, slightly expanded, epandrial lobes straight. Epiproct not easily distinguished from epandrial lobes, posterior margin straight. Posteromedial stylus absent. Hypoproct ovoid plate, subepandrial sclerite closely associated with hypoproct, forming distinct transverse bar.

Parameres separate, spine directed medially from medial surface of gonocoxite before bending dorsally.

Gonocoxal apodeme dorsoventrally flattened, narrow; dorsal spur acutely pointed, directed dorsally. Gonocoxite extremely large, quadrate slanted slightly anterior. Dorsal gonocoxal lobes present, directed medially at base of gonostylus; secondary set of dorsally directed paired spines located

near dorsal spur of gonocoxal lobe. Gonostylus with basal lobe directed medially, finger-like curved posterior. Apical stylus massive, broadly triangular, dorsal margin curving ventrally, ventral margin straight, margins simple. Secondary and tertiary lobes absent.

Basal division band-like, broad, margins simple; spathate lobes absent; basal scale present, divided, dorsoventrally compressed subquadrate fleshy lobes fused at base and simple margins. Terminal division with constricted, articulated base, lateral sclerites extremely narrow, small ventrally curved spine near base; apex with prominent lateral extensions free of basal division, subquadrate tapering ventrally; apex spade-like, with prominent stout trichoid sensillae on lateral base. Membranous window slit-like, stretching nearly entire length of terminal division, dividing base.

Aedeagus vertical. Aedeagal sclerites with apex rounded, simple, parallel sided. Lateral ejaculatory processes with base straight, as tall as sperm sac, extended straight laterally; discoid apodemes simple, directed ventrally, directed both dorsally and ventrally. Sperm sac subspherical. Ejaculatory apodeme flag-like, not closely associated with aedeagal sclerites, larger than sperm sac, not closely paralleling anterior margin of sperm sac. Subapical sclerite cylindrical with bullet shaped apex.

Female Genitalia. Tergite VII yellow. Cerci light orange, lateral ridge poorly defined, dorsal furrow poorly developed. Cercus length:width, 3:1. Hypogynium yellow, rotated dorsally approximately 30 degrees from vertical; with constricted transversely 1/3 from base. Apical margin triangular, lateral corner simple. Lateral margin concealed.

Figures. Male Genitalia: 142, Wing: 143, Distribution: 144.

Material Examined. Holotype. Hong San SE, Kiangsi, Ohi, na. VI-30-36/ L. Gressitt Collector (Pinned: 1 m#) (USNM) **Other Material.** As type (Pinned: 1 f#)

Ptychoptera chalybeata* Alexander, 1956*Diagnosis**

Adult. Epandrial clasper length shorter than width of epandrium, gonostylus with simple basal lobe, apex with notch.

Description

Adult. Measurements (n=1). Overall length ? (fragmentary). **Head.** Width: ?, Height: ?, Length: ?; Antenna flagellum length: ?. **Thorax.** Length: 1.76mm, Height: 1.65mm; Wing length: 5.4mm, Width: 1.6mm. **Abdomen.** Length: ? (missing).

Head. Vertex shining dark brown, evenly provided with elongate trichoid sensilla posteriorly weakly pollinose; frons extremely narrow strip, black. Occiput and genae with dense elongate yellow trichoid sensilla. Antennae: scape bright yellow, oblong cylinder with ring of long black trichoid sensilla well separated from dorsal apex; pedicel yellow, globular, ring of trichoid sensilla on lateral margin. Flagellomeres yellow, fusiform. Facial sclerite indistinct from clypeus. Clypeus rhomboidal, inflated, generally covered in yellow sensilla, russet brown. Maxillary palpus with all segments yellow. Labrum broadly spade shaped, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae bright yellow.

Thorax. Anteprenotum with transverse fold narrower than height of anterior ridge, medial lobe approximately one fifth width of remainder of anteprenotum, lateral margins rounded, dorsal surface with medial notch. Prescutum and scutum obscurely shining russet brown, with microtrichia vestiture; medial and prescutal suture with row of minute clear trichoid sensilla, long clear prealar sensilla present. Scutellum brown. Mediotergite of metanotum russet brown, with light pollinosity. Laterotergite of metanotum pollinose russet brown,. Pleural sclerites all russet brown, shining. Anepisternal cleft broad,

trapezoidal, membrane yellow. Suture between epimeron and metapleurite complete. **Wing.** Two broad bands, proximal extending from base of R_5 to angle of CuA_2 fork, distal from R_{1+2} fork nearly to CuA_1 fork extending to margin; membrane with macrotrichia in all cells except br, bm and A. All veins covered in short stout macrotrichia. Sc: 3.31mm, Apex of Sc to Apex of R_1 1.23mm, R_{3+4+5} stem 0.20mm, straight; R_{4+5} stem 1.25mm; R_4 after fork 1.34mm, R_5 after fork 1.46mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.0 : 6.25 : 6.7$. r-m 0.22mm; M distal to r-m 1.48mm; M_1 1.06mm, arcuate, M_2 0.88mm; $M_{\text{distal}}:M_1 = 1.0:0.71$, $R_{3+4+5}:M_{\text{distal}} = 1.0:7.4$, $R_4:M_1 = 1.0:0.79$. CuA_1 proximal 0.25mm, distal 1.60mm; CuA_2 0.99mm with anterior angle well developed, posterior angle absent. CuA_2 to A_1 1.58mm. r-m joins R_3 with point contact at r-m.. Prehalter orange. **Legs.** All coxae yellow. Femur and tibia yellow, darkening slightly at shared joint, joint of tibia and first tarsomere brown. First tarsomere light brown proximally, darkening distally. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Male Genitalia. Epandrial collar complete, closely appressed to epandrial lobes; epandrial apodemes present, extent impossible to determine on holotype. Epandrial lobes nematoform, short, extending posterior less than width of epandrium, curving weakly ventrally, broadly tapering at base, apex expanding to rounded bulb, brush of trichoid sensilla on ventroanterior surface; epandrial clasper indistinguishable from epandrial lobe. Epiproct prominent, posterior margin rounded V-shape, epandrial lobes not in contact. Posteromedial stylus not present. Hypoproct tonguelike. Subepandrial membrane not apparent in holotype preparation. Parameral bridge attached narrowly to gonocoxite; base directed medial with prominent posterior short, broad quadrate lobe, anterior margin with elongate flattened spine directed with distinct bend laterally at base, extending laterally beyond paramere base, point acute. Apical lobe directed dorsally, laterally compressed, leaflike. Gonocoxal apodeme triangular, apex rounded, $1/3^{\text{rd}}$ length of gonocoxite. Dorsal spur of gonocoxite present, nearly as large as remainder of apodeme anterior margin straight, posterior margin curved. Gonocoxite

lozenge shaped, dorsal margin straight, directed ventrally near base of gonocoxite, ventral margin broadly curved. Gonocoxal lobes absent. Gonostylus with basal lobe directed medially, knob-like, covered in trichoid sensilla. Apical stylus finger-like, gently curved medially, somewhat laterally convex and expanding towards apex; apex notched, ventral division longer than dorsal division. Hypandrium difficult to interpret on holotype. Basal division with fingerlike spathate lobes which expand weakly at apex. Aedeagus orientation not readily apparent in holotype. Aedeagal sclerites with apex rounded, small laterally curved spine on either side of phallotrema. Subapical sclerite wrapping around apex of aedeagal sclerites, each lateral margin forming a posterior directed broad triangular point above aedeagal sclerites; apex conical with rounded tip. Lateral ejaculatory processes narrow at base.

Figures. Male Genitalia: 145, Wing: 146, Distribution: 147.

Material Examined. Holotype. Thailand, Huey Kao, VI-14-53 (Manop Ruttanapradith) (Pinned & Slide: 1 m#) (USNM)

***Ptychoptera clitellaria* Alexander, 1935**

Diagnosis

Adult. Wing tinged yellow, Rs greater than twice length of rm.

Description

Adult. Measurements (n=1). Overall length ? (abdomen missing). **Head.** Width: 1.11mm, Height: 1.13mm, Length: 0.74mm; Antenna flagellum length: ? (missing), . **Thorax.** Length: 2.4mm, Height: 2.65mm; Wing length: 11.29mm, Width: 2.86mm. **Abdomen.** ? (missing)..

Head. Vertex dull black; frons extremely narrow strip, black. Occiput and genae yellow, with dense elongate yellow trichoid sensilla. Antennae: scape bright yellow, pedicel yellow. Facial sclerite

indistinct from clypeus. Clypeus rectangular, inflated, generally covered in yellow sensilla, yellow. Maxillary palpus with segments 1&2 yellow, distal segments darkening to brown. Labrum narrowly subcircular, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae muddy yellow.

Thorax. Antepronotum with transverse fold broader than height of anterior ridge, yellow, medial lobe approximately equal to width of remainder of antepronotum, rounded, dorsal surface without medial notch. Prescutum and scutum subshining black, lateral margins yellow, vestiture of microtrichia present. Scutellum yellow. Mediotergite of metanotum yellow, shining. Laterotergite of metanotum yellow, shining. Pleural sclerites all yellow, shining. Anepisternal cleft narrow, membrane yellow. Suture between epimeron and metapleurite complete, **Wing.** Hyaline, weak infuscation extending from base of R_{1+2} to CuA_1+CuA_2 fork; membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 8.0mm, Apex of Sc to Apex of R_1 1.48mm, R_{3+4+5} stem 1.85mm, long, with angle at base; R_{4+5} stem 2.17mm; R_4 after fork 2.59mm, R_5 after fork 2.59mm; $R_{3+4+5}:R_{4+5}$ stem: R_4 , 1.0 : 1.17 : 1.4. r-m 0.27; M distal to r-m 3.44mm; M_1 1.01mm, M_2 0.74mm; Mdistal: M_1 , 1.0:0.29, $R_{3+4+5}:M$ distal, 1.0:1.85, $R_4:M_1$, 1.0:0.38. CuA_1 proximal 0.35mm, distal 2.92mm; CuA_2 1.96mm with anterior angle well developed, posterior angle absent. CuA_2 to A_1 3.00mm. R_3 branching after r-m. Halter yellow. Prehalter yellow. **Legs.** Coxae yellow. Femur , darkening slightly at distal joint, tibia light brown proximally, darkening distally. All tarsi brown. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Tergites and sternites yellow, posterior margins of all segments posterior to seg. II with brown band.

Figures. Wing: 148, Distribution: 149.

Material Examined. W. China, Yachow, Szech. 1930,(D.C. Graham) (Pinned & Slide: 1 f#) (USNM). **Other Material.** Bet. Yin Kuan, Chian & Tatlu, Si Kang 10-13, 000ft. VII-22-28/ Szechwan China, DC Graham (Pinned: 1 f#) (USNM)

***Ptychoptera distincta* Brunetti, 1911**

Diagnosis

Adult. Wing with dark band along cord, dark field at apex of wing, oblong spot along CuA₁.

Description

Adult. Measurements (n=1). Overall length 6.8mm. **Head.** Width: 0.78mm, Height: 0.7mm, Length: 0.5mm; Antenna flagellum length: ? (damaged). **Thorax.** Length: 2.1mm, Height: 2.2mm; Wing length: 8.2mm, Width: 2.3mm. **Abdomen.** Length: 4.2mm.

Head. Vertex shining russet brown, glabrous; frons inevident. Occiput and genae with dense elongate yellow trichoid sensilla. Antennae: scape bright yellow, oblong cylinder with ring of long black trichoid sensilla well separated from dorsal apex; pedicel yellow, globular, ring of trichoid sensilla on lateral margin. Flagellomeres yellow, fusiform. Facial sclerite yellow, indistinct from clypeus. Clypeus inversely triangular, inflated, generally covered in yellow sensilla, yellow. Maxillary palpus with segments 1&2 yellow, posterior segments brown, terminal segment extended. Labrum not readily apparent, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae yellow.

Thorax. Anteprenotum with transverse fold broader than height of anterior ridge, anterior ridge yellow, remainder brown, medial lobe approximately one quarter width of remainder of anteprenotum, rounded trapezoid, dorsal surface without medial notch. Prescutum and scutum obscurely shining dark brown, microtrichia vestiture present; medial and prescutal suture with row of minute clear trichoid

sensilla; shortclear prealar sensilla present. Scutellum brown. Mediotergite of metanotum brown, weakly shining, Laterotergite of metanotum shining brown. Pleural sclerites brown, shining. Anepisternal cleft broad, membrane yellow. Suture between epimeron and metapleurite complete.

Wing. Three bands, basal band proximal to h, medial band extending from base of R_{1+2} to CuA_2 bend, apical band extending proximal to R_{4+5} and M fork to apex of CuA_1 , extending to apex, anterior margin of wing with cells C and Sc infuscated, oval spot on CuA_1 ; membrane with macrotrichia in all cells except br & bm. All veins covered in short stout macrotrichia. Sc: 5.13mm, Apex of Sc to Apex of R_1 1.32, R_{3+4+5} stem 0.35mm, straight, nearly traverse; R_{4+5} stem 1.85mm; R_4 after fork 1.78mm, R_5 after fork 1.73mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4$, 1.0 : 5.28 : 5.08. r-m 0.39mm; M distal to r-m 2.4mm; M_1 1.04mm, broadly arced, M_2 0.74mm; Mdistal: M_1 , 1.0:0.43, R_{3+4+5} :Mdistal, 1.0:6.85, $R_4:M_1$, 1.0:0.58. CuA_1 proximal 0.30mm, distal 2.24mm; CuA_2 1.36mm with anterior angle well developed, posterior angle absent. CuA_2 to A_1 2.10mm. R_3 with point contact at r-m. Halter yellow. **Legs.** Coxae yellow. Femur and tibia yellow, darkening slightly at shared joint, joint of tibia and first tarsomere brown. First tarsomere light brown proximally, darkening distally. All other tarsi brown. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Segments brown, segment II with yellow band, segment VII yellow.

Female Genitalia. Tergite VII yellow. Cerci orange, lateral ridge inevident, dorsal furrow poorly developed. Cercus length:width, 3.5:1. Hypogynium yellow, rotated dorsally approximately 15 degrees from vertical; tapering ventrally. Apical margin rounded, lateral corner rounded. Lateral margin hidden.

Figures. Wing: 150, Distribution: 151.

Taxonomic Notes.

Material Examined. Darjiling, c. 6000 ft. E.. Himalayas, 3-9-VI-09, F.M. Howlett (Pinned: 1 f#) (BMNH). **Other Material.** Nafra 3,500-4,000 ft, 24-26-VI-1961, Fernand Schmid/ INDIA – Assam – NEFA – Kameng, NAFRA, 4000' VI-26-'61 (Schmid) (Pinned & Slide: 1 f#) (USNM)

Ptychoptera formosensis* Alexander, 1924.*Diagnosis**

Adult. Gonostylus with apical stylus and secondary lobe crossing at apex, hypandrium with indistinct medial apex of terminal division but with prominent dorsally directed lateral lobes.

Description

Adult. Measurements (n=1). Overall length ? (abdomen dissected). **Head.** Width: 1.1mm, Height: 0.91mm, Length: 0.57mm; Antenna flagellum length: 4.85mm. **Thorax.** Length: 2.2mm, Height: 2.3mm; Wing length: 8.7mm, Width: 2.0mm. **Abdomen.** ? (dissected).

Head. Vertex shining russet brown, sparsely provided with elongate trichoid sensilla posteriorly; frons inevident. Occiput and genae with dense elongate yellow trichoid sensilla. Antennae: scape bright yellow, oblong cylinder with ring of long black trichoid sensilla well separated from dorsal apex; pedicel yellow, globular, ring of trichoid sensilla on lateral margin. Flagellomeres brown, fusiform. Facial sclerite yellow, indistinct from clypeus. Clypeus subquadrate, inflated, generally covered in yellow sensilla, dark yellow. Maxillary palpus with segments 1&2 yellow, posterior segments brown, terminal segment extended. Labrum broadly spade shaped, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae orange yellow.

Thorax. Anteprenotum with transverse fold broader than height of anterior ridge, yellow, medial lobe approximately one third width of remainder of anteprenotum, weak trapezoid, dorsal surface with medial notch. Prescutum and scutum obscurely shining dark brown, microtrichia vestiture present; medial and prescutal suture with row of minute clear trichoid sensilla; short clear prealar sensilla present. Scutellum yellow medially, lateral ridges brown. Mediotergite of metanotum brown, weakly shining, Laterotergite of metanotum pollinose brown dorsally, yellow anteroventrally. Pleural sclerites yellow, shining. Anepisternal cleft narrow, membrane yellow. Suture between epimeron and metapleurite complete. **Wing.** Two broad bands, proximal extending from base of R_s to CuA_1+CuA_2 fork, distal from R_{1+2} fork to base of M fork; membrane with macrotrichia in all cells except br & bm. All veins covered in short stout macrotrichia. Sc: 5.57mm, Apex of Sc to Apex of R_1 1.73mm, R_{3+4+5} stem 0.27mm, straight; R_{4+5} stem 1.85mm; R_4 after fork 1.93mm, R_5 after fork 1.83mm; $R_{3+4+5}:R_{4+5}$ -stem: R_4 , 1.0 : 6.85 : 7.14. r-m 0.30mm; M distal to r-m 2.30mm; M_1 1.21mm, arcuate, M_2 0.86mm; Mdistal: M_1 , 1.0:0.52, $R_{3+4+5}:M$ distal, 1.0:8.51, $R_4:M_1$, 1.0:0.62. CuA_1 proximal 0.35mm, distal 2.47mm; CuA_2 1.34mm with anterior angle well developed, posterior angle absent. CuA_2 to A_1 2.24mm. R_3 with point contact at r-m. Halter yellow. **Legs.** Forecoxa yellow dorsoanterior margin with dark brown spot and ventral margin with broad brown band sloping anterior, midcoxa yellow with dark brown spot on dorsoanterior apex and ventral margin with broad brown band sloping anterior, hindcoxa dark brown with yellow spot dorsally on posterior surface. Femur and tibia yellow, darkening slightly at shared joint, joint of tibia and first tarsomere brown. First tarsomere light brown proximally, darkening distally. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Segments brownish black, with yellow patches medially. **Male Genitalia.** Epandrial collar complete, closely appressed to epandrial lobes; epandrial apodemes well developed, thread-like across gonocoxal apodeme to hypandrium, breaks present at epandrium and hypandrium. Epandrial

lobes nematoform, elongate, narrow; epandrial clasper not well delineated from epandrial lobe, apex rounded bulb, epandrial lobes strongly curved ventrally with distinct arc of greater than 30 degrees. Epiproct readily apparent, small, lateral apices not developed, medial notch very shallow. Posteromedial stylus absent. Hypoproct fused to subepandrial sclerite, quadrate, paired posterior lobes present.

Parameral bridge attached narrowly to gonocoxite, directed dorsally then abruptly angled medially, medial portion weakly bowed anterior. Apical lobe placed at posterolateral corner, forming two spines, one directed dorsolaterally and the other ventroposterior.

Gonocoxal apodeme laterally compressed, tall, apex rounded, dorsal spur shifted to dorsal surface of gonocoxite, equilateral, nearly the same size as the remainder of the gonocoxal apodeme, directed dorsally. Gonocoxite expanding to gonostylus, dorsal margin with peak at 1/3 length, remainder straight to gonocoxite, ventral margin forming broad arc peaking subapically. Gonocoxal lobes absent. Gonostylus with basal lobe banana shaped, anterior lobe weakly flattened, with notch subapically on dorsal surface, medial lobe low paddle-like, apex weakly squared. Apical stylus shorter than gonocoxite, fingerlike, round in cross section, curved dorsally, apex pointed. Secondary lobe of apical stylus placed at base of apical stylus, proximal portion rounded, forming ridge tapering distally, apex fingerlike, curved ventrally and provided with cluster of short trichoid sensillae. Tertiary lobe absent.

Basal division band-like, heavily sloping dorsally, with rounded medial lobe near gonopods; spathate lobes present, flattened fingerlike directed dorsally; basal scale absent. Terminal division with constricted, articulated base, lateral sclerites extremely broad, small ventrally curved spine near base; apex with prominent lateral extensions fused to basal division; apex spine-like with keel terminating in blunt spine, lateral corners formed to paired spines bent dorsally. Membranous window broad, deeply inset, stretching nearly entire length of terminal division, base undivided.

Aedeagus within approximately 15 degrees of vertical. Aedeagal sclerites with apex laterally compressed, with dorsal corner extended dorsoanterior, straight sided and convergent, base broad. Lateral ejaculatory processes with base straight, narrow, extended straight anterolaterally; discoid apodemes with elongate ovoid dorsal extension. Sperm sac subspherical. Ejaculatory apodeme flag-like, closely associated with aedeagal sclerites, subequal to sperm sac, paralleling anterior margin of sperm sac. . Subapical sclerite subconical, tapering posterior to aedeagal sclerites. **Female Genitalia.** Tergite VII yellow. Cerci orange, lateral ridge well defined, dorsal furrow poorly developed. Cercus length:width, 3:1. Hypogynium yellow, rotated dorsally approximately 30 degrees from vertical; expanding semibulbously at apex. Apical margin triangular, medial apex with weak emargination, lateral corner rounded. Lateral margin visible distally.

Figures. Male Genitalia: 152, Wing: 153, Distribution: 154.

Taxonomic Notes

There are strong similarities between the gonostyle of *P. formosensis*, *P. persimilis*, and *P. pseudosimilis*. Further collection of these species (as *P. persimilis* and *P. pseudosimilis* are known only from slide mounted genitalia) is warranted as they may represent a monophyletic species group or potential subgenus.

Material Examined. Holotype. Funkiko, 25 IV 1917, col. T. Shiraki (Pinned: 1 m#, wing on slide) (USNM). **Other Material.** TAIWAN: Chiayi County, Chu-Chi Township, Fen-Chi-Hu 1405m, 23-30-11N: 120-41-42E, 31 Mar 2009 Chen Young (Pinned: 1 m#, 1 f#) (CMNH). TAIWAN: Hsinchu, Jianshan, woods near Yuan Yang Lake, 24.5903N: 121.4261E 1645m, 22 Apr. 2010 Chen Young (Pinned: 1 m#) (CMNH).

***Ptychoptera gutianshana* Yang & Chen, 1995.**

Ptychoptera gutianshana Yang & Chen, 1995: 180-182 (original description)

Ptychoptera gutianshana Yang & Chen; Kang, Wang, & Yang 2013:

Diagnosis

Adult. Epandrium nematoform, simple. Parameres separate, simple spines. Gonopod with gonocoxite quadrate, gonostylus having triangular apical stylus with massive semicircular lobe on dorsal surface. Hypandrium lacking spathate lobes, divided basal scale present.

Description

Adult. Measurements (n=1). Overall length ? (abdomen dissected). **Head.** Width: 0.97mm, Height: 0.88mm, Length: 0.57mm; Antenna flagellum length: 3.1mm. **Thorax.** Length: 2.15mm, Height: 2.15mm; Wing length: 8.4mm, Width: 2.2mm. **Abdomen.** Length: ? (dissected).

Head. Vertex shining black, sparsely provided with elongate trichoid sensilla posteriorly; frons extremely narrow strip, black. Occiput and genae glabrous. Antennae: scape yellow, oblong cylinder with ring of long black trichoid sensilla well separated from dorsal apex; pedicel yellow, globular, ring of trichoid sensilla on lateral margin. Flagellomeres yellow, fusiform. Facial sclerite indistinct from clypeus. Clypeus rhomboidal, inflated, generally covered in clear sensilla, bright yellow. Maxillary palpus yellow. Labrum narrowly spade shaped, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae bright yellow.

Thorax. Anteprenotum with transverse fold narrower than height of anterior ridge, brown with yellow anteriolateral corner, medial lobe approximately one fifth width of remainder of anteprenotum, highly tapered trapezoid, dorsal surface without medial notch. Prescutum and scutum shining ruddy brown, with microtrichia vestiture; medial and prescutal suture lacking sensilla, short clear prealar

sensilla present. Scutellum dark brown. Mediotergite of metanotum ruddy brown, shining. Laterotergite of metanotum shining ruddy brown, dorsal patch of short orange trichoid sensilla. Pleural sclerites all ruddy brown, shining. Anepisternal cleft narrow, triangular with membrane yellow. Suture between epimeron and metapleurite complete. **Wing.** Two broad bands and a large spot, proximal extending from base of R_5 to beyond r-m, not extending below M, distal band extending from R_2 through R_{4+5} fork to the M fork, spot oval at base of R_5 , membrane with macrotrichia in all cells except br & bm. All veins covered in short stout macrotrichia. Sc: 5.3mm, Apex of Sc to Apex of R_1 1.65mm, R_{3+4+5} stem 1.23mm, elongate, with angle at base; R_{4+5} stem 1.75mm; R_4 after fork 1.92mm, R_5 after fork 1.92mm; $R_{3+4+5}:R_{4+5}$ stem: R_4 = 1.0 : 1.42 : 1.56. r-m 0.30mm; M distal to r-m 1.96mm; M_1 1.36mm, arcuate, M_2 0.99mm; Mdistal: M_1 = 1.0:0.69, $R_{3+4+5}:Mdistal$ = 1.0:0.62mm, $R_4:M_1$ = 1.0:0.70. CuA_1 proximal 0.25mm, distal 2.10mm; CuA_2 1.11mm with anterior angle well developed, posterior angle absent. CuA_2 to A_1 straight for 1.98mm. R_3 branches at r-m. Halter yellow. **Legs.** Coxae yellow. Femur and tibia yellow, darkening slightly at shared joint, joint of tibia and first tarsomere brown. First tarsomere light brown proximally, darkening distally. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Segments brown, yellow band on segments II and III **Male Genitalia.** Epandrial collar complete, closely appressed to epandrial lobes; epandrial apodemes well developed, thread-like across gonocoxal apodeme to hypandrium, breaks present at epandrium and hypandrium. Epandrial lobes nematoform, elongate, narrow; epandrial clasper not well delineated from epandrial lobe, apex rounded bulb, epandrial lobes moderately curved ventrally without distinct angle. Epiproct readily apparent, small, with weakly developed lateral apices, medial notch extremely narrow U-shape longer than broad. Posteromedial stylus absent. Hypoproct short, tonguelike, subepandrial sclerite weakly developed as fused paired circular plates anterior to gonocoxal bridge.

Parameres separate, simple spine with expanded base placed on medial surface of gonocoxite.

Gonocoxal apodeme dorsoventrally flattened, narrow, dorsal spur shifted to dorsal surface of gonocoxite, acutely point, directed medially. extremely broad, quadrate slanted slightly anterior. Dorsal gonocoxal lobes present, directed medially at base of gonostylus. Gonostylus with basal lobe directed medially, small setose ball-like knob. Apical stylus massive, broadly triangular, dorsal margin curving ventrally, ventral margin straight, apex forming triangular spine. Secondary lobe of apical stylus placed at base, forming massive semicircular laterally compressed lobe directed dorsally nearly as large as remained of apical stylus. Tertiary lobe placed subapically on medial surface of apical stylus, scallop-shaped knob with small triangular notch ventrally.

Basal division band-like, broad, with low triangular apex near base of terminal division; spatulate lobes absent; basal scale present, divided, dorsoventrally compressed semicircular fleshy lobes fused at base and with small notch on medial margin near apex. Terminal division with constricted, articulated base, lateral sclerites extremely narrow, small ventrally curved spine near base; apex with prominent lateral extensions free of basal division, subquadrate tapering ventrally; apex spine-like. Membranous window slit-like, stretching nearly entire length of terminal division, dividing base.

Aedeagus vertical. Aedeagal sclerites with apex rounded, simple, parallel sided. Lateral ejaculatory processes with base straight, as tall as sperm sac, extended straight lateroanterior; discoid apodemes kidney shaped, directed both dorsally and ventrally. Sperm sac subspherical. Ejaculatory apodeme flag-like, not closely associated with aedeagal sclerites, larger than sperm sac, not closely paralleling anterior margin of sperm sac. Subapical sclerite mushroom shaped, apex expanded semicircle, base cylindrical.

Figures. Male Genitalia: 155, Wing: 156, Distribution: 157.

Material Examined. E. China, Fukien, Ta-chu-lan, May 1943, Maa (Pinned: 1 m#, 1 f#) (USNM)

***Ptychoptera javensis* Alexander, 1937.**

Ptychoptera javensis Alexander, 1937: 368-369 (original description)

Diagnosis

Adult. Epandrium with nematoform lobes with a spatulate apex. Paramere with apical lobes straight and dagger-like. Gonopod with threadlike secondary lobe at 1/2 length of apical stylus, dorsolaterally directed tertiary lobe at apex does not extend to epandrial claspers. Hypandrium with terminal division apex forming squared plate with rounded lateral margins and spine-like dorsal apex.

Description

Adult. Measurements (n=1). Overall length ? (dissected). **Head.** Width: 1.16mm, Height: 0.94mm, Length: 0.62mm; Antenna flagellum length: 5.75mm. **Thorax.** Length: 2.0mm, Height: 1.95mm; Wing length: 8.7mm, Width: 2.1mm. **Abdomen.** Length: ? (dissected).

Head. Vertex shining russet brown, glabrous; frons extremely narrow strip, brown. Occiput and genae yellow with dense elongate yellow trichoid sensilla. Antennae: scape bright yellow, oblong cylinder with ring of long black trichoid sensilla; pedicel yellow, globular, ring of trichoid sensilla on lateral margin. Flagellomeres brown, bacilliform. Facial sclerite yellow, indistinct from clypeus. Clypeus quadrate, inflated, generally covered in yellow sensilla, dark yellow. Maxillary palpus with segments 1-3 yellow, distal segments brown, terminal segment extended. Labrum triangular pressed to clypeus, yellow; hypopharynx and epipharynx yellow, labium and labellae yellow.

Thorax. Antepronotum with transverse fold narrower than height of anterior ridge, brown medially, yellow laterally, medial lobe approximately nearly the width of remainder of antepronotum,

rounded, dorsal surface with medial notch. Prescutum and scutum with yellow stripe medially, laterally russet brown incised with dull orange posterior, mictrichia vestiture present; medial and prescutal suture with row of minute clear trichoid sensilla, long clear prealar sensilla present. Scutellum dull orange. Mediotergite of metanotum yellow, with shining. Laterotergite of metanotum shining yellow. Pleural sclerites all yellow, shining. Anepisternal cleft narrow, membrane yellow. Suture between epimeron and metapleurite complete. **Wing.** Two broad bands, proximal extending from base of R_5 to CuA_1+CuA_2 fork, distal from R_{1+2} fork to base of M fork; membrane with macrotrichia in all cells except br & bm, CuA, A. All veins covered in short stout macrotrichia. Sc: 5.31mm, Apex of Sc to Apex of R_1 1.60mm, R_{3+4+5} stem 0.37mm, straight; R_{4+5} stem 1.93mm; R_4 after fork 1.80mm, R_5 after fork 1.73mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4$, 1.0 : 5.21 : 4.86. r-m 0.32mm; M distal to r-m 2.47mm; M_1 1.09mm, arcuate, M_2 0.69mm; Mdistal: M_1 , 1.0:0.44, $R_{3+4+5}:M\text{distal}$, 1.0:6.67, $R_4:M_1$, 1.0:0.60. CuA_1 proximal 0.27mm, distal 2.47mm; CuA_2 1.50mm with anterior angle well developed, posterior angle absent. CuA_2 to A_1 2.29mm. R_3 with point contact at r-m. Halter yellow. Prehalter dark yellow. **Legs.** Coxae yellow. Femur and tibia yellow, darkening slightly at shared joint, joint of tibia and first tarsomere brown. First tarsomere light brown proximally, darkening distally. All other tarsi brown. 5th tarsomere cannot fold back on pentultimate tarsomere. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Tergites and sternites yellow, posterior margins of all segments posterior to seg. II with brown band. **Male Genitalia.** Epandrial collar complete, closely appressed to epandrial lobes; epandrial apodemes well developed, thread-like across gonocoxal apodeme to hypandrium, breaks present at epandrium and hypandrium. Epandrial lobes nematoform, elongate, narrow; epandrial clasper not well delineated from epandrial lobe, apex weakly spatulae, dorsal corner weakly extended, epandrial lobes moderately curved ventrally without distinct angle. Epiproct readily apparent, small,

posterior margin simple, V-shaped, completely separating epandrial lobes. Posteromedial stylus absent. Hypoproct fused to subepandrial sclerite, quadrate, paired posterior lobes present.

Parameral bridge attached narrowly to gonocoxite, directed dorsally then abruptly angled medially, band-like in dorsal view; anterior margin simple arc, posterior margin with subcircular posterior bulge with fingerlike extension medially. Apical lobe placed submedially on posterior margin, elongate spike extending posterior beyond apex of aedeagus.

Gonocoxal apodeme narrow, weakly tapering, apex pointed, greater than half length of gonocoxite, dorsal spur subobtusate, over half length of apodeme, ventral margin simple, weakly angled. Gonocoxite elongate, weakly expanding to gonostylus, dorsal margin straight dorsally, ventral margin loose arc. Gonocoxal lobes absent. Gonostylus with basal lobe having three subdivisions, anterior lobe simple rounded point, dorsal and medial lobes directed medially, dorsal lobe subtriangular paddle-like with broad base, medial lobe oval, paddle-like, with petiolate base. Apical stylus fingerlike, round in cross section, apex curved dorsally, weakly expanding, over twice length of external portion of gonocoxite. Secondary lobe directed dorsally at 1/3 length of apical stylus, narrow threadlike process extended dorsally, expanding slightly at apex. Tertiary lobe present, fingerlike, placed at apex of apical stylus and directed dorsolaterally, not approaching epandrial clasper.

Basal division band-like, broad; spathate lobes present at base of terminal division, base subrhomboidal with apical corner extended to rounded point; basal scale present, divided, ribbon like base expanding to brush-like apex below spathate lobes. Terminal division with constricted, articulated base, lateral sclerites extremely narrow; apex with prominent lateral extensions fused to basal division, square plate with rounded lateral margins and notch in ventral margin, dorsal margin with medial spine-like apex. Membranous window slit-like, stretching nearly entire length of terminal division, expanding subcircularly at base.

Aedeagus within approximately 15 degrees of vertical. Aedeagal sclerites with apex pointed, simple, base narrow. Lateral ejaculatory processes with base straight, narrow, extended straight lateroanterior; discoid apodemes with elongate ovoid dorsal extension. Sperm sac subspherical. Ejaculatory apodeme flag-like, not closely associated with aedeagal sclerites, larger than sperm sac, not closely paralleling anterior margin of sperm sac. . Subapical sclerite with constriction at apex of aedeagal sclerites, apex turnip shaped, lateral margins rounded, tapering.

Figures. Male Genitalia: 158, Wing: 159, Distribution: 160.

Taxonomic Notes

P. javensis and *P. sumatrensis* appear to represent sister species, and suggest that allopatric speciation may have occurred on the islands of the Malay Archipelago, though further sampling is needed for confirmation.

Material Examined. Holotype. Soember, ronantas, Java, 6000' Jan. '36, Walsh (Pinned: 1m#, Slide: Wing) (USNM)

***Ptychoptera malaisei* Alexander, 1946**

Diagnosis.

Adult. Basal lobe of gonostylus mushroom shaped.

Description.

Adult. Measurements. Wing length 9.2mm, width 2.4mm.

Head. Unknown.

Thorax. Unknown. **Wing.** Faint infuscation from R_5 to CuA fork and R_{4+5} fork, membrane with macrotrichia in all cells except br and bm. All veins covered in short stout macrotrichia. Sc: 6.4mm, Apex of Sc to Apex of R_1 1.58mm, R_{3+4+5} stem 1.68mm, long, angle at base; R_{4+5} stem 2.03mm; R_4 after fork 2.37mm, R_5 after fork 2.37mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.0 : 1.20 : 1.41$. r-m 0.32mm; M distal to r-m 3.12mm; M_1 0.86mm, M_2 0.57mm; Mdistal: $M_1 = 1.0:0.27$, $R_{3+4+5}:M\text{distal} = 1.0:1.85$, $R_4:M_1 = 1.0:0.36$. CuA₁ proximal 0.30, distal 2.72mm; CuA₂ 1.78mm with anterior angle well developed, posterior angle absent. CuA₂ to A₁ 2.50mm. R_3 with point contact at r-m. **Legs.** Unknown.

Pre-genital Abdomen. Unknown. **Male Genitalia.** Epandrial collar complete; epandrial apodemes well developed, ribbon-like across gonocoxal apodeme to hypandrium. Epandrial lobes short, triangular extending posterior less than half the width of the epandrium; epandrial clasper very short, distinctly delineated from epandrial lobe, circular in cross section, curved medially, apex round. Epiproct weakly delineated, posterior margin straight, epandrial lobes with point contact anteriorly. Posteromedial stylus possibly present as thickened cuticle on medial surface of epandrial clasper. Hypoproct tonguelike, as broad as epiproct. Subepandrial membrane with distinct T-shaped subepandrial sclerite, lateral apices squared, heavily sclerotized, broad, weakly sclerotized medially.

Parameral bridge attached narrowly to gonocoxite, directed medially; base very broad, with triangular anterior directed lobe, medial point with distinct anterior bend. Apical lobe located very close to base, directed posteriorly, triangular beak-like, approximately half length of paramere.

Gonocoxal apodeme triangular, apex rounded, 1/4th length of gonocoxite, dorsal margin straight, ventral margin emarginate. Dorsal spur of gonocoxite present, anterior margin sloped, posterior margin straight. Gonocoxite expanding to gonostylus, dorsal margin straight, ventral margin straight anteriorly, directed obliquely ventrally for 2/3rds length, posterior portion parallel to horizontal axis. Gonocoxal lobes absent. Gonostylus with basal lobe directed dorsomedially, base petiolate, apex

forming broad, mushroom-like cone covered in short, stout trichoid sensilla. Apical stylus subdivided, ventral to secondary lobe, curving weakly medially, shorter than secondary stylus, expanding slightly to weakly bifurcated apex, dorsal lobe flattened, narrower than basal lobe; secondary lobe round in cross section, curved medially, longer than remainder of apical stylus, apex abruptly cut to flattened plate.

Hypandrium difficult to interpret on specimen examined. Basal division broad, with three massive trichoid sensilla in a vertical line 1/3rd length dorsally from base along posterior margin, secondary patch of stout trichoid sensilla placed directly anterior. Spathate lobes present, small round knobs located ventrally from massive sensilla, covered with trichoid sensilla. Terminal division narrowly attached medially on basal division, junction acutely ax shaped plate, base of slit-like membranous window present. Remainder of terminal division obliterated. Aedeagus orientation not readily apparent in holotype.

Aedeagal sclerites with apex rounded simple. Subapical sclerite simple, flattened conical. Ejaculatory apodeme much larger than sperm sac, slightly longer than tall, closely paralleling contour of sperm sac. Lateral ejaculatory processes narrow at base, discoid apodemes extended ventrally.

Figures. Male Genitalia: 162, Wing: 163, Distribution: 164.

Material Examined. Holotype. n.e. Burma, Kambaiti, 6800', Apr. 1, '34, (Rene Malaise) (Slide: 1m#) (USNM).

***Ptychoptera perbona* Alexander, 1946**

Ptychoptera perbona flaviventris Alexander, 1946

Diagnosis.

Adult. Epandrial clasper longer than width of epandrium, apical stylus of gonostylus with apical notch.

Description.

Adult. Measurements. Wing length 5.7mm, width 1.9mm.

Head. Unknown.

Thorax. Unknown. **Wing.** Faint infuscation from R_5 to CuA fork and R_{4+5} fork to M fork, membrane with macrotrichia in all cells except br and bm. All veins covered in short stout macrotrichia. Sc: 5.00mm, Apex of Sc to Apex of R_1 1.78mm, R_{3+4+5} stem 0.32mm, short, straight; R_{4+5} stem 1.91mm; R_4 after fork 1.68mm, R_5 after fork 1.68mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.0 : x : x$. r-m 0.37mm; M distal to r-m 2.50mm; M_1 1.04mm, M_2 0.76mm; Mdistal: $M_1 = 1.0:x$, $R_{3+4+5}:M\text{distal} = 1.0:x$, $R_4:M_1 = 1.0:x$. CuA₁ proximal 0.37mm, distal 2.45mm; CuA₂ 1.41mm with anterior angle well developed, posterior angle absent. CuA₂ to A₁ CuA₂ 2.35mm. R_3 with point contact at r-m. **Legs.** Unknown.

Pre-genital Abdomen. Unknown. **Male Genitalia.** Epandrial collar incomplete, broken medially at epiproct, closely appressed to epandrial lobes; epandrial apodemes not distinguishable on specimens examined. Epandrial lobes nematoform, elongate, narrow, much long than epandrium is wide; epandrial clasper weakly delineated from epandrial lobe with internal crease, approximately half length of epandrial lobe, weakly constricted before apex, apex distinct oblong rounded bulb, weakly curved medially at apex. Epiproct readily apparent, posterior margin heavily incised in V-shape, lateral margins rounded, epandrial lobes with no contact. Posteromedial stylus absent. Hypoproct and subepandrial membrane not preserved on specimens examined. Parameral bridge attached narrowly to gonocoxite at ventral margin of gonocoxite near gonostylus, directed anterior at base, anterior arc in dorsal view;

posterior margin simple arc, anterior margin with low triangular lobes near base, probably represent apical lobes. Gonocoxal apodeme weakly tapering, apex rounded, 1/3rd length of gonocoxite. Dorsal spur of gonocoxal apodeme present, shifted anterior on gonocoxal apodeme, about half as large as remainder of gonocoxal apodeme, subacute. Gonocoxite subcylindrical, dorsal margin heavily straight, ventral margin formed of two loose ventrally directed arcs, meeting midway along length. Gonocoxal lobes absent. Gonostylus with basal lobe on dorsal surface, subdivided to two lobes, anterior lobe tapering to rounded apex, with elongate trichoid sensilla, posterior lobe located somewhat lateral to anterior lobe, round with petiolate base, covered in elongate trichoid sensilla. Apical stylus fingerlike, weakly laterally compressed, elongate expanding to clavate apex, apex weakly bifurcate, dorsal lobe smaller than ventral lobe. Hypandrium damaged on specimens examined. Basal division of hypandrium bandlike, broad. Spathate lobes not apparent, possibly represented by weak bulge on lateral edge of posterior margin with elongate trichoid sensilla. Eversible sac absent. Terminal division with well-developed lateral extensions, medial sclerotized heavily reduced to setose strips; apex divided medially, broadly triangular with lateral apices elongate, laterally directed spines curving dorsally at apex. Aedeagus orientation not readily apparent in specimens examined. Aedeagal sclerites with apex rounded, very short. Subapical sclerite with extremely broad triangle basally, constricting near apex of aedeagal sclerites, terminal portion broadly blade-like, tapering to acute point. Sperm sac oblong. Ejaculatory apodeme flag-like, not closely associated with aedeagal sclerites, smaller than sperm sac, weakly paralleling anterior margin of sperm sac. Lateral ejaculatory processes not readily diagnosed in specimen examined.

Figures. Male Genitalia: 164, Wing: 165, Distribution: 166.

Material Examined. Paratypes. N.E. Burma, Kambaiti, 2000m, VI-16-VI (Malaise) (Slide: 1m#) (USNM). N.E. Burma, Kambaiti, 7000' VI-12-VI (Rene Malaise) (Slide: 1m#, as *Ptychoptera perbona flaviventris*) (USNM)

***Ptychoptera persimilis* Alexander, 1947**

Diagnosis.

Adult. Male genitalia with epandrium nematoform, apex expanded and slipper-like; paramere forming bridge, trapezoidal in shape, posterolateral corners formed for acute medioposterior directed spines which cross at apex; gonostylus with basal lobe with anterior and dorsal portions forming banana shape, medial portion fingerlike, dorsal surface of apical stylus with sail-like subtriangular lobe, apical stylus and secondary lobe subequal in length, crossing at apices.

Description.

Adult. Measurements. Wing length 6.8mm, width 1.8mm.

Head. Unknown.

Thorax. Unknown. **Wing.** Band from R_5 to CuA fork, infuscation at R_{4+5} fork and M fork, membrane with macrotrichia in all cells except br and bm. All veins covered in short stout macrotrichia. Sc: 4.5mm, Apex of Sc to Apex of R_1 1.34mm, R_{3+4+5} stem 0.27mm, short, straight; R_{4+5} stem 1.58mm; R_4 after fork 1.55mm, R_5 after fork 1.48mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.0 : 5.85 : 5.74$. r-m 0.25mm; M distal to r-m 2.10mm; M_1 0.88mm, M_2 0.60mm; $M\text{distal}:M_1 = 1.0:0.41$, $R_{3+4+5}:M\text{distal} = 1.0:7.77$, $R_4:M_1 = 1.0:0.56$. CuA₁ proximal 0.30mm, distal 1.98mm; CuA₂ 1.21mm with anterior angle well developed, posterior angle absent. CuA₂ to 1.01mm. R_3 with point contact at r-m. **Legs.** Unknown.

Pre-genital Abdomen. Unknown. **Male Genitalia.** Epandrial collar complete, closely appressed to epandrial lobes; epandrial apodemes well developed, thread-like across gonocoxal apodeme to hypandrium, breaks present at epandrium and hypandrium. Epandrial lobes nematoform, broad, very weakly tapering, longer than width of epandrium; epandrial clasper not well delineated from epandrial lobe, apex weakly expanded, slipper-shaped, epandrial lobes with distinct ventral angle. Epiproct very reduced, posterior margin simple shallow U-shaped notch, epandrial lobes not in contact. Posteromedial stylus absent. Hypoproct indistinct. Subepandrial membrane weakly sclerotized, weakly attached to epandrium, quadrate, paired posterior lobes present.

Parameral bridge attached narrowly to gonocoxite, directed medially; arced weakly dorsally; ventroposterior margin with medially directed elongate flattened spine placed near base. Apical lobe placed dorsally, short triangular spine 2/3rds distance between paramere base and medial point. Gonocoxal apodeme weakly tapering, apex rounded, greater than half length of gonocoxite, dorsal margin broken by dorsal spur, ventral margin sloped weakly dorsally. Dorsal spur of gonocoxal apodeme present, shifted anterior on gonocoxal apodeme, nearly as long as remainder of gonocoxal apodeme, subequilateral. Gonocoxite ovoid, dorsal margin heavily arced dorsally, ventral margin looser arc. Gonocoxal lobes absent. Gonostylus with basal lobe on dorsal surface, anterior and dorsal combine to form banana shape, attached on medially along ventral arc, medial stylus present as finger-like extension. Apical stylus fingerlike, round in cross section, apex curved laterally, weakly expanding, shorter than gonocoxite. Secondary lobe subdivided, basal portion directed dorsally, laterally compressed, round, broader than remainder of apical stylus complex, covered in fine trichoid sensilla; posterior portion fingerlike, directed posterior, curving medially, expanding at apex, with numerous stout trichoid sensilla on medial surface apically. Posterior portion of secondary lobe and primary apical stylus with apices crossing. Hypandrium damaged on specimen examined. Basal division with spatulate lobes present, near medial point, broadly elongate with rounded apex. Terminal division with

pentagonal apex, lateral apices quadrate, with ventrally curved spine. Aedeagus orientation not readily apparent in holotype. Aedeagal sclerites with apex pointed, simple. Subapical sclerite with constriction at apex of aedeagal sclerites, apex turnip shaped, lateral margins straight, tapering. Sperm sac damaged. Ejaculatory apodeme and lateral ejaculatory processes not readily diagnosed in specimen examined.

Figures. Male Genitalia: 167, Wing: 168, Distribution: 169.

Material Examined. Holotype. Burma, So. Shan States, Shwenyoung, Aug. 1930.

***Ptychoptera praescutellaris* Alexander, 1946**

Diagnosis

Adult. Epandrial clasper nematoform, with medial swelling at 1/3rd length, gonostylus with secondary lobe subquadrate with dorsoposterior corner extended.

Description.

Adult. Measurements. Wing length 7.9mm, 2.4mm.

Head. Unknown. **Thorax.** Unknown. **Wing.** Faint infuscation from R_5 to CuA fork as well as R_{4+5} fork and M fork, membrane with macrotrichia in all cells except br and bm. All veins covered in short stout macrotrichia. Sc: 5.06mm, Apex of Sc to Apex of R_1 1.58mm, R_{3+4+5} stem 0.49mm, short, straight; R_{4+5} stem 1.83mm; R_4 after fork 2.05mm, R_5 after fork 2.03mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.0 : 3.73 : 4.18\text{mm}$. r-m 0.42mm; M distal to r-m 2.47mm; M_1 1.28mm, M_2 0.99mm; $M\text{distal}:M_1 = 1.0:0.51$, $R_{3+4+5}:M\text{distal} = 1.0:5.04$, $R_4:M_1 = 1.0:0.62$. CuA_1 proximal 0.37, distal 2.47mm; CuA_2 1.48mm with anterior angle well developed, posterior angle absent. CuA_2 to A_1 2.42mm. R_3 with point contact at r-m. **Legs.** Fore- and midcoxae yellow with dark band on dorsal margin, hindcoxae black. Femur and tibia yellow. First

tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensillae.

Abdomen. Unknown. **Male Genitalia.** Epandrial collar complete; epandrial apodemes well developed, ribbon-like across gonocoxal apodeme to hypandrium, breaks not distinguishable in specimen examined. Epandrial lobes nematoform, triangular extending posterior approximately 3/4ths width of epandrium; epandrial clasper very elongate, distinctly delineated from epandrial lobe, circular in cross section, directed straight posterior, lateral margin with ovoid swelling on medial margin near delineation of epandrial clasper, apex expanding to rounded bulb. Epiproct readily apparent, posterior margin simple steep V-shaped notch, epandrial lobes not in contact, extending halfway to junction of epandrial clasper and epandrial lobe. Posteromedial stylus possibly present as ovoid swelling near division of epandrial lobe and epandrial clasper. Hypoproct short, triangular. Subepandrial membrane heavily sclerotized, but not defined into distinct subepandrial sclerite. Parameral bridge attached narrowly to gonocoxite, directed medially; medioposterior extension present, apex simple rounded point. Apical lobe placed submedially, directed posterior, flattened, with distinct angle directed medially, apex acutely pointed. Gonocoxal apodeme parallel sided, apex rounded, 1/3rd length of gonocoxite, dorsal margin straight, ventral margin emarginate. Dorsal spur of gonocoxite present, nearly equilateral, subequal in size to remainder of gonocoxal apodeme. Gonocoxite subcylindrical, dorsal margin evenly arced dorsally, ventral margin with tight arc anteriorly, flattening at midpoint, rounded angle to joint with gonostylus. Gonocoxal lobes absent. Gonostylus with basal lobe subdivided into three portions, two directed dorsally, anterior projection recumbent anteriorly directed cylindrical lobe with rounded apex, posterior projection directed dorsally, both lobes with trichoid sensilla, third portion directed medially, low short conical lobe on medial surface. Apical stylus fingerlike, expanding to apex, shorter than gonocoxite; secondary lobe present on dorsal surface at 1/3rd length of apical stylus,

flaglike, dorsoposterior corner extended dorsoposteriorly, covered with short stout trichoid sensilla, base with short triangular lobe on medial surface near posterior margin. Hypandrium damaged on specimen examined. Basal division with spatulate lobes present, near medial point, subtriangular lifelike lobes directed dorsally, heavily provided with elongate trichoid sensilla. Terminal division narrowly attached medially on basal division, small semicircular lobules at junction of basal and terminal division; apex of terminal division glabrous, triangular folded medially forming trough. Aedeagus orientation not readily apparent in holotype. Aedeagal sclerites with apex pointed, simple. Subapical sclerite somewhat flattened, closely appressed to aedeagal sclerites, transverse notch located subapically on ventral surface, dorsal surface with minute spicules. Sperm sac oblong. Ejaculatory apodeme and lateral ejaculatory processes not readily diagnosed in specimen examined.

Figures. Male Genitalia: 170, Wing: 171, Distribution: 172.

Material Examined. Holotype. n.e. Burma, Kambaiti, 6500', V-16-'34, (Malaise) (USNM) (Slide, 1m#). **Paratype.** n.e. Burma, Kambaiti, 7000', VI-4-'34, (Malaise) (USNM) (Slide, 1m#)

***Ptychoptera pseudosimilis* Fasbender, sp. n.**

Adult. Male genitalia with epandrium nematoform, apex expanded and evenly round; paramere forming bridge, trapezoidal in shape, posterolateral corners with flattened squared apices; gonostylus with basal lobe with anterior and dorsal portions forming banana shape, medial portion absent, dorsal surface of apical stylus with sail-like subtriangular lobe, apical stylus and secondary lobe subequal in length, crossing at apices.

Females and immature stages unknown.

Description.

Adult. Measurements. Wing length 7.9mm, 2.2mm.

Head. Unknown. **Thorax.** Unknown. **Wing.** Faint infuscation from R_5 to CuA fork and R_{4+5} fork, membrane with macrotrichia in all cells except br and bm. All veins covered in short stout macrotrichia. Sc: 5.18mm, Apex of Sc to Apex of R_1 1.60mm, R_{3+4+5} stem 0.35mm, short, straight; R_{4+5} stem 1.80mm; R_4 after fork 1.80mm, R_5 after fork 1.71mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.00 : 5.14 : 5.14$. r-m 0.30mm; M distal to r-m 2.29mm; M_1 1.05mm, M_2 0.74mm; $M\text{distal}:M_1 = 1.00:0.45$, $R_{3+4+5}:M\text{distal} = 1.00:6.54$, $R_4:M_1 = 1.00:0.58$. CuA₁ proximal 0.30mm, distal 2.35mm; CuA₂ 1.43mm with anterior angle well developed, posterior angle absent. A₁ straight for x. R_3 with point contact at r-m. **Legs.** Fore- and midcoxae yellow with dark band on dorsal margin, hindcoxae black. Femur and tibia yellow. First tarsomere yellow proximally, turning brown distally. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. Mid and hind 1st tarsomere with widely spaced row of minute, spine-like trichoid sensillae.

Pre-genital Abdomen. Unknown. **Male Genitalia.** Epandrial collar complete, closely appressed to epandrial lobes; epandrial apodemes well developed, thread-like across gonocoxal apodeme to hypandrium, breaks present at epandrium and hypandrium. Epandrial lobes nematoform, elongate, narrow; epandrial clasper not well delineated from epandrial lobe, apex strongly expanded, rounded bulb, epandrial lobes moderately curved ventrally without distinct angle. Epiproct readily apparent, posterior margin simple, weakly emarginate, epandrial lobes with point contact on anterior margin. Posteromedial stylus absent. Hypoproct indistinct. Subepandrial membrane weakly sclerotized, weakly attached to epandrium, quadrate, paired posterior lobes present.

Parameral bridge attached narrowly to gonocoxite, directed medially, trapezoidal in dorsal view; posterior margin simple arc, anterior margin with lateral portions straight posteromedial, angled medially at half width from base to midpoint, angle with scallop-shaped extension, medial portion with

low triangular lobes laterally, low semicircular lobe medially. Apical lobe placed dorsally, short triangular spine 2/3rds distance between paramere base and medial point, spine with internal crease near lateral margin. Gonocoxal apodeme weakly tapering, apex rounded, greater than half length of gonocoxite, dorsal margin broken by dorsal spur, ventral margin sloped weakly dorsally. Dorsal spur of gonocoxal apodeme present, shifted anterior on gonocoxal apodeme, nearly as long as remainder of gonocoxal apodeme, subequilateral. Gonocoxite ovoid, dorsal margin heavily arched dorsally, ventral margin looser arc. Gonocoxal lobes absent. Gonostylus with basal lobe on dorsal surface, banana-shaped, attached on medially along ventral arc. Apical stylus fingerlike, round in cross section, apex curved laterally, weakly expanding, shorter than gonocoxite. Secondary lobe subdivided, basal portion directed dorsally, laterally compressed, round, broader than remainder of apical stylus complex, covered in fine trichoid sensilla; posterior portion fingerlike, directed posterior, curving medially, expanding at apex, with numerous stout trichoid sensilla on medial surface apically. Posterior portion of secondary lobe and primary apical stylus with apices crossing. Hypandrium damaged on specimen examined. Basal division with spatulate lobes present, near medial point, broadly elongate with rounded apex. Terminal division with pentagonal apex, lateral apices quadrate, with ventrally curved spine, apex damaged. Membranous window slit-like, stretching nearly entire length of terminal division. Aedeagus orientation not readily apparent in holotype. Aedeagal sclerites with apex pointed, simple. Subapical sclerite with constriction at apex of aedeagal sclerites, apex turnip shaped, lateral margins rounded, tapering. Sperm sac oblong. Ejaculatory apodeme flag-like, not closely associated with aedeagal sclerites, smaller than sperm sac, weakly paralleling anterior margin of sperm sac. Lateral ejaculatory processes not readily diagnosed in specimen examined.

Figures. Male Genitalia: 174, Wing: 175, Distribution: 176.

Taxonomic Notes

This species has been described from a pair of slide mounted specimens consisting primarily of the male genitalia. Based on the structure of the gonostylus this species appears to be the sister taxon of *P. persimilis*.

Material Examined. Holotype. assam – Kameng, Nyukmadong, 8000' IV-21.61, 465 (Schmid) (Slide: 1m#) (USNM) **Paratype.** INDIA – Assam, NEFA – Kameng, Shergaon, 6400' V-8.61, 585 (Schmid) (Slide: 1m#) (USNM)

Ptychoptera sumatrensis Alexander, 1936.

Ptychoptera sumatrensis Alexander, 1936: 165-167 (original description)

Diagnosis

Adult. Epandrium with nematoform lobes with a squared apex. Paramere with apical lobes dorsally curved triangles with acutely pointed spine on dorsal margin. Gonopod lacking threadlike secondary lobe at 1/2 length of apical stylus, and dorsolaterally directed tertiary lobe at apex extends beyond epandrial claspers. Hypandrium with terminal division apex forming squared plate with rounded lateral margins and spine-like dorsal apex.

Description

Adult. Measurements (n=1). Overall length ? (abdomen dissected). **Head.** Width: 1.0mm, Height: 0.86mm, Length: 0.58mm; Antenna flagellum length: ? (dissection). **Thorax.** Length: 1.95mm, Height: 1.9mm; Wing length: 7.8mm, Width: 1.8mm. **Abdomen.** Length: ? (dissected).

Head. Vertex shining blue, sparsely provided with elongate trichoid sensilla posteriorly; frons extremely narrow strip, yellow. Occiput and genae yellow, with dense elongate yellow trichoid sensilla. Antennae: scape bright yellow, oblong cylinder with ring of long black trichoid sensilla well separated from dorsal apex; pedicel yellow basally, brown dorsally, globular, ring of trichoid sensilla on lateral margin. Flagellomeres brown, fusiform. Facial sclerite ellow, indistinct from clypeus. Clypeus rectangular, inflated, generally covered in yellow sensilla, bright yellow. Maxillary palpus with segments 1&2 yellow, segment three and four muddy yellow, terminal segment brown. Labrum bluntly triangular, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae yellow.

Thorax. Antepronotum with transverse fold narrower than height of anterior ridge, yellow, medial lobe approximately equal in width to remainder of antepronotum, rounded margins, dorsal surface with medial notch. Prescutum and scutum dark brown obscurely shining, with microtrichia vestiture; medial and prescutal suture with row of minute black trichoid sensilla; long clear prealar sensilla present. Scutellum dark brown. Mediotergite of metanotum yellow dorsally brown ventrally, with light pollinosity. Laterotergite of metanotum shining brown. Pleural sclerites yellow, except episternum brown, shining. Anepisternal cleft narrow, membrane yellow. Suture between epimeron and metapleurite complete, weak. **Wing.** Two broad bands, proximal extending from base of R_s to angle of CuA_2 fork, distal from R_{1+2} fork to M fork; membrane with macrotrichia in all cells except br, bm and A. All veins covered in short stout macrotrichia. Sc: 4.25mm, Apex of Sc to Apex of R_1 1.48mm, R_{3+4+5} stem 0.27, weakly bowed at base; R_{4+5} stem 1.78; R_4 after fork 1.48mm, R_5 after fork 1.50mm; $R_{3+4+5}:R_{4+5}$ -stem: R_4 = 1.0 : 6.59 : 5.48. r-m 0.32mm; M distal to r-m 2.15mm; M_1 0.94mm, arcuate, M_2 0.64; Mdistal: M_1 = 1.0:0.43, R_{3+4+5} :Mdistal = 1.0:7.96, $R_4:M_1$ = 1.0:0.63. CuA_1 proximal 0.30mm, distal 2.0; CuA_2 1.13mm with anterior angle well developed, posterior angle absent. CuA_2 to A_1 2.12. r-m joins R_3 with point contact at r-m. Halter yellow. Prehalter dark yellow. **Legs.** Coxae yellow. Femur and tibia yellow, darkening slightly at shared joint, joint of tibia and first tarsomere brown. First tarsomere light brown

proximally, darkening distally. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Segments yellow anterior, brown posterior, except segment II brown with yellow band medially, segment VII yellow. **Male Genitalia.** Epandrial collar complete, closely appressed to epandrial lobes; epandrial apodemes well developed, thread-like across gonocoxal apodeme to hypandrium, breaks present at epandrium and hypandrium. Epandrial lobes nematoform, elongate, narrow; epandrial clasper not well delineated from epandrial lobe, apex bluntly squared, dorsal corner not extended, epandrial lobes moderately curved dorsally without distinct angle. Epiproct readily apparent, small, posterior margin simple, V-shaped, epandrial lobes completely separating epandrial lobes. Posteromedial stylus absent. Hypoproct fused to subepandrial sclerite, quadrate, paired posterior lobes present.

Parameral bridge attached narrowly to gonocoxite, directed dorsally then abruptly angled medially, band-like in dorsal view; anterior margin simple arc, posterior margin with subcircular posterior bulge with fingerlike extension medially. Apical lobe placed submedially on posterior margin, broad dorsally curved triangle extending posterior beyond apex of aedeagus, dorsal margin with acute spine.

Gonocoxal apodeme narrow, weakly tapering, apex narrowly rounded, greater than half length of gonocoxite, dorsal spur nearly equilateral, partially shifted to dorsal surface of gonocoxite, ventral margin simple, weakly angled. Gonocoxite elongate, weakly expanding to gonostylus, dorsal margin straight dorsally, ventral margin loose arc. Gonocoxal lobes absent. Gonostylus with basal lobe having three subdivisions, anterior lobe simple rounded point, dorsal and medial lobes directed medially, dorsal lobe weakly crescent shaped paddle-like with broad base, medial lobe T-shaped, flattened, apices

rounded. with elongate petiolate base. Apical stylus fingerlike, round in cross section, apex curved dorsally, weakly expanding, over subequal in length to external portion of gonocoxite. Secondary lobe no more than a small bump at 2/3 length of apical stylus, on medial surface. Tertiary lobe present, elongate fingerlike, placed at apex of apical stylus and directed dorsolaterally beyond epandrial clasper.

Basal division band-like, broad; spathate lobes present at base of terminal division, elongate flattened stylus directed posterior at base, curved dorsally after less the 1/5 length; basal scale present, divided, ribbon like base with rounded apex below spathate lobes. Terminal division with constricted, articulated base, lateral sclerites extremely narrow; apex with prominent lateral extensions fused to basal division, square plate with straight, weakly convergent lateral margins and notch in ventral margin, dorsal margin with medial spine-like apex with distinct posterior bend near keel-like base. Membranous window slit-like, stretching nearly entire length of terminal division, expanding subcircularly at base.

Aedeagus within approximately 15 degrees of vertical. Aedeagal sclerites with apex pointed, simple, base narrow. Subapical sclerite with constriction at apex of aedeagal sclerites, apex turnip shaped, lateral margins of basal portion straight, divergent ventrally forming trapezoid shielding base of aedeagal sclerites. Lateral ejaculatory processes with base straight, narrow, extended straight lateroanterior; discoid apodemes with elongate ovoid dorsal extension. Sperm sac subspherical. Ejaculatory apodeme flag-like, not closely associated with aedeagal sclerites, smaller than sperm sac, not closely paralleling anterior margin of sperm sac.

Female Genitalia. Tergite VII yellow. Cerci yellow, lateral ridge poorly defined, dorsal furrow poorly developed. Cercus length:width, 5.5:1. Hypogynium yellow, rotated dorsally approximately 30 degrees from vertical; expanding weakly transversely halfway from base. Apical margin triangular, medial apex with weak emargination, lateral corner simple. Lateral margin visible distally.

Figures. Male Genitalia: 176, Wing: 177, Distribution: 178.

Material Examined. Holotype. Pagar Alam, Palembang, Sumatra 2250' V-23-35, Walsh (Pinned: 1m#, Slide: Wing) (USNM) **Other Material.** As holotype (Pinned: 1 f#) (USNM).

***Ptychoptera yasumatsui* Tokunaga, 1939**

Diagnosis

Adult. Gonostylus with dorsal lobe of basal lobe paddle-like, hypandrium without spathate lobes.

Description

Adult. Measurements (n=1). Overall length 8.15mm. **Head.** Width: 1.0mm, Height: 0.8mm, Length: 0.55mm; Antenna flagellum length: 3.88mm. **Thorax.** Length: 2.3mm, Height: 2.2mm; Wing length: 9.6mm, Width: 2.5mm. **Abdomen.** Length: 5.3mm

Head. Vertex shining black, sparsely provided with elongate trichoid sensilla posteriorly; frons extremely narrow strip, black. Occiput and genae glabrous. Antennae: scape brown, oblong cylinder with ring of long black trichoid sensilla well separated from dorsal apex; pedicel brown, globular, ring of trichoid sensilla on lateral margin. Flagellomeres brown, fusiform. Facial sclerite quadrate, distinct from clypeus, flat. Clypeus triangular, inflated, generally covered in clear sensilla, pollinose black. Maxillary palpus yellow. Labrum not apparent, yellow; hypopharynx and epipharynx not externally apparent, labium and labellae dark orange.

Thorax. Antepronotum with transverse fold broader than height of anterior ridge, black, medial lobe approximately triangular, dorsal surface with medial notch. Prescutum and scutum shining black, with microtrichia vestiture; medial and prescutal suture with sensilla, short clear prealar sensilla present. Scutellum dark brown. Mediotergite of metanotum shining black, with heavy pollinosity.

Laterotergite of metanotum shining black, dorsal patch of short yellow trichoid sensilla. Pleural sclerites black, fading to ruddy brown medially, shining. Anepisternal cleft narrow, trapezoidal with membrane orange brown. Suture between epimeron and metapleurite complete. **Wing.** Two broad bands and two large spots, proximal extending from base of R_5 to beyond r-m, not extending below M, distal band extending from R_2 through R_{4+5} fork to the M fork, spot oval at base of R_5 , second spot in br distal of h, membrane with macrotrichia in all cells. All veins covered in short stout macrotrichia. Sc: 6.8mm, Apex of Sc to Apex of R_1 1.3mm, R_{3+4+5} stem 1.6mm, elongate, with angle at base; R_{4+5} stem 2.45mm; R_4 after fork 2.27mm, R_5 after fork 2.22mm; $R_{3+4+5}:R_{4+5}\text{-stem}:R_4 = 1.0 : x : x$. r-m 0.32mm; M distal to r-m 3.0mm; M_1 1.3mm, arcuate, M_2 1.0mm; Mdistal: $M_1 = 1.0:x$, $R_{3+4+5}:M\text{distal} = 1.0:x$, $R_4:M_1 = 1.0:x$. CuA_1 proximal 0.37mm, distal 3.1mm; CuA_2 1.65mm with anterior angle well developed, posterior angle absent. CuA_2 to A_1 2.4mm. R_3 branches at r-m. Halter yellow. **Legs.** Fore- and midcoxae dark orange, hind coxa dark brown. Femur and tibia yellow, darkening slightly at shared joint, joint of tibia and first tarsomere brown. First tarsomere light brown proximally, darkening distally. All other tarsi brown. 5th tarsomere can fold back on pentultimate tarsomere. 1st tarsomere on all legs with widely spaced row of minute, spine-like trichoid sensillae across length.

Abdomen. Tergites and sternites dark brown, segments II, III, and IV with yellow bands. **Male Genitalia.** Epandrial collar complete, narrow, epandrial apodemes well developed, extending to lateroanterior apex of hypandrium, ribbonlike across gonocoxal apodeme, breaks at epandrium and hypandrium. Epandrial lobes nematoform, epandrial clasper indistinguishably fused, tapering weakly at base, cylindrical to tapering rounded apex. Epiproct prominent, epandrial lobes in contact for less than 1/5th of epiproct length anteriorly; posterior margin with medial notch subtrapezoidal. Posteromedial stylus not developed. Hypoproct heavily reduced, subepandrial membrane weakly sclerotized, divided medially. Parameral bridge attached broadly to dorsoanterior surface of gonocoxite, base subquadrate, directed obliquely posterior and weakly ventrally; medial portion forming broad arc, flattened. Apical

lobes directed dorsoposterior, laterally compressed, apex spatulate, dorsal corner weakly extended.

Gonocoxal apodeme as broad as gonocoxite, apex broadly rounded, dorsal spur directed medially, short and triangular. Gonocoxite broadly oblong, ventral margin bulging, dorsal margin with anterior portion straight, dropping slightly at halfway point and continuing straight and parallel to gonostylus, ventral margin broadly rounded anteriorly, arc becoming more acute posterior near gonostylus, ventral margin extending posterior beyond dorsal margin. Gonostylus with basal lobe complex, anteriomedial with petiolate knob directed medially, posteromedial corner slightly extended; dorsal surface with laterally compressed, paddle-like blade with broad, rounded apex, extending nearly to the apex of the apical stylus, medial surface with laterally compressed leaf-like lobe directed medially, apex curving medially, nearly as tall as long. Apical stylus directed posteriorly, with medial curve, furcate at apex, dorsal spur directed dorsoposterior, ventral spur directed posterior, longer than dorsal spur, flattened semicircular lobe present subapically on medial surface. Basal division of hypandrium simple, bandlike, expanding midway along length of lateral portion. Eversible sac absent, hypandrial spathate lobes absent. Terminal division narrowly attached to basal division, weakly articulated, extending 2x the height of basal division, membranous window absent, expanding weakly from base to quadrate apex bent to form prominent trough, bulging posterior, dorsal and lateral margins bent anterior, pair of hemispherical lateral lobules located at base of quadrate apex. Aedeagus oriented approximately 45 degrees from vertical, ejaculatory apodeme with base narrow, much broader larger than sperm sac, approximately as tall as long; dorsal margin of lateral ejaculatory process straight, lateral ejaculatory processes 3/4ths size of ejaculatory apodeme; apex of aedeagal sclerites tapering, rounded. Subapical sclerite narrowly conical, weakly arced posteroventrally, apex more acutely curved. Lateral plates of subapical sclerite absent.

Figures. Male Genitalia: 179 Wing: 180, Distribution: 181.

Material Examined. Japan Kyushu I. Hiko San (mt.) 17 May 1954 600m, Mitsuo Takahashi
(Pinned: 4 m#) (KU).

Discussion

Morphological Phylogenies

The phylogenetic analyses undertaken demonstrated the existence of several monophyletic clades, though the relationships between these clades and the placement of the majority of Afrotropical and Asian *Ptychoptera* was not resolved. Four of these clades and one distinctive species are named as subgenera: *P. (Amblyptycha)*, *P. (Chrysoptycha)*, *P. (Rheoptycha)*, *P. (Tigrimya)* and *P. (Unguptycha)*. Two other clades correspond to *P. (Parapteroptera)* and a constrained *P. (Ptychoptera)*. Although the phylogeny is not fully resolved, the authors feel that further resolution of the phylogeny will require a deeper understanding of the species diversity of Asia and sub-Saharan Africa as both regions are especially poorly sampled. Zwick & Stary (2003) established a precedent of the recognition of subgenera within *Ptychoptera* and it may be years before significant progress is made in understanding the diversity of the aforementioned region, thus the authors feel that the formal naming of these clades as subgenera is merited to facilitate recognition of the phylogenetic and ecological diversity within *Ptychoptera*. Those species not currently placed in the current subgenera should be treated as *Ptychoptera* incertae sedis and not assigned to *P. (Ptychoptera)*, as that subgenus has been constrained to the clade containing *Ptychoptera contaminata* and allies.

Much of the instability in the subgeneric classification can be attributed to the recognition of two potential “apical” clades, as the recovery of one group as the monophyletic “apical” clade inevitably results in the breakdown of the other group as a grade branching in series at more “basal” positions along the branch. These two groups can be broadly categorized as Group A: *P. (Chrysoptycha)*, *P. (Parapteroptera)*, *P. (Ptychoptera)*, and *P. (Rheoptycha)*; and Group B: *P. (Amblyptycha)*, *P.*

(*Unguptycha*) and those species with spathate lobes of the hypandrium. Group A can be best recognized with the hypandrium having the terminal division poorly articulated, its base divided, and spathate lobes absent, and a distinct eversible sac present and reaching the base of the terminal division. Group B has the terminal division at least partially articulated, the base undivided and constricted, and spathate lobes usually (though not universally) present, and the eversible sac absent (though there often is a membranous window in the terminal division).

The conflicting “apical” clade in the phylogenies is the result of differing character polarizations, as both taxa are defined by a suite of characters (particularly of the gonopod, hypandrium and aedeagus) of which some are shared by taxa that do not belong to either clade, or belong outside the clade containing both groups (“intermediate taxa”). Some characters are also likely differing developments of homologous structures: the membranous window in the terminal division of many Group B taxa probably represents the remnant of the eversible sac of Group A & *P. (Tigrimya)*. In particular, the eversible sac in *P. (Chrysotypcha)*, *P. (Paraptychoptera)*, and *P. (Rheotypcha)* heavily incises the terminal division, suggesting a possible evolutionary series. *P. (Tigrimya)* contributes significantly to this problem of polarization: while the subgenus has a bittacomorphine-like sperm pump that consistently places outside the clade with an enlarged ejaculatory apodeme and smaller sperm sac, the presence of a medial gonocoxal lobe, eversible sac and detached lateral plates of the subapical sclerite of the aedeagus suggest that these features in *P. (Chrysotypcha)*, *P. (Paraptychoptera)* and *P. (Rheotypcha)* are symplesiomorphies. Alternately, the undivided base of the hypandrium of *P. (Tigrimya)* may indicate that the similar condition in Group B is a symplesiomorphy.

P. (Tigrimya) is one of the most readily distinguished subgenera. Aside from its orange and black banded abdomen, the scutum of *P. (Tigrimya)* is greasy black, with a distinct microtrichia vestiture lacking in *P. (Unguptycha)*. The male genitalia of the subgenus is distinguished by the epandrial claspers

reduced, with the subepandrial membrane with only weak sclerotization at the base of the hypoproct, the gonocoxites having the dorsal surface nearly divided sagittally by an anterior incision, with the medial surface forming the base of the paramere, the hypandrium subhemispherical and stretched in the dorsal plane, and the eversible sac leaflike and not approaching the ventral margin of the terminal division. While *P. (Tigrimya)* shares symplesiomorphies of the aedeagus and hypandrium with Group C (described below), it shares the distinctive medial gonocoxal lobe with Group A.

The phylogeny of species with plesiomorphic features of the male genitalia is problematic (from here on referred to as *Ptychoptera* Group C). The species included in this analysis are *P. alexanderi*, *P. ichitai*, *P. japonica*, and *P. yamato*. These species share the plesiomorphic (for Ptychopterinae) characters of a bittacomorphine-like sperm pump, laterally directed lateral ejaculatory processes, nematoform epandrium, gonocoxal apodeme pointed, simple cylindrical apical stylus of gonostylus, basal lobe of gonostylus with single lobe, and hypandrium subhemispherical. The three latter species (*P. japonica* morphotype) are all distributed in Japan, and have the hypothetical synapomorphies of discoid apodeme of lateral ejaculatory process scythe shaped and directed dorsally, medial portion of paramere conical, and basal lobe of gonostylus reduced to peg. Additionally, there is a reversion to a sclerotized medial surface of the gonocoxite, while the remainder of *Ptychoptera* and Bittacomorphinae have the medial surface membranous. However, these species were not recovered as a monophyletic clade, instead being placed in a grade leading to *P. alexanderi*, *P. (Tigrimya)* and *Ptychoptera* Groups A&B in the Maximum Parsimony analysis, and as a polytomy with *P. alexanderi* and *P. (Tigrimya)* in the Bayesian Inference Analysis.

P. alexanderi shares characteristics with both the *P. japonica* morphotype and *P. (Tigrimya)* and *Ptychoptera* Group A. The hypothetical synapomorphy shared with the *P. japonica* Morphotype is the nearly indistinguishable fusion of the basal and terminal divisions of the hypandrium. The hypothetical

synapomorphy shared with *P. (Tigrimya)* and *Ptychoptera* Group A is a well-developed dorsal gonocoxal lobe, while the presence of the dorsal spur of the gonocoxal apodeme is shared with all *Ptychoptera* except the *P. japonica* Morphotype or *P. (Amblyptycha)*.

P. (Chrysoptycha) warrants recognition as a subgenus based on the morphological characters that unambiguously place it as a member of Group A (“higher” ptychopterine sperm pump, eversible sac reaching base of terminal division of hypandrium, poorly articulated basally divided terminal division), yet exhibits distinctive autapomorphies (lateral plates placed at base of subapical sclerite, ovoid gonocoxite) and one symplesiomorphy not shared by other Group A taxa (nematiform epandrium). There are also several characters that suggest a close relationship to *P. (Paraptychoptera)* and especially *P. (Rheoptycha)*: apical stylus of gonostylus poorly sclerotized and pendulous (*P. (Rheoptycha)* and some *P. (Paraptychoptera)*), sclerotized portion of paramere floating on membrane without distinct apical lobes as in *P. (Rheoptycha)*.

P. (Rheoptycha) can be readily recognized by the scutum shining and lacking microtrichia, and the male genitalia synapomorphies of: epandrial claspers reduced, paired subepandrial sclerites present covering much of the ventral surface of the epandrium, paramere a simple dorsally directed arc floating on the parameral membrane, and the apex of the hypandrium triangular with lateral lobules present. All species also have the distinctive poorly sclerotized pendulant apical stylus. Some members of *P. (Rheoptycha)* lack a dorsal spur of the gonocoxal apodeme

Though *P. (Paraptychoptera)* has typically been delineated based on the presence of the male auxiliary sexual organ and the branching of R_3 before r-m, there are several features of the male genitalia which support the monophyly of the group. These are the presence of poorly sclerotized, articulated epandrial claspers without a flattened basal medial lobe, the parameres fused to the supraedeagal membrane forming a floor of the genital chamber on the dorsal surface of the

hypandrium, the medial gonocoxal lobe directed posterior, and the gonostylus with a scythe-like medial lobe of the basal lobe. In other aspects *P. (Paraptychoptera)* is somewhat intermediate between *P. (Ptychoptera)* and *P. (Rheoptycha)*: *P. (Paraptychoptera)* shares the articulated epandrial claspers and has a similar configuration to the epandrial lobes of *P. (Ptychoptera)*, yet has a poorly sclerotized gonostylus which is often pendulant as seen in *P. (Rheoptycha)*.

P. (Ptychoptera) has never been delineated except in opposition to *P. (Paraptychoptera)*. Here *P. (Ptychoptera)* is constrained to a clade of species related to *P. contaminata*. This clade is extremely distinctive in the structure of the male genitalia: epandrial claspers present, heavily sclerotized, with flattened basal lobe, hypoproct reduced, paired quadrate subepandrial sclerites present, paramere trapezoidal with apical lobes having elongate ventral spines, paramere with posteromedial extension, gonostylus with basal lobe having scythe-like anterior lobe and trapezoidal dorsal lobe, aedeagus with ventral arms rod-like, attached by narrow band to medial portion. Much like *P. (Rheoptycha)*, *P. (Ptychoptera)* has a shining scutum lacking a microtrichia vestiture. *P. (Ptychoptera)* lacks the medial gonocoxal lobe of the remainder of Group A and *P. (Tigrimyia)*. With the delineation of an explicit concept of *P. (Ptychoptera)* unplaced species should be referred to *Ptychoptera incertae sedis*, and not the nominal subgenus.

Intermediate taxa between Group A and Group B include *P. bellula*, *P. gutianshana*, *P. perbona*, and *P. yasumatsui*. While the first three have been grouped within Group B in these analyses, *P. yasumatsui* has been consistently placed in a position between Group A and Group B. All of these taxa have the hypandrium without spathate lobes, but with a constricted, articulated base. The first three taxa additionally have the membranous window and lateral extensions of the terminal division apex which are lacking in *P. yasumatsui*. These species may represent an evolutionary series, though *P. perbona* does not group with *P. bellula* and *P. gutianshana*, and neither group represents an early

diverging lineage, suggesting the lack of spathate lobes may represent a secondary loss. The placement of *P. yasumatsui* has been consistently between Group A and Group B, so it may represent a true intermediate taxon.

Although the resolution of taxa within Group A is well supported, the interrelationships between these clades are not well resolved even outside of the aforementioned “apical clade” problem. *P. (Chrysoptycha)* and *P. (Rheoptycha)* are recovered as sister taxa in both analyses, though not with strong support. The relationships of this clade, *P. (Ptychoptera)* and *P. (Paraptychoptera)* are not well resolved.

Relationships within Group B are exceptionally poorly resolved, with many species having radically different placements between analyses, with the group collapsing into a large polytomy in the Bayesian Inference analysis. The only consistently recovered clades are *P. (Amblyptycha)* and *P. (Unguiptycha)*, and a larger clade containing both subgenera and *P. albimana* and *P. alina* which is distinguished largely by the presence of a ventromesal lobe of the epandrial clasper, though all species except *p. alina* have a glabrous dorsal ridge of the apical stylus of the gonostylus. *P. (Amblyptycha)* and *P. (Unguiptycha)* are consistently recovered as sister taxa with high support, with the placement of *P. albimana* and *P. alina* not well resolved.

The three species of *P. (Amblyptycha)* are readily distinguished from other Group B species with the ventromesal lobe by the blunt apex of the epandrial clasper. The synapomorphies supporting *P. (Amblyptycha)* are anteprenotum with medial apex broad, epandrial collar incomplete, epandrial lobes fused medially at base, epandrial apex blunt, posteromedial stylus fingerlike with basal plate on surface of epandrium, dorsal spur of gonocoxal apodeme absent, basal lobe of gonostylus forming ridge on medial surface of apical stylus. This subgenus is allied with *P. (Unguiptycha)* based on the lack of a break at the epandrium of the epandrial apodeme and the epandrial apodeme being broad and triangular.

Synapomorphies of *P. (Unguiptycha)* include the epandrial clasper claw-like (shared with *P. alina*), male posteromedial stylus forming elongate raised strip bordering epiproct, dorsal spur of gonocoxal apodeme directed posterior, ventral gonocoxal lobe present, lateral ejaculatory processes directed anterior at nearly a right angle, subapical sclerite rodlike, with triangular lobe at phallotreme.

The other species of Group B show a wide range of morphological features. In general, they can be recognized by these characters: nematoform epandrium, lack of gonocoxal lobes, hypandrial spathate lobes (except *P. bellula*, *P. gutianshana*, and *P. perbona*), base of terminal division constricted, with some degree of articulation. Unfortunately the material examined for many of these species was mounted on slides and the hypandrium and aedeagus were damaged, making assessment of these and other characters difficult.

Molecular Phylogeny

Taxa were included in the molecular study based on sampling by the authors for material suitable for molecular analysis. Outgroups were selected based on availability of sequence (*Drosophila* (Ephydroidea: Drosophilidae)) and phylogenetic proximity to Ptychopteridae (*Anopheles* (Culicomorpha: Culicidae), *Edwardsina* (Psychodomorpha: Blephariceridae)). Species of Bittacomorphinae were also included to reduce long-branch effects. Both mitochondrial (Cytochrome Oxidase I) and nuclear genes (TUFT) were used to provide resolution of both species and higher level phylogeny.

P. (Rheoptycha), *P. (Tigrimya)*, and *P. (Unguiptycha)* were strongly supported in the molecular analysis, lending support to the results of the morphological analyses. The most significant difference from the morphological phylogenies was the support of clade containing (*P. (Chrysotycha)*)+*P. (Rheoptycha)*)+*P. (Tigrimya)*. While there are some morphological characters which would support such

a clade, comparison with Group C species suggests that the most significant of these characters may represent symplesiomorphies. Molecular sampling of Group C taxa should be undertaken before this clade is given serious credence.

Ecological Discussion

Ptychoptera is known throughout the Holarctic and Afrotropical regions, as well as the Central American portion of the Neotropics. The subgroups of *Ptychoptera* are not evenly distributed, with most of the taxa having distributions localized to a particular subregion. *P. (Ptychoptera)* is an exception, with species being found throughout the northern regions of the Holarctic. As the fieldwork of this study was conducted in the Nearctic, the taxa of that region will be the most thoroughly explored.

The taxa of Group A are not known from the Afrotropics or eastern Asia, with the exception of *P. (Ptychoptera)* in northern Asia. *P. (Parapterychoptera)* is known from Europe, North Africa, and the Middle East. *P. (Parapterychoptera)* is sympatric through much of Europe with *P. (Ptychoptera)*, as well as *P. albimana*. The best examination of sympatry between these taxa is Stubbs (1993).

P. (Rheopterycha) is distributed in western North America, sympatric with *P. (Chrysopterycha)*, *P. (Unguipterycha)* and species of both *Bittacomorpha* and *Bittacomorphella*. *P. (Rheopterycha)* specializes in the depositional zones and margins of lotic habitats, being found in areas with higher water flow and shallower sediments than sympatric taxa. *P. (Chrysopterycha)* is similarly found in shallower sediments than *P. (Unguipterycha)* is typically collected, and is distributed in the Cascade Range and west on the Pacific Coast of North America.

Group B has a much more extensive range than Group A, dominating the fauna of eastern Asia and the Afrotropics, and having significant diversity in western North America and a species complex in Europe (Ujvárosi *et al* 2011). *P. (Amblypterycha)* is recorded only from the southern margin of the

Himalayas, though sampling in eastern Asia is poor enough that the subgenus may have a more extensive range. *P. (Unguptycha)* is diverse in North America west of the Rocky Mountains, with *P. daimio* recorded from Hokkaido, Japan (Nakamura & Saigusa 2009). In the Nearctic *P. (Unguptycha)* is associated with deep organic sediments with low water flow, such as seepages and beaver ponds. The distribution and ecology of the other members of Group B are poorly understood.

P. (Tigrimya) is known only from the eastern Nearctic. It is widely distributed through the region, occurring from the Atlantic coast to the foothills of the Rocky Mountains, with the northern and southern limits of the subgenus poorly defined. Larvae are found in both stream margins and depositional zones as well as more conventional seepage habitats, though it appears that *Bittacomorpha clavipes* outcompetes *P. (Tigrimya)* in areas with low rates of flow (Harris & Carlson 1978).

There is a distinct disjunction in the distributions of Group C, with the *P. japonica* Morphotype restricted to Japan, while *P. alexanderi* is endemic to Central America. While both of these regions are isolated in the wider distribution of *Ptychoptera*, little more is known about the biogeography of these taxa. The widely disjunct distribution reinforces the probable non-monophyletic nature of these species. The description of *P. alexanderi* describes the streamside environment from which it was collected, though little else is known ecologically about any of these species.

There is another disjunction between the *Ptychoptera* subgenera and species diversity of the eastern versus western Nearctic. *P. (Tigrimya)* is the dominant taxon of the eastern Nearctic, with *P. (Ptychoptera) metallica* being the only other *Ptychoptera* species present. *P. (Ptychoptera) metallica* has a disjunct distribution, being found both in the boreal and sub-boreal regions of the US and Canada as well as the Front Range of the Colorado Rockies. *B. clavipes* is also a common component of the ptychopterid fauna of the eastern Nearctic, in contrast to the lesser density of bittacomorphine collections in the western Nearctic. From the Rocky Mountains west the ptychopterid niche is divided

between *P. (Rheoptycha)* in lotic habitats and *P. (Unguiptycha)* in seepages, lake margins and other areas with lesser water flow. West of the Cascade Range *P. (Chrysoptycha)* is also found, as well as a more speciose (though not as dense) bittacomorphine species assemblage.

As discussed in Chapter 6, there are potentially differences in phenology between the eastern and western fauna, with the eastern fauna being multivoltine or continuously emerging (Bowles 1998, Rogers 1942) and the western fauna being univoltine with an extended emergence period (Hodkinson 1973), though this may not hold true for all species in all habitats (see *P. (U.) lacrimiformis* material examined). These differences may be accounted for by the generally more shorter summer conditions of the western United States, especially at altitude where most *Ptychoptera* are collected.

Ecological specialization is readily apparent at the subgenus level in the Nearctic, as indicated above. There is a broad distinction between those taxa that specialize or tolerate lotic environments (*P. (Rheoptycha)*, *P. (Tigrimya)*) and those found in more lentic microhabitats (*P. (Unguiptycha)*, *P. (Chrysoptycha)* and Bittacomorphinae). *P. (Tigrimya)* show the greatest flexibility in microhabitat usage, seemingly largely constrained by their interactions with *B. clavipes*, while the other taxa are much more constrained in their microhabitat usage.

The ecology of *P. (Pt.) metallica* remains poorly understood. The only collection of this species by the authors was at a fen in northwest Iowa, with a large seepage and a large (>400 hectare) lake and a 3-4 hectare complex of ponds and wetlands, with a small hillside seepage. As only adults were collected it is difficult to determine the larval habitat due to the heterogenous nature of the collection area.

Species distributions throughout the Nearctic are allopatric within subgenera, with only two notable exceptions. These exceptions are between *P. (R.) pendula* and *P. (R.) townesi* on in the Coast Range of Oregon, and *P. (T.) osceola* and *P. (T.) quadrifasciata* in Florida. *P. (R.) pendula* is distributed

primarily in the intermountain West, but is also known from the east side of the Cascade Range, and the authors have collected this species at Ecola State Park and Lower Deer Creek in the Coast Range of Oregon. *P. (R.) townesi* is recorded from the Pacific Coast west of the Cascades, occupying the same niche as *P. (R.) pendula*. At this point it is difficult to determine the mechanism or permanence of this invasion of *P. (R.) pendula* into the range of *P. (R.) townesi*. This is further confounded by the incidence of *P. (R.) townesi* at the Lower Deer Creek site in 2011, yet *P. (R.) pendula* was collected from the same locality in 2012.

As *P. (T.) osceola* was not collected in the course of this study only preliminary inferences about its ecology can be drawn based on the publication of Rogers (1933), who collected what would become the type series described by Alexander (1959). This series of specimens was collected from an acidic sphagnum bog, and this may be the microhabitat of *P. (T.) osceola*. Thus sympatry may be facilitated by the differential utilization of the sphagnum bog habitat versus the more conventional stream margin habitat of *P. (T.) quadrifasciata*.

Outside of these instances the allopatric range allocation among species within particular subgenera is strongly reinforced. *P. (Unguptycha)* is a particularly strong example with species distributed based on the ecoregions of western North America. The various subregions of the Rocky Mountains are inhabited by the *P. (U.) coloradensis* complex, which likely can be further broken into cryptic species with more extensive molecular sampling (see below), and *P. (U.) coloradensis* metapopulations are also present in the Sonoran region. *P. (U.) uta* has been collected only on the northern shore of the Great Salt Lake of Utah, and may be extinct due to ecological changes in the latter half of the 20th century. The Great Basin is populated by *P. (U.) byersi*, which does not cross beyond the east side of the Cascade Range, though it is present in the Trinity Alps. West of the Cascade Range is dominated by *P. (U.) lacrimiformis*, which extends considerably to the margin of the Canadian Rockies in

British Columbia. *P. (U.) bilobata* is known only from the east coast of Puget Sound and Fraser River Valley, and as it is known from so few specimens the true range is hard to discern. *P. (U.) minor* is also known only from limited specimens, but appears to be endemic to the California Coast Ranges, a poorly sampled area. Finally, *P. (U.) lenis* is endemic to both slopes of the Sierra Nevada Range.

Species in other subgenera tend to have wider ranges, though there remains correlation to established ecoregions. As stated previously, *P. (R.) pendula* has a wide range across the intermountain West east of the Cascade Range, while *P. (R.) townesi* is distributed west of the Cascades. *P. (R.) espica* is known from the Olympic Peninsula and terminus of the range to the southeast. *P. (R.) monoensis* is endemic to the Sierra Nevada Range. *P. (Chrysotypcha) sculleni* is the sole member of its subgenus, but is distributed west of the Cascade Range.

The eastern Nearctic has had much more extensive historical glaciation, which probably has negatively affected the species diversity of *P. (Tigrimylia)*. *P. (T.) osceola* is known only from Georgia and Florida currently, though the southeastern U.S. is poorly sampled. *P. (T.) quadrifasciata* is distributed throughout the Eastern Temperate Forest Region, though the current conception of *P. (T.) quadrifasciata* represents a species complex. *P. (T.) abbreviata* is distributed through the Prairie/Great Plains ecoregion, though the eastern limit of *P. (T.) abbreviata* and the western limit of *P. (T.) quadrifasciata* is currently poorly defined.

There is extensive sympatry between different subgenera of *Ptychoptera* and Bittacomorphinae. A table of sympatric associations is provided in Table X, which covers species collected at the same general locality, although some species also utilize the same microhabitat (as denoted by an asterisk). Some of the most obvious of these are situations where both lotic and lentic water occur in close association, such as the lentic pond above a beaver dam and the flowing stream with depositional zones below, which permits the combined of the taxa adapted to these habitats. Less readily evaluated is the

coexistence of taxa which are typically found in similar microhabitats, such as the associations of *P. (Chrysoptycha)*, *P. (Unguptycha)*, and species of Bittacomorphinae.

All species found in these microhabitat sympatry can be found at different localities alone or in association with other taxa, suggesting that there are differing ecological conditions which are optimal for these taxa, or perhaps some taxa are more tolerant of suboptimal conditions but are inferior competitors in higher quality habitats compared with species that cannot survive in the lower quality habitat. If this is the case it is possible for these lower quality habitats to serve as reservoirs for those weaker competitors to continually “invade” higher quality habitats from which they would be outcompeted.

Taxonomic Discussion

One major limitation to the taxonomic work of this study was limited access to type material ,as many institutions were not comfortable shipping type specimens long distances. Thus, some of the species figured and described here were done based on non-type material, though the determination of specimens was based on the excellent treatments of Peus (1958) and Nakamura & Saigusa (2009), supplemented by Tjeder (1968) for *P. (Pt.) hugoi* and Yang & Chen (1996) for *P. gutianshana*. Elaine deConinck of the Royal Central African Museum also supplied images of the type specimens of several Afrotropical *Ptychoptera*, though full descriptions could not be composed.

As in many other taxa, species concepts in *Ptychoptera* have changed over time with the development of new techniques and examination of larger sets of material. The use of molecular techniques in the taxonomy of *Ptychoptera* is still in its infancy, and species are still essentially delineated and determined based on morphology. Most the morphological characters in both taxonomy and phylogeny of *Ptychoptera* are in the male genitalia which was discussed in detail in Chapter 4, and

will not be discussed further here. The other major character systems in adult *Ptychoptera* are body coloration and wing coloration, with minor variations in antennal flagellomere shape, anteprepronotum shape, and wing venation.

Body coloration in *Ptychoptera* varies from species that are nearly neon orange or yellow to other taxa that are solid black. The abdomen is often banded, and thoracic sclerites may be solid or have broad splotches or stripes of color. Some taxa have metallic iridescence, particularly on the scutum and thoracic pleurites. The usefulness of coloration in species determination is highly variable, generally being more useful for distinguishing subgenera and species groups. For example, *P. (Ptychoptera)* and *P. (Rheoptycha)* can be readily distinguished from other *Ptychoptera* by the glassy shining scutum without microtrichia, and from each other by the narrow yellow bands on the posterior margins of the abdominal segments of *P. (Rheoptycha)* versus the uniform coloration or limited bands of *P. (Ptychoptera)*. On the other hand, *P. albimana*, *P. alina*, *P. (Amblyptycha)* and *P. (Unguipitycha)* can be distinguished from other *Ptychoptera* by the yellow triangles at the dorsolateral corners of the mediotergite of the metanotum, except that *P. (A.) sikkimensis* has a uniformly yellow mediotergite. This inconsistency of color across the phylogeny thus degrades its utility in keys or other determination schemes. Body color is further hampered by the fact that many species exhibit increased melanism with higher latitude, readily seen in *P. (C.) sculleni* (which is entirely yellow in California, but becomes black with yellow highlights in Washington) and several species of *P. (Unguipitycha)* (which have black or brown abdomens in the north of their range, and orange abdomens in the south).

Wing coloration in *Ptychoptera* can be broadly summarized that the presence/absence of three primordial sagittal bands on the wing and the extent to which those bands are developed. The three primordial bands are placed at h, the wing cord, and across the R_{4+5} and M_{1+2} forks. Additionally, the leading edge of the wing sometimes has a transverse band, and in *P. (Tigrimya)* a secondary band is

developed between the h and cord bands. Accessory spots appear to be derived from these primordial bands, especially if they do not fully traverse the wing. Sometimes the distal band is extended to the wing apex, forming a broad dark field as seen in *P. africana*, *P. chalybeata*, *P. distincta* and *P. uelensis*. The combined presence of specific bands or spots can be used to distinguish some species, but the size (or extent in the case of bands) of these markings is somewhat plastic and not a reliable determiner. Of note is that all species have at least infuscation along the cord.

Antennal flagellomeres in most *Ptychoptera* are fusiform, though those in Group C and a few Group B species are more elongate and bacilliform. The anteprenotum as a transverse fold in *Ptychoptera*, with the posterior ridge formed to a high trapezoid in most species, sometimes with a notch medially. Finally, while the structure of the wing venation is largely homogenous there is some variability. The most distinctive form of this variation is the length of R_{stem} , though it is difficult to place this variation in a phylogenetic context. Several taxa (*P. (Paraptychoptera)*, *P. (Rheoptycha)* and *P. (Tigrimya)*) have a short R_{stem} with a distinct bend midway along its length. Other aspects of the wing venation (proportions of R_{4+5} and M_{1+2} , degree of curvature of CuA_2) are of little utility in taxonomy or phylogenetics.

Based on this work there are two definite cryptic species complexes known in North America, *P. (T.) quadrifasciata* and *P. (U.) coloradensis*, based on molecular data. This should not be taken as an indication that these are the only species complexes in the Nearctic, rather that these species are the ones from which sufficient molecular sampling was available to uncover this cryptic diversity. Outside of North America there are other probably species complex in the material examined in this study, but lack of access to type specimens of the nominal species or good male specimens have led the authors to take a conservative approach and not give these morphospecies names which may prove unstable. In particular the *P. (Pt.) hugoi/scutellaris* complex probably has two undescribed species in eastern Asia, as

the Mongolian and Kyrgyz material examined differs from the illustrations in Tjeder (1968) and also between the localities, but lack of access to types precludes naming these species. The Angolan female specimen of *P. africana* also differs from the Nigerian material based on the coloration of the wing and details of the body coloration, and probably represents a distinct species. Additionally, while the specimen described here as “*P. gutianshana*” matches the limited illustration of the species from Yang & Chen (1996), it does not fit the key provided in Kang *et al* (2013), and thus the determination should be treated circumspectly.

While the European and North American faunas merit continued investigation, the *Ptychoptera* of the Afrotropics and Eastern Asia remain extremely poorly known. Extensive collecting is still needed to get a basic understanding of species diversity, and the ecology of the species endemic to these regions remains essentially unknown. For the Afrotropical region the work that is simultaneously most helpful yet also most taxonomically problematic is Freeman (1959). While keying and illustrating *P. africana* and *P. uelensis* Freeman synonymized five other species into these two. However, *P. schoutedeni* is synonymous with *P. uelensis* (not *P. africana*) and *P. stuckenbergi* is easily distinct enough in the pattern of wing coloration to merit recognition as a distinct species until the male is described. The phylogenetic position of these species is closely tied to the similar Group B taxa in eastern Asia, and as such is poorly resolved.

The greatest difficulty in assessing the eastern Asian species is the fragmentary nature of much of the material examined during this study. The slide mounting of earlier workers often destroyed or distorted structures not typically used in species diagnoses, especially the hypandrium and aedeagus. The combined effects of fragmentary material and a poor understanding of the species diversity of the region have made recovering a resolved phylogeny of these taxa impossible at the current time. In both

Asia and Africa collection localities have been highly localized, and collection coverage of the regions is poor. In Asia the fauna in localities less than 500km apart is completely different, and some sites demonstrate sympatry of at least three species of *Ptychoptera*.

Further Research

There remain significant gaps in the understanding of *Ptychoptera*. As with all works, this study was limited by external factors and time was focused on character systems and life stage which provided the most information. There remains significant work to be undertaken on the structure of the female genitalia and female genital tract in *Ptychoptera*, as this study was covered only gross external anatomy. Preliminary work undertaken here indicates that *P. (Ptychoptera)*, *P. (Rheoptycha)* and *P. (Unguptycha)* have three well sclerotized spermathecae, while *P. (Tigrimyia)* has no sclerotized spermathecae, though there has not been a comprehensive examination to determine if the structures are membranous. The genital fork also holds promise for determining higher taxa or possibly species. Similarly, the male soft tissue genital tract was not examined as part of this study, though Sinclair *et al* (2007) examined several ptychopterid species as part of a wider survey of this system in lower Diptera.

Larval and pupal morphology and taxonomy are extremely poorly known in Ptychopterinae. The structure of immature stages is much more homogenous in *Ptychoptera* than in Bittacomorphinae, and though efforts were made to associate immatures with adults for the Nearctic taxa this work was confounded by the high degree of sympatry among *Ptychoptera* species. While larvae were collected from four of the five Nearctic subgenera, species coverage was often poor. As such, confidently assigning morphological character states to species was impossible. Diagnoses for the larvae of *P. (Tigrimyia)* and *P. (Unguptycha)* are provided, as well as a combined diagnosis for *P. (Chrysoptycha)* + *P. (Rheoptycha)*, require further character development to distinguish from each other. The pupal

morphology is even more homogenous and less understood than that of the larvae, and as such is not approached in this work.

Although the molecular dataset examined here represents the first quantitative phylogenetic assessment of *Ptychoptera* there remain significant improvements that could be made in future analyses. The most obvious of these would greater development of immature and female character states, as well as the incorporation of soft tissue internal characters. Further, many taxa included in this analysis were based on fragmentary material, and access to more complete material will likely improve resolution within the phylogeny, if not suggest new characters. Similarly, while the majority of extant *Ptychoptera* were included in this analysis there are still a number of described species which were not included, and the diversity of the Afrotropical and eastern Asian regions is still poorly known, thus wider taxon sampling will improve the phylogeny.

Similarly, limited taxon sampling is the greatest weakness of the molecular analysis presented here. The most obvious step is inclusion of taxa from outside the Nearctic, though even within the Nearctic there remain species and populations which were not sampled, such as *P. (Pt.) metallica*, *P. (T.) osceola* and *P. (U.) minor*.

Though some biogeographic inferences are presented here, there remain many unanswered questions about the historical development of the group, which could be elucidated by quantitative ecological or biogeographic analyses. Techniques such as ecological niche modeling could provide needed insight into the factors facilitating sympatry, the allopatric limits of species, and future predictions. At the higher levels of the classification there is little understanding of the historical ranges and origins of the subgenera, and why Group A and Group B seem to have formed a largely exclusionary relationship in the Old World is worth exploration.

Finally, basic ecological questions remain about *Ptychoptera*. Rogers (1933, 1942), Hodkinson (1973), Harris & Carlson (1978), Mattingly (1987, 1988), Bowles (1998) and Wolf *et al* (1997) and Wolf & Zwick (2001) have provided information about the feeding ecology, survival rate, and phenology, but these have only been based on a limited number of taxa. Further exploration of the phenology of species of different regions and microhabitats is needed. Further, our understanding of microhabitat utilization remains at an infant stage, and categorization and quantification of factors which delimit niche usage remains to be explored.

Conclusion

This work is the first attempt to place the global diversity of *Ptychoptera* into an organized, predictive framework. The first comprehensive key was constructed, and descriptions and illustrations were produced for all species for which substantial material is available, facilitating the determination of numerous taxa which were previously only identifiable with consultation of type material. The phylogenies presented here represent the first published analysis of the relationships within *Ptychoptera*, and support the erection of five subgenera to recognize distinct clades within the genus.

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Appendix I: Morphological Characters of *Ptychoptera*

Larva

1. Dentition on postmentum: (0), 2 or less; (1), 3-14; (2), >14
2. Postmentum and subgenal sclerite fused: (0), absent; (1), present
3. Larval cuticle with tubercles or extensions: (0), absent; (1), present
4. Larval respiratory siphon: (0), longer than remainder of anal division; (1), shorter than remainder of anal division

Adult

Head

5. Antennal flagellomeres: (0), nodiform; (1), cylindrical; (2), fusiform; (3), bacilliform
6. Flagellomeres with verticillate sensilla: (0), absent; (1), present
7. Posterior sensilla on occiput: (0), absent; (1), present
8. Ultimate segment of maxillary palpus extended, longer than preceeding segments: (0), absent; (1), present

Thorax

9. Antepronotum: (0), broad, flat; (1), with transverse fold; (2), plate-like
10. Antepronotum with transverse fold: (0), broad; (1), narrow
11. Antepronotum with medial apex: (0), broad; (1), narrow
12. Antepronotum medial notch: (0), absent; (1), present
13. Anterior margin of prescutum: (0), convex; (1), flattened
14. Prescutum & scutum: (0), dull; (1), shining; (2), greasy
15. Prescutum and scutum surface: (0), smooth; (1), with microscopic punctures; (2), with microtrichia vestiture
16. Posterior apex of prescutum: (0), rounded; (1), indistinct; (2), triangular
17. Epimeron-metapleuron suture: (0), strongly developed; (1), incomplete, weak

18. Metapleural suture: (0), present; (1), absent

Wing

19. R_{2+3+4} length: (0), $>2\times$ length of rm ; (1), $<2\times$ length of rm

20. R_{2+3+4} with distinct angle: (0), absent; (1), simple angle present at base; (2), angle midway along length

21. M forked: (0), present; (1), absent

22. Median angle of CuA_2 : (0), inevident; (1), weakly developed; (2), strong

23. Marginal angle of CuA_2 : (0), absent; (1), weak; (2), strong

Legs

24. Legs strongly banded: (0), absent; (1), present

25. Forecoxae: (0), distinctly separated; (1), closely appressed

26. Foretibial spur membranous and bifid: (0), absent; (1), present

27. First tarsomere with stout spines: (0), absent; (1), present

28. Final tarsomere can fold back on penultimate: (0), absent; (1), present

Pregenital Abdomen

29. Posterior abdominal segments telescoped into preceding segment: (0), absent; (1), present

30. Auxiliary sexual organ developed on Sternite III: (0), absent; (1), present

31. Medial extension present on Sternite VII: (0), absent; (1), present

Female Genitalia

32. Tergite VII covers epigynium: (0), present; (1), present

33. Epigynium: (0), platelike; (1), reduced to band

34. Epiproct: (0), poorly distinguished; (1), distinct

- 35. Cerci: (0), heavily sclerotized, elongate; (1), weakly sclerotized, short
- 36. Cercus with longitudinal ridge: (0), absent; (1), present
- 37. Hypoproct: (0), absent, or fused to cerci; (1), present
- 38. Hypogynial valves: (0), well developed; (1), poorly developed
- 39. Median portion of hypogynium constricted: (0), absent; (1), present
- 40. Lateral lobes on posterior margin of hypogynium: (0), absent; (1), triangular spines; (2), broad domes

Epandrium

- 41. Epandrial collar: (0), absent; (1), partial; (2), complete
- 42. Lateral margin of epandrial collar (epandrial apodeme): (0), simple angle; (1), extended ventrally to articulate with hypandrium
- 43. Epandrial apodeme break at epandrium: (0), absent; (1), present
- 44. Epandrial apodeme break at hypandrium: (0), absent; (1), present
- 45. Epandrial apodeme: (0), narrow and ribbon-like; (1), stout and triangular
- 46. Epandrium: (0), simple plate; (1), bilobate
- 47. Epandrial lobes fused medially at base: (0), absent; (1), present
- 48. Epandrial claspers: (0), absent or reduced; (1), present
- 49. Epandrial clasper articulation: (0), well-articulated; (1), contiguous
- 50. Epandrial clasper distinguished from epandrial lobe: (0), present; (1), absent
- 51. Epandrial clasper apex: (0), rounded; (1), pad; (2), point; (3), blunt
- 52. Epandrial clasper sclerotized: (0), well sclerotized; (1), poorly sclerotized
- 53. Epandrial clasper configuration: (0), nematoform; (1), simple curving cylindrical style; (2), cylindrical style with basal lobes; (3) composite structure articulating on the epiproct
- 54. Epandrial clasper flattened: (0), absent; (1) present
- 55. Epandrial clasper with medial angle: (0), absent; (1), present
- 56. Epandrial clasper with lateral lobe: (0), absent; (1), present

- 57. Epandrial lobe and clasper length: (0), 2x or greater as long as width of epandrium; (1), longer than width, less than 2x as long as wide; (2), length and width equivalent, or wider than long
- 58. Epandrial clasper curved ventrally: (0), less than 30 degree arc; (1), greater than 30 degree arc
- 59. Ventromesal lobe present on epandrial clasper: (0), absent; (1), present
- 60. Ventromesal lobe petiolate: (0), absent; (1), present
- 61. Ventromesal lobe apex: (0), expanding; (1), tapering
- 62. Ventromesal lobe with apical margin emarginate: (0), present; (1), absent
- 63. Ventromesal lobe bent posterior: (0), absent; (1), present
- 64. Subapical spine: (0), absent; (1), present
- 65. Subapical spine: (0), spine-like; (1), knob-like; (2), conical; (3), filamentous
- 66. Lateral subapical spine: (0), absent; (1), present
- 67. Portion of medial margin of epandrial clasper inflated: (0), absent; (1), present

Proctiger

- 68. Male cerci/Posteromedial stylus: (0), absent; (1), present
- 69. Cercus/Posteromedial stylus form: (0), fleshy lobe (1), triangular acute stylet; (2), subobtus triangular lobe; (3), low knob; (4), elongate strip bordering epiproct; (5), plate with finger-like extension; (6), small hook; (7), scallop-shaped
- 70. Posteromedial stylus with internal spine: (0), absent; (1), present
- 71. Epiproct: (0), not readily apparent, membranous; (1), easily distinguishable
- 72. Epiproct reaching epandrial collar: (0), present; (1), absent
- 73. Epiproct with medial notch: (0), absent; (1) present
- 74. Epiproct with weakly developed lateral lobules on margin: (0), absent; (1), present
- 75. Hypoproct: (0), completely membranous; (1), ovoid sclerite suspended in membrane; (2), tongue-like; (3), emarginate plate
- 76. Subepandrial sclerite: (0), absent; (1), sclerotized, single sclerite associated with hypoproct; (2), sclerotised, divided into paired sclerites

77. Extent of divided subepandrial sclerite: (0), small strips floating on subepandrial membrane; (1), large plates extending across ventral surface of epandrium; (2), fused to base of epandrial claspers

Paramere

78. Parameres: (0), fused; (1), paired and separate
79. Basal portion of paramere directed medially: (0), present; (1), absent
80. Base of paramere shifted anterior on medial surface of gonocoxite: (0), absent; (1), present
81. Paramere attachment with dorsal surface of gonocoxite: (0), broad; (1), narrow; (2), floating on membrane
82. Spine at paramere base: (0), absent; (1), present
83. Basal paramere spine directed: (0), lateral; (1), ventral; (2), posterior; (3), dorsal
84. Anterior margin: (0), concave; (1), convex; (2), straight
85. Posterior margin with flattened sublateral lobes: (0), absent; (1), present
86. Paramere flexed dorsally: (0), absent; (1), present
87. Medial portion of paramere conical: (0), absent; (1), present
88. Medioposterior extension of paramere: (0), absent; (1) present
89. Medioposterior extension of paramere furcate: (0), absent; (1), present
90. Apices of Paramere: (0), inevident; (1), distinguishable
91. Apical lobes of paramere directed: (0), posterior; (1), dorsal; (2), ventral
92. Apical lobes of paramere with lateral lobe: (0), absent; (1), present
93. Shape of apical lobes: (0), spine-like; (1), dorsoventrally flattened; (2), laterally compressed; (3), conical
94. Apical lobe of paramere with notch at tip: (0), absent; (1), present
95. Dorsal surface of paramere with secondary spines or lobes: (0), absent; (1), present

Gonopod

- 96.** Gonocoxal apodeme extent: (0), confined to anterior margin of hypandrium, not extended as narrow process; (1), elongate, extending well beyond anterior margin of hypandrium
- 97.** Dorsal spur of gonocoxal apodeme: (0), absent; (1), present
- 98.** Dorsal spur of gonocoxal apodeme shifted posterior: (0), absent; (1), present
- 99.** Dorsal spur of gonocoxal apodeme: (0), directed dorsally; (1), directed medially; (2), directed posterior
- 100.** Apex of dorsal spur: (0), pointed; (1), rounded
- 101.** Apex of gonocoxal apodeme rounded in lateral view: (0), absent; (1), present
- 102.** External portion of gonocoxite curved dorsally to articulate with epandrium: (0), absent; (1), present
- 103.** Gonocoxite shape: (0), tapering to gonostylus; (1), expanding to gonostylus; (2), ovoid; (3), cylindrical
- 104.** Dorsal surface of gonocoxite: (0), simple, undivided; (1), divided longitudinally, separating paramere base
- 105.** Medial surface of gonocoxite: (0), sclerotized posteriorly; (1), completely membranous, or at most with a thin strip supporting the paramere
- 106.** Dorsal gonocoxal lobe: (0), present; (1), absent
- 107.** Dorsal gonocoxal lobe placement: (0), near midpoint of gonocoxite; (1), near posterior margin of gonocoxite
- 108.** Dorsal gonocoxal lobe: (0), tall, near height of basal lobe of gonostylus; (1) short, little more than a nodule
- 109.** Medial gonocoxal lobe: (0), present; (1), absent
- 110.** Medial gonocoxal lobe fused to paramere: (0), absent; (1), present
- 111.** Ventral gonocoxal lobe: (0), absent; (1), present
- 112.** Basal lobe of gonostylus: (0), present; (1), absent
- 113.** Number of lobules associated with basal lobe of gonostylus: (0), 1; (1), 2; (2), 3
- 114.** Shape of anterior lobule: (0), scythe-like; (1), peg-like; (2), knob-like; (3), finger-like, (4); paddle-like

- 115.** Shape of dorsal lobule: (0), peg-like; (1), knob-like; (2), finger-like, (3); paddle-like; (4), triangular; (5), scythe-like
- 116.** Shape of medial lobule: (0), peg-like; (1), knob-like; (2), finger-like, (3); paddle-like
- 117.** Basal lobe of gonostylus with stout trichoid sensilla: (0), absent; (1), present
- 118.** Apical stylus of gonostylus: (0), complex (1), simple
- 119.** Apical stylus of gonostylus: (0), well sclerotized; (1); poorly sclerotized
- 120.** Apical stylus of gonostylus pendulant: (0), absent; (1), present
- 121.** Apical stylus of gonostylus length: (0), shorter than external portion of gonocoxite; (1), longer than external portion of gonocoxite; (2), subequal
- 122.** Apex of apical stylus furcate: (0), absent; (1), present
- 123.** Apical stylus with glabrous dorsal ridge: (0), absent; (1), present
- 124.** Secondary lobe of apical stylus: (0), present; (1), absent
- 125.** Secondary lobe length: (0), shorter than apical stylus; (1), subequal to apical stylus
- 126.** Secondary lobe of apical stylus placement: (0), near basal lobe; (1), subapical
- 127.** Secondary lobe of apical stylus flattened: (0), rounded; (1), flattened; (2) flattened, petiolate base
- 128.** Apical stylus and secondary lobe cross at apex: (0), absent; (1), present
- 129.** Tertiary lobe of apical stylus present: (0), present; (1), absent
- 130.** Tertiary lobe placement: (0), apical; (1), proximal
- 131.** Gonostylus with stout sensillae on medial apex: (0), absent; (1), present, forming ordered lines; (2) present, scattered

Hypandrium

- 132.** Shape of hypandrium: (0), band-like; (1) roughly triangular; (2), sub-hemispherical; (3), indistinct
- 133.** Parameres and gonocoxal lobes fused to dorsal hypandrial membrane, forming floor of genital chamber: (0), absent; (1), present
- 134.** Eversible sac of hypandrium: (0), absent; (1), present

- 135.** Eversible sac extent: (0), extending to base of terminal division; (1), well separated from base of terminal division
- 136.** Eversible sac extended anterior nearly to margin: (0), absent; (1), present
- 137.** Basal scale of hypandrium: (0), absent; (1), present
- 138.** Hypandrial spathate lobes: (0), absent; (1), present
- 139.** Spathate lobe shape: (0), rounded; (1) subquadrate; (2), triangular; (3), knob-like; (4), finger-like
- 140.** Spathate lobe extent: (0), not extending to gonocoxites; (1), extending to ventral margin of gonocoxite; (2), extending beyond ventral margin of gonocoxite
- 141.** Spathate lobe petiolate: (0), absent; (1), present
- 142.** Terminal division of hypandrium: (0), absent; (1), present
- 143.** Terminal division articulation: (0), poorly articulated; (1), well-articulated; (2), almost inevident
- 144.** Terminal division shape: (0), divided basally (1), undivided basally
- 145.** Base of terminal division constricted: (0), absent; (1), present, (2), separated from basal division
- 146.** Terminal division recumbent anteriorly: (0), absent; (1), present
- 147.** Apex of terminal division: (0), spine-like; (1), triangular; (2), circular plate; (3), quadrate; (4), scallop shaped; (5), subdivided; (6), reduced
- 148.** Terminal division forming trough: (0), absent; (1), present
- 149.** Apex of terminal division cloaked in trichoid sensilla: (0), absent; (1), present
- 150.** Apical trichoid sensilla divided into discrete patches: (0), absent; (1), present
- 151.** Apex of terminal division inflated: (0), absent; (1), present
- 152.** Apex of terminal division curved posterior, flume-like: (0), absent; (1), present
- 153.** Lateral extensions of terminal division apex: (0), absent; (1), present
- 154.** Lateral extensions of terminal division apex: (0), attached to basal division; (1), floating
- 155.** Rounded secondary lobe near lateral extension: (0), absent; (1), present
- 156.** Membranous window of terminal division: (0), absent; (1), present
- 157.** Membranous window extent: (0), does not extend to basal division margin; (1), extends to basal division margin

158. Membranous window inflated: (0), absent; (1), present

159. Lateral lobules of terminal division: (0), absent; (1), present

Aedeagus

160. Terminal division and aedeagus rotated dorsally: (0), unrotated; (1), rotated

161. Shape of ejaculatory apodeme: (0), narrow, tapering; (1), fanlike; (2), reduced

162. Ejaculatory apodeme size: (0), smaller than sperm sac; (1), larger than sperm sac; (2), subequal

163. Ejaculatory apodeme closely associated with sperm sac: (0), absent; (1), present

164. Ejaculatory apodeme longer than tall (0), present; (1), absent; (2), subequal

165. Ejaculatory apodeme closely associated with aedeagal sclerites: (0), absent; (1), present

166. Lateral ejaculatory processes: (0), absent; (1), present

167. Lateral ejaculatory process orientation: (0), directed laterally; (1), directed anterior; (2), directed anterior at nearly right angle

168. Dorsal margin of lateral ejaculatory process convex: (0), absent; (1), present

169. Apex of lateral ejaculatory process: (0), rounded apodeme directed anteroventrally; (1), large rounded apodeme directed anterodorsally; (2), scythe-like directed dorsally; (3), curved blunt blade directed ventrally

170. Ventral portion of lateral ejaculatory process: (0), absent; (1), present

171. Ventral portion of lateral ejaculatory process: (0), does not extend into sperm sac; (1), extends into sperm sac

172. Tubercles associated with base of lateral ejaculatory process: (0), absent; (1), present

173. Aedeagal sclerites: (0), aedeagus uniformly sclerotized; (1) aedeagus composed of lateral sclerotized regions joined by medial membrane; (2), aedeagus membranous

174. Aedeagal sclerites shortened: (0), more than 2x as long as combined width at base; (1), less than 2x as long as combined width at base

175. Aedeagal sclerites flattened: (0), absent; (1), present

176. Apex of aedeagal sclerites: (0), angled; (1), rounded; (2), with expanded apex

177. Base of aedeagal sclerites constricted: (0), absent; (1), present

- 178.** Ventral apical apodemes of aedeagus: (0), absent; (1), present
- 179.** Ventral plate/Subapical Sclerite: (0), absent; (1), present
- 180.** Subapical sclerite shape: (0) conical; (1), platelike, (2), spine-like; (3), rod-like; (4), reduced; (5), winglike; (6), trough-like
- 181.** Ventral arm of subapical sclerite: (0), present, attached; (1), present, detached (lateral plate); (2), absent
- 182.** Ventral arm of subapical sclerite forming bar-like structures. (0), absent; (1), present
- 183.** Ventral keel on subapical sclerite: (0), absent; (1), present
- 184.** Filament on ventral surface of subapical sclerite: (0), absent; (1), present
- 185.** Ventral surface of subapical sclerite: (0), smooth; (1), serrated
- 186.** Dorsal triangular lobe at phallotrema: (0), absent; (1), present

Appendix II:

Morphological Dataset

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	
<i>Tricyphona inconstans</i>	?	?	?	?	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Araucoderus gloriosus</i>	0	0	0	-	2	1	1	0	0	-	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	
<i>Protoplasia fitchii</i>	0	0	0	-	0	1	1	0	0	-	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
<i>Edwardsina gigantea</i>	?	?	?	?	2	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Culicoides crepuscularis</i>	?	?	?	?	?	0	0	0	2	-	0	0	0	0	0	?	?	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Dixa modesta</i>	?	?	?	?	1	0	1	0	2	-	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	
<i>Bittacomorpha clavipes</i>	0	1	1	0	1	0	0	0	2	-	0	0	1	0	0	1	0	0	0	1	2	2	1	1	1	1	0	0	0	0	0	0	0	1	
<i>Bittacomorphella fenderiana</i>	0	1	1	1	1	0	0	0	2	-	1	0	1	0	0	1	0	1	1	0	1	2	2	1	1	1	0	0	0	0	0	0	0	1	
<i>Bittacomorphella pacifica</i>	?	?	?	?	1	0	0	0	2	-	0	0	1	0	0	1	0	0	1	0	1	2	2	1	0	1	0	0	0	0	0	0	0	?	
<i>Ptychoptera abbreviata</i>	?	?	?	?	2	1	1	1	1	0	0	0	0	0	2	2	0	1	1	2	0	1	0	0	0	0	0	1	1	0	0	1	1	0	
<i>Ptychoptera africana</i>	?	?	?	?	2	1	1	1	1	1	1	0	0	1	2	2	0	1	1	0	0	1	1	0	0	0	?	?	1	0	0	1	1	0	
<i>Ptychoptera albimana</i>	?	?	?	?	2	1	1	1	1	1	0	0	0	2	1	2	1	1	1	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	
<i>Ptychoptera alexanderi</i>	?	?	?	?	3	1	1	?	?	1	1	1	0	0	1	2	2	0	1	1	0	0	1	1	0	0	0	0	0	1	0	0	1	1	0
<i>Ptychoptera alina</i>	?	?	?	?	2	1	1	1	1	1	0	0	0	1	2	2	1	1	1	0	0	1	0	0	0	0	1	1	1	0	0	?	?	?	
<i>Ptychoptera annandalei</i>	?	?	?	?	1	1	?	1	?	?	?	?	0	?	?	?	?	?	1	0	0	1	1	1	?	0	1	0	1	0	0	?	?	?	
<i>Ptychoptera bellula</i>	?	?	?	?	2	1	1	0	1	0	1	1	0	1	2	2	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	1	1	0	
<i>Ptychoptera bilobata</i>	?	?	?	?	2	1	1	1	2	1	1	1	0	2	1	2	1	1	0	1	0	1	1	0	0	0	1	1	1	0	0	?	?	?	
<i>Ptychoptera byersi</i>	?	?	?	?	2	1	1	1	1	1	0	0	0	2	1	2	1	1	0	1	0	0	1	0	0	0	1	1	1	0	1	1	1	0	
<i>Ptychoptera camerounensis</i>	?	?	?	?	?	?	0	1	1	1	1	1	0	1	2	?	0	1	1	0	0	1	1	0	0	0	1	?	1	0	0	?	?	?	
<i>Ptychoptera capensis</i>	?	?	?	?	?	?	1	1	1	1	1	1	0	1	2	2	0	1	1	0	0	1	2	0	0	0	1	0	?	?	?	?	1	1	0
<i>Ptychoptera chalybeata</i>	?	?	?	?	?	1	?	0	1	0	1	0	0	1	2	2	0	1	1	1	0	1	1	0	0	1	1	0	?	?	?	?	?	?	
<i>Ptychoptera coloradensis</i>	1	0	0	0	2	1	1	0	1	1	1	0	2	1	2	1	1	0	1	0	1	0	0	0	0	0	1	1	1	0	1	1	1	1	0
<i>Ptychoptera contaminata</i>	?	?	?	?	2	1	1	0	1	1	1	0	0	1	0	2	1	1	0	0	0	1	0	0	0	0	1	1	1	2	0	1	1	0	
<i>Ptychoptera daimio</i>	?	?	?	?	2	1	1	1	1	1	1	0	1	0	2	?	?	?	0	0	0	1	0	0	0	0	1	1	?	?	?	?	?	?	
<i>Ptychoptera espica</i>	?	?	?	?	2	1	1	1	1	0	1	1	0	1	0	2	0	1	0	1	0	1	1	0	0	0	1	1	1	0	0	1	1	0	
<i>Ptychoptera formosensis</i>	?	?	?	?	2	1	1	0	1	0	0	0	1	2	2	0	1	1	0	0	2	0	0	0	0	0	1	0	1	0	0	1	1	0	
<i>Ptychoptera garhwalensis</i>	?	?	?	?	2	1	1	1	1	1	0	1	0	1	2	2	1	1	1	0	1	0	1	0	0	0	0	1	1	?	0	?	?	?	
<i>Ptychoptera gutianshana</i>	?	?	?	?	2	1	1	1	1	1	0	0	1	2	2	0	1	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0	1	1	0
<i>Ptychoptera handlirschi</i>	?	?	?	?	2	1	1	1	1	0	1	1	0	1	2	2	0	1	1	2	0	1	1	0	0	0	1	1	1	1	0	1	1	0	
<i>Ptychoptera helena</i>	?	?	?	?	2	1	1	1	1	1	1	0	0	1	2	2	0	1	1	2	0	2	1	0	0	0	1	0	1	1	0	1	1	0	
<i>Ptychoptera hugoi</i>	?	?	?	?	2	1	0	1	1	0	0	0	0	1	0	2	1	1	1	1	0	1	0	0	0	0	1	1	1	2	0	1	1	0	
<i>Ptychoptera ichitai</i>	?	?	?	?	3	1	1	?	?	1	0	1	0	0	1	2	2	0	1	1	0	0	1	0	0	0	0	1	0	1	0	0	?	?	?
<i>Ptychoptera japonica</i>	?	?	?	?	?	?	1	?	?	0	1	0	0	?	0	2	0	1	1	0	0	1	0	0	0	0	0	?	1	0	0	1	1	0	
<i>Ptychoptera javensis</i>	?	?	?	?	3	1	0	1	1	1	1	0	0	1	2	2	0	1	1	0	0	2	0	0	0	0	0	0	1	0	0	?	?	?	
<i>Ptychoptera lacustris</i>	?	?	?	?	2	1	1	1	1	1	1	1	0	1	2	2	1	1	1	2	0	1	0	0	0	0	1	0	1	1	0	1	1	0	
<i>Ptychoptera lacrimiformis</i>	1	0	0	0	2	1	1	1	1	1	0	0	0	2	1	2	1	1	1	0	0	1	0	0	0	0	1	1	1	0	0	1	1	0	
<i>Ptychoptera lenis</i>	?	?	?	?	2	1	1	1	1	0	1	1	0	2	1	2	1	1	1	0	1	0	0	0	0	0	1	1	1	0	0	1	1	0	
<i>Ptychoptera longicauda</i>	?	?	?	?	2	1	1	1	1	1	0	0	0	1	2	2	0	1	0	2	0	1	1	0	0	0	0	1	0	1	1	0	?	?	?
<i>Ptychoptera madagascariensis</i>	?	?	?	?	?	1	?	?	?	1	0	0	0	0	?	0	2	0	1	?	?	?	?	?	?	0	?	0	0	1	0	0	?	?	?
<i>Ptychoptera malaisei</i>	?	?	?	?	2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	?	?	1	1	?	?	?	?	?	
<i>Ptychoptera metallica</i>	?	?	?	?	2	1	1	1	1	1	0	0	0	1	0	2	0	1	1	1	0	1	0	0	0	0	1	1	1	2	0	1	1	0	
<i>Ptychoptera minor</i>	?	?	?	?	2	1	1	0	1	1	1	1	0	2	1	2	1	1	1	0	0	1	1	0	0	0	1	1	1	0	0	?	?	?	
<i>Ptychoptera minuta</i>	?	?	?	?	2	1	1	1	1	1	1	1	0	1	0	2	1	1	0	0	0	1	0	0	0	0	0	1	1	1	2	0	1	1	0
<i>Ptychoptera monoensis</i>	?	?	?	?	2	1	1	1	1	0	0	0	0	1	0	2	0	1	0	1	0	1	1	0	0	0	1	1	1	0	0	1	1	0	
<i>Ptychoptera obscura</i>	?	?	?	?	2	1	1	0	1	1	1	0	0	2	1	2	1	1	1	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	
<i>Ptychoptera osceola</i>	?	?	?	?	3	1	1	1	1	1	1	1	0	2	1	2	0	1	1	2	0	1	0	0	0	0	1	1	1	0	0	1	1	0	
<i>Ptychoptera paludosa</i>	?	?	?	?	2	1	1	1	1	1	1	0	0	1	2	2	0	1	1	2	0	1	1	0	0	0	1	1	1	1	0	1	1	0	
<i>Ptychoptera pendula</i>	2	0	0	1	2	1	1	1	1	1	0	0	0	1	0	2	1	1	0	0	0	1	0	0	0	0	1	1	1	0	0	1	1	0	
<i>Ptychoptera perbona</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	1	1	?	?	?	?	?	?	?	?	?	
<i>Ptychoptera persimilis</i>	?	?	?	?	3	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	1	1	0	?	?	0	0	1	?	0	?	?
<i>Ptychoptera praescutellaris</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	1	1	?	?	?	?	?	?	?	?	?	
<i>Ptychoptera pseudosimilis</i>	?	?	?	?	2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	1	1	0	0	0	0	0	1	0	0	?	?
<i>Ptychoptera quadrifasciata</i>	2	0	0	0	1	1	1	0	1	1	1	0	0	2	2	0	1	1	2	0	1	1	0	0	0	0	1	1	1	0	0	1	1	0	
<i>Ptychoptera resseli</i>	?	?	?	?	2	1	0	1	1	1	1	1	0	1	2	2	0	1	1	2	0	?	?	0	0	0	0	1	0	1	1	0	1	1	0
<i>Ptychoptera sculleni</i>	2	0	0	1	2	1	1	1	1	0	0	0	0	1	2	2	0	1	0	0	0	1	0												

Appendix II:

Morphological Dataset

	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66		
<i>Tricyphona inconstans</i>	0	0	0	0	0	0	0	-	-	-	-	0	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-		
<i>Araucoderus gloriosus</i>	1	0	0	0	0	0	0	-	-	-	-	0	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-		
<i>Protoplasma fitchii</i>	1	0	0	0	0	0	0	-	-	-	-	0	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-		
<i>Edwardsina gigantea</i>	1	0	0	0	0	0	0	-	-	-	-	0	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-		
<i>Culicoides crepuscularis</i>	1	0	0	0	0	0	0	-	-	-	-	0	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0		
<i>Dixa modesta</i>	?	?	?	?	?	?	0	-	-	-	-	0	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-		
<i>Bittacomorpha clavipes</i>	1	0	1	0	0	0	0	-	-	-	-	0	-	1	0	0	1	0	1	0	1	0	2	0	0	-	-	-	-	0	-	-		
<i>Bittacomorphella fenderiana</i>	1	0	1	0	1	1	0	0	-	-	-	1	0	1	0	0	2	0	1	0	1	0	2	0	0	-	-	-	-	0	-	-		
<i>Bittacomorphella pacifica</i>	1	0	1	0	1	1	0	0	-	-	-	0	-	1	0	0	2	0	1	0	1	0	2	0	0	-	-	-	-	0	-	-		
<i>Ptychoptera abbreviata</i>	0	1	?	1	0	0	2	1	0	0	0	1	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-		
<i>Ptychoptera africana</i>	0	1	0	1	0	0	1	1	0	1	0	1	0	1	1	1	2	0	0	0	0	0	0	0	0	-	-	-	-	0	-	-		
<i>Ptychoptera albimana</i>	0	1	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	3	0	
<i>Ptychoptera alexanderi</i>	1	1	0	1	0	0	2	1	1	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	-	-	-	-	0	-	-	
<i>Ptychoptera alina</i>	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	1	1	0	0	3	0	1	0	1	0	1	0	0	0	0	1	2	0	
<i>Ptychoptera annandalei</i>	?	?	?	?	?	?	?	2	1	1	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	-	-	-	-	0	-	-	
<i>Ptychoptera bellula</i>	0	1	0	1	0	0	?	?	?	?	?	?	1	0	1	1	1	1	0	0	0	0	0	1	0	0	-	-	-	-	0	-	-	
<i>Ptychoptera bilobata</i>	?	?	?	?	?	?	2	1	0	1	1	1	0	1	1	1	0	0	3	0	1	0	1	0	1	0	1	1	0	1	0	1		
<i>Ptychoptera byersi</i>	0	1	0	1	1	1	2	1	0	1	1	1	0	1	1	1	0	0	3	0	1	0	1	0	1	0	1	1	0	1	0	0		
<i>Ptychoptera camerounensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	1	1	0	0	0	0	0	0	0	0	0	-	-	-	-	0	-	-	
<i>Ptychoptera capensis</i>	0	1	0	1	1	0	2	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	-	-	-	0	-	-	
<i>Ptychoptera chalybeata</i>	?	?	?	?	?	?	2	1	1	1	0	1	0	1	1	1	0	0	0	0	0	0	0	1	0	0	-	-	-	-	0	-	-	
<i>Ptychoptera coloradensis</i>	0	1	0	1	0	1	2	1	0	1	1	1	0	1	1	1	0	0	3	0	1	0	1	0	1	0	1	1	1	1	?	0		
<i>Ptychoptera contaminata</i>	0	1	0	1	0	1	2	1	1	1	0	1	0	1	0	0	0	0	2	0	1	0	1	0	0	-	-	-	-	0	-	-		
<i>Ptychoptera daimio</i>	?	?	?	?	?	?	2	1	0	1	1	0	1	0	1	1	0	0	3	0	1	0	0	0	1	0	1	0	1	0	1	0	1	
<i>Ptychoptera espica</i>	0	1	0	1	1	1	2	1	0	1	0	1	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-		
<i>Ptychoptera formosensis</i>	0	1	0	1	0	0	2	?	?	?	?	?	1	0	1	1	1	0	0	0	0	0	0	0	1	0	-	-	-	-	0	-	-	
<i>Ptychoptera garhwalensis</i>	?	?	?	?	?	?	1	1	0	1	1	1	1	1	1	1	3	0	3	0	0	0	0	2	0	1	0	1	1	0	1	2	0	
<i>Ptychoptera gutianshana</i>	0	1	0	1	0	0	2	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0	-	-	-	-	0	-	-	
<i>Ptychoptera handlirschi</i>	0	1	0	1	0	0	2	1	1	1	0	1	0	1	0	0	0	0	1	2	0	0	1	0	0	0	-	-	-	-	0	-	-	
<i>Ptychoptera helena</i>	0	1	0	1	0	0	?	?	?	?	?	?	1	0	1	0	0	0	1	1	0	0	0	0	0	0	-	-	-	-	0	-	-	
<i>Ptychoptera hugoi</i>	0	1	0	1	?	0	1	1	1	1	0	1	0	1	0	0	0	0	2	0	1	0	1	0	0	-	-	-	-	0	-	-		
<i>Ptychoptera ichitai</i>	?	?	?	?	?	?	2	1	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	0	-	-	
<i>Ptychoptera japonica</i>	0	1	0	1	0	0	2	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	-	-	-	-	0	-	-
<i>Ptychoptera javensis</i>	?	?	?	?	?	?	2	1	1	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	-	-	-	-	0	-	-	
<i>Ptychoptera lacustris</i>	0	1	0	1	0	0	2	1	1	1	0	1	0	1	0	0	0	0	1	1	0	1	0	2	0	0	-	-	-	-	0	-	-	
<i>Ptychoptera lacrimiformis</i>	0	1	0	1	1	1	2	1	0	1	1	1	0	1	1	1	0	0	3	0	1	0	1	0	1	1	1	1	0	1	0	0		
<i>Ptychoptera lenis</i>	0	1	0	1	1	1	2	1	0	1	1	1	0	1	1	1	0	0	3	0	1	0	1	0	1	0	0	0	0	1	2	0		
<i>Ptychoptera longicauda</i>	?	?	?	?	?	?	2	1	1	1	0	1	0	1	0	0	0	1	1	0	0	1	1	0	0	-	-	-	-	0	-	-		
<i>Ptychoptera madagascariensis</i>	?	?	?	?	?	?	2	1	1	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	-	-	-	-	0	-	-	
<i>Ptychoptera malaisei</i>	?	?	?	?	?	?	2	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	2	0	0	-	-	-	-	0	-	-	
<i>Ptychoptera metallica</i>	0	1	0	1	1	1	2	1	1	1	0	1	0	1	0	0	0	0	2	1	1	0	1	0	0	-	-	-	-	0	-	-		
<i>Ptychoptera minor</i>	?	?	?	?	?	?	2	1	0	1	1	1	0	1	1	1	0	0	3	0	1	0	1	0	1	1	1	1	0	1	0	-	-	
<i>Ptychoptera minuta</i>	0	1	0	1	1	1	2	1	1	1	0	1	0	1	0	0	0	0	2	1	1	0	1	0	0	-	-	-	-	0	-	-		
<i>Ptychoptera monoensis</i>	0	1	0	1	1	1	2	1	1	1	0	1	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	0		
<i>Ptychoptera obscura</i>	0	1	0	1	1	1	2	1	0	1	1	1	0	1	1	1	0	0	3	0	1	0	1	0	1	0	1	1	1	1	2	0		
<i>Ptychoptera osceola</i>	0	1	0	1	1	0	2	1	1	0	0	1	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-		
<i>Ptychoptera paludosa</i>	0	1	0	1	0	0	2	1	1	0	0	1	0	1	0	0	0	0	1	1	0	0	1	2	0	0	-	-	-	-	0	-	-	
<i>Ptychoptera pendula</i>	0	1	0	1	1	2	2	1	1	0	0	1	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	0		
<i>Ptychoptera perbona</i>	?	?	?	?	?	?	2	1	1	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0	-	-	-	-	0	-	-	
<i>Ptychoptera persimilis</i>	?	?	?	?	?	?	2	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	-	-	-	-	0	-	-	
<i>Ptychoptera praescutellaris</i>	?	?	?	?	?	?	2	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	0	-	-	
<i>Ptychoptera pseudosimilis</i>	?	?	?	?	?	?	2	1	1	0	0	1	0	1	1	1	0	0	0	0	0	0	0	1	0	-	-	-	-	0	-	-		
<i>Ptychoptera quadrifasciata</i>	0	1	0	1	1	0	2	1	1	1	0	1	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-		
<i>Ptychoptera resseli</i>	0	1	0	1	1	2	2	1	1	1	0	1	0	1	0	0	2	1	1	0	0	0	2	0	0	-	-	-	-	0	-	-		
<i>Ptychoptera sculleni</i>	0	1	0	1	0	0	2	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	-	-	-	-	1	1	-	
<i>Ptychoptera sikkimensis</i>	0	1	0	1	1	0	1	1	0	1	1	1	1	1	1	3	0	3	0	0	0	2	0	1	0	1	0	1	1	0	1	2	1	
<i>Ptychoptera subscutellaris</i>	?	?	?	?	?	?	2	1	1	1	0	1	0	1	0	0	0	0	0	1	1	0	1	0	0	-	-	-	-	0	-	-		
<i>Ptychoptera sumatrensis</i>	0	1	0	1	0	0	2	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	-	-	-	-	0	-	-	
<i>Ptychoptera tibialis</i>	?	?	?																															

Appendix II:

Morphological Dataset

	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	
<i>Triclyphona inconstans</i>	-	0	-	-	0	-	-	-	0	0	-	0	0	0	-	0	-	0	0	0	0	0	-	0	-	-	-	-	0	0	0	-	
<i>Araucoderus gloriosus</i>	-	1	0	0	0	-	-	-	0	0	-	0	0	0	-	0	-	0	0	0	0	0	-	1	0	0	1	0	0	0	0	-	
<i>Protoplasma fitchii</i>	-	1	0	0	0	-	-	-	0	0	-	0	0	0	-	0	-	0	0	0	0	0	-	1	0	0	2	1	0	0	0	-	
<i>Edwardsina gigantea</i>	-	1	0	0	0	-	-	-	0	0	-	0	0	0	-	0	-	0	0	0	0	0	-	1	0	0	0	0	0	0	0	-	
<i>Culicoides crepuscularis</i>	-	1	0	0	0	-	-	-	0	0	-	1	1	0	-	0	-	0	-	0	0	0	-	1	0	0	0	0	0	0	0	-	
<i>Dixa modesta</i>	-	1	0	0	0	-	-	-	0	0	-	0	0	0	-	0	-	0	0	0	0	0	-	1	1	0	1	0	0	0	0	-	
<i>Bittacomorpha clavipes</i>	0	1	2	0	0	-	-	-	1	2	2	1	1	0	-	0	-	-	0	-	0	0	-	1	0	1	2	1	1	1	0	-	
<i>Bittacomorphella fenderiana</i>	0	1	1	0	0	-	-	-	1	2	2	1	1	0	-	1	3	-	0	-	0	0	-	1	1	0	0	0	0	1	0	-	
<i>Bittacomorphella pacifica</i>	0	1	3	0	0	-	-	-	1	1	-	1	1	0	-	0	-	0	-	0	0	0	-	1	0	0	0	0	0	1	0	-	
<i>Ptychoptera abbreviata</i>	-	0	-	-	1	1	0	0	2	0	-	0	0	1	0	0	-	2	0	0	0	0	-	1	1	0	3	0	0	1	1	0	
<i>Ptychoptera africana</i>	0	0	-	-	1	0	1	1	2	1	-	0	0	1	1	1	2	1	0	0	0	0	-	1	1	0	2	0	0	1	1	1	
<i>Ptychoptera albimana</i>	0	1	3	0	1	0	1	1	2	0	-	0	0	1	0	0	-	1	0	0	0	1	0	0	-	-	-	-	0	1	1	0	
<i>Ptychoptera alexanderi</i>	0	0	-	-	1	0	1	1	2	0	-	0	0	1	2	0	-	2	0	1	0	0	-	1	1	0	2	0	0	1	1	0	
<i>Ptychoptera alina</i>	0	0	-	-	1	0	1	1	2	?	?	0	0	1	0	?	?	?	0	0	0	0	-	1	0	0	1	1	0	1	1	0	
<i>Ptychoptera annandalei</i>	0	0	-	-	1	1	1	0	2	0	-	0	0	1	1	0	-	1	0	?	0	0	-	1	0	0	1	0	0	1	1	0	
<i>Ptychoptera bellula</i>	0	1	2	0	1	0	0	0	1	1	-	0	0	1	1	0	-	0	0	0	0	0	-	0	-	-	-	-	0	1	1	1	
<i>Ptychoptera bilobata</i>	0	1	4	0	1	0	1	1	2	0	-	1	0	1	0	0	-	-	0	-	0	0	-	1	1	1	2	0	0	1	1	0	
<i>Ptychoptera byersi</i>	0	1	4	0	1	0	1	1	2	0	-	1	0	1	0	0	-	-	0	-	0	0	-	1	1	1	2	0	0	1	1	0	
<i>Ptychoptera camerounensis</i>	0	0	-	-	1	0	1	1	?	?	?	0	0	?	?	?	?	?	?	1	0	0	-	1	0	?	1	0	0	?	?	?	
<i>Ptychoptera capensis</i>	0	0	-	-	1	0	1	1	?	?	?	0	0	1	1	0	-	2	2	?	0	0	-	1	1	0	0	0	0	1	1	1	
<i>Ptychoptera chalybeata</i>	0	0	-	-	1	0	1	0	?	?	?	0	0	1	1	1	2	2	0	0	0	0	-	1	1	0	0	0	0	1	1	1	
<i>Ptychoptera coloradensis</i>	0	1	4	0	1	0	1	1	2	0	-	1	0	1	0	0	-	0	-	0	0	0	-	1	1	1	2	0	0	1	1	0	
<i>Ptychoptera contaminata</i>	0	1	7	1	1	1	1	0	0	2	0	0	0	1	0	0	-	0	0	1	0	1	1	1	1	0	3	0	1	1	1	0	
<i>Ptychoptera daimio</i>	0	1	4	0	1	0	1	1	2	0	-	1	0	1	0	0	-	-	0	0	0	0	-	1	0	0	1	0	0	1	1	0	
<i>Ptychoptera espica</i>	-	1	3	0	1	1	1	1	1	2	1	0	0	1	2	0	-	0	0	1	0	0	-	0	-	-	-	-	0	1	0	-	
<i>Ptychoptera formosensis</i>	0	0	-	-	1	0	1	1	2	?	?	0	0	1	0	1	0	2	0	0	0	0	-	1	1	0	0	0	0	1	1	1	
<i>Ptychoptera garhwalensis</i>	0	1	5	0	1	1	0	0	2	?	?	0	0	1	0	1	2	2	1	?	0	0	-	1	2	0	2	0	0	1	0	-	
<i>Ptychoptera gutianshana</i>	0	0	-	-	1	0	1	1	2	1	-	1	1	1	0	0	-	-	0	-	0	0	-	1	0	0	0	0	0	1	1	0	
<i>Ptychoptera handlirschi</i>	0	1	2	0	1	0	1	0	2	0	-	0	1	1	1	1	3	0	0	0	0	0	-	1	1	0	2	1	0	1	1	0	
<i>Ptychoptera helena</i>	0	1	1	0	1	0	1	0	2	?	?	0	1	1	1	0	-	0	0	0	0	0	-	1	1	0	2	0	0	1	1	1	
<i>Ptychoptera hugoi</i>	0	1	7	1	1	1	1	0	0	2	0	0	0	1	0	0	-	0	0	1	0	1	1	1	1	1	0	2	0	1	1	1	
<i>Ptychoptera ichitai</i>	1	0	-	-	1	0	1	1	2	0	-	0	0	1	0	0	-	0	0	0	1	0	-	1	0	0	0	0	0	1	1	0	
<i>Ptychoptera japonica</i>	0	0	-	-	1	0	1	1	2	0	-	0	0	0	0	0	-	0	0	0	1	0	-	1	0	0	0	0	0	1	1	1	
<i>Ptychoptera javensis</i>	0	0	-	-	1	0	1	1	3	1	-	0	0	1	0	0	-	0	0	0	0	0	-	1	0	0	0	0	0	1	1	1	
<i>Ptychoptera lacustris</i>	1	0	-	-	1	1	1	0	2	0	-	0	1	1	1	2	0	0	0	0	0	0	-	1	1	0	2	1	0	1	1	1	
<i>Ptychoptera lacrimiformis</i>	0	1	4	0	1	0	1	1	2	0	-	1	0	1	0	0	-	-	0	0	0	0	-	1	1	0	2	0	0	1	1	0	
<i>Ptychoptera lenis</i>	0	1	4	0	1	1	1	1	2	0	-	1	0	1	0	0	-	-	0	0	0	0	-	1	0	0	1	0	0	1	1	0	
<i>Ptychoptera longicauda</i>	0	1	1	0	1	1	1	0	2	0	-	0	1	1	1	1	3	0	0	0	0	0	-	1	1	0	2	0	0	1	1	1	
<i>Ptychoptera madagascariensis</i>	1	0	-	-	1	0	1	0	2	1	-	0	0	1	0	0	-	0	0	0	0	0	-	1	1	0	0	0	0	1	1	1	
<i>Ptychoptera malaisei</i>	0	0	-	-	1	1	0	1	2	1	-	0	0	1	1	0	-	0	0	?	0	0	-	1	0	0	1	0	0	1	1	1	
<i>Ptychoptera metallica</i>	0	1	7	1	1	1	1	0	0	2	0	0	0	1	0	1	0	0	0	1	0	1	1	1	1	1	0	3	0	1	1	1	1
<i>Ptychoptera minor</i>	0	1	4	0	1	0	1	1	2	0	-	1	0	1	0	0	-	-	0	0	0	0	-	1	1	0	2	0	0	1	1	0	
<i>Ptychoptera minuta</i>	0	1	7	1	1	1	1	0	0	2	0	0	0	1	0	1	0	0	0	1	0	1	1	1	1	1	0	3	0	1	1	1	1
<i>Ptychoptera monoensis</i>	-	1	3	0	1	0	1	0	1	2	1	0	0	1	2	0	-	0	0	1	0	0	-	0	-	-	-	-	0	1	1	1	
<i>Ptychoptera obscura</i>	0	1	4	0	1	0	1	1	2	0	-	1	0	1	0	0	-	-	0	0	0	0	-	1	1	1	2	0	0	1	1	0	
<i>Ptychoptera osceola</i>	-	0	-	-	1	0	0	0	2	0	-	0	0	1	0	0	-	2	0	0	0	0	-	1	0	0	1	0	0	1	1	0	
<i>Ptychoptera paludosa</i>	0	1	1	0	1	0	1	0	2	1	-	0	1	1	1	3	3	0	0	0	0	0	-	1	1	0	2	0	0	1	1	1	
<i>Ptychoptera pendula</i>	-	0	1	0	1	1	1	0	1	2	1	0	0	1	2	0	-	0	0	1	0	0	-	0	-	-	-	-	0	1	1	1	
<i>Ptychoptera perbona</i>	0	0	-	-	1	0	1	1	?	?	?	0	0	1	1	0	-	1	0	?	0	0	-	0	-	-	-	-	0	1	1	1	
<i>Ptychoptera persimilis</i>	0	0	-	-	1	0	1	0	3	1	-	0	0	1	1	1	3	?	0	1	0	0	-	1	0	0	0	0	1	1	1	1	
<i>Ptychoptera praescutellaris</i>	1	0	-	-	1	0	1	0	2	0	-	0	0	1	0	0	-	?	0	0	0	1	0	1	0	0	0	0	0	1	1	0	
<i>Ptychoptera pseudosimilis</i>	0	0	-	-	1	0	1	0	3	1	-	0	0	1	0	0	-	0	0	?	0	0	-	1	0	0	1	0	0	1	1	0	
<i>Ptychoptera quadrifasciata</i>	-	0	-	-	1	1	0	0	2	0	-	0	0	1	0	0	-	2	0	0	0	0	-	1	1	0	2	0	0	1	1	0	
<i>Ptychoptera resseli</i>	0	1	1	0	1	0	1	0	2	0	-	0	1	1	1	0	-	1	0	0	0	0	-	1	1	0	2	0	0	1	1	1	
<i>Ptychoptera sculleni</i>	0	0	-	-	1	1	1	0	2	1	-	0	0	1	2	0	-	2	0	0	0	1	0	0	-	-	-	-	0	1	1	1	
<i>Ptychoptera sikkimensis</i>	0	1	0	0	1	1	1	1	?	?	?	0	0	1	0	0	-	2	1	0	0	0	-	1	0	0	1	0	0	1	0	-	
<i>Ptychoptera subscutellaris</i>	0	1	2	1	1	1	1	1	0	2	0	0	0	1	0	0	-	0	0	0	0	1	1	1	2	0	0	0	1	1	1	0	
<i>Ptychoptera sumatrensis</i>	0	0	-	-	1	0	1	0	1	?	?	0	0	1	0	0	-	0	0	1	0	0	-										

Appendix II:

Morphological Dataset

	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122
<i>Tricyphona inconstans</i>	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	0	0	0	0	0	0
<i>Araucoderus gloriosus</i>	-	-	0	0	0	0	0	1	-	-	1	-	0	1	-	-	-	-	-	1	0	0	1	0
<i>Protoplasma fitchii</i>	-	-	0	0	0	0	0	1	-	-	1	-	0	1	-	-	-	-	-	2	0	0	1	1
<i>Edwardsina gigantea</i>	-	-	0	0	0	0	0	0	1	0	1	-	0	1	-	-	-	-	-	1	0	0	0	0
<i>Culicoides crepuscularis</i>	-	-	0	0	0	0	0	1	-	-	1	-	0	1	-	-	-	-	-	1	0	0	0	0
<i>Dixa modesta</i>	-	-	0	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	-	1	0	0	0	0
<i>Bittacomorpha clavipes</i>	-	-	0	0	1	0	1	1	-	-	1	-	0	1	-	-	-	-	-	1	0	0	1	0
<i>Bittacomorphella fenderiana</i>	-	-	0	0	1	0	1	1	-	-	1	-	0	0	1	-	-	-	0	1	0	0	1	0
<i>Bittacomorphella pacifica</i>	-	-	0	0	3	0	1	1	-	-	1	-	0	0	-	-	-	-	-	1	0	0	1	0
<i>Ptychoptera abbreviata</i>	0	0	0	0	1	1	1	0	1	1	0	0	0	0	1	2	-	-	1	1	0	0	2	0
<i>Ptychoptera africana</i>	1	0	1	0	0	0	1	1	-	-	1	-	0	0	0	4	-	-	1	0	0	0	0	0
<i>Ptychoptera albimana</i>	0	0	0	0	1	0	1	1	-	-	1	-	0	0	0	2	-	-	1	0	0	0	1	0
<i>Ptychoptera alexanderi</i>	0	0	0	0	0	0	1	0	0	1	1	-	0	0	0	0	-	-	0	1	0	0	1	0
<i>Ptychoptera alina</i>	0	0	0	0	1	0	1	1	-	-	1	-	0	0	0	4	-	-	0	1	0	1	0	0
<i>Ptychoptera annandalei</i>	0	0	0	0	2	0	1	1	-	-	1	-	0	0	1	3	-	1	1	0	0	0	0	1
<i>Ptychoptera bellula</i>	0	0	0	0	2	0	1	0	0	0	1	-	0	0	0	3	-	-	1	1	0	0	2	0
<i>Ptychoptera bilobata</i>	2	0	0	0	1	0	1	1	-	-	1	-	1	0	0	2	-	-	1	1	0	0	1	0
<i>Ptychoptera byersi</i>	2	0	0	0	1	0	1	1	-	-	1	-	1	0	0	2	-	-	1	1	0	0	1	0
<i>Ptychoptera camerounensis</i>	?	?	?	0	2	0	?	0	1	0	1	-	0	0	0	4	-	-	0	0	0	0	0	0
<i>Ptychoptera capensis</i>	0	0	1	0	0	0	1	1	-	-	1	-	0	0	0	2	-	-	1	1	0	0	0	0
<i>Ptychoptera chalybeata</i>	0	0	1	0	2	0	1	1	-	-	1	-	0	0	0	2	-	-	1	0	0	0	2	1
<i>Ptychoptera coloradensis</i>	2	0	0	0	1	0	1	1	-	-	1	-	1	0	0	2	-	-	1	1	0	0	1	0
<i>Ptychoptera contaminata</i>	0	0	0	0	1	0	1	0	0	0	1	-	0	0	1	0	3	-	1	0	0	0	2	0
<i>Ptychoptera daimio</i>	2	0	0	0	1	0	1	1	-	-	1	-	1	0	0	2	-	-	1	1	0	0	1	0
<i>Ptychoptera espica</i>	-	-	0	0	0	0	1	0	0	0	0	1	0	0	1	3	0	-	0	0	1	1	1	0
<i>Ptychoptera formosensis</i>	0	?	0	0	1	0	1	1	-	-	1	-	0	0	1	4	3	-	1	0	0	0	0	1
<i>Ptychoptera garhwalensis</i>	-	-	0	0	?	0	1	1	-	-	1	-	1	0	1	2	4	-	1	1	0	0	1	0
<i>Ptychoptera gutianshana</i>	0	0	0	0	2	0	1	0	1	0	1	-	0	0	1	2	3	-	1	0	0	1	2	1
<i>Ptychoptera handlirschi</i>	1	0	0	0	2	0	1	0	1	0	0	0	0	0	1	1	5	-	1	0	1	1	1	0
<i>Ptychoptera helena</i>	1	0	0	0	2	0	1	0	1	0	0	0	0	0	1	4	5	-	1	0	1	1	0	0
<i>Ptychoptera hugoi</i>	0	0	0	1	1	0	1	0	0	0	1	-	0	0	1	3	3	-	1	0	0	0	2	0
<i>Ptychoptera ichitai</i>	0	0	0	0	2	0	0	1	-	-	1	-	0	0	0	1	-	-	1	1	0	0	1	0
<i>Ptychoptera japonica</i>	0	0	0	0	0	0	0	1	-	-	1	-	0	0	0	1	-	-	1	1	0	0	1	0
<i>Ptychoptera javensis</i>	0	0	0	0	3	0	1	1	-	-	1	-	0	0	3	1	1	2	1	0	0	0	1	0
<i>Ptychoptera lacustris</i>	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	4	5	-	1	0	1	1	0	0
<i>Ptychoptera lacrimiformis</i>	2	0	0	0	1	0	1	1	-	-	1	-	1	0	0	2	-	-	1	1	0	0	1	0
<i>Ptychoptera lenis</i>	2	0	0	0	1	0	1	1	-	-	1	-	1	0	0	2	-	-	1	1	0	0	1	0
<i>Ptychoptera longicauda</i>	1	0	0	0	1	0	1	0	1	0	0	0	0	0	1	2	5	-	1	0	1	1	1	0
<i>Ptychoptera madagascariensis</i>	0	0	1	0	0	0	1	1	-	-	1	-	0	0	1	2	2	-	1	0	0	0	1	0
<i>Ptychoptera malaisei</i>	0	0	1	0	2	0	1	1	-	-	1	-	0	0	1	2	2	-	1	0	1	0	0	0
<i>Ptychoptera metallica</i>	0	0	0	1	3	0	1	0	1	1	1	-	0	0	1	0	3	-	1	0	0	0	1	0
<i>Ptychoptera minor</i>	2	0	0	0	1	0	1	1	-	-	1	-	1	0	0	2	-	-	1	1	0	0	1	0
<i>Ptychoptera minuta</i>	0	0	0	1	3	0	1	0	1	1	1	-	0	0	1	0	3	-	1	0	0	0	1	0
<i>Ptychoptera monoensis</i>	1	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	-	-	1	0	1	1	1	0
<i>Ptychoptera obscura</i>	2	0	0	0	1	0	1	1	-	-	1	-	1	0	1	2	-	-	1	1	0	0	1	0
<i>Ptychoptera osceola</i>	0	0	0	0	1	1	1	0	1	0	1	0	0	0	0	2	-	-	1	1	0	0	0	0
<i>Ptychoptera paludosa</i>	1	0	0	0	2	0	1	0	1	0	0	1	0	0	1	2	5	-	1	1	1	0	2	0
<i>Ptychoptera pendula</i>	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	-	-	1	0	1	1	1	0
<i>Ptychoptera perbona</i>	0	0	1	0	2	0	1	1	-	-	1	-	0	0	0	2	-	-	1	0	0	0	1	1
<i>Ptychoptera persimilis</i>	0	0	1	0	1	0	1	1	-	-	1	-	0	0	2	3	3	2	1	0	0	0	0	0
<i>Ptychoptera praescutellaris</i>	0	1	1	0	3	0	1	1	-	-	1	-	0	0	2	4	3	3	1	0	0	0	0	0
<i>Ptychoptera pseudosimilis</i>	0	1	1	0	0	0	1	1	-	-	1	-	0	0	2	3	3	2	1	0	0	0	0	0
<i>Ptychoptera quadrifasciata</i>	0	0	0	0	3	1	1	1	1	1	0	0	0	0	0	2	-	-	1	1	0	0	0	0
<i>Ptychoptera resseli</i>	1	0	0	0	1	0	1	0	1	0	0	1	0	0	0	4	5	-	1	-	-	-	-	-
<i>Ptychoptera sculleni</i>	1	0	1	0	2	0	1	0	1	1	0	0	0	0	0	2	-	-	1	0	1	1	1	0
<i>Ptychoptera sikkimensis</i>	-	-	0	0	1	0	1	1	-	-	1	-	0	0	1	1	4	-	1	1	0	0	1	0
<i>Ptychoptera subscutellaris</i>	0	0	0	0	1	0	1	0	1	0	1	-	0	0	1	4	3	-	1	0	0	0	2	0
<i>Ptychoptera sumatrensis</i>	0	0	0	0	2	0	1	1	-	-	1	-	0	0	2	2	2	3	1	0	0	0	0	0
<i>Ptychoptera tibialis</i>	-	-	0	0	1	0	1	1	-	-	1	-	0	0	1	1	4	-	1	1	0	0	1	0
<i>Ptychoptera townesi</i>	-	-	0	0	0	0	1	0	0	0	0	1	0	0	0	0	-	-	0	0	1	1	1	0
<i>Ptychoptera uta</i>	2	0	0	0	1	0	1	1	-	-	1	-	1	0	0	2	-	-	1	1	0	0	1	0
<i>Ptychoptera yamato</i>	0	1	0	0	0	0	1	1	-	-	1	-	0	0	0	1	-	-	1	1	0	0	1	0
<i>Ptychoptera yankovskiana</i>	0	0	0	0	1	0	1	1	0	0	1	-	0	0	1	4	3	-	1	0	0	0	2	0
<i>Ptychoptera yasumatsui</i>	1	0	1	0	2	0	1	1	-	-	1	-	0	0	2	3	3	3	0	0	0	0	0	0

Appendix II:

Morphological Dataset

	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146
<i>Tricyphona inconstans</i>	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	-	-	-	0	-	-	-	-
<i>Araucoderus gloriosus</i>	0	1	-	-	-	-	1	-	0	3	0	0	-	-	0	0	-	-	-	0	-	-	-	-
<i>Protoplasma fitchii</i>	0	0	0	1	0	0	1	-	0	4	0	0	-	-	0	0	-	-	-	0	-	-	-	-
<i>Edwardsina gigantea</i>	0	1	-	-	-	-	1	-	0	4	0	0	-	-	0	0	-	-	-	0	-	-	-	-
<i>Culicoides crepuscularis</i>	0	1	-	-	-	-	1	-	0	0	0	0	-	-	0	0	-	-	-	0	-	-	-	-
<i>Dixa modesta</i>	0	1	-	-	-	-	1	-	0	0	0	0	-	-	0	0	-	-	-	0	-	-	-	-
<i>Bittacomorpha clavipes</i>	0	1	-	-	-	-	1	-	2	2	0	0	-	-	0	0	-	-	-	1	1	0	0	0
<i>Bittacomorphella fenderiana</i>	0	1	-	-	-	-	1	-	1	2	0	0	-	-	0	0	-	-	-	1	1	0	0	0
<i>Bittacomorphella pacifica</i>	0	1	-	-	-	-	1	-	1	1	0	0	-	-	0	0	-	-	-	1	0	0	0	0
<i>Ptychoptera abbreviata</i>	0	1	-	-	-	-	1	-	0	2	1	1	1	0	0	0	-	-	-	1	0	1	0	0
<i>Ptychoptera africana</i>	0	1	-	-	-	-	1	-	0	0	0	0	-	-	0	1	2	0	1	1	1	1	2	0
<i>Ptychoptera albimana</i>	1	0	0	0	1	0	1	-	0	0	0	0	-	-	0	1	0	0	1	1	1	1	1	0
<i>Ptychoptera alexanderi</i>	0	1	-	-	-	-	1	-	1	2	0	0	-	-	0	0	-	-	-	1	2	1	0	0
<i>Ptychoptera alina</i>	1	1	-	-	-	-	1	-	0	0	0	0	-	-	0	1	0	1	0	1	1	1	1	0
<i>Ptychoptera annandalei</i>	0	0	1	1	0	1	1	-	2	0	0	0	-	-	0	1	4	0	0	1	1	1	1	0
<i>Ptychoptera bellula</i>	0	1	-	-	-	-	1	-	0	0	0	0	-	-	1	0	-	-	-	1	?	?	?	?
<i>Ptychoptera bilobata</i>	1	1	-	-	-	-	1	-	0	0	0	0	-	-	0	1	2	2	0	1	1	1	1	0
<i>Ptychoptera byersi</i>	1	1	-	-	-	-	1	-	0	0	0	0	-	-	0	1	2	2	0	1	1	1	1	0
<i>Ptychoptera camerounensis</i>	0	0	0	0	1	0	1	-	0	0	0	0	-	-	1	1	2	0	0	1	1	1	1	0
<i>Ptychoptera capensis</i>	0	1	-	-	-	-	1	-	0	0	0	0	-	-	0	1	0	0	1	1	1	1	1	0
<i>Ptychoptera chalybeata</i>	0	1	-	-	-	-	1	-	0	0	0	0	-	-	0	1	4	0	0	1	?	?	?	?
<i>Ptychoptera coloradensis</i>	1	1	-	-	-	-	1	-	0	0	0	0	-	-	0	1	2	1	0	1	1	1	1	0
<i>Ptychoptera contaminata</i>	0	0	0	0	2	0	1	-	0	0	0	1	0	0	0	0	-	-	-	1	0	0	0	0
<i>Ptychoptera daimio</i>	1	1	-	-	-	-	1	-	0	0	0	0	-	-	0	1	0	0	0	1	1	1	1	0
<i>Ptychoptera espica</i>	0	0	0	1	1	0	1	0	2	0	0	1	0	0	0	0	-	-	-	1	0	0	1	0
<i>Ptychoptera formosensis</i>	0	0	0	1	0	1	1	-	0	0	0	0	-	-	0	1	0	0	0	1	1	1	1	0
<i>Ptychoptera garhwalensis</i>	1	1	-	-	-	-	1	-	0	0	0	0	-	-	0	1	0	0	1	1	1	1	1	0
<i>Ptychoptera gutianshana</i>	0	0	0	1	0	0	1	-	0	0	0	0	-	-	1	0	-	-	-	1	1	1	1	1
<i>Ptychoptera handlirschi</i>	0	0	1	0	0	0	1	-	0	0	1	1	0	0	1	0	-	-	-	1	0	0	0	0
<i>Ptychoptera helena</i>	0	0	1	0	0	0	1	-	0	0	1	1	0	1	1	0	-	-	-	1	0	0	0	0
<i>Ptychoptera hugoi</i>	0	0	0	0	2	0	1	-	0	0	0	1	0	0	0	0	-	-	-	1	0	0	0	0
<i>Ptychoptera ichitai</i>	0	1	-	-	-	-	1	-	0	2	0	0	-	-	0	0	-	-	-	1	2	1	0	0
<i>Ptychoptera japonica</i>	0	1	-	-	-	-	1	-	0	2	0	0	-	-	0	0	-	-	-	1	2	1	0	0
<i>Ptychoptera javensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	-	-	1	1	4	0	0	1	1	1	1	1
<i>Ptychoptera lacustris</i>	0	0	0	0	0	0	1	-	0	0	1	1	0	1	0	0	-	-	-	1	0	0	0	0
<i>Ptychoptera lacrimiformis</i>	1	1	-	-	-	-	1	-	0	0	0	0	-	-	0	1	2	1	0	1	1	1	1	0
<i>Ptychoptera lenis</i>	1	1	-	-	-	-	1	-	0	0	0	0	-	-	0	1	1	0	0	1	1	1	0	0
<i>Ptychoptera longicauda</i>	0	0	0	0	0	0	1	-	0	0	1	1	0	1	1	0	-	-	-	1	0	0	0	0
<i>Ptychoptera madagascariensis</i>	0	0	0	0	0	0	1	-	0	0	0	0	-	-	0	1	0	0	1	1	1	1	1	1
<i>Ptychoptera malaisei</i>	0	0	1	1	0	0	1	-	0	0	0	0	-	-	0	1	0	0	0	1	1	1	1	?
<i>Ptychoptera metallica</i>	0	0	0	1	2	0	1	-	0	0	0	1	0	0	0	0	-	-	-	1	0	0	0	0
<i>Ptychoptera minor</i>	1	1	-	-	-	-	1	-	0	0	0	0	-	-	0	1	2	1	0	1	1	1	1	0
<i>Ptychoptera minuta</i>	0	0	0	1	2	0	1	-	0	0	0	1	0	0	0	0	-	-	-	1	0	0	0	0
<i>Ptychoptera monoensis</i>	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	-	-	-	1	0	0	0	0
<i>Ptychoptera obscura</i>	1	1	-	-	-	-	1	-	0	0	0	0	-	-	0	1	2	1	0	1	1	1	1	0
<i>Ptychoptera osceola</i>	1	1	-	-	-	-	1	-	0	2	0	1	1	0	0	0	-	-	-	1	0	1	0	0
<i>Ptychoptera paludosa</i>	0	1	-	-	-	-	1	-	0	0	1	1	0	0	1	0	-	-	-	1	0	0	0	0
<i>Ptychoptera pendula</i>	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	-	-	-	1	0	0	0	0
<i>Ptychoptera perbona</i>	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	-	-	-	1	0	1	2	0
<i>Ptychoptera persimilis</i>	0	0	1	0	0	1	1	-	0	0	0	0	-	-	0	1	0	0	0	1	1	1	1	0
<i>Ptychoptera praescutellaris</i>	0	0	0	0	2	0	1	-	0	0	0	0	-	-	0	1	2	0	0	1	1	1	1	0
<i>Ptychoptera pseudosimilis</i>	0	0	1	0	0	1	1	-	0	0	0	0	-	-	0	1	0	0	0	1	1	1	1	0
<i>Ptychoptera quadrifasciata</i>	1	1	-	-	-	-	1	-	0	2	1	1	1	0	0	0	-	-	-	1	0	1	0	0
<i>Ptychoptera resseli</i>	-	-	-	-	-	-	-	-	0	1	1	0	0	1	0	-	-	-	-	1	1	0	0	0
<i>Ptychoptera sculleni</i>	0	0	0	0	0	0	1	-	0	0	0	1	1	0	0	0	-	-	-	1	0	0	0	1
<i>Ptychoptera sikkimensis</i>	1	1	-	-	-	-	1	-	0	0	0	0	-	-	0	1	0	0	0	1	1	1	1	0
<i>Ptychoptera subscutellaris</i>	0	0	0	0	2	0	0	-	0	0	0	1	0	0	0	0	-	-	-	1	0	0	0	0
<i>Ptychoptera sumatrensis</i>	0	0	0	1	0	0	1	-	0	0	0	0	-	-	1	1	4	0	0	1	1	1	1	1
<i>Ptychoptera tibialis</i>	1	1	-	-	-	-	1	-	0	0	0	0	-	-	0	1	0	0	0	1	1	1	1	0
<i>Ptychoptera townesi</i>	0	0	0	1	1	0	0	0	2	0	0	1	0	0	0	0	-	-	-	1	0	0	1	0
<i>Ptychoptera uta</i>	1	1	-	-	-	-	1	-	0	0	0	0	-	-	0	1	2	1	0	1	1	1	1	0
<i>Ptychoptera yamato</i>	0	1	-	-	-	-	1	-	0	2	0	0	-	-	0	0	-	-	-	1	2	1	0	0
<i>Ptychoptera yankovskiana</i>	0	0	0	0	2	0	1	-	0	0	0	1	1	1	0	0	-	-	-	1	0	0	0	0
<i>Ptychoptera yasumatsui</i>	0	0	0	1	0	0	0	0	0	0	0	0	-	-	0	0	-	-	-	1	1	1	1	0

Appendix II:

Morphological Dataset

[illegible]

Appendix II:

Morphological Dataset

	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185	186
<i>Tricyphona inconstans</i>	-	-	0	-	-	-	-	0	0	-	-	-	-	-	-	-
<i>Araucoderus gloriosus</i>	-	-	0	-	-	-	-	0	0	-	-	-	-	-	-	-
<i>Protoplasma fitchii</i>	-	-	0	-	-	-	-	0	0	-	-	-	-	-	-	-
<i>Edwardsina gigantea</i>	-	-	0	-	-	-	-	0	0	-	-	-	-	-	-	-
<i>Culicoides crepuscularis</i>	-	-	2	-	-	-	-	-	1	1	2	-	-	-	0	0
<i>Dixa modesta</i>	-	-	2	-	-	-	-	-	1	1	2	-	-	-	0	0
<i>Bittacomorpha clavipes</i>	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0
<i>Bittacomorphella fenderiana</i>	1	0	1	0	0	0	1	1	1	4	0	0	0	0	0	0
<i>Bittacomorphella pacifica</i>	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0
<i>Ptychoptera abbreviata</i>	1	1	1	1	0	1	0	1	1	0	1	0	0	0	0	0
<i>Ptychoptera africana</i>	-	0	1	1	0	1	0	0	1	2	2	-	0	0	0	0
<i>Ptychoptera albimana</i>	0	1	1	1	0	1	1	0	1	5	0	-	0	0	0	0
<i>Ptychoptera alexanderi</i>	0	1	1	1	1	0	0	1	1	2	2	-	0	0	1	0
<i>Ptychoptera alina</i>	?	?	1	1	0	1	1	0	1	5	0	0	0	0	?	0
<i>Ptychoptera annandalei</i>	?	?	1	1	0	2	0	0	1	2	2	-	0	0	1	0
<i>Ptychoptera bellula</i>	-	0	1	1	0	1	0	0	1	0	2	-	0	1	0	0
<i>Ptychoptera bilobata</i>	-	1	1	1	0	1	1	0	1	3	2	-	0	0	0	1
<i>Ptychoptera byersi</i>	-	1	1	1	0	1	1	0	1	3	2	-	0	0	0	1
<i>Ptychoptera camerounensis</i>	?	?	?	?	?	?	?	?	1	2	?	?	?	0	?	?
<i>Ptychoptera capensis</i>	-	0	1	1	0	0	0	0	1	2	2	-	0	0	0	0
<i>Ptychoptera chalybeata</i>	-	?	1	1	0	2	1	0	1	0	2	-	?	0	?	0
<i>Ptychoptera coloradensis</i>	-	1	1	1	0	1	1	0	1	3	2	-	0	0	0	1
<i>Ptychoptera contaminata</i>	-	1	1	1	1	0	0	1	1	6	0	1	0	0	0	0
<i>Ptychoptera daimio</i>	-	1	1	1	0	1	1	0	1	3	2	-	0	0	0	1
<i>Ptychoptera espica</i>	-	1	1	1	1	0	0	0	1	0	1	-	1	0	0	0
<i>Ptychoptera formosensis</i>	-	1	1	1	0	2	0	0	1	2	2	-	0	0	1	0
<i>Ptychoptera garhwalensis</i>	-	?	1	1	0	1	1	0	1	?	?	?	?	0	?	?
<i>Ptychoptera gutianshana</i>	-	1	1	1	0	1	0	1	1	0	2	-	0	0	0	0
<i>Ptychoptera handlirschi</i>	-	1	1	1	1	0	0	1	1	2	1	-	0	0	0	0
<i>Ptychoptera helena</i>	-	1	1	1	1	0	0	1	1	0	1	-	0	0	0	0
<i>Ptychoptera hugoi</i>	-	1	1	1	1	0	0	1	1	6	0	1	0	0	0	0
<i>Ptychoptera ichitai</i>	0	1	1	1	1	0	0	1	1	2	1	-	0	0	1	0
<i>Ptychoptera japonica</i>	0	1	1	1	1	0	0	1	1	2	2	-	0	0	1	0
<i>Ptychoptera javensis</i>	-	1	1	1	1	0	0	0	1	2	2	-	0	1	0	0
<i>Ptychoptera lacustris</i>	-	1	1	1	1	0	0	1	1	2	1	-	1	0	0	0
<i>Ptychoptera lacrimiformis</i>	-	1	1	1	0	1	1	0	1	3	2	-	0	0	0	1
<i>Ptychoptera lenis</i>	-	1	1	1	0	1	1	0	1	3	2	-	0	0	0	1
<i>Ptychoptera longicauda</i>	-	1	1	1	1	0	0	1	1	2	1	-	1	0	0	0
<i>Ptychoptera madagascariensis</i>	-	1	1	1	0	2	0	0	1	0	2	-	0	0	0	0
<i>Ptychoptera malaisei</i>	-	?	1	1	0	0	1	0	1	0	2	-	0	0	0	0
<i>Ptychoptera metallica</i>	-	1	1	1	1	0	0	1	1	6	0	1	0	0	0	0
<i>Ptychoptera minor</i>	-	1	1	1	0	1	0	0	1	3	2	-	0	0	0	1
<i>Ptychoptera minuta</i>	-	1	1	1	1	0	0	1	1	6	0	1	0	0	0	0
<i>Ptychoptera monoensis</i>	-	1	1	1	1	0	0	0	1	0	1	-	1	0	0	0
<i>Ptychoptera obscura</i>	-	1	1	1	0	1	1	0	1	3	2	-	0	0	0	1
<i>Ptychoptera osceola</i>	0	1	1	1	1	0	0	1	1	1	1	-	0	0	0	0
<i>Ptychoptera paludosa</i>	-	1	1	1	1	0	0	1	1	1	1	-	0	0	0	0
<i>Ptychoptera pendula</i>	-	1	1	1	1	0	0	0	1	0	1	-	1	0	0	0
<i>Ptychoptera perbona</i>	-	1	1	1	0	0	1	0	1	2	2	-	0	0	0	0
<i>Ptychoptera persimilis</i>	-	?	1	1	0	2	0	0	1	0	2	-	0	0	0	0
<i>Ptychoptera praescutellaris</i>	-	?	1	1	0	2	0	0	1	0	2	-	0	0	0	0
<i>Ptychoptera pseudosimilis</i>	-	1	1	1	0	2	0	0	1	0	2	-	?	0	?	0
<i>Ptychoptera quadrifasciata</i>	0	1	1	1	1	0	0	1	1	0	1	-	0	0	0	0
<i>Ptychoptera resseli</i>	-	1	1	1	1	0	0	1	1	2	1	-	0	0	0	0
<i>Ptychoptera sculleni</i>	-	1	1	1	1	0	0	0	1	0	1	-	0	0	0	0
<i>Ptychoptera sikkimensis</i>	-	1	1	1	0	1	1	0	1	?	?	?	?	0	?	?
<i>Ptychoptera subscutellaris</i>	-	1	1	1	1	0	0	1	1	6	0	1	0	0	0	0
<i>Ptychoptera sumatrensis</i>	-	1	1	1	0	1	0	0	1	0	2	-	0	0	0	0
<i>Ptychoptera tibialis</i>	-	1	1	1	0	1	1	0	1	5	0	0	0	0	0	0
<i>Ptychoptera townesi</i>	-	1	1	1	1	0	0	0	1	0	1	-	1	0	0	0
<i>Ptychoptera uta</i>	-	1	1	1	0	1	1	0	1	3	2	-	0	0	0	1
<i>Ptychoptera yamato</i>	0	1	1	1	1	0	0	1	1	2	2	-	0	0	1	0
<i>Ptychoptera yankovskiana</i>	-	1	1	1	1	0	0	1	1	6	0	1	0	0	0	0
<i>Ptychoptera yasumatsui</i>	-	1	1	1	1	0	0	0	1	0	2	-	0	0	0	0

Table I.
Sympatric Associations of
***Ptychoptera* in the Nearctic**

<i>P. (Chrysoptycha)</i>	<i>P. (Rheoptycha)</i>	<i>P. (Tigrimya)</i>	<i>P. (Unguptycha)</i>
<i>P. (C.) sculleni</i>	<i>P. (R.) espica</i>	<i>P. (T.) abbreviata</i>	<i>P. (U.) byersi</i>
<i>P. (R.) espica</i>	<i>P. (C.) sculleni</i>	<i>P. (Pt.) metallica</i>	<i>B. occidentalis*</i>
<i>P. (R.) pendula</i>	<i>P. (U.) lacrimiformis</i>	<i>P. (U.) coloradensis</i>	
<i>P. (R.) townesi</i>	<i>Bl. fenderiana</i>	<i>B. clavipes*</i>	<i>P. (U.) coloradensis</i>
<i>P. (U.) lacrimiformis*</i>			<i>P. (R.) pendula</i>
<i>B. occidentalis</i>	<i>P. (R.) pendula</i>	<i>P. (T.) quadrifasciata</i>	<i>P. (T.) abbreviata</i>
<i>Bl. fenderiana</i>	<i>P. (C.) sculleni</i>	<i>B. clavipes*</i>	<i>B. clavipes*</i>
	<i>P. (R.) townesi*</i>	<i>Bl. jonesi</i>	
<i>P. (Ptychoptera)</i>	<i>P. (U.) coloradensis</i>		<i>P. (U.) lacrimiformis</i>
<i>P. (Pt.) metallica</i>	<i>P. (U.) lacrimiformis</i>		<i>P. (C.) sculleni*</i>
<i>P. (T.) abbreviata</i>			<i>P. (R.) townesi</i>
<i>B. clavipes</i>	<i>P. (R.) townesi</i>		
	<i>P. (R.) pendula*</i>		
	<i>P. (U.) lacrimiformis</i>		
	<i>B. occidentalis</i>		
	<i>Bl. fenderiana</i>		

*Collected in direct association.

Figure Abbreviations

AEA: Ejaculatory Apodeme, AES: Aedeagal Sclerite, AEV: Ventral Apical Apodeme of Aedeagus, ALP: Lateral Ejaculatory Process AS: Sperm Sac, ASA, Subapical Sclerite of Aedeagus, ASP: Lateral Plate of Subapical Sclerite, AVA: Ventral Arm of Subapical Sclerite, CRC: Cercus, ECA: Epandrial Apodeme, ECB: Epandrial clasper basal lobe, ECL: Epandrial Collar, ECP: Epandrial Clasper, ECV: Epandrial Clasper Ventral Lobe, EL: Epandrial Lobe, EMS: Epandrial Clasper medial swelling, EPI: Epiproct, EPG: Epigynium, EPP: Epandrial Plate, EPS: Posteromedial Stylus of Epandrium, ESS, Subapical Spine of Epandrium, EVL: Ventromesal Lobe of Epandrium, GAS: Apical stylus of gonostylus, GAT: Tertiary lobe of Apical Stylus of Gonostylus, GBA: Anterior lobe of basal lobe of gonostylus, GBL: Basal lobe of gonostylus, GBM: Medial lobe of basal lobe of gonostylus, GBP: Posterior lobe of basal lobe of gonostylus, GCT: Gonocoxite, GCA: Gonocoxal Apodeme, GDS: Dorsal spur of gonocoxal apodeme, GLD: Dorsal Gonocoxal Lobe, GLM: Medial Gonocoxal Lobe, GLV: Ventral Gonocoxal Lobe, GSL: Secondary lobe of Apical Stylus of Gonostylus, GFK: Genital Fork, GST: Gonostylus, HBD: Basal Division of Hypandrium, HBS: Basal scale of Hypandrium HES: Eversible sac of Hypandrium, HLT: Lateral lobule of terminal division, HMW: Membranous Window of Terminal Division, HPG: Hypogynium, HSL: Spathate Lobe of Hypandrium, HTD: Terminal Division of Hypandrium, HTE: Lateral Extension of Terminal Division, HVL: Hypogynial Valves, HYP: Hypoproct, PMB: Paramere Base, PME: Posteromedial Extension of Paramere, PPA: Apical Process of Paramere

Figure Captions

Figure 1. Bayesian phylogeny of the Nearctic Ptychopterinae based on the COI and TUFT genes, posterior probabilities below branches.

Figure 2. Maximum parsimony morphological phylogeny of Ptychopterinae, Bremer support above branches, bootstrap support below.

Figure 3. Bayesian inference morphological phylogeny of Ptychopterinae, posterior probabilities below branches.

Figure 4. Thoracic sclerites of *Ptychoptera (Unguipitycha) coloradensis*.

Figure 5. *Ptychoptera (Ptychoptera) contaminata* Linnaeus, 1758 male genitalia: a. overall, lateral view; b. epandrium, lateral view; c. epandrium, dorsal view; d. aedeagus, anterior view; e. aedeagus, lateral view; f. hypandrium, posterior view; h. gonopod, dorsal view; i. gonopod, lateral view; j. paramere, posterior view; k. paramere, dorsal view.

Figure 6. *P. (Ptychoptera) contaminata*, wing.

Figure 7. *P. (Ptychoptera) contaminata*, distribution of material examined.

Figure 8. *Ptychoptera (Ptychoptera) hugoi* Tjeder, 1968 male genitalia: a. overall, lateral view; b. epandrium, lateral view; c. epandrium, dorsal view; d. aedeagus, anterior view; e. aedeagus, lateral

view; f. hypandrium, posterior view; h. gonopod, lateral view; i. gonopod, dorsal view; j. paramere, posterior view; k. paramere, dorsal view.

Figure 9. *P. (Ptychoptera) hugoi*, wing.

Figure 10. *P. (Ptychoptera) hugoi*, distribution of material examined.

Figure 11. *Ptychoptera (Ptychoptera) metallica* Walker, 1848 male genitalia: a. overall, lateral view; b. epandrium, lateral view; c. epandrium, dorsal view; d. aedeagus, anterior view; e. aedeagus, lateral view; f. hypandrium, posterior view; h. gonopod, lateral view; i. gonopod, dorsal view; j. paramere, posterior view; k. paramere, dorsal view.

Figure 12. *P. (Ptychoptera) metallica*, wing.

Figure 13. *P. (Ptychoptera) metallica*, distribution of material examined.

Figure 14. *Ptychoptera (Ptychoptera) minuta* Tonnoir, 1919 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, dorsal view.

Figure 15. *P. (Ptychoptera) minuta*, wing.

Figure 16. *P. (Ptychoptera) minuta*, distribution of material examined.

Figure 17. *Ptychoptera (Ptychoptera) scutellaris* Wiedemann, 1818, wing.

Figure 18. *P. (Ptychoptera) scutellaris*, distribution of material examined.

Figure 19. *Ptychoptera (Ptychoptera) subscutellaris* Alexander, 1921 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, dorsal view.

Figure 20. *P. (Ptychoptera) subscutellaris*, wing.

Figure 21. *P. (Ptychoptera) subscutellaris*, distribution of material examined.

Figure 22. *Ptychoptera (Ptychoptera) yankovskiana* Alexander, 1945 male genitalia: a. overall, lateral view; b. epandrium, lateral view; b. epandrium, dorsal view; d. aedeagus, anterior view; e. aedeagus, lateral view; f. hypandrium, posterior view; g. gonopod, lateral view; h. gonopod, dorsal view; i. paramere, dorsal view; j. paramere, posterior view.

Figure 23. *P. (Ptychoptera) yankovskiana*, wing.

Figure 24. *P. (Ptychoptera) yankovskiana*, distribution of material examined.

Figure 25. *Ptychoptera (Amblyptycha) garhwalensis* Alexander, 1959 male genitalia: a. epandrium, dorsal view; b. gonopod, dorsal view; c. paramere, dorsal view; d. detail of apical lobe of paramere.

Figure 26. *P. (Amblyptycha) garhwalensis*, wing.

Figure 27. *P. (Amblyptycha) garhwalensis*, distribution of material examined.

Figure 28. *Ptychoptera (Amblyptycha) sikkimensis* Alexander, 1965 male genitalia: a. epandrium, dorsal view; b. gonopod, dorsal view; c. paramere, dorsal view.

Figure 29. *P. (Amblyptycha) sikkimensis*, wing.

Figure 30. *P. (Amblyptycha) sikkimensis*, distribution of material examined.

Figure 31. *Ptychoptera (Amblyptycha) tibialis* Brunetti, 1911 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, dorsal view; i. paramere, posterior view.

Figure 32. *P. (Amblyptycha) tibialis*, wing.

Figure 33. *P. (Amblyptycha) tibialis*, distribution of material examined.

Figure 34. *Ptychoptera (Chrysoptycha) sculleni* Alexander, 1943 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, dorsal view; g. gonopod, lateral view; h. paramere, dorsal view.

Figure 35. *P. (Chrysoptycha) sculleni*, wing.

Figure 36. *P. (Chrysoptycha) sculleni*, distribution of material examined.

Figure 37. *Ptychoptera (Paraptychoptera) handlirschi* Cizek, 1919 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, dorsal view.

Figure 38. *P. (Paraptychoptera) handlirschi*, wing.

Figure 39. *P. (Paraptychoptera) handlirschi*, distribution of material examined.

Figure 40. *Ptychoptera (Paraptychoptera) helena* Peus, 1958 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, dorsal view.

Figure 41. *P. (Paraptychoptera) helena*, wing.

Figure 42. *P. (Paraptychoptera) helena*, distribution of material examined.

Figure 43. *Ptychoptera (Paraptychoptera) lacustris* Meigen, 1830 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, dorsal view.

Figure 44. *P. (Parapychoptera) lacustris*, wing.

Figure 45. *P. (Parapychoptera) lacustris*, distribution of material examined.

Figure 46. *Ptychoptera (Parapychoptera) longicauda* Tonnoir, 1830 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, dorsal view.

Figure 47. *P. (Parapychoptera) longicauda*, wing.

Figure 48. *P. (Parapychoptera) longicauda*, distribution of material examined.

Figure 49. *Ptychoptera (Parapychoptera) paludosa* Meigen, 1804 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, dorsal view.

Figure 50. *P. (Parapychoptera) paludosa*, wing.

Figure 51. *P. (Parapychoptera) paludosa*, distribution of material examined.

Figure 52. *Ptychoptera (Parapychoptera) resli* Theischinger, 1978 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, dorsal view.

Figure 53. *P. (Parapychoptera) resli*, distribution of material examined.

Figure 54. *Ptychoptera (Parapychoptera) silvicola*, Zwyrtek & Rozkosny, 1967 wing.

Figure 55. *P. (Parapychoptera) silvicola*, distribution of material examined.

Figure 56. *Ptychoptera (Rheoptycha) espica* Fasbender & Courtney, male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, posterior view.

Figure 57. *P. (Rheoptycha) espica*, wing.

Figure 58. *P. (Rheoptycha) espica*, distribution of material examined.

Figure 59. *Ptychoptera (Rheoptycha) monoensis* Alexander, 1947 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, posterior view.

Figure 60. *P. (Rheoptycha) monoensis*, wing.

Figure 61. *P. (Rheoptycha) monoensis*, distribution of material examined.

Figure 62. *Ptychoptera (Rheoptycha) pendula* Alexander, 1937 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, dorsal view.

Figure 63. *P. (Rheoptycha) pendula*, wing.

Figure 64. *P. (Rheoptycha) pendula*, distribution of material examined.

Figure 65. *Ptychoptera (Rheoptycha) townesi* Alexander, 1943 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, posterior view.

Figure 66. *P. (Rheoptycha) townesi*, wing.

Figure 67. *P. (Rheoptycha) townesi*, distribution of material examined.

Figure 68. *Ptychoptera (Tigrimya) abbreviata* Fasbender & Courtney, male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. epandrium, alternate form, dorsal view; d. aedeagus, anterior view; e. aedeagus, lateral view; f. hypandrium, posterior view; g. gonopod, lateral view; h. gonopod, dorsal view; i. lateral plate, posterior view; j. paramere, posterior view; k. paramere, dorsal view.

Figure 69. *P. (Tigrimya) abbreviata*, wing.

Figure 70. *P. (Tigrimya) abbreviata*, distribution of material examined.

Figure 71. *Ptychoptera (Tigrimya) osceola* Alexander, 1959 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, dorsal view.

Figure 72. *P. (Tigrimya) osceola*, wing.

Figure 73. *P. (Tigrimya) osceola*, distribution of material examined.

Figure 74. *Ptychoptera (Tigrimya) quadrifasciata* Say, 1824 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, dorsal view; i. paramere, posterior view.

Figure 75. *P. (Tigrimya) quadrifasciata*, wing.

Figure 76. *P. (Tigrimya) quadrifasciata*, distribution of material examined.

Figure 77. *Ptychoptera (Unguptycha) bilobata* Copley & Canning, male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, lateral view; d. aedeagus, dorsal view; e. gonopods and parameres, dorsal view; f. hypandrium, posterior view; g. hypandrium, lateral view; h. gonopod, lateral view.

Figure 78. *P. (Unguptycha) bilobata*, wing.

Figure 79. *P. (Unguptycha) bilobata*, distribution of material examined.

Figure 80. *Ptychoptera (Unguptycha) byersi* Alexander, 1966 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod & paramere, dorsal view; h. paramere, dorsal view.

Figure 81. *P. (Unguptycha) byersi*, wing.

Figure 82. *P. (Unguptycha) byersi*, distribution of material examined.

Figure 83. *Ptychoptera (Unguptycha) coloradensis* Alexander, 1937 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, dorsal view.

Figure 84. *P. (Unguptycha) coloradensis*, wing.

Figure 85. *P. (Unguptycha) coloradensis*, distribution of material examined.

Figure 86. *Ptychoptera (Unguptycha) daimio* Alexander, 1921 male genitalia: a. epandrium, dorsal view; b. aedeagus, anterior view; c. aedeagus, lateral view; d. hypandrium, posterior view; e. gonopod, lateral view; f. gonopod, dorsal view; g. paramere, dorsal view.

Figure 87. *P. (Unguptycha) daimio*, wing.

Figure 88. *P. (Unguptycha) daimio*, distribution of material examined.

Figure 89. *Ptychoptera (Unguptycha) lacrimiformis* Fasbender & Courtney, male genitalia: a. overall, lateral view; b. ventromesal lobe, medial view; c. epandrium, dorsal view; d. aedeagus, anterior view; e. aedeagus, lateral view; f. hypandrium, posterior view; g. gonopod, lateral view; h. gonopod, dorsal view; i. paramere, dorsal view; j. paramere, lateral view.

Figure 90. *P. (Unguptycha) lacrimiformis*, wing.

Figure 91. *P. (Unguptycha) lacrimiformis*, distribution of material examined.

Figure 92. *Ptychoptera (Unguptycha) lenis* Osten Sacken, 1877 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod & paramere, dorsal view.

Figure 93. *P. (Unguptycha) lenis*, wing.

Figure 94. *P. (Unguptycha) lenis*, distribution of material examined.

Figure 95. *Ptychoptera (Unguptycha) minor* Alexander, 1920 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. ventromesal lobe, medial view; d. aedeagus, anterior view; e. aedeagus,

lateral view; f. hypandrium, posterior view; g. gonopod, lateral view; h. gonopod, dorsal view; i. paramere, dorsal view; j. paramere, lateral view.

Figure 96. *P. (Unguptycha) minor*, wing.

Figure 97. *P. (Unguptycha) minor*, distribution of material examined.

Figure 98. *Ptychoptera (Unguptycha) obscura* Peus, 1958 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, dorsal view; i. paramere apex, alternate form, dorsal view.

Figure 99. *P. (Unguptycha) obscura*, wing.

Figure 100. *P. (Unguptycha) obscura*, distribution of material examined.

Figure 101. *Ptychoptera (Unguptycha) uta* Alexander, 1947 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. gonopod, dorsal view; d. paramere, dorsal view.

Figure 102. *P. (Unguptycha) uta*, wing.

Figure 103. *P. (Unguptycha) uta*, distribution of material examined.

Figure 104. *Ptychoptera* (incertae sedis) *albimana* Fabricius, 1781 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, dorsal view; i. paramere posterior.

Figure 105. *P. albimana*, wing.

Figure 106. *P. albimana*, distribution of material examined.

Figure 107. *Ptychoptera* (incertae sedis) *alina* Krzeminski & Zwick, 1993 male genitalia: a. overall, lateral view; b. epandrium, dorsal view.

Figure 108. *P. alina*, wing.

Figure 109. *P. alina*, distribution of material examined.

Figure 110. *Ptychoptera* (incertae sedis) *alexanderi* Hancock, 2006 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, dorsal view; i. paramere posterior.

Figure 111. *P. alexanderi*, wing.

Figure 112. *P. alexanderi*, distribution of material examined.

Figure 113. *Ptychoptera* (incertae sedis) *ichitai* Nakamura & Saigusa, 2009 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, dorsal view.

Figure 114. *P. ichitai*, wing.

Figure 115. *Ptychoptera* (incertae sedis) *japonica* Alexander, 1913 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, dorsal view.

Figure 116. *P. japonica*, distribution of material examined.

Figure 117. *Ptychoptera* (incertae sedis) *yamato* Nakamura & Saigusa, 2009 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, dorsal view.

Figure 118. *P. yamato*, wing.

Figure 119. *P. yamato*, distribution of material examined.

Figure 120. *Ptychoptera* (incertae sedis) *africana* Alexander, 1920 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, dorsal view; i. paramere, posterior view.

Figure 121. *P. africana*, wing.

Figure 122. *P. africana*, distribution of material examined.

Figure 123. *Ptychoptera* (incertae sedis) *camerounensis* Alexander, 1921 male genitalia: a. overall, lateral view; b. overall, dorsal view.

Figure 124. *P. camerounensis*, wing.

Figure 125. *P. camerounensis*, distribution of material examined.

Figure 126. *Ptychoptera* (incertae sedis) *capensis* Alexander, 1917 male genitalia: a. epandrium, dorsal view; b. gonopod, lateral view; c. paramere, dorsal view.

Figure 127. *P. capensis*, wing.

Figure 128. *P. capensis*, distribution of material examined.

Figure 129. *Ptychoptera* (incertae sedis) *madagascariensis* Alexander, 1937 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, posterior view.

Figure 130. *P. madagascariensis*, distribution of material examined.

Figure 131. *Ptychoptera* (incertae sedis) *matongoensis* Alexander, 1958 wing.

Figure 132. *P. matongoensis*, distribution of material examined.

Figure 133. *Ptychoptera* (incertae sedis) *pauliani* Alexander, 1957 gonopod, lateral view.

Figure 134. *P. pauliani*, distribution of material examined.

Figure 135. *Ptychoptera* (incertae sedis) *stuckenbergi* Alexander, 1956 wing.

Figure 136. *P. stuckenbergi*, distribution of material examined.

Figure 137. *Ptychoptera* (incertae sedis) *uelensis* Alexander, 1928 wing (*Ptychoptera basilewskyi* holotype).

Figure 138. *P. uelensis*, distribution of material examined.

Figure 139. *Ptychoptera* (incertae sedis) *annandalei* Brunetti, 1918 male genitalia: a. epandrium, dorsal view; b. gonopod, lateral view; c. paramere, dorsal view.

Figure 140. *P. annandalei*, wing.

Figure 141. *P. annandalei*, distribution of material examined.

Figure 142. *Ptychoptera* (incertae sedis) *bellula* Alexander, 1937 male genitalia: a. epandrium, dorsal view; b. gonopod, lateral view; c. gonopod, dorsal view; d. aedeagus, lateral view; e. aedeagus; anterior view.

Figure 143. *P. bellula*, wing.

Figure 144. *P. bellula*, distribution of material examined.

Figure 145. *Ptychoptera* (incertae sedis) *chalybeata* Alexander, 1956 male genitalia: a. epandrium, dorsal view; b. gonopod, lateral view; c. paramere, dorsal view.

Figure 146. *P. chalybeata*, wing.

Figure 147. *P. chalybeata*, distribution of material examined.

Figure 148. *Ptychoptera* (incertae sedis) *clitellaria* Alexander, 1935 wing.

Figure 149. *P. clitellaria*, distribution of material examined.

Figure 150. *Ptychoptera* (incertae sedis) *distincta* Brunetti, 1911 wing.

Figure 151. *P. distincta*, distribution of material examined.

Figure 152. *Ptychoptera* (incertae sedis) *formosensis* Alexander, 1924 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, posterior view.

Figure 153. *P. formosensis*, wing.

Figure 154. *P. formosensis*, distribution of material examined.

Figure 155. *Ptychoptera* (incertae sedis) *gutianshana* Yang & Chen, 1995 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, posterior view.

Figure 156. *P. gutianshana*, wing.

Figure 157. *P. gutianshana*, distribution of material examined.

Figure 158. *Ptychoptera* (incertae sedis) *javensis* Alexander, 1937 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view.

Figure 159. *P. javensis*, wing.

Figure 160. *P. javensis*, distribution of material examined.

Figure 161. *Ptychoptera* (incertae sedis) *malaisei* Alexander, 1946 male genitalia: a. epandrium, dorsal view; b. gonopod, lateral view; c. paramere, dorsal view.

Figure 162. *P. malaisei*, wing.

Figure 163. *P. malaisei*, distribution of material examined.

Figure 164. *Ptychoptera* (incertae sedis) *perbona* Alexander, 1946 male genitalia: a. epandrium, dorsal view; b. gonopod, lateral view; c. paramere, dorsal view.

Figure 165. *P. perbona*, wing.

Figure 166. *P. perbona*, distribution of material examined.

Figure 167. *Ptychoptera* (incertae sedis) *persimilis* Alexander, 1947 male genitalia: a. epandrium, dorsal view; b. gonopod, lateral view; c. gonostylus, dorsal view d. paramere, posterior view.

Figure 168. *P. persimilis*, wing.

Figure 169. *P. persimilis*, distribution of material examined.

Figure 170. *Ptychoptera* (incertae sedis) *praescutellaris* Alexander, 1946 male genitalia: a. epandrium, dorsal view; b. gonopod, lateral view; c. paramere, posterior view.

Figure 171. *P. praescutellaris*, wing.

Figure 172. *P. praescutellaris*, distribution of material examined.

Figure 173. *Ptychoptera* (incertae sedis) *pseudosimilis* Fasbender, male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. gonopod, lateral view; d. gonostylus, dorsal view e. paramere, dorsal view.

Figure 174. *P. pseudosimilis*, wing.

Figure 175. *P. pseudosimilis*, distribution of material examined.

Figure 176. *Ptychoptera* (incertae sedis) *sumatrensis* Alexander, 1936 male genitalia: a. epandrial lobe, dorsal view; b. gonopod, lateral view; c. paramere, dorsal view.

Figure 177. *P. sumatrensis*, wing.

Figure 178. *P. sumatrensis*, distribution of material examined.

Figure 179. *Ptychoptera* (incertae sedis) *yasumatsui* Tokunaga, 1939 male genitalia: a. overall, lateral view; b. epandrium, dorsal view; c. aedeagus, anterior view; d. aedeagus, lateral view; e. hypandrium, posterior view; f. gonopod, lateral view; g. gonopod, dorsal view; h. paramere, dorsal view.

Figure 180. *P. yasumatsui*, wing.

Figure 181. *P. yasumatsui*, distribution of material examined.

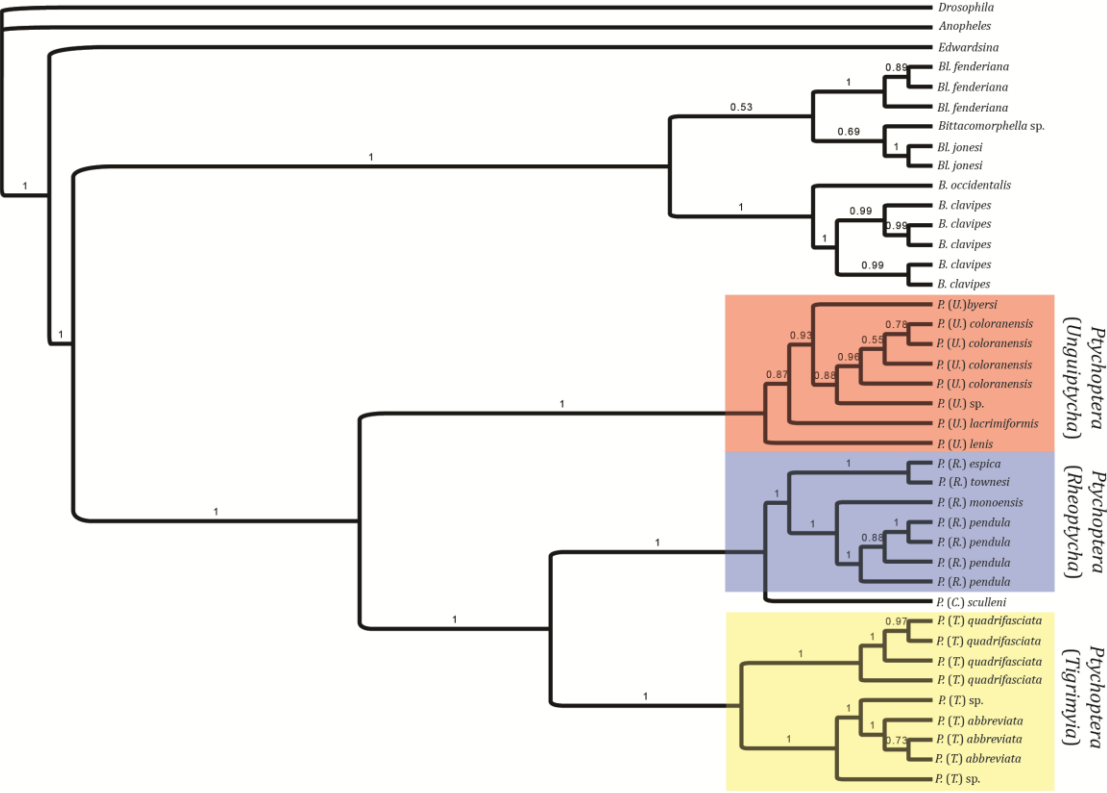


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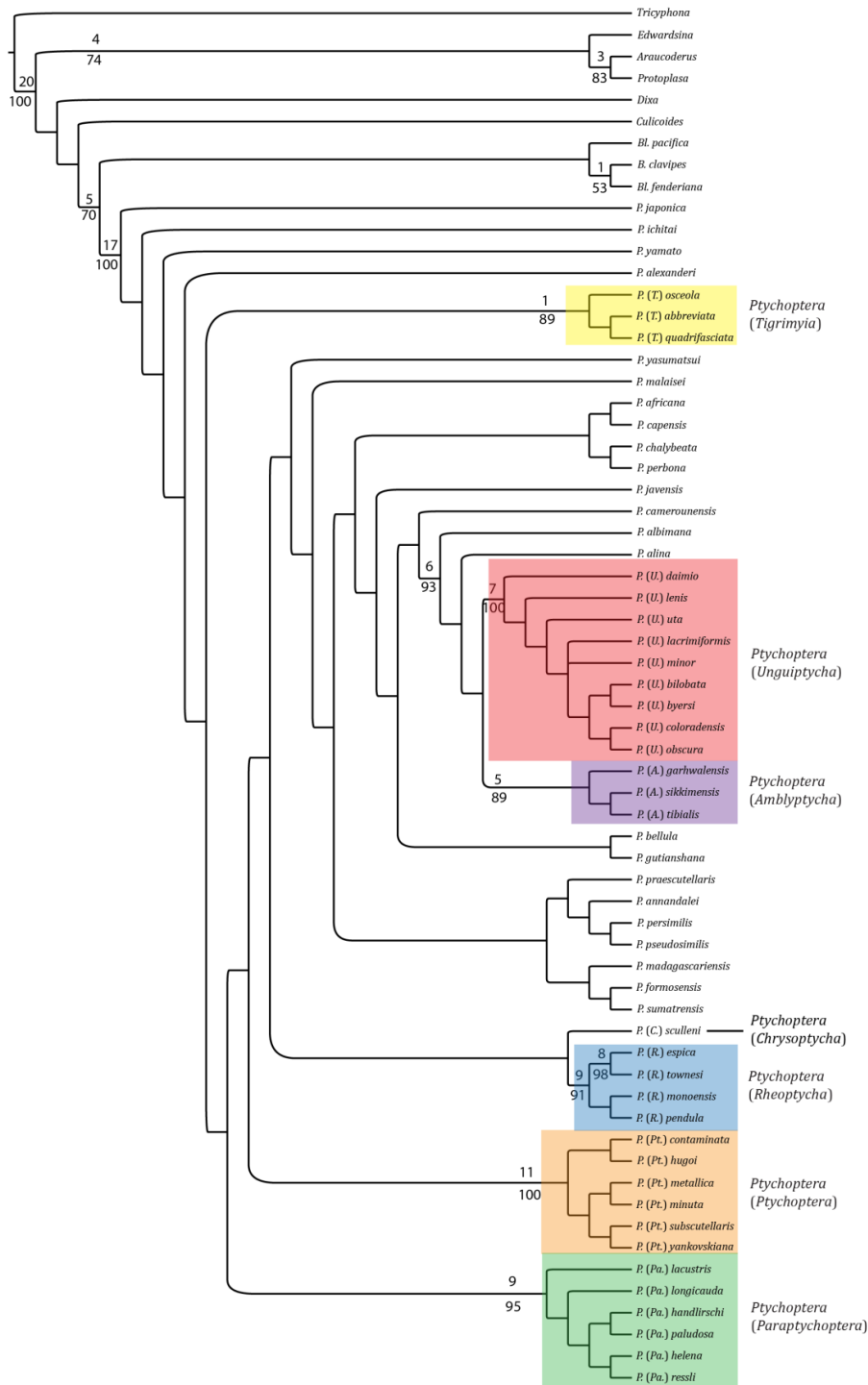


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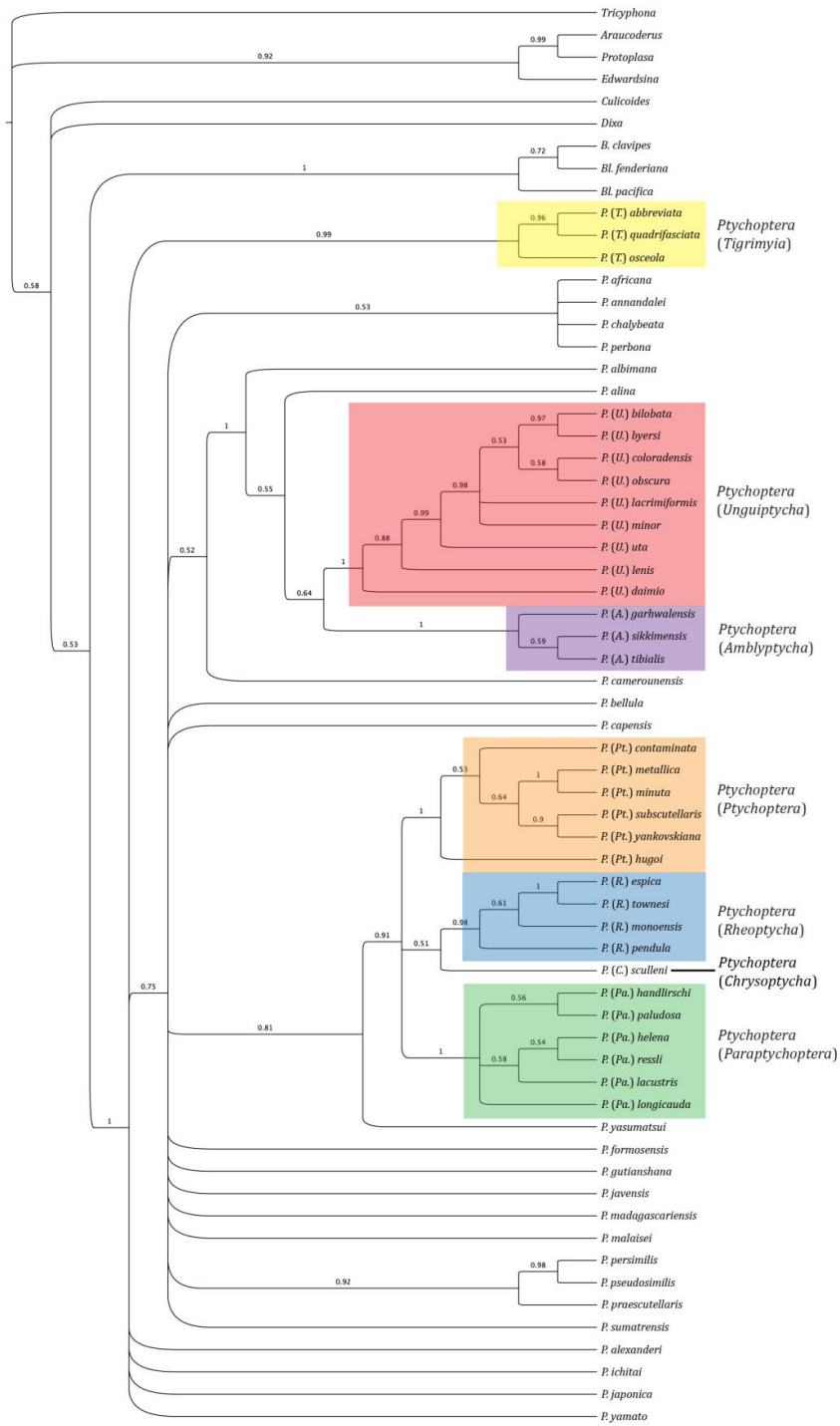


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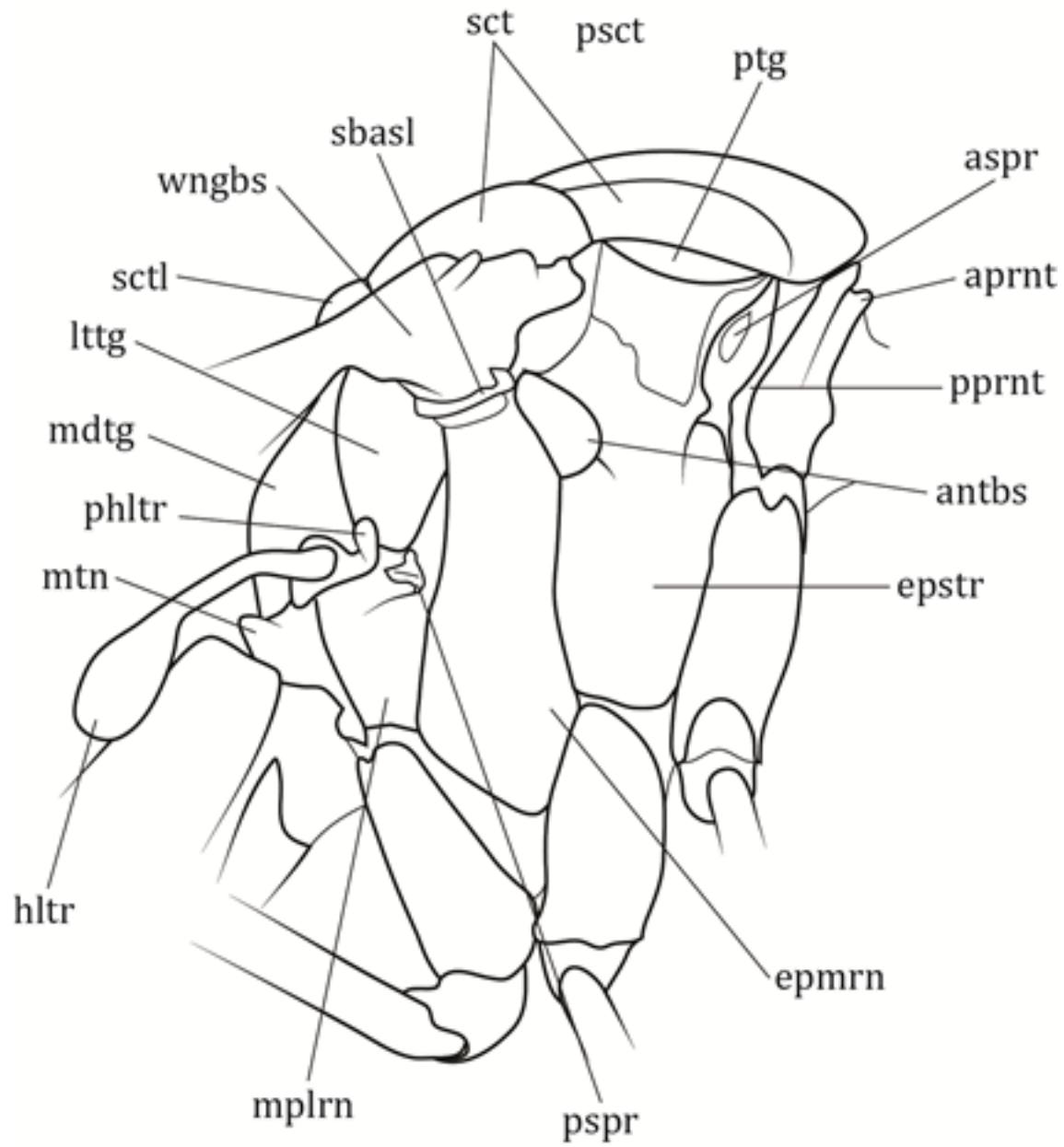


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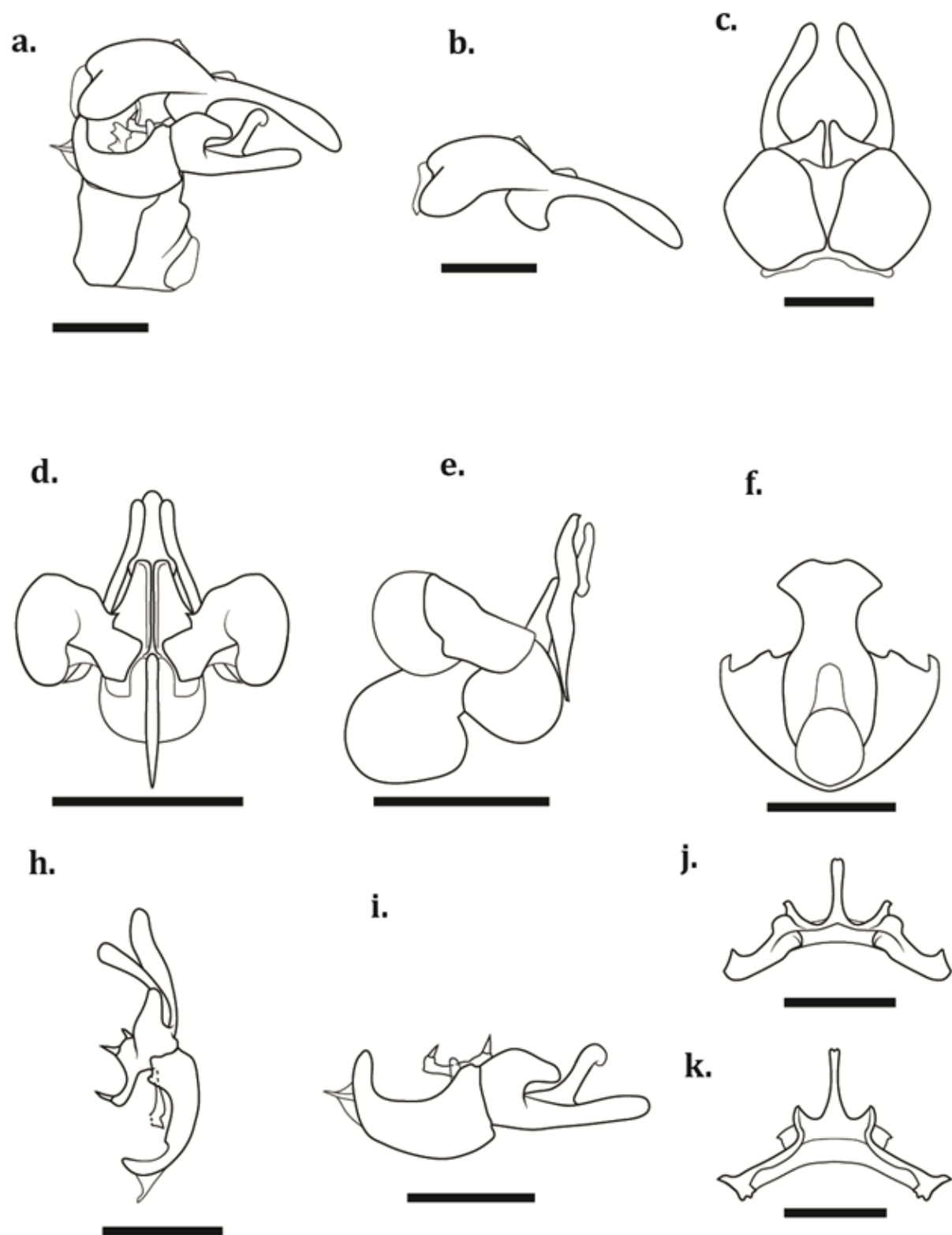


Figure 5.



Figure 6.



Figure 7.

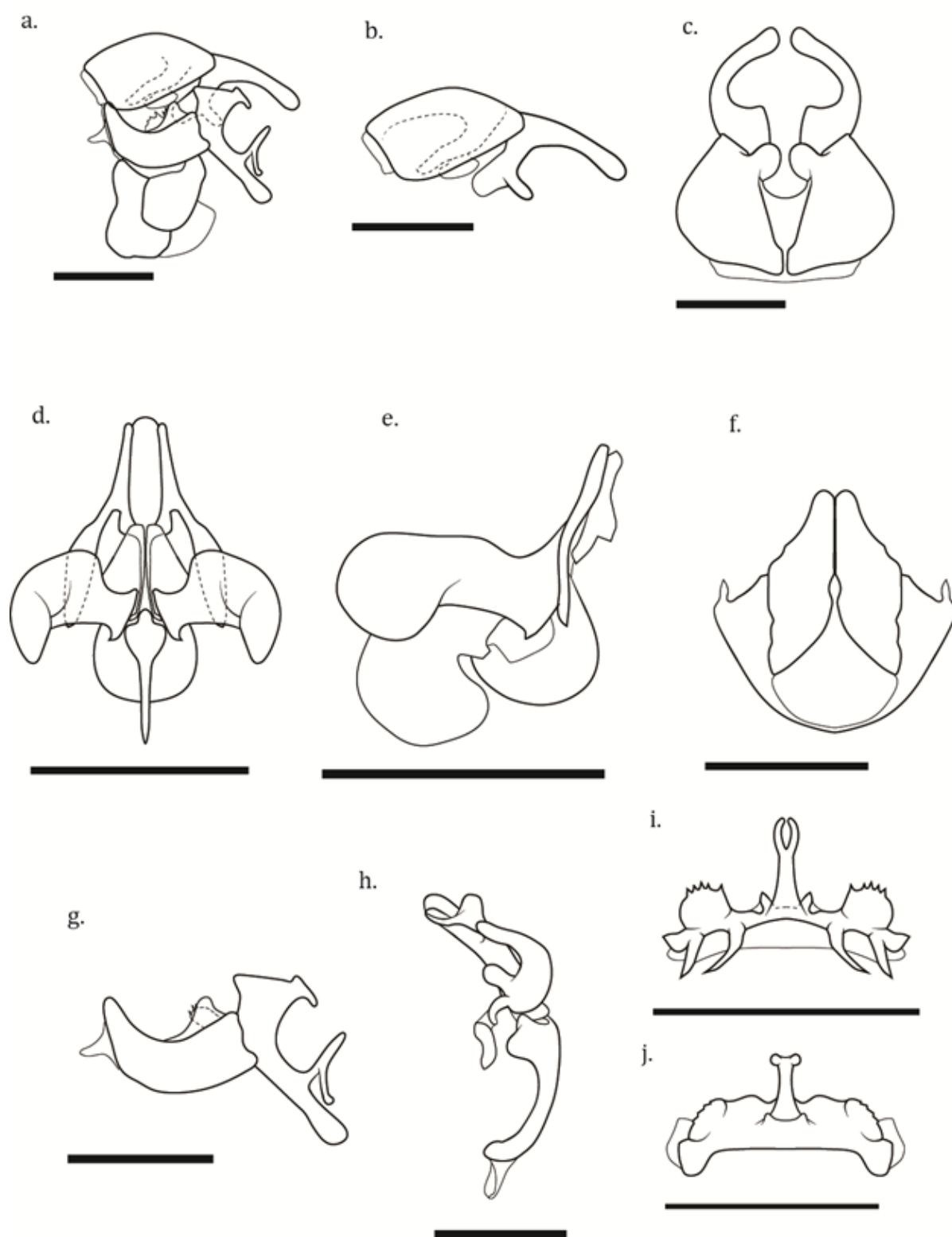
**Figure 8.**



Figure 9.



Figure 10.

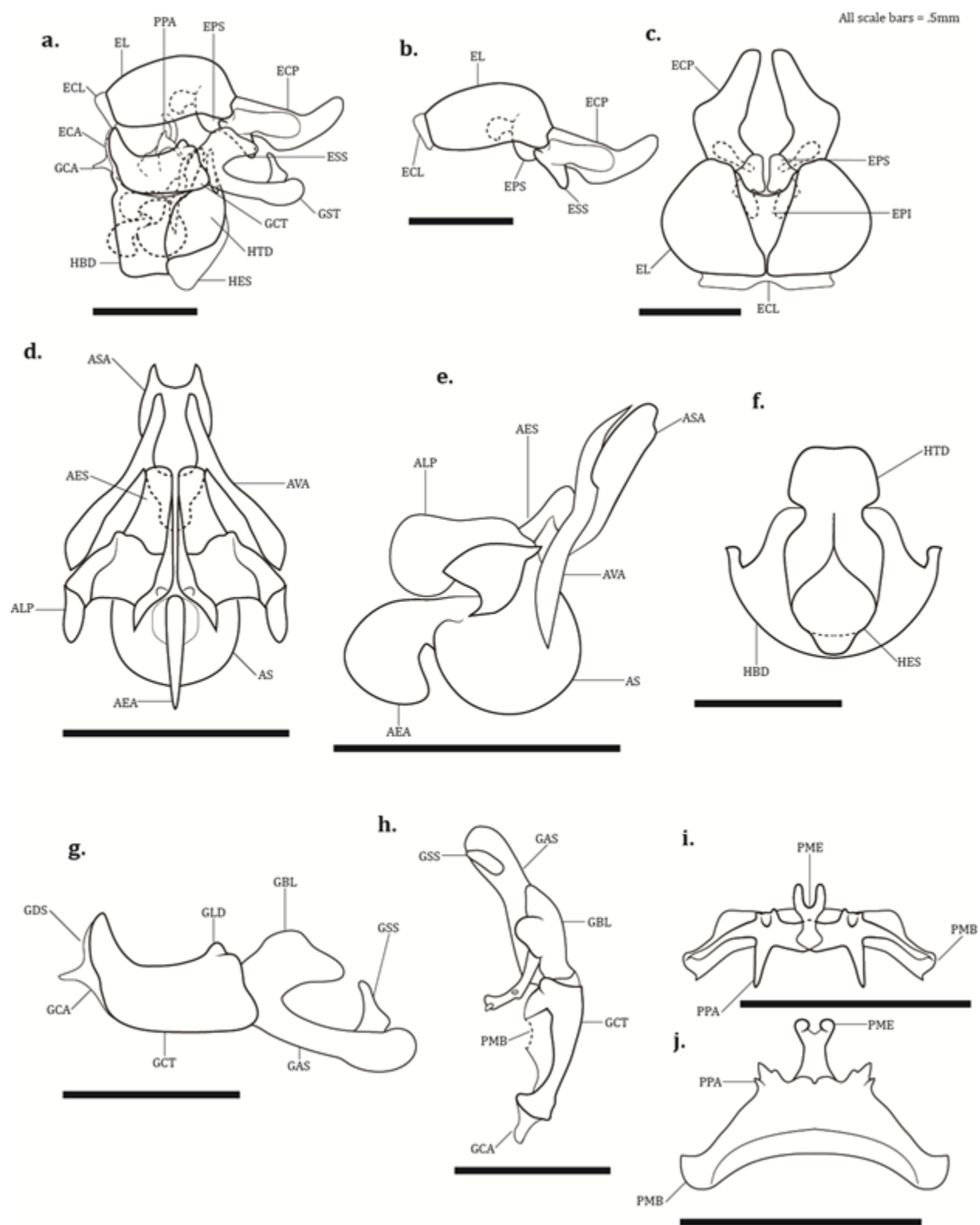


Figure 11.



Figure 12.



Figure 13.

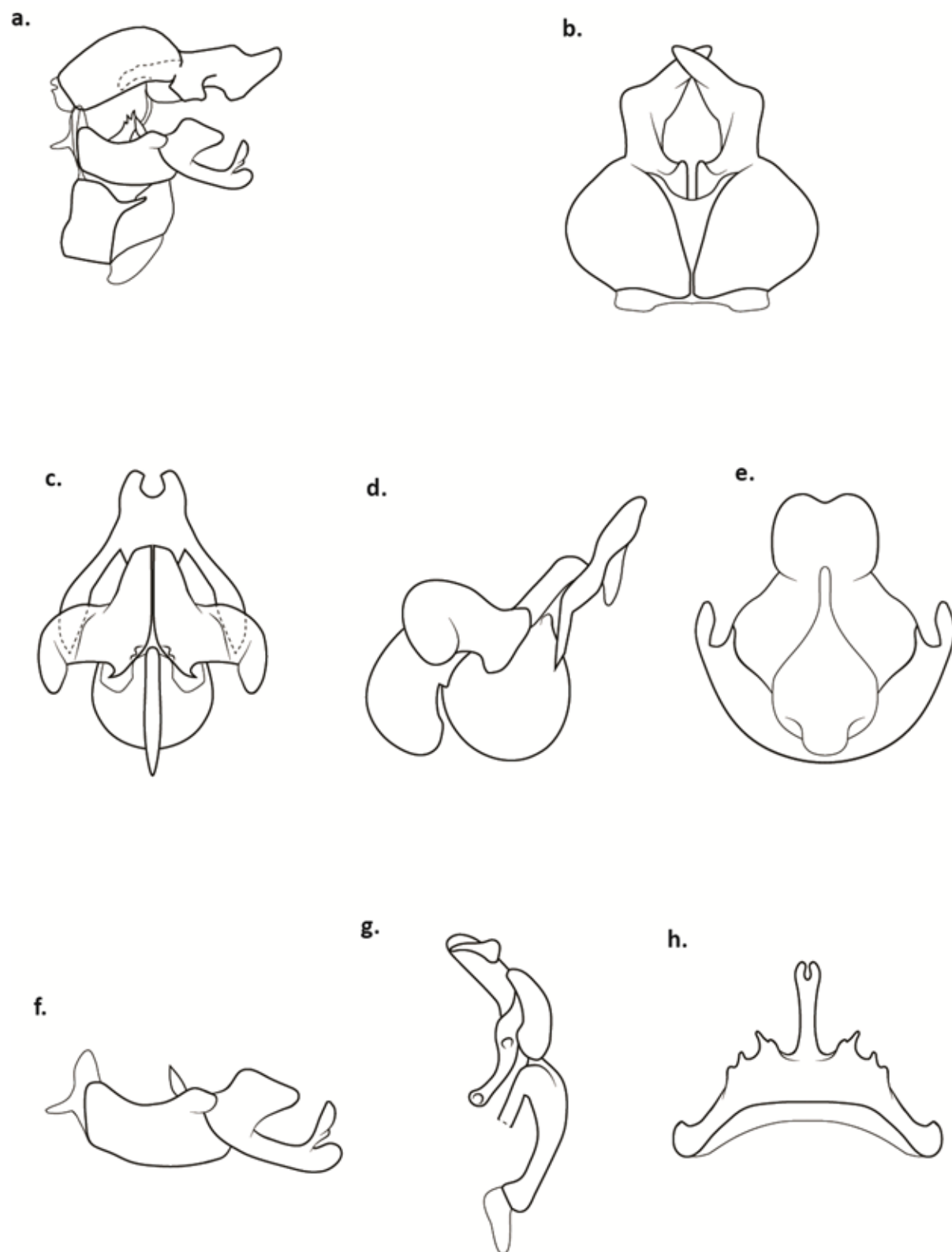


Figure 14.



Figure 15.



Figure 16.

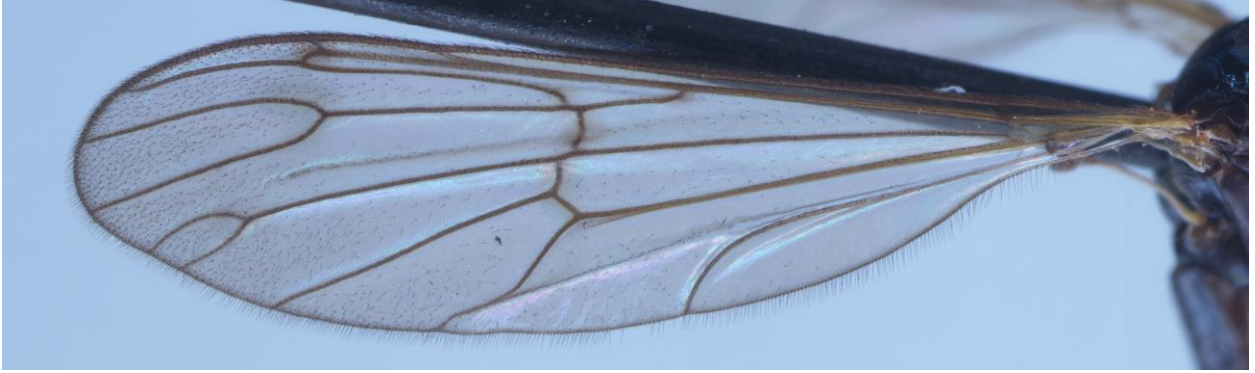


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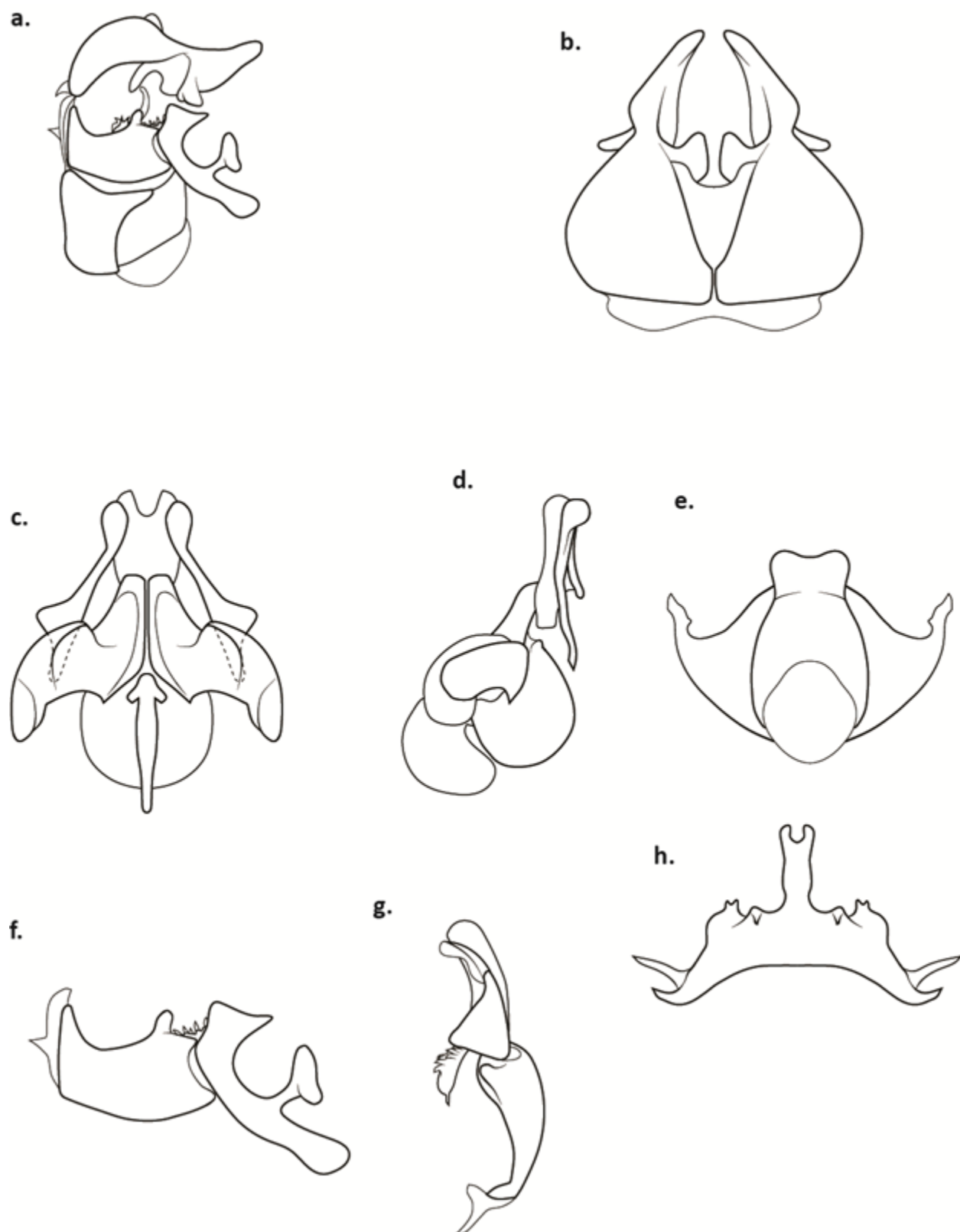


Figure 19.



Figure 20.



Figure 21.

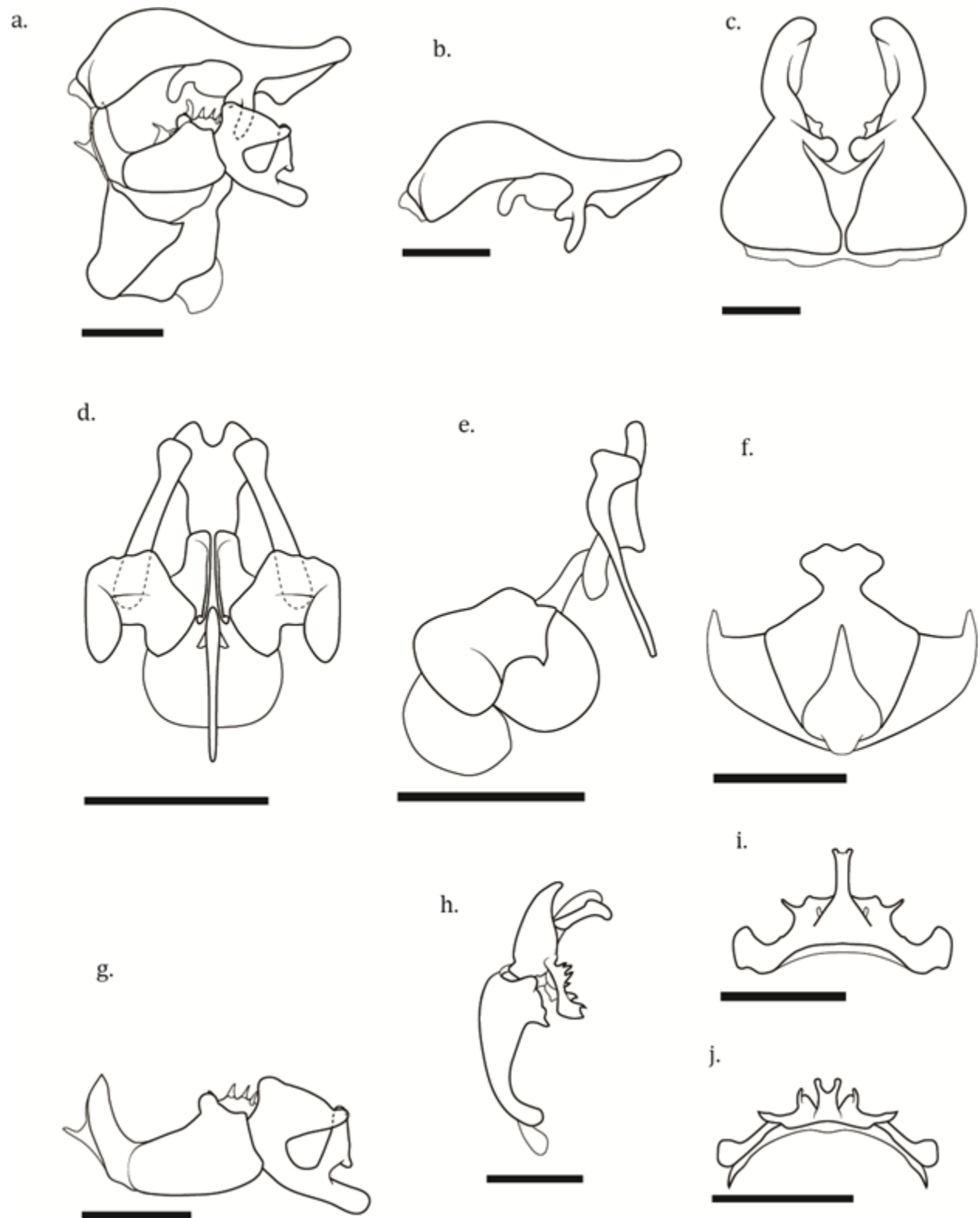


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Figure 23.



Figure 24.

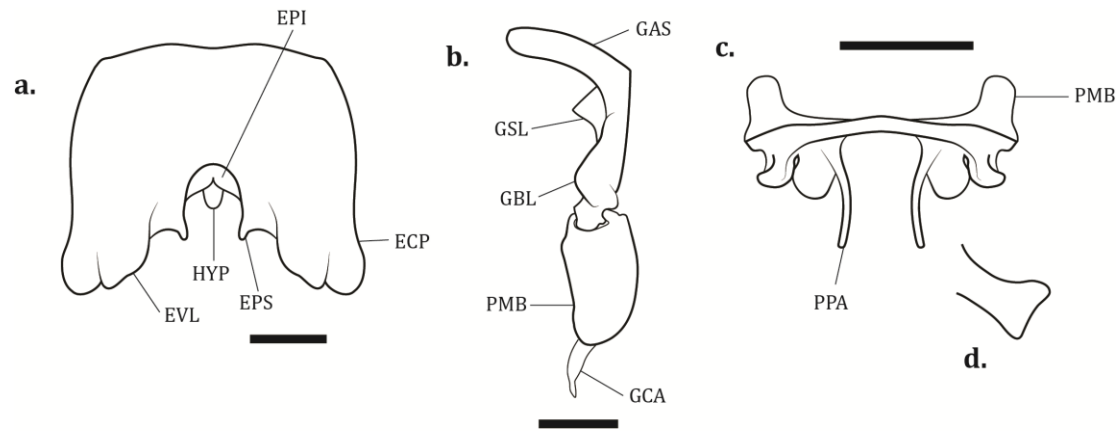


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Figure 26.



Figure 27.

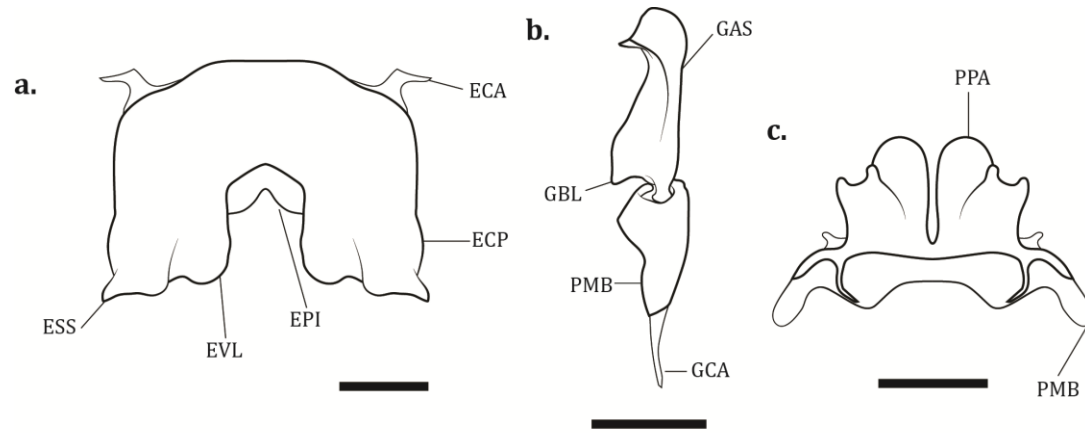


Figure 28.



Figure 29.



Figure 30.

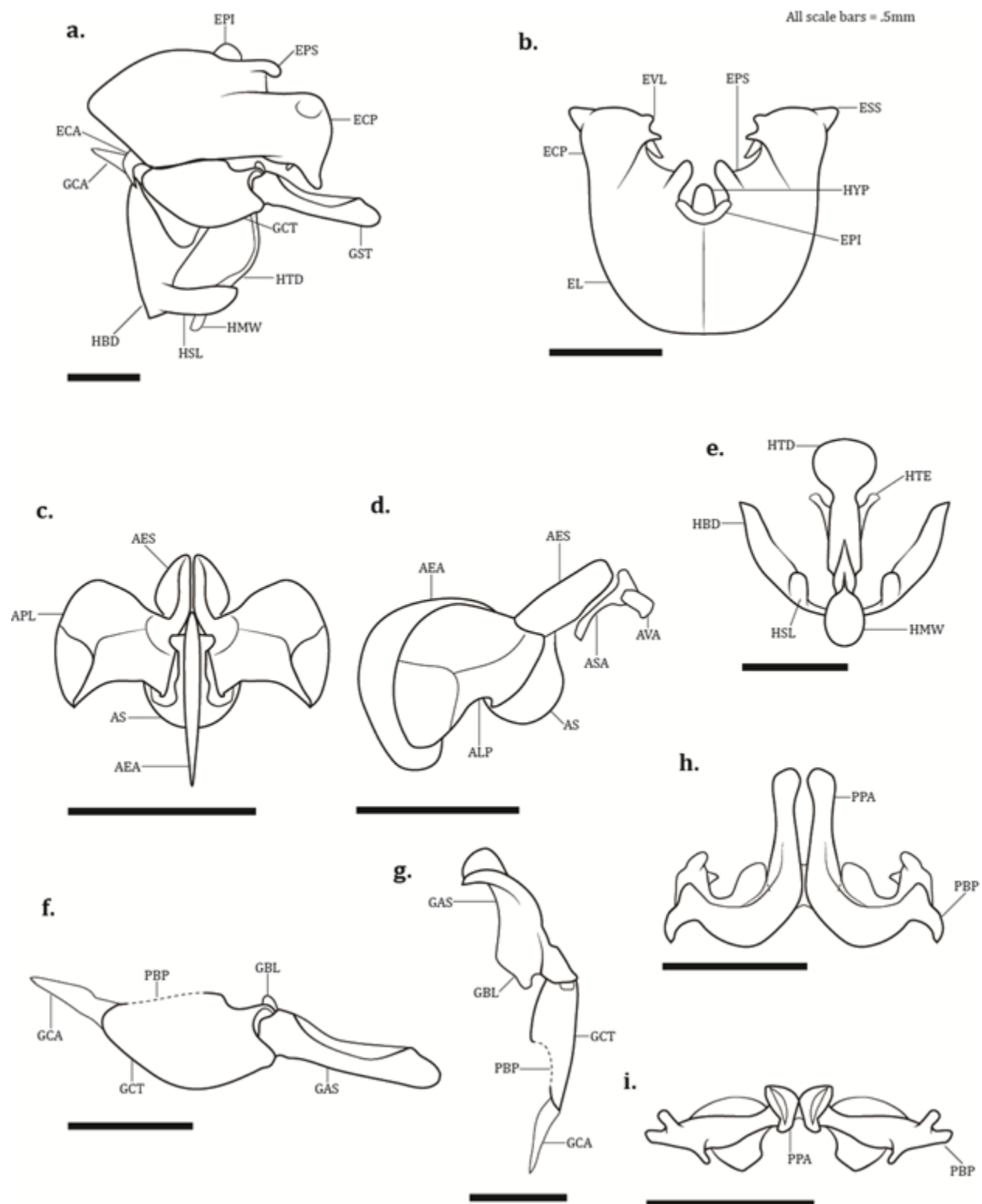


Figure 31.



Figure 32.



Figure 33.

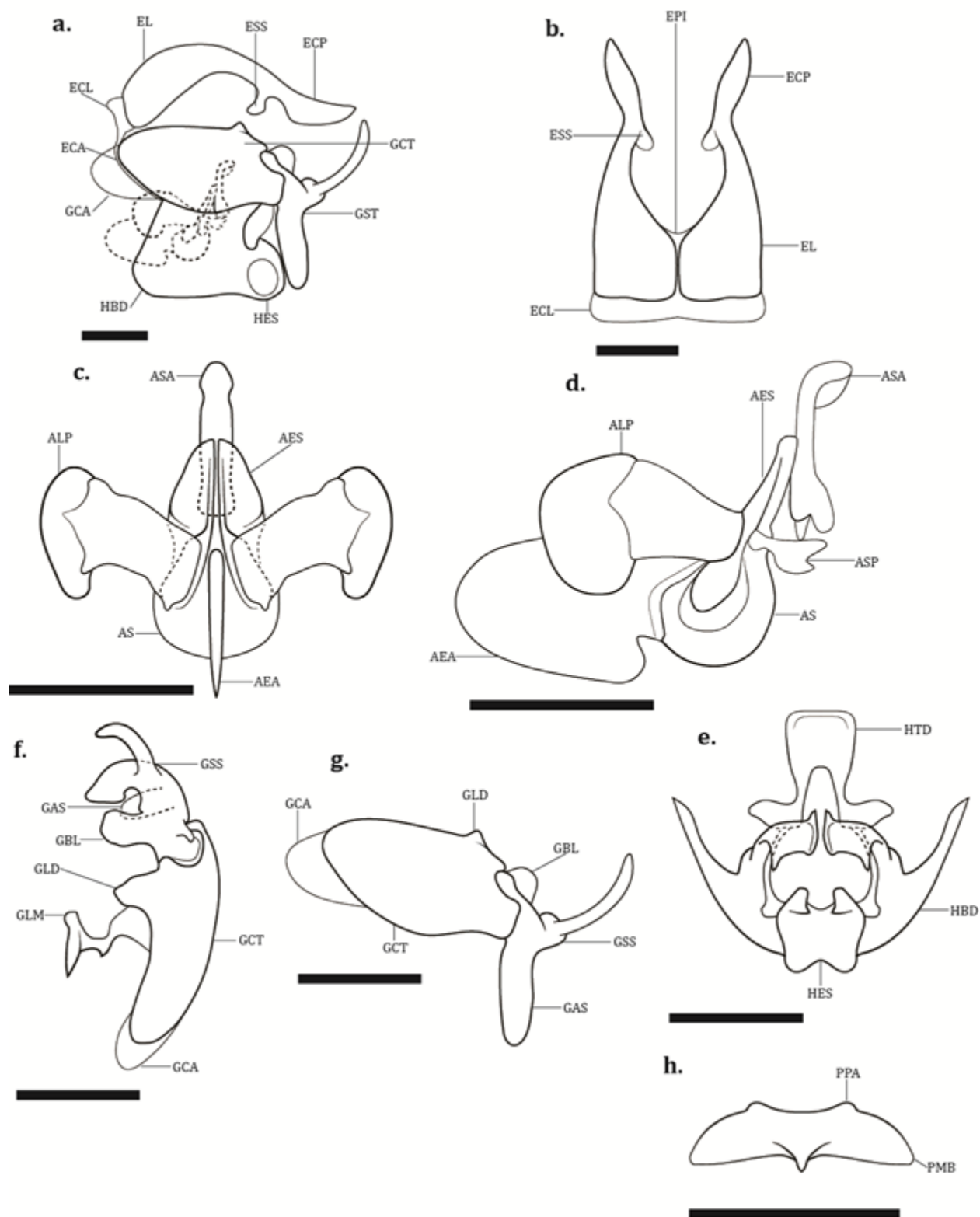


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Figure 35.



Figure 36.

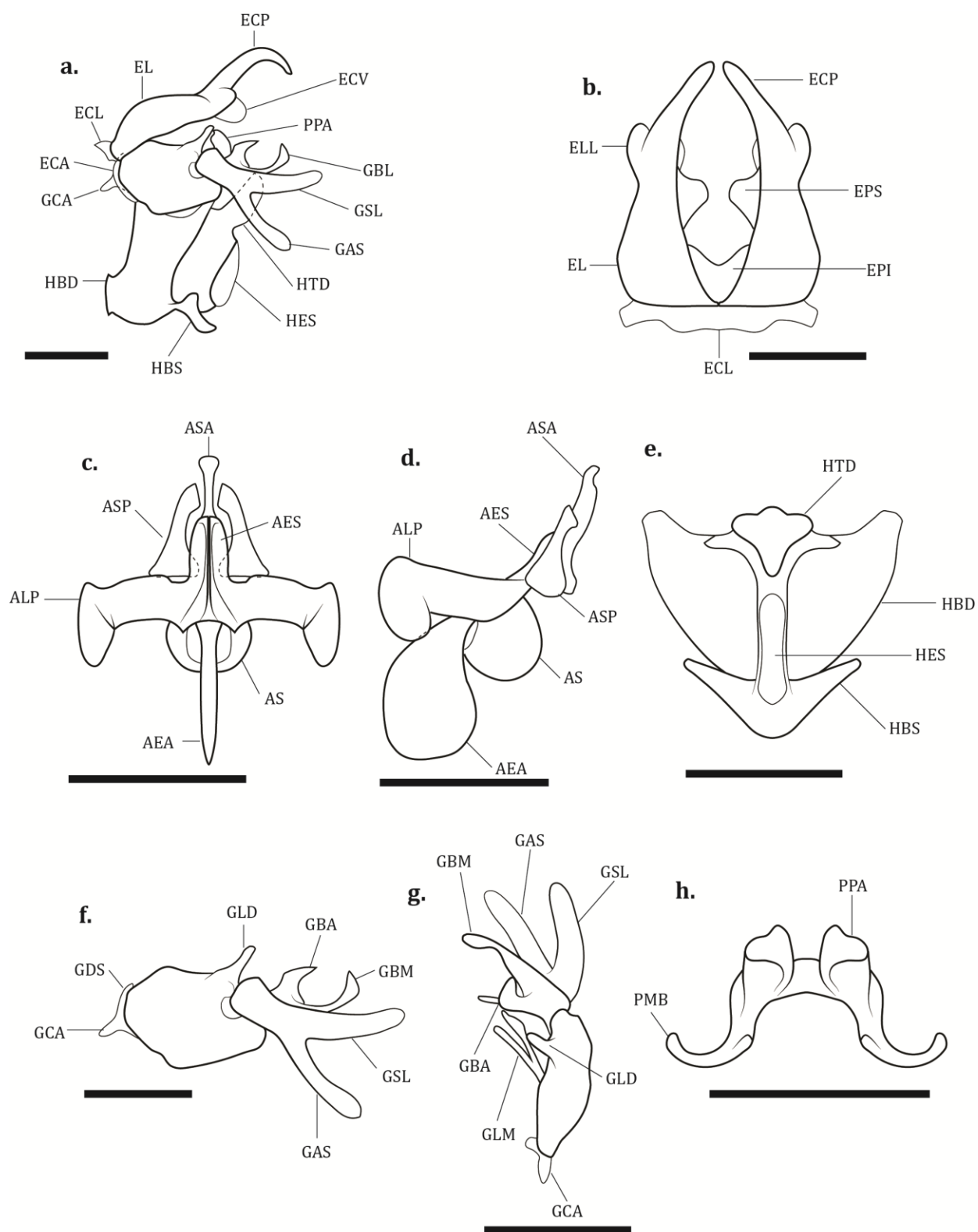


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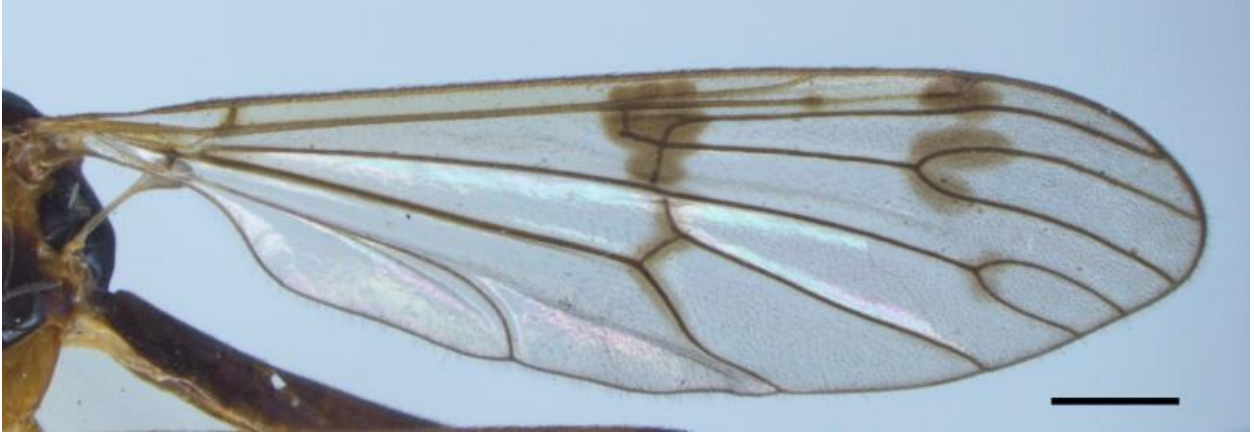


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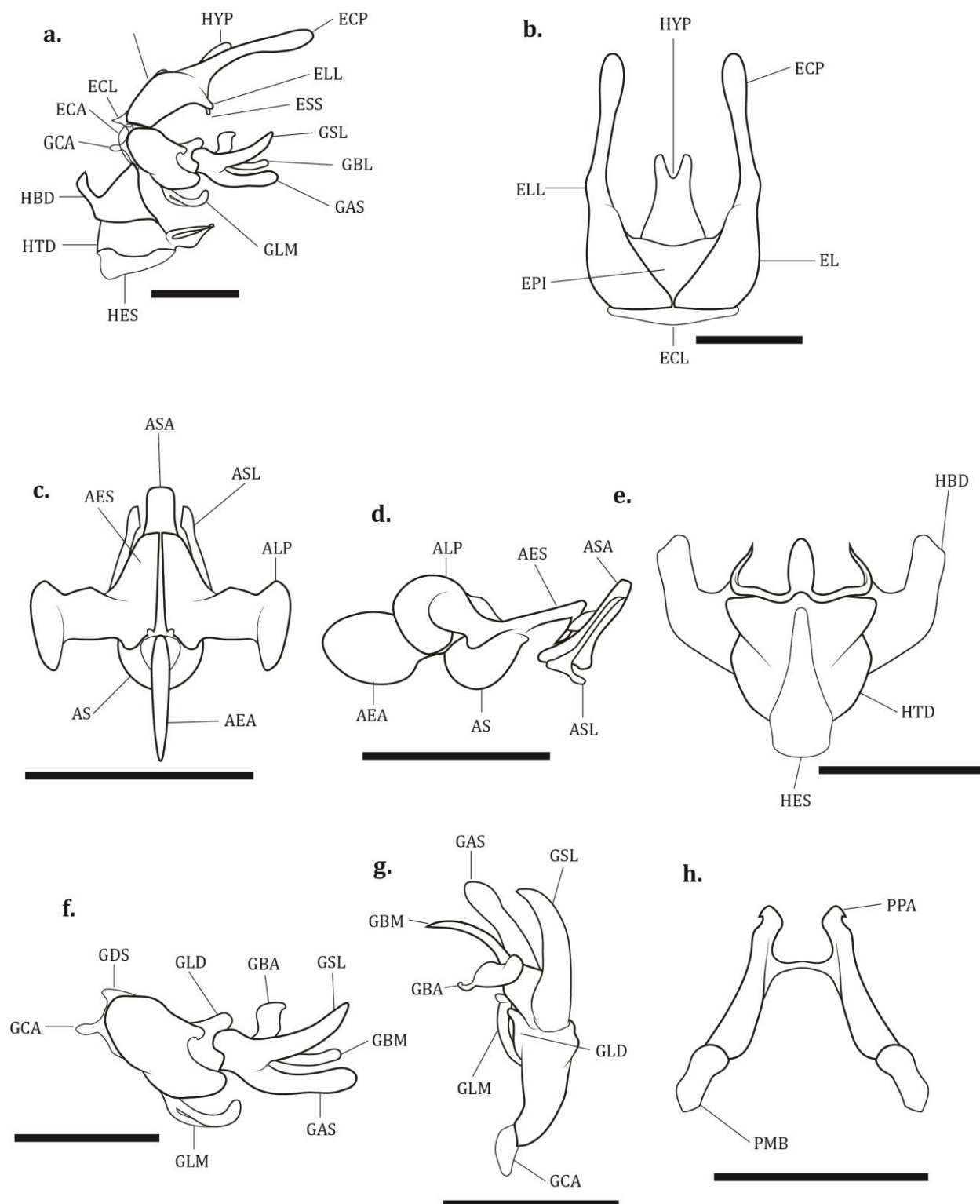


Figure 40.



Figure 41.



Figure 42.

All scale bars = .5mm

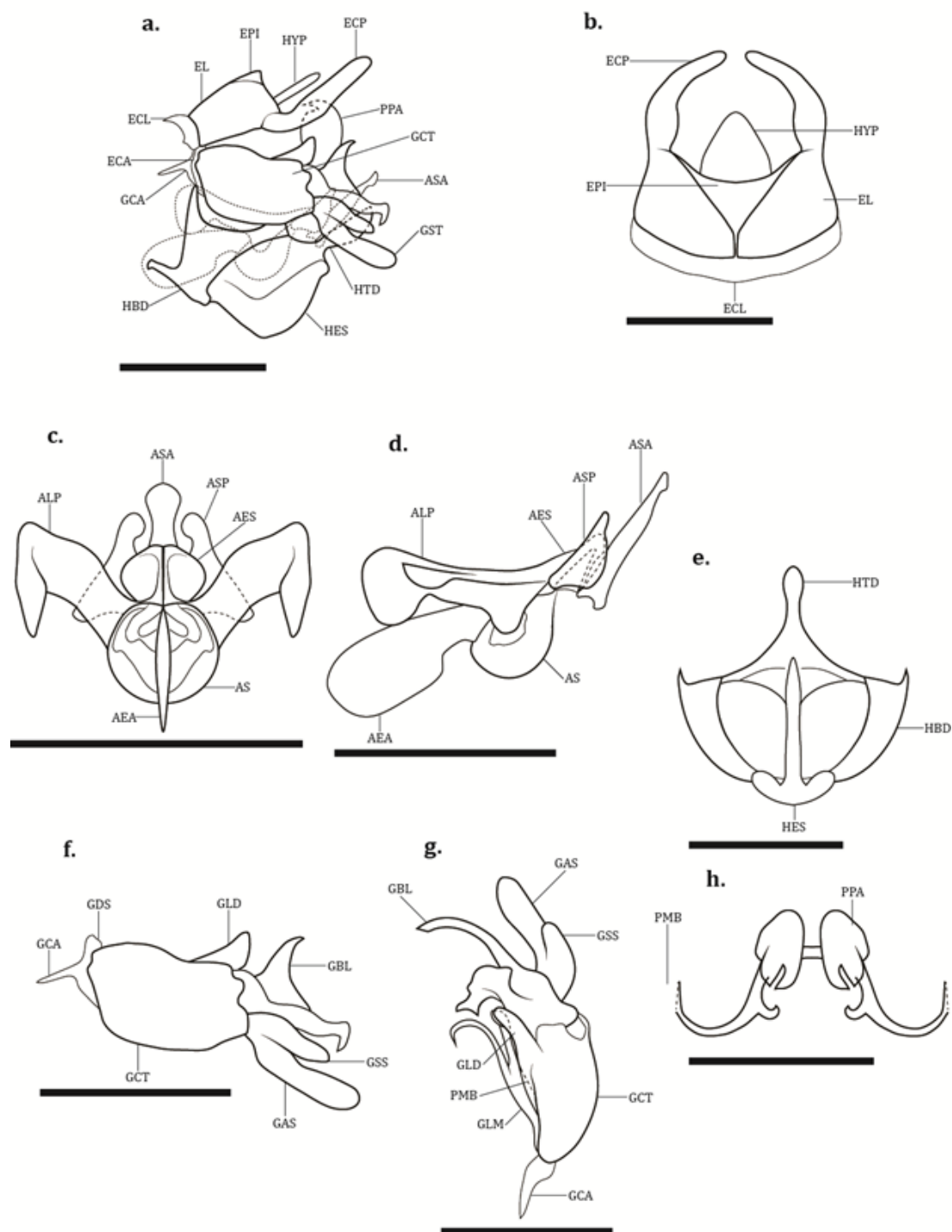


Figure 43.



Figure 44.



Figure 45.

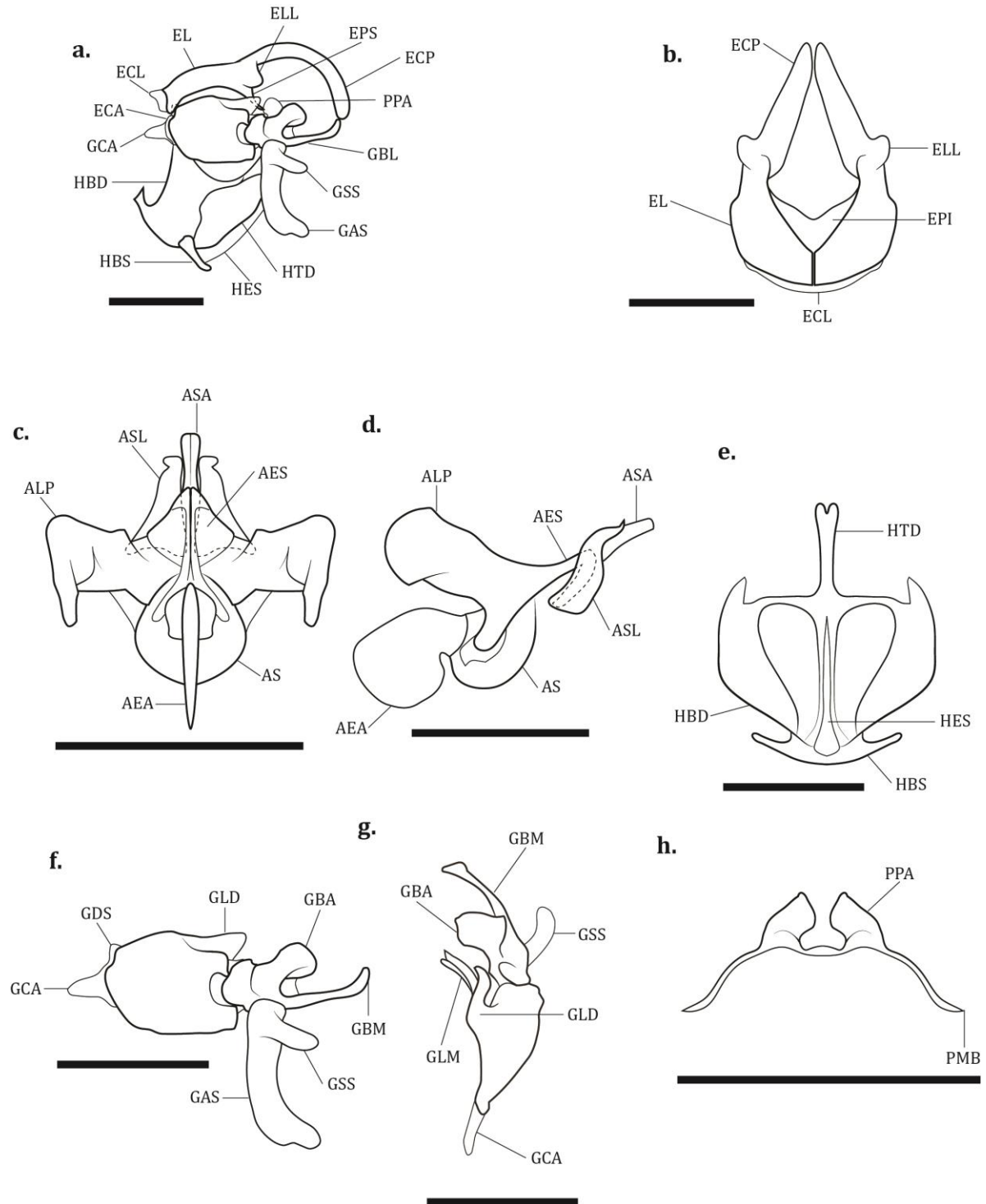


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Figure 47.



Figure 48.

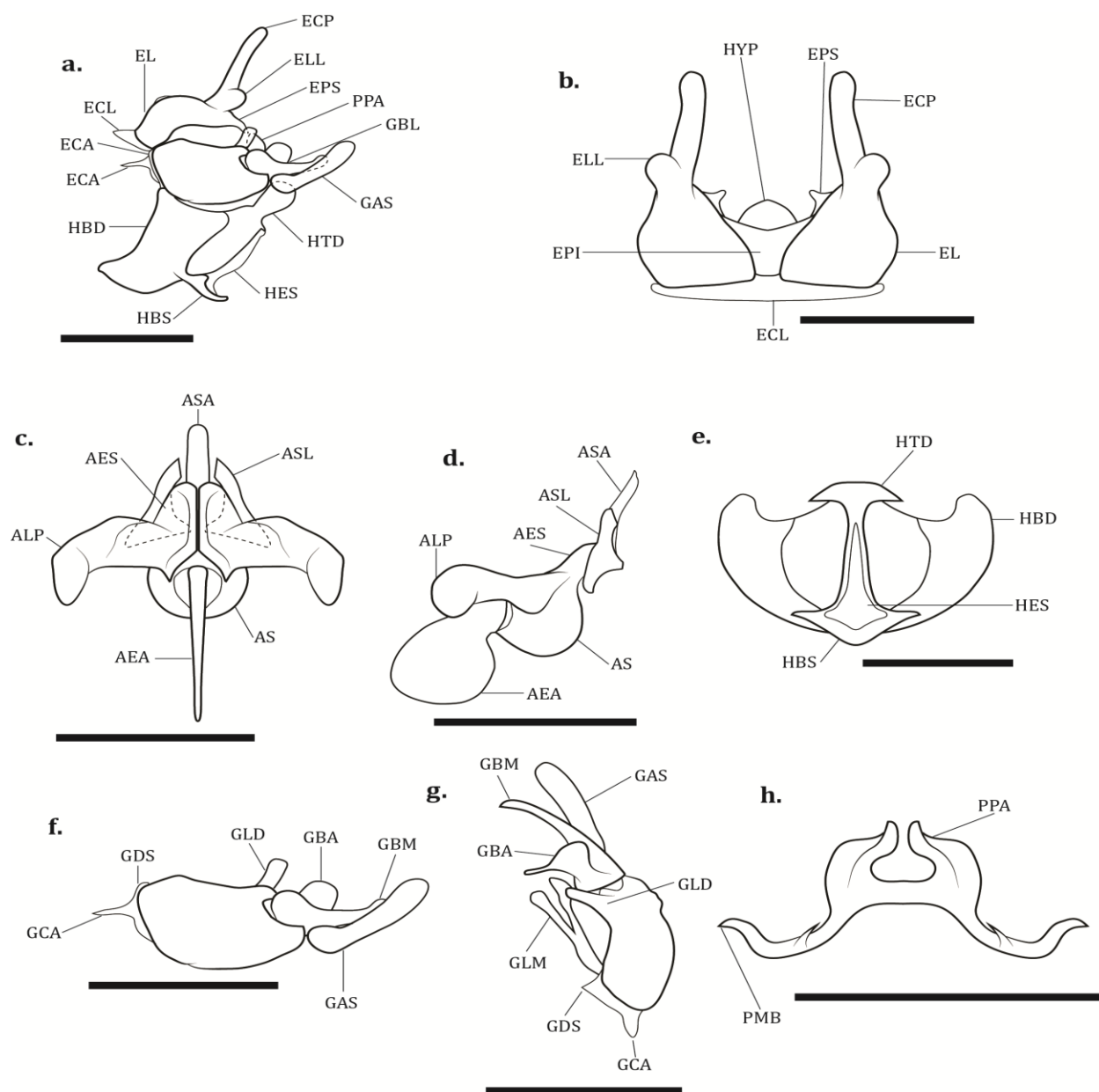


Figure 49.



Figure 50.



Figure 51.

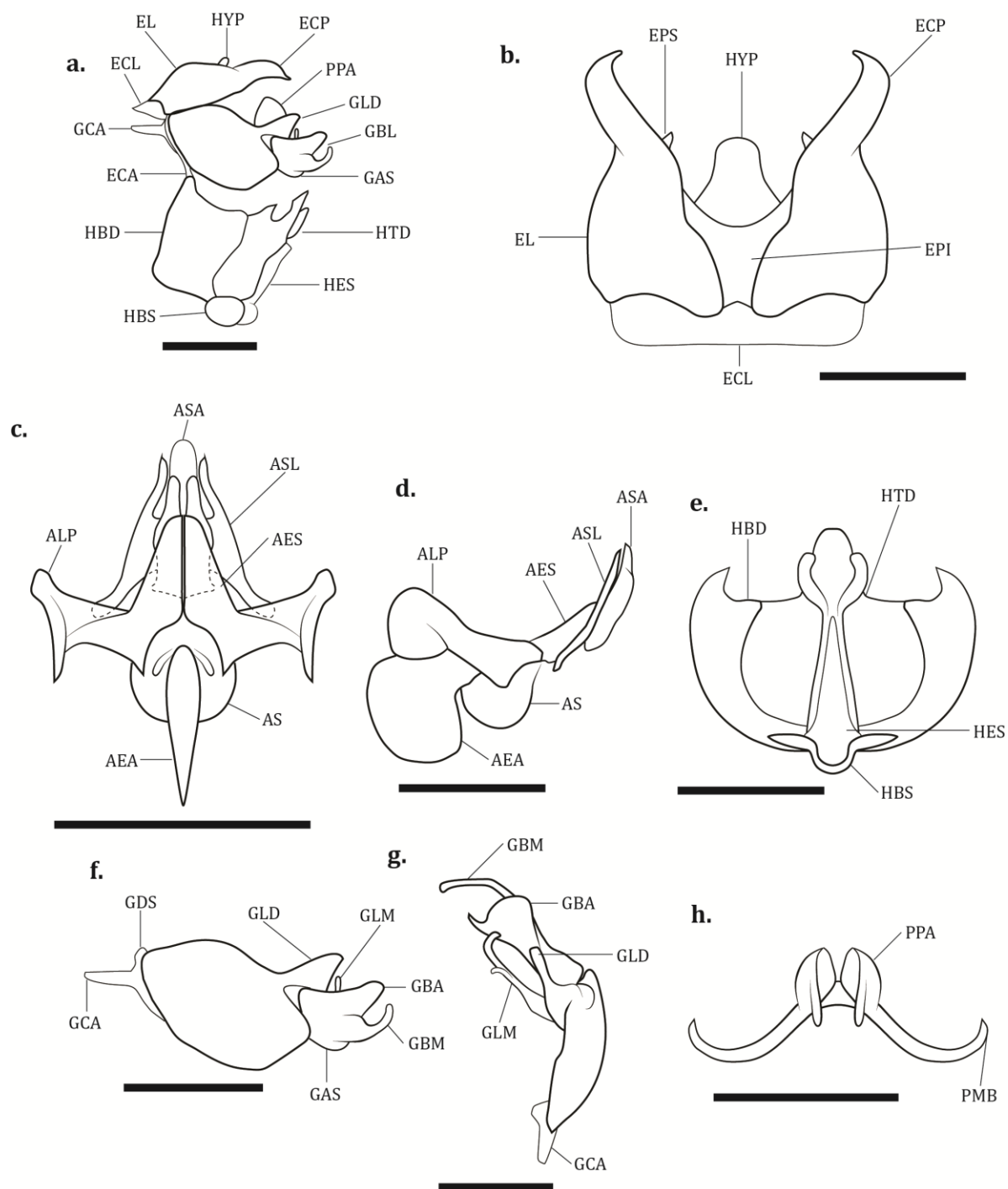


Figure 52.



Figure 53.



Figure 54.



Figure 55.

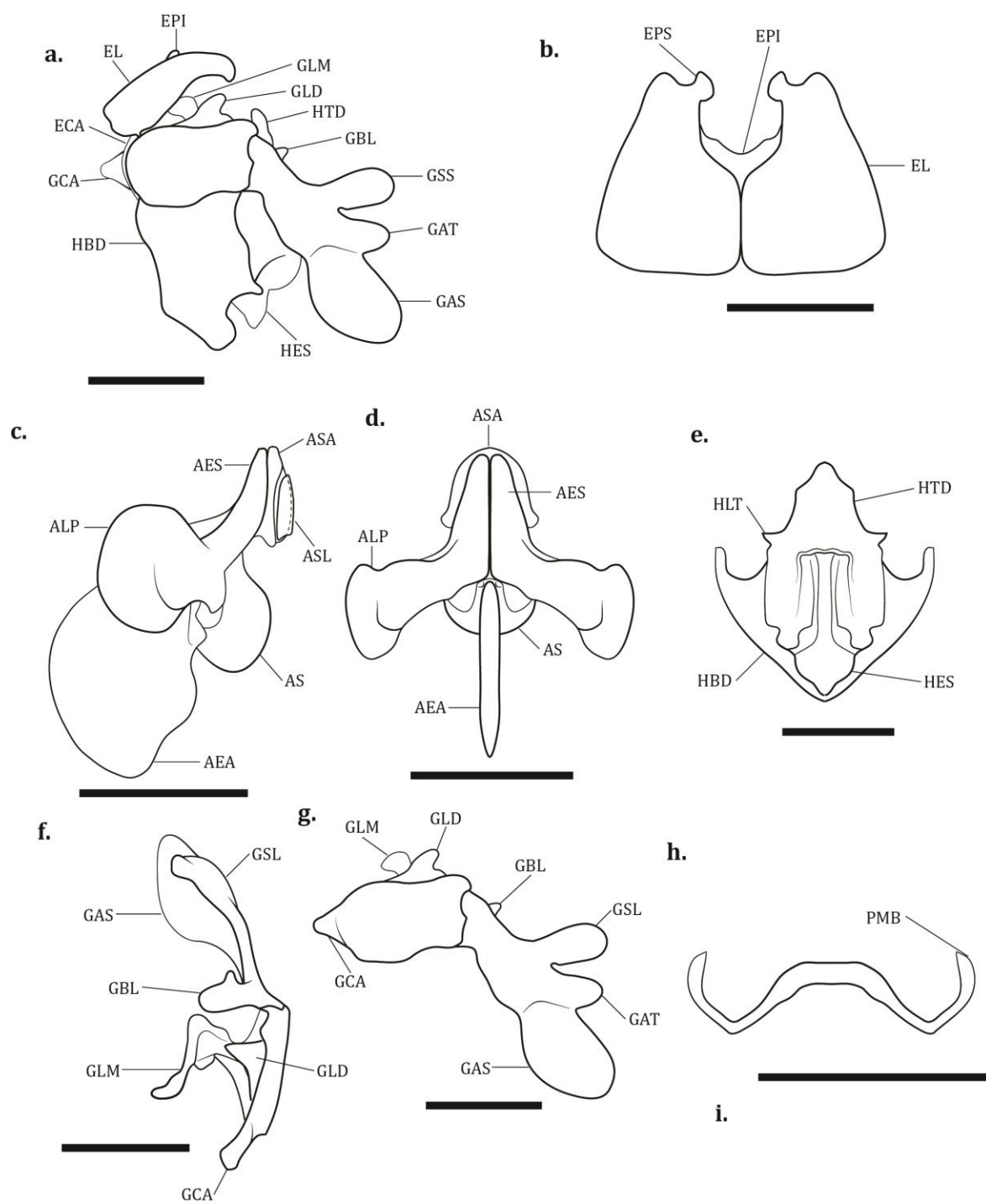


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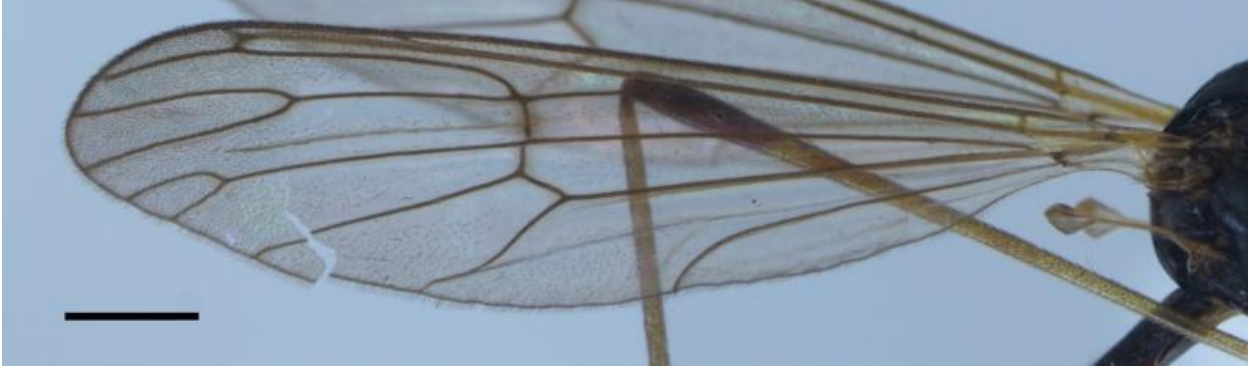


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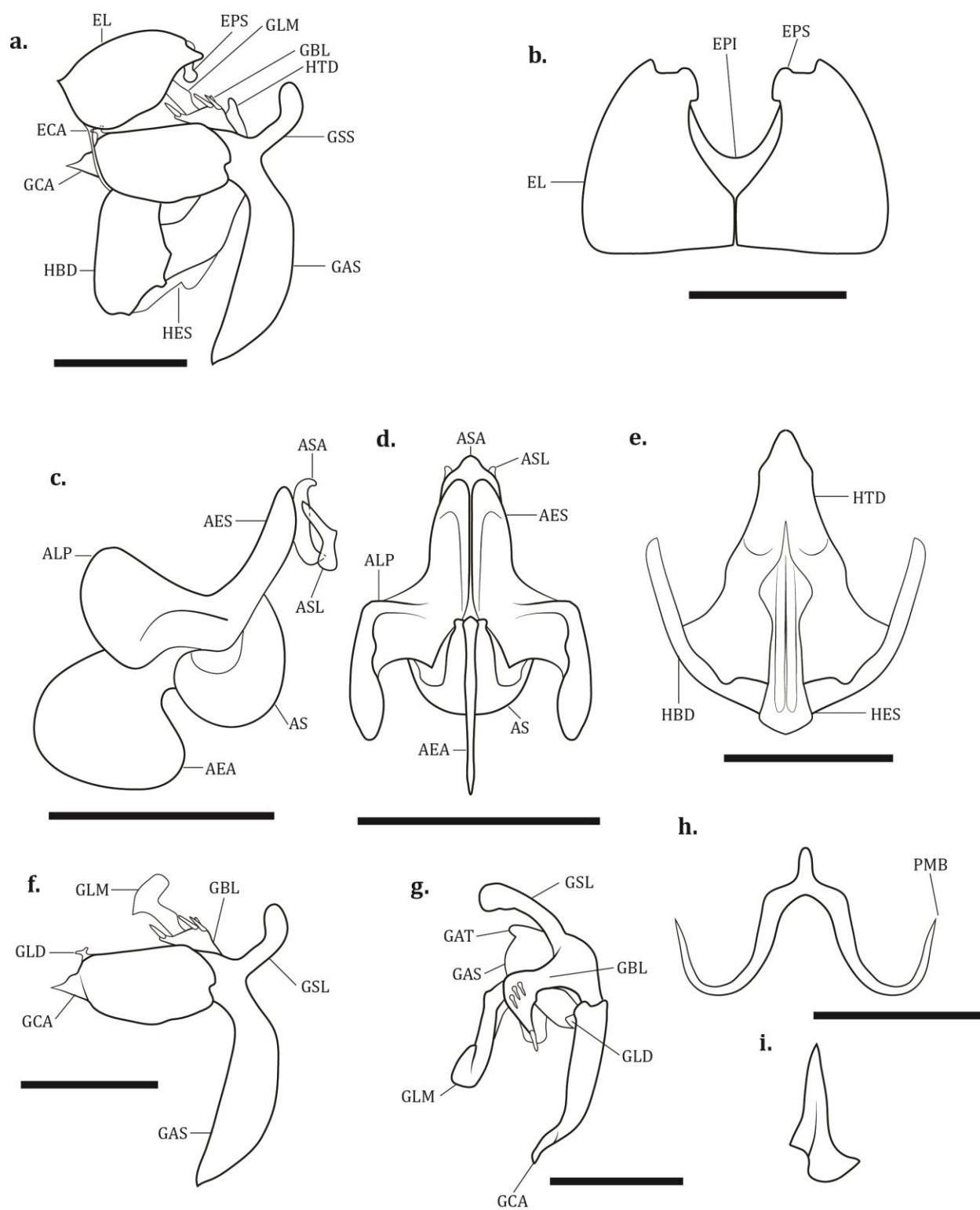


Figure 59.



Figure 60.



Figure 61.

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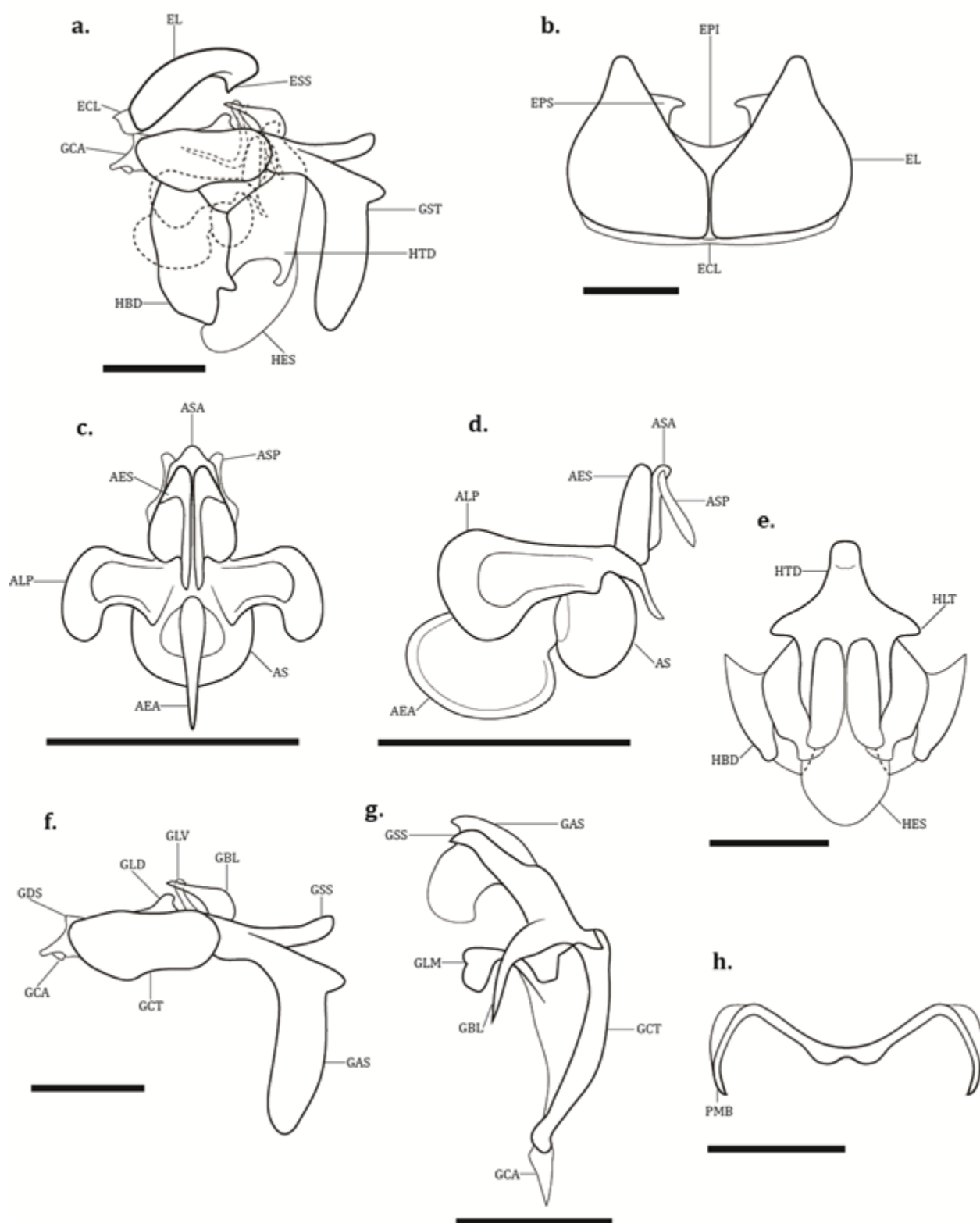


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Figure 63.



Figure 64.

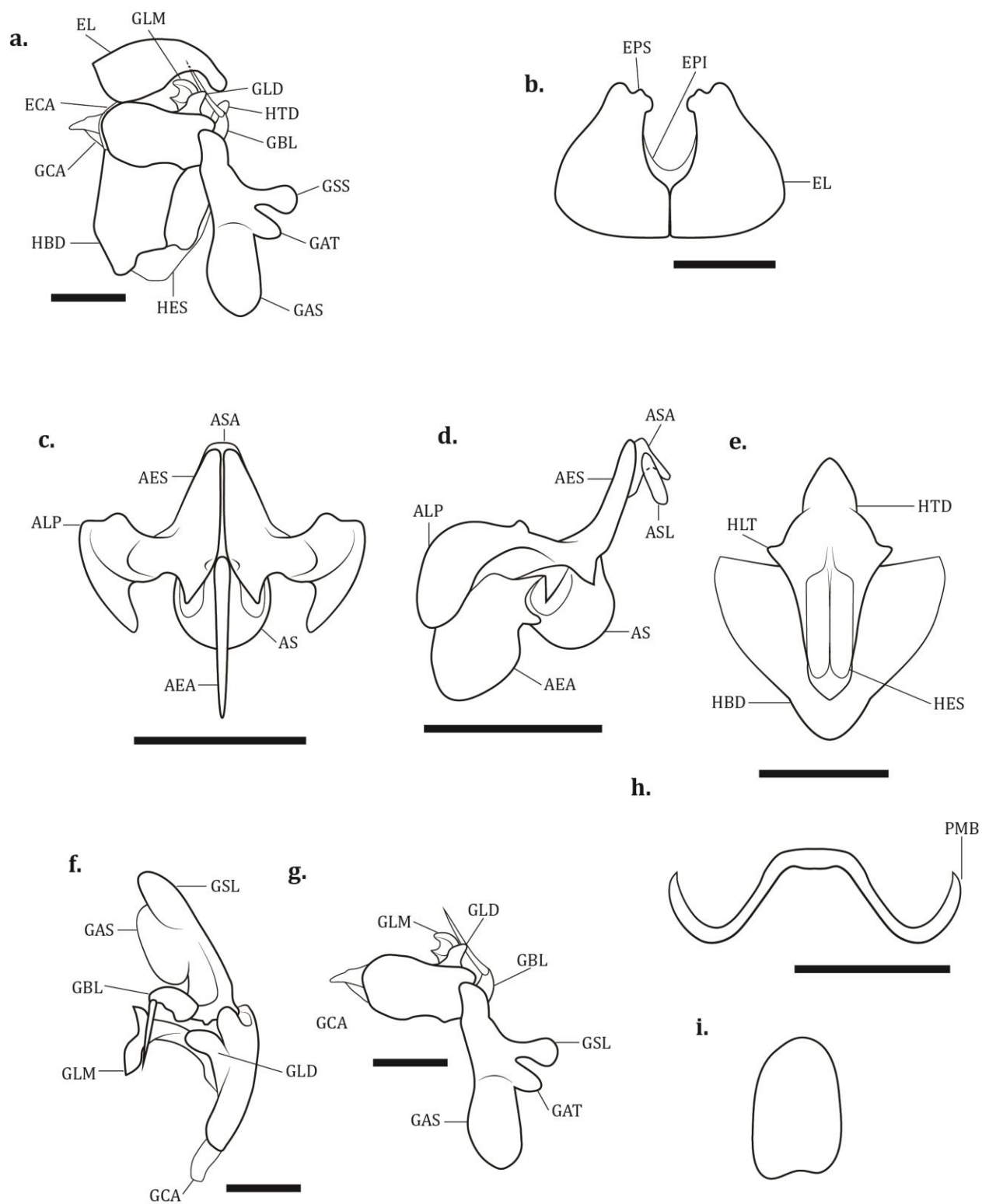


Figure 65.



Figure 66.



Figure 67.

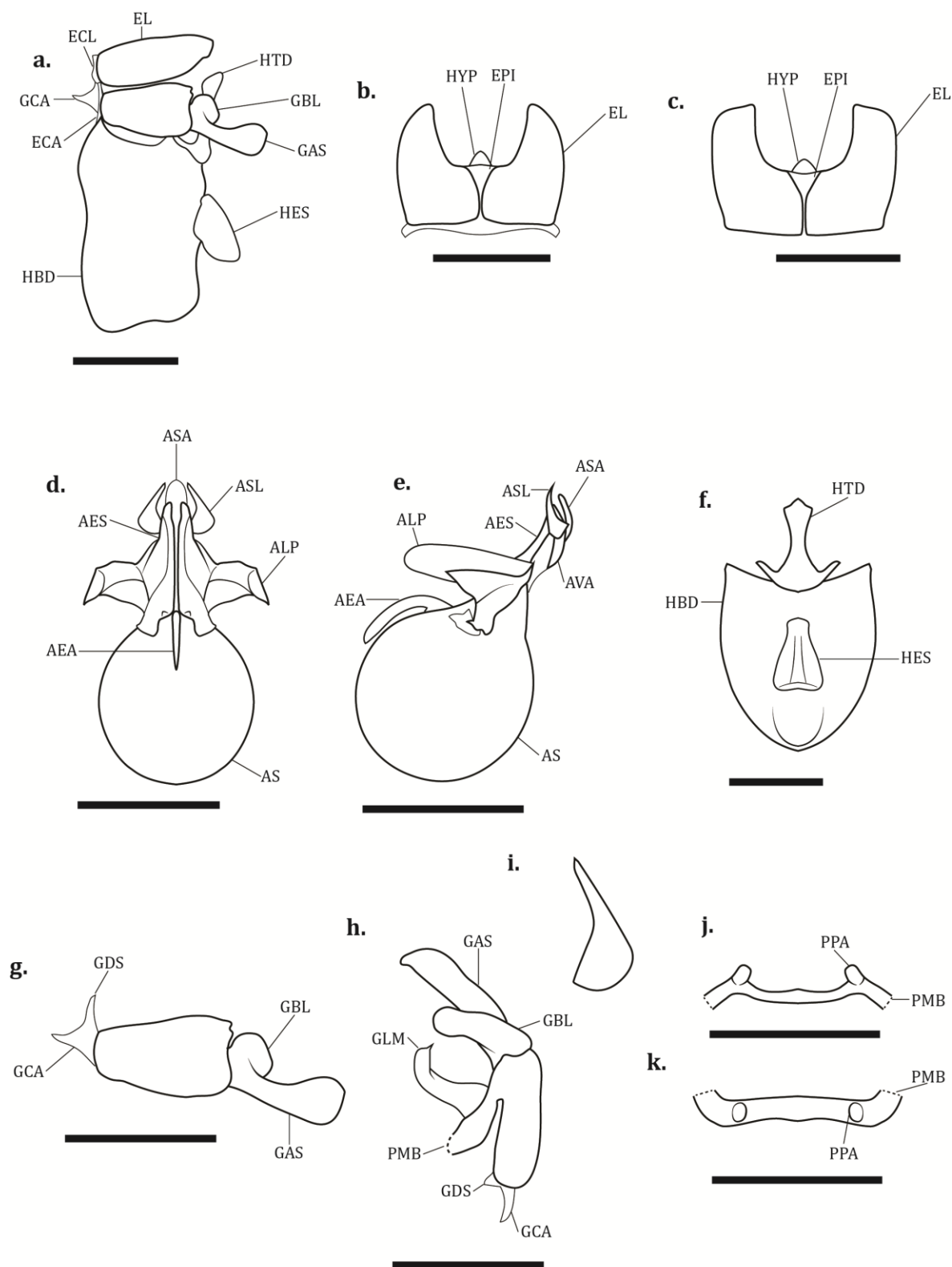


Figure 68



Figure 69.



Figure 70.

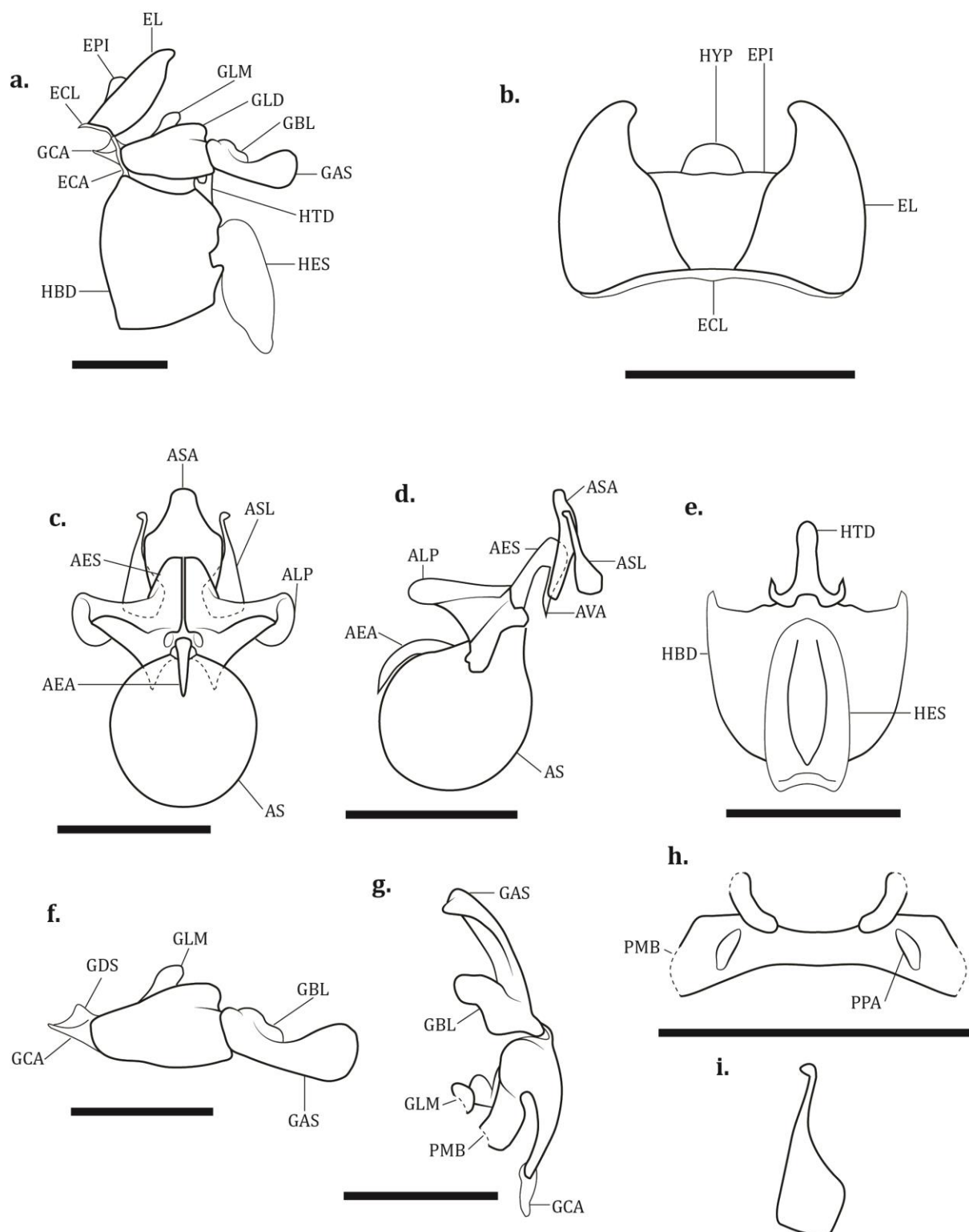


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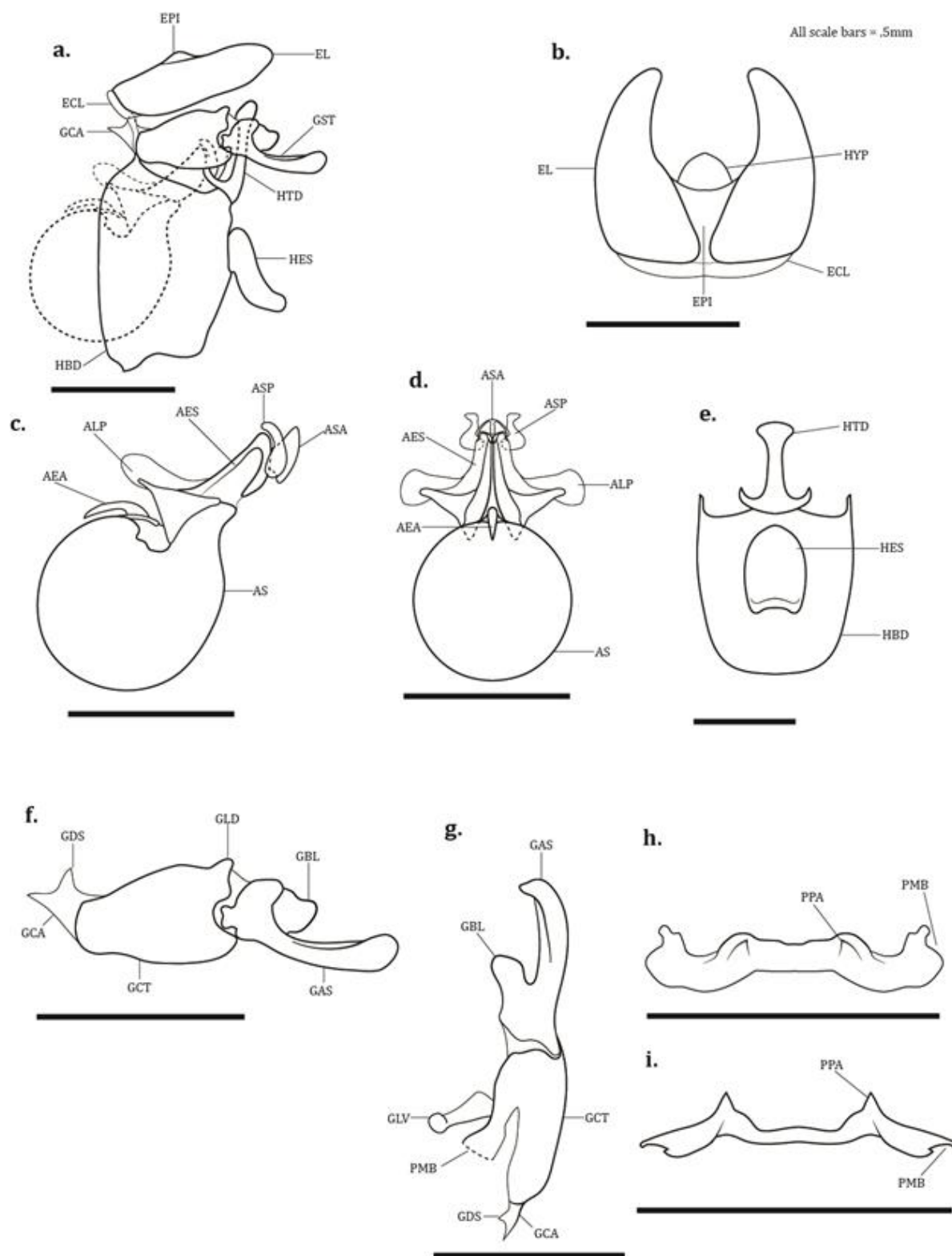


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Figure 75.



Figure 76.

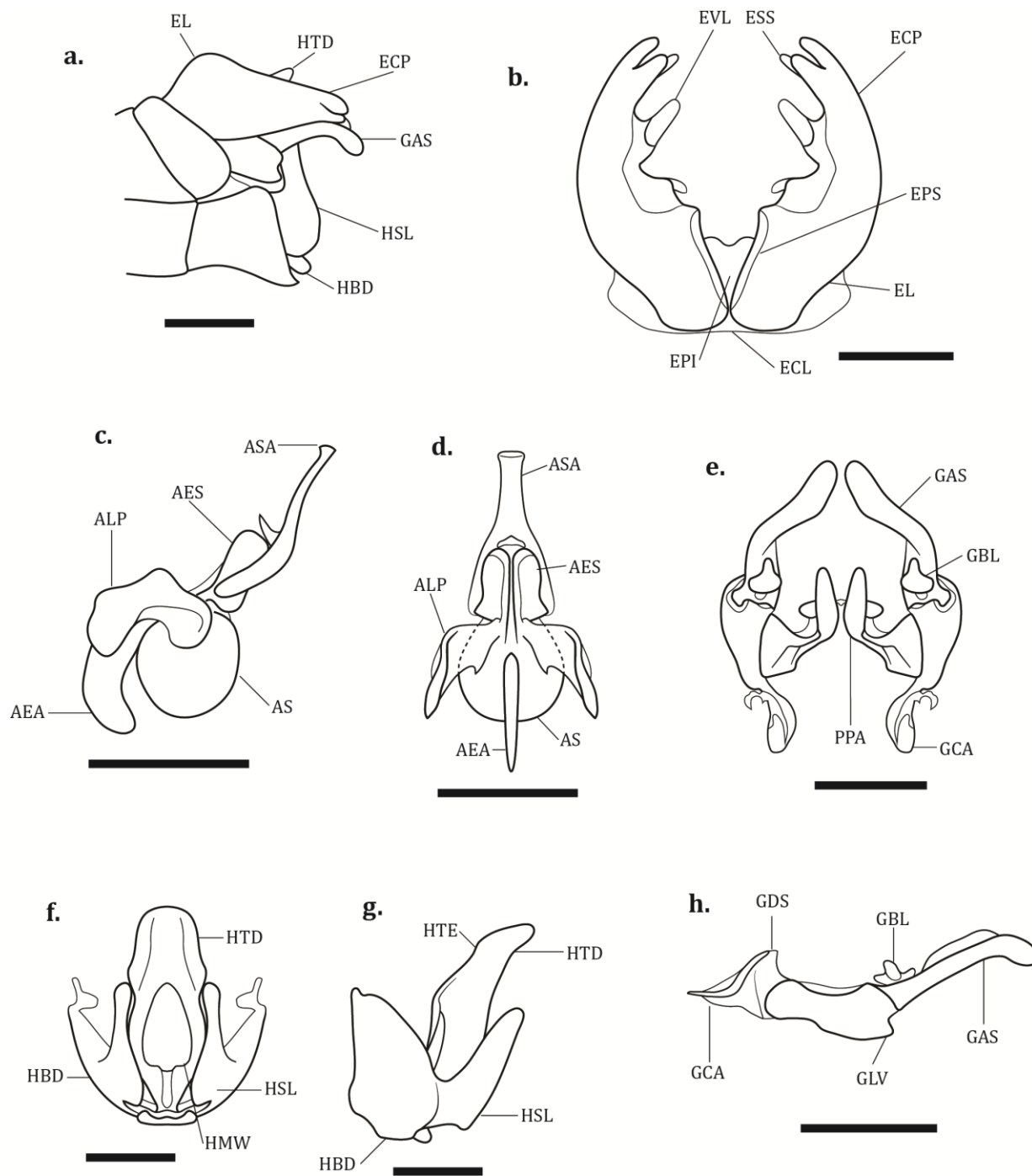


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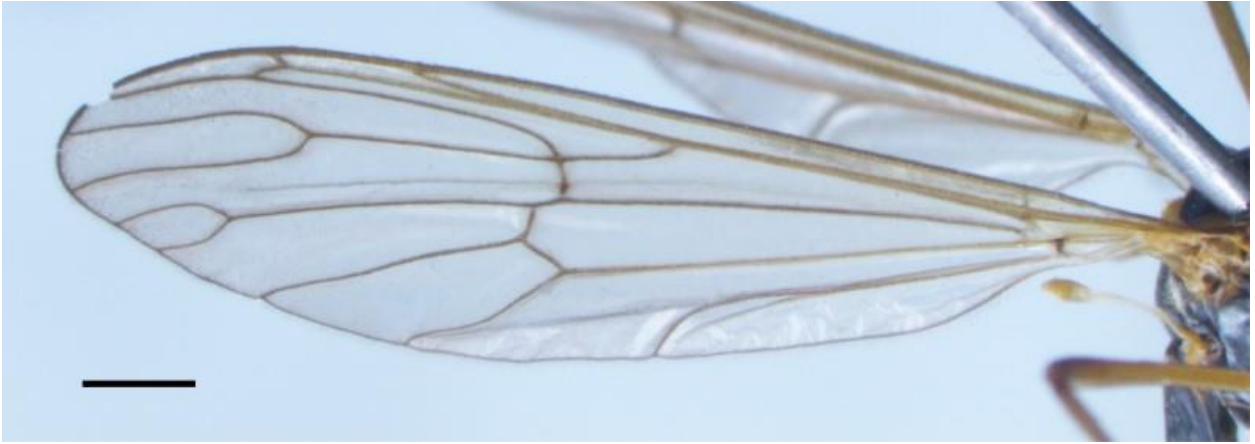


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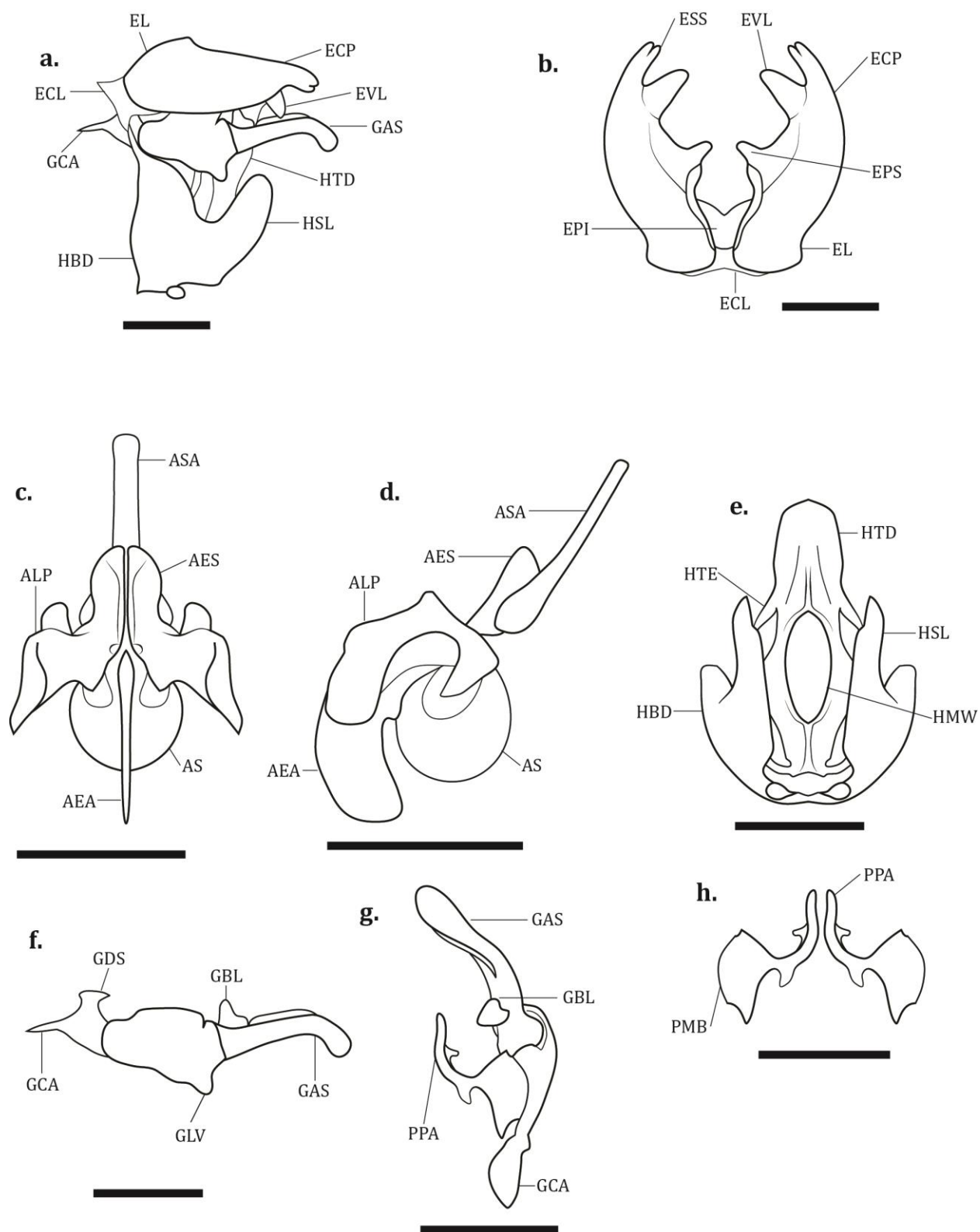


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Figure 81.



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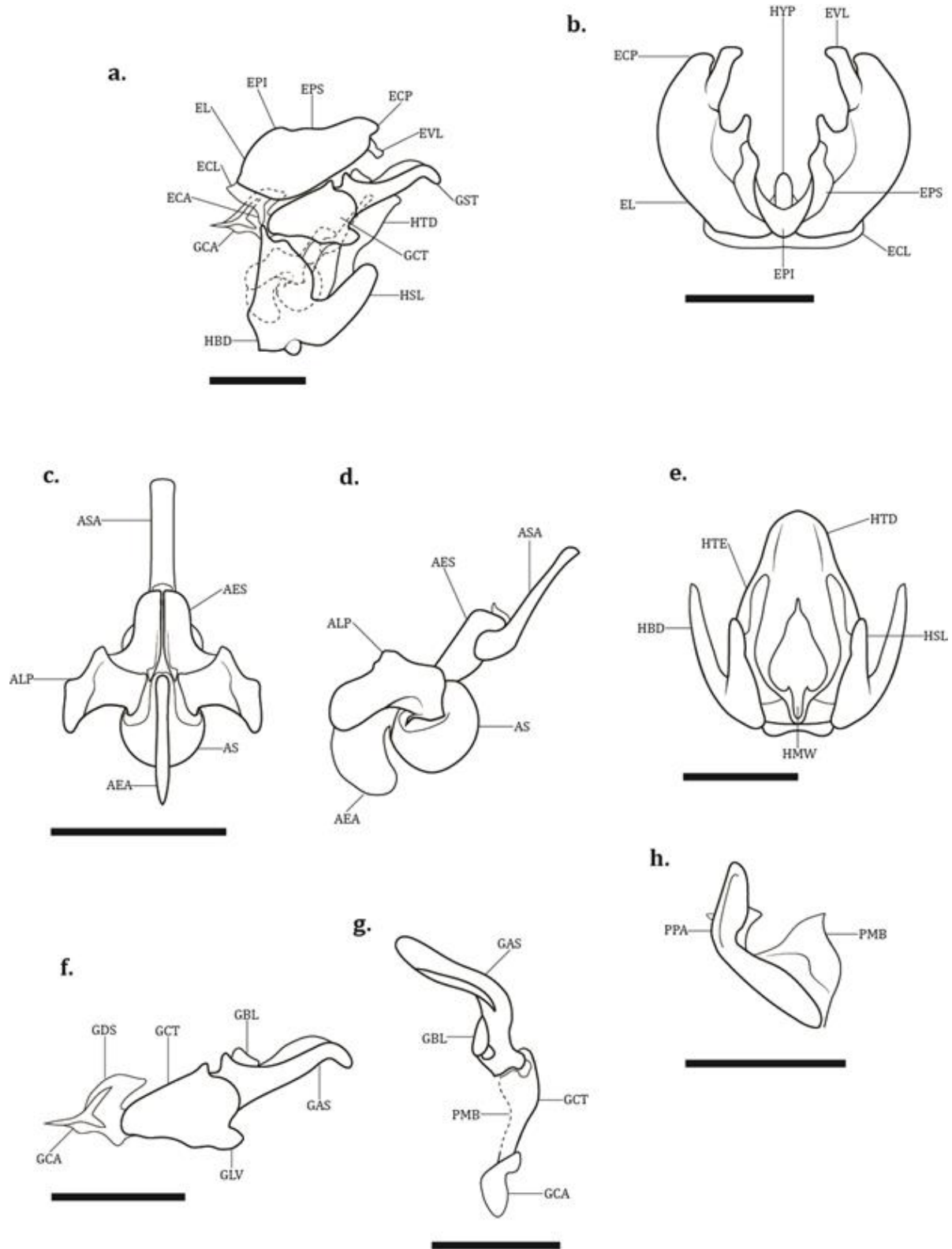


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Figure 84.



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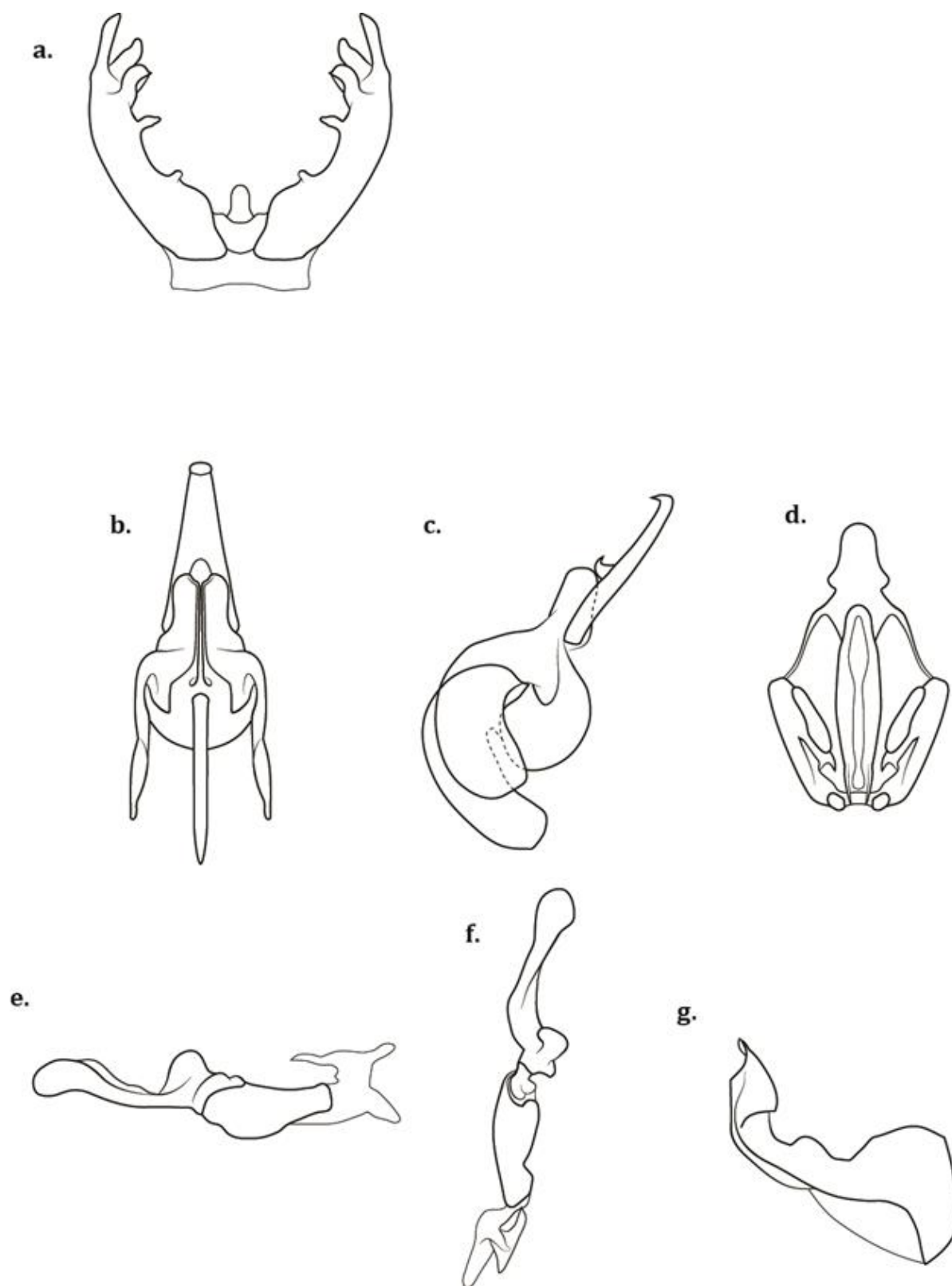


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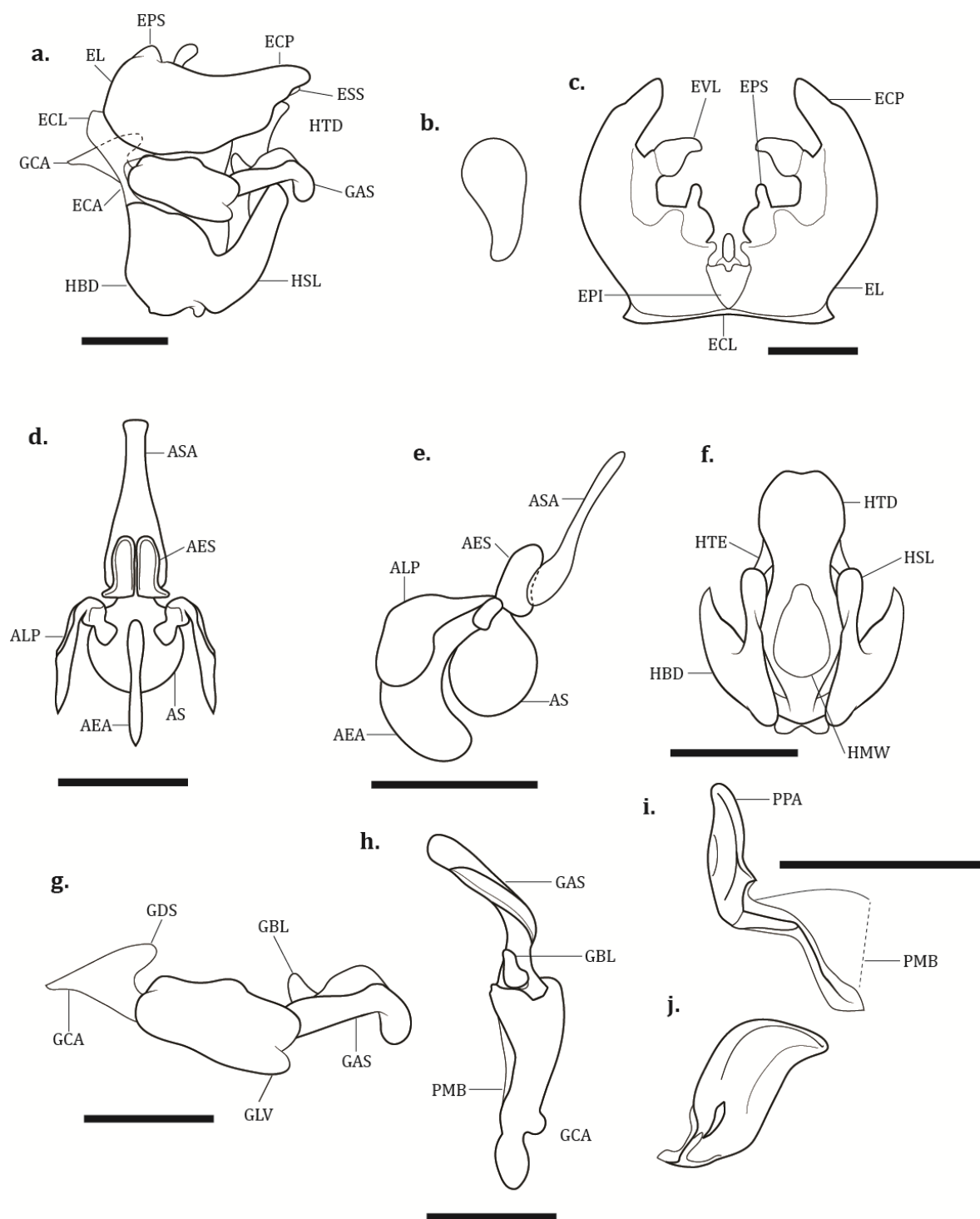


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Figure 90.



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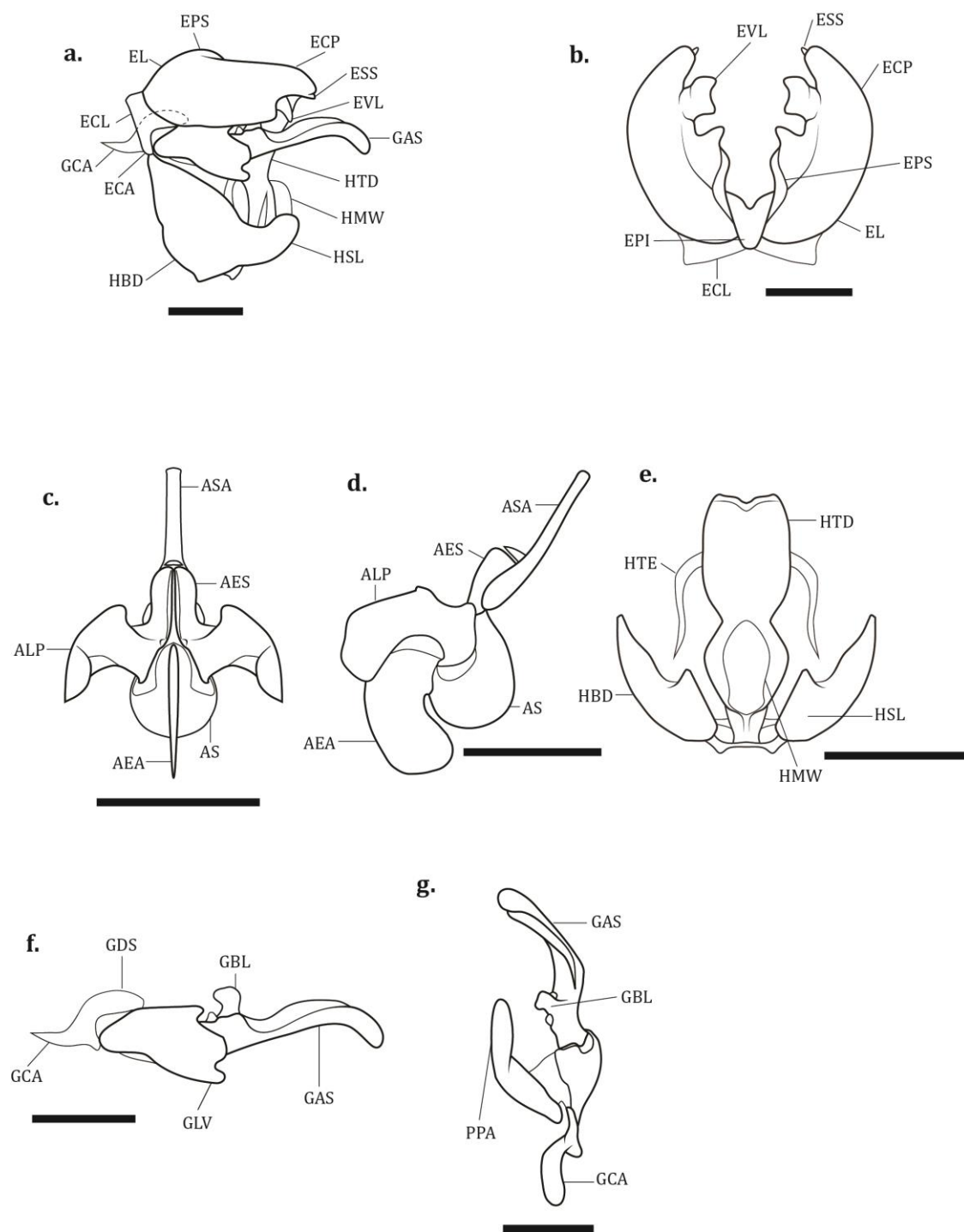


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Figure 93.



Figure 94.

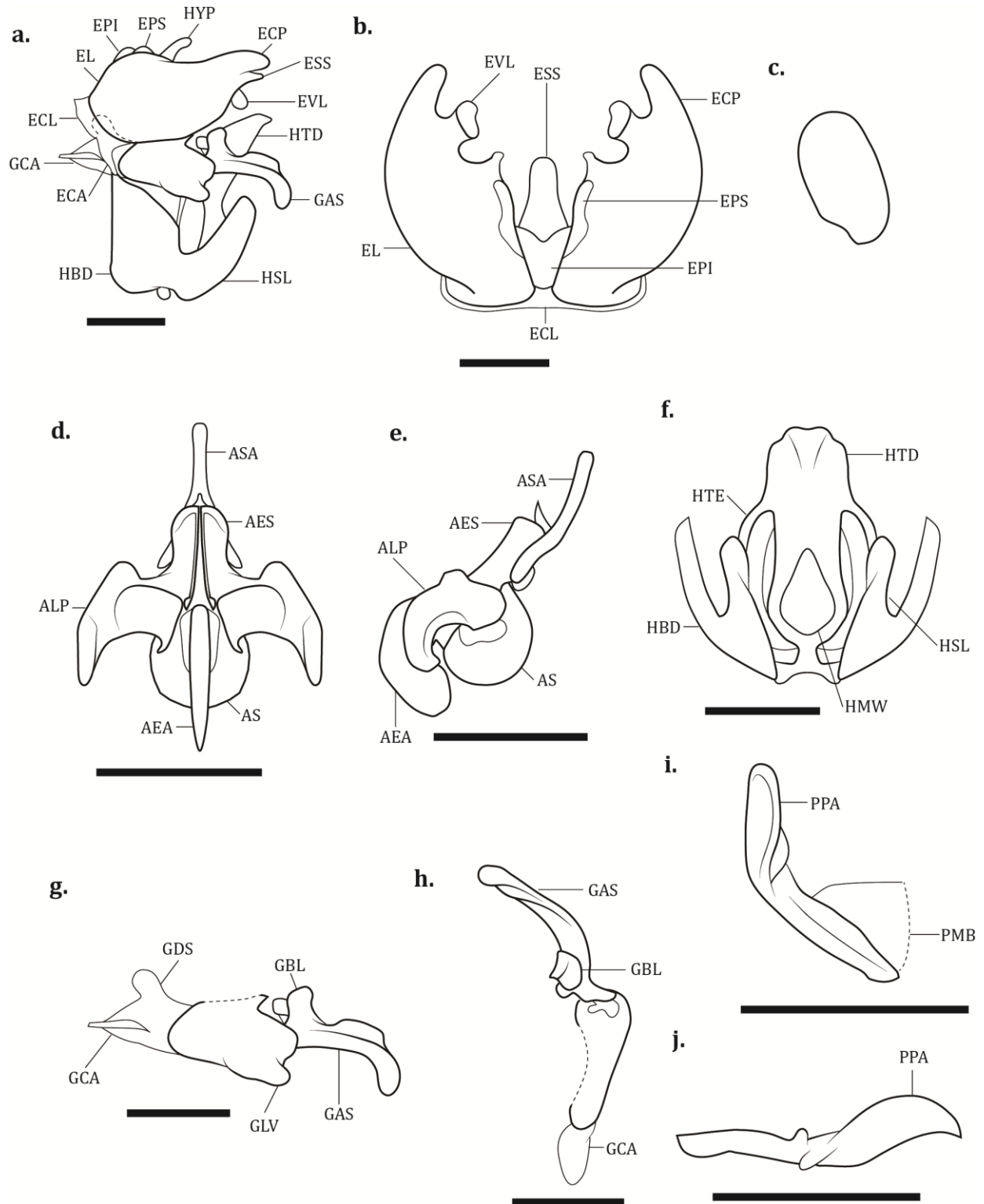


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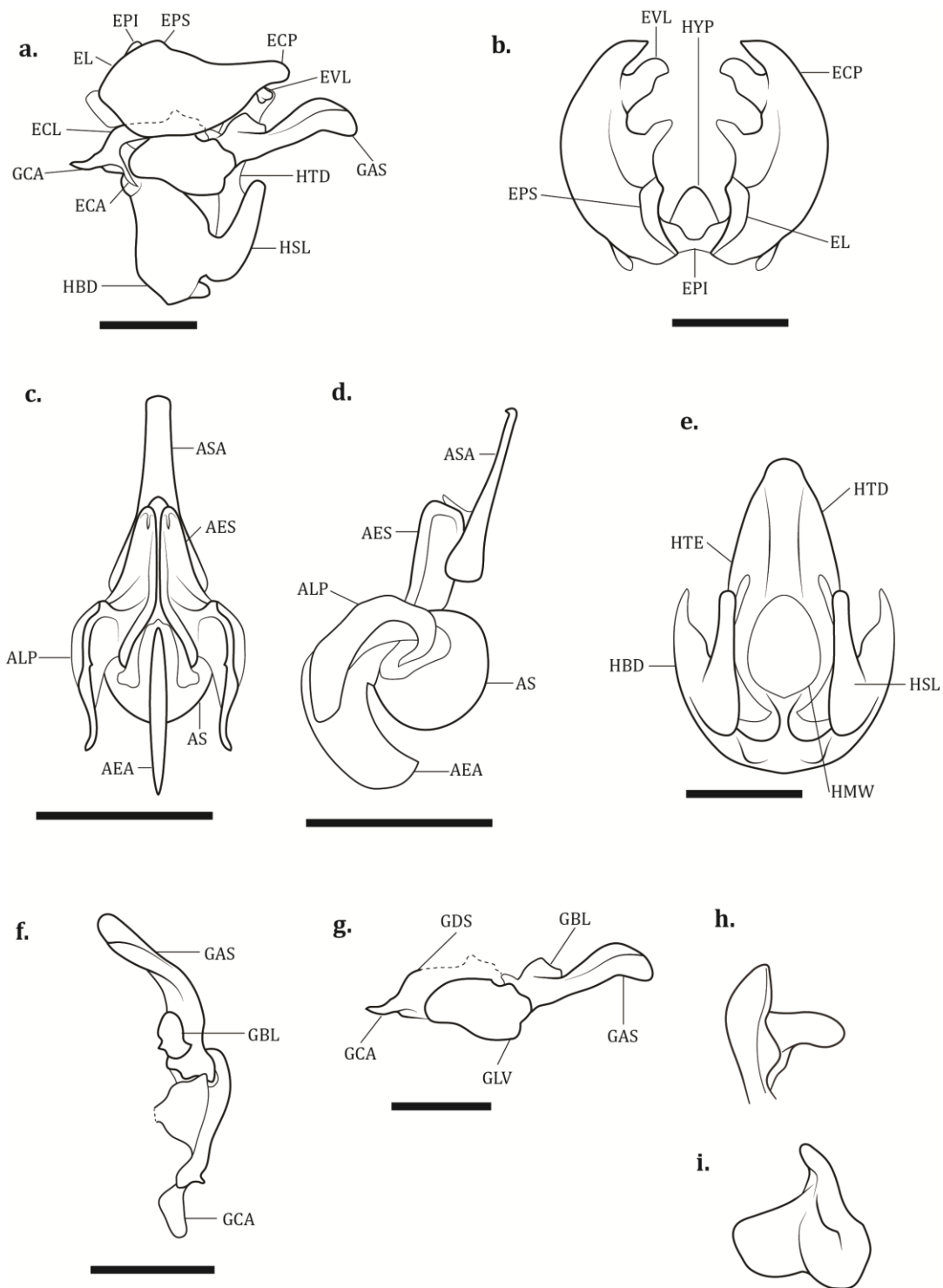


Figure 98.



Figure 99.



Figure 100.

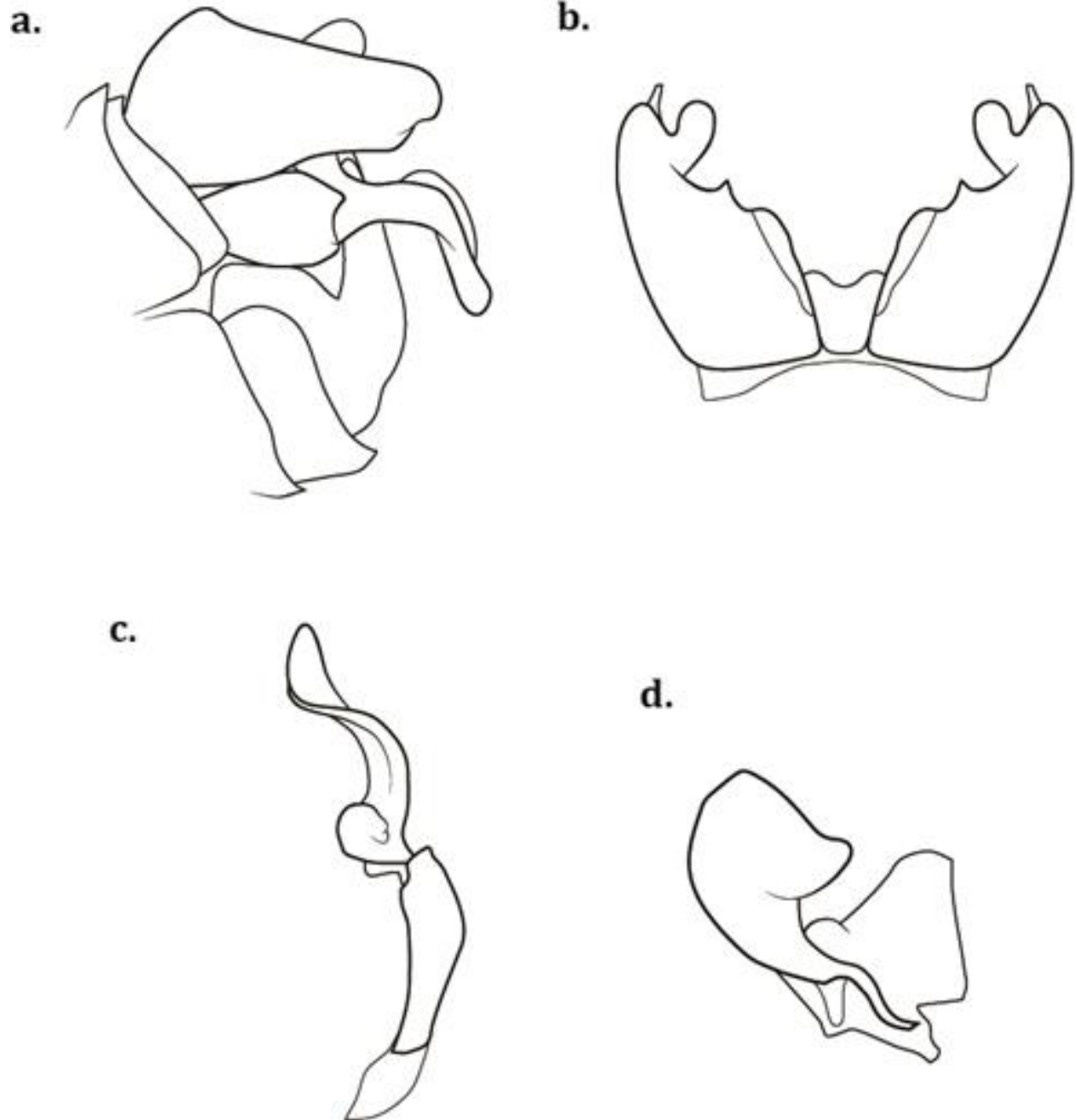


Figure 101.



Figure 102.



Figure 103.

All scale bars = .5mm

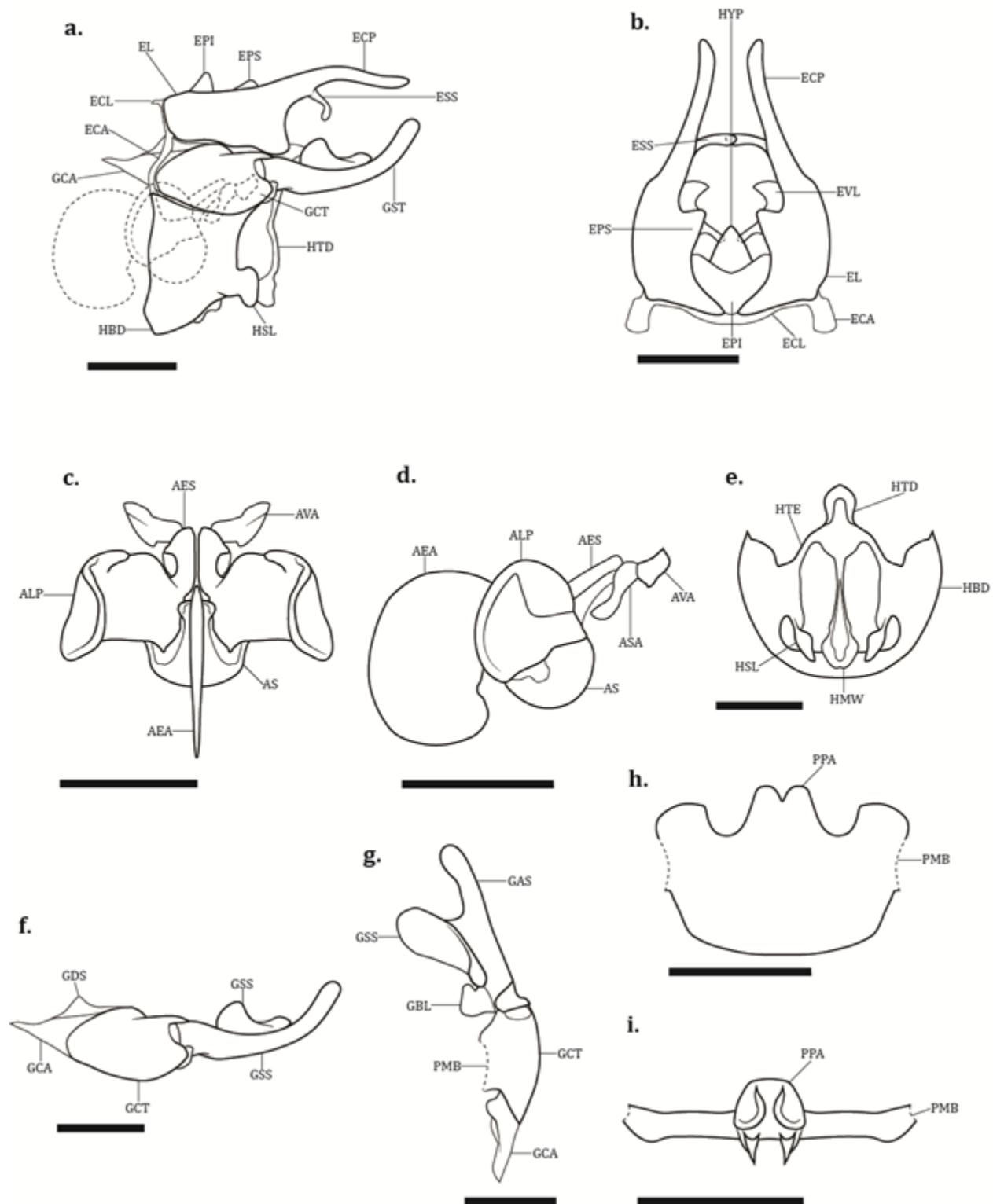


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Figure 105.



Figure 106.

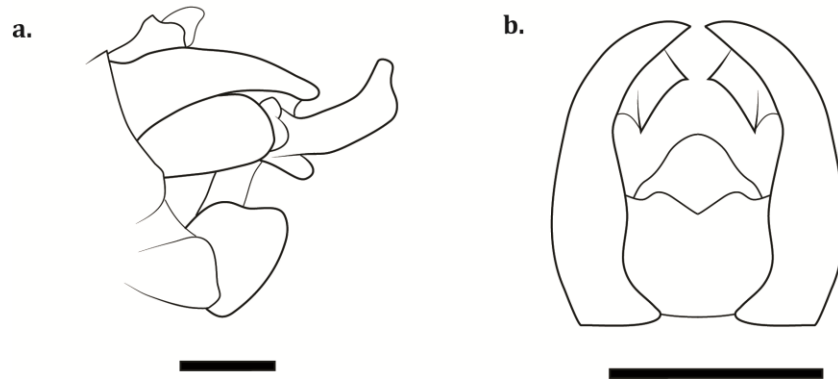


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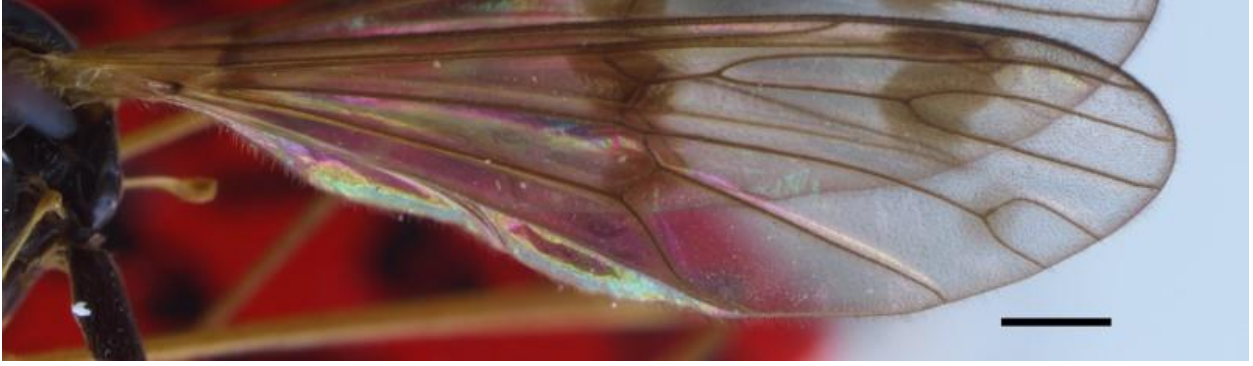


Figure 108.



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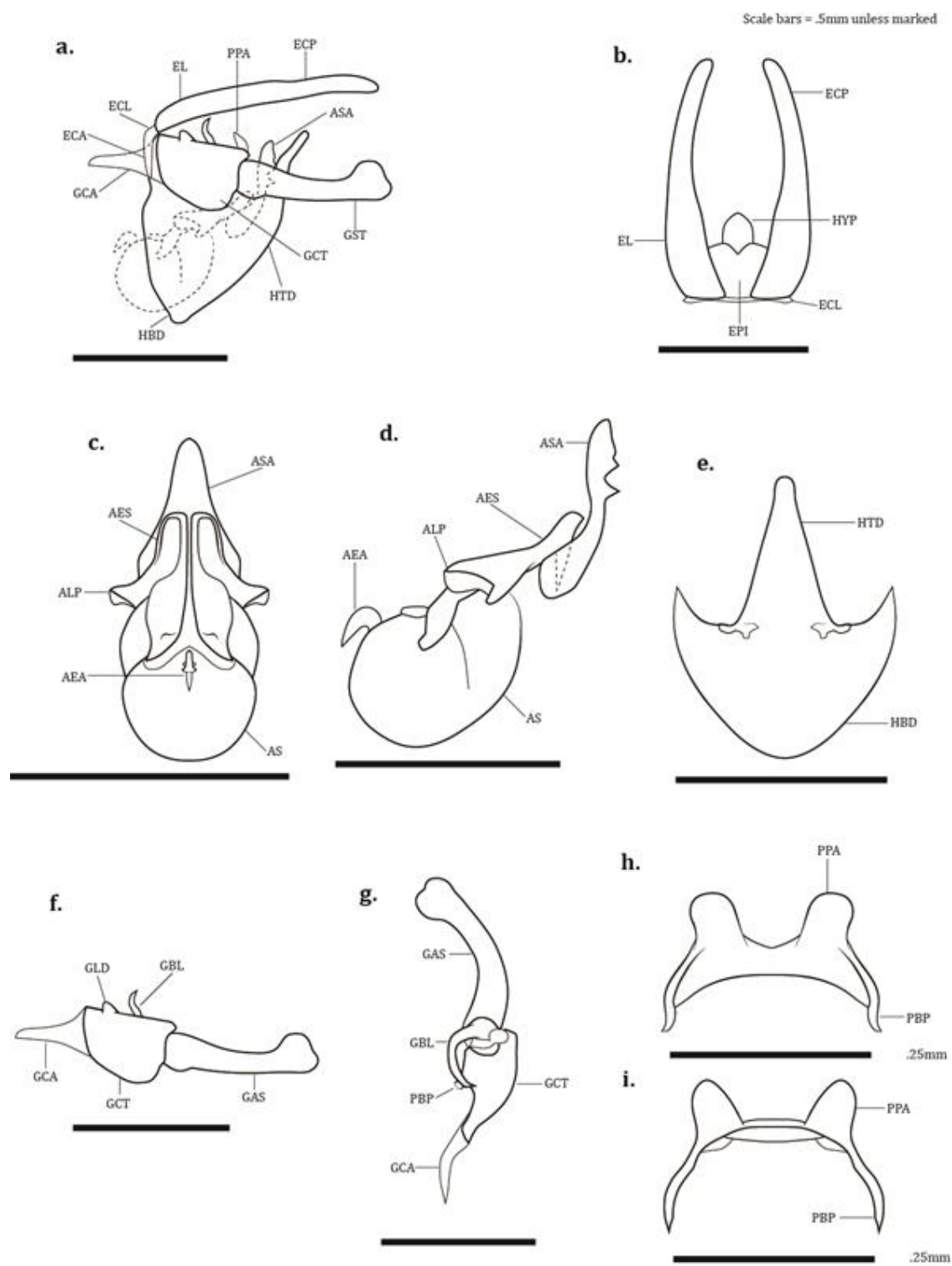


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Figure 111.



Figure 112.

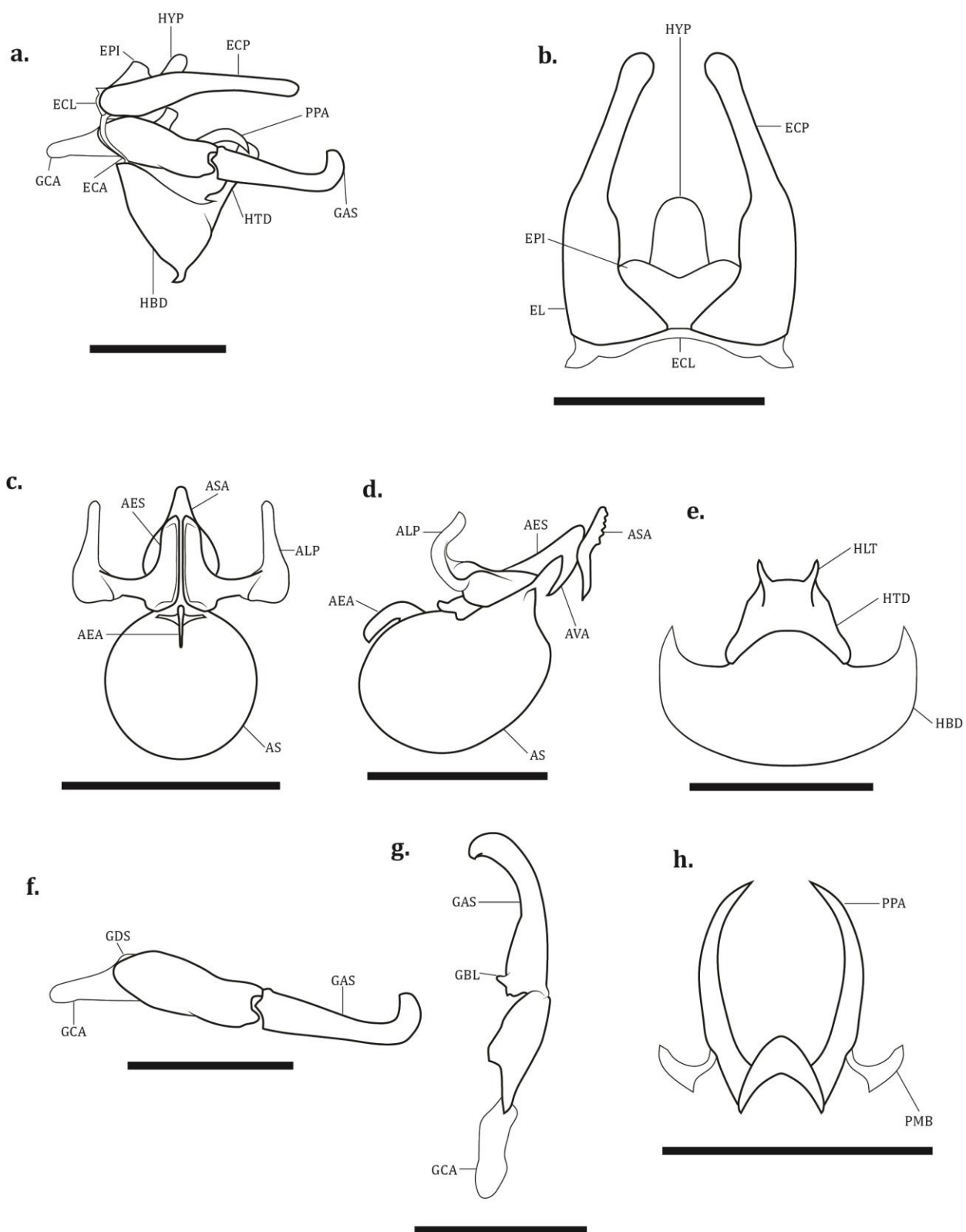


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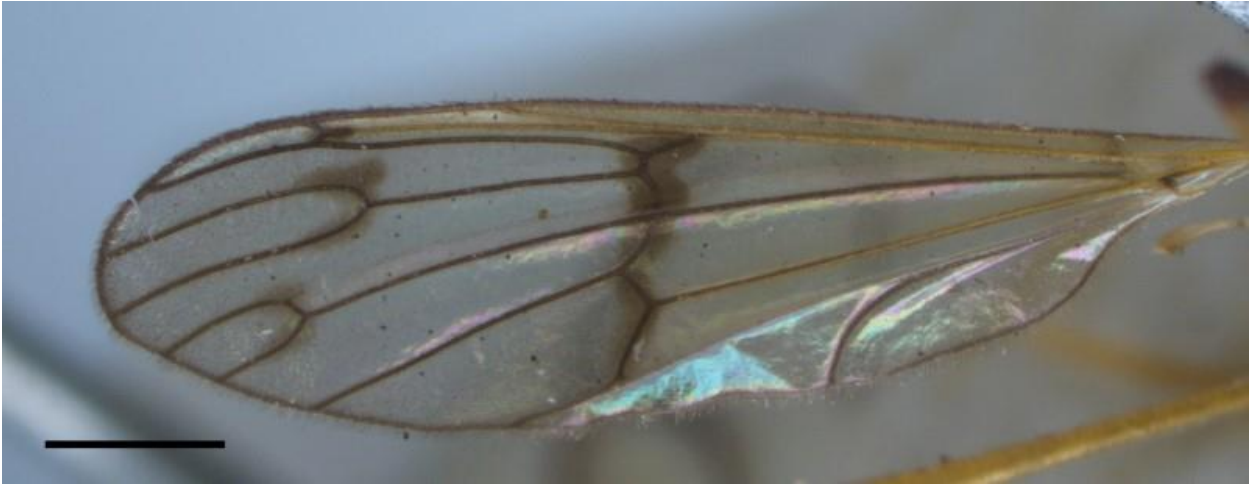


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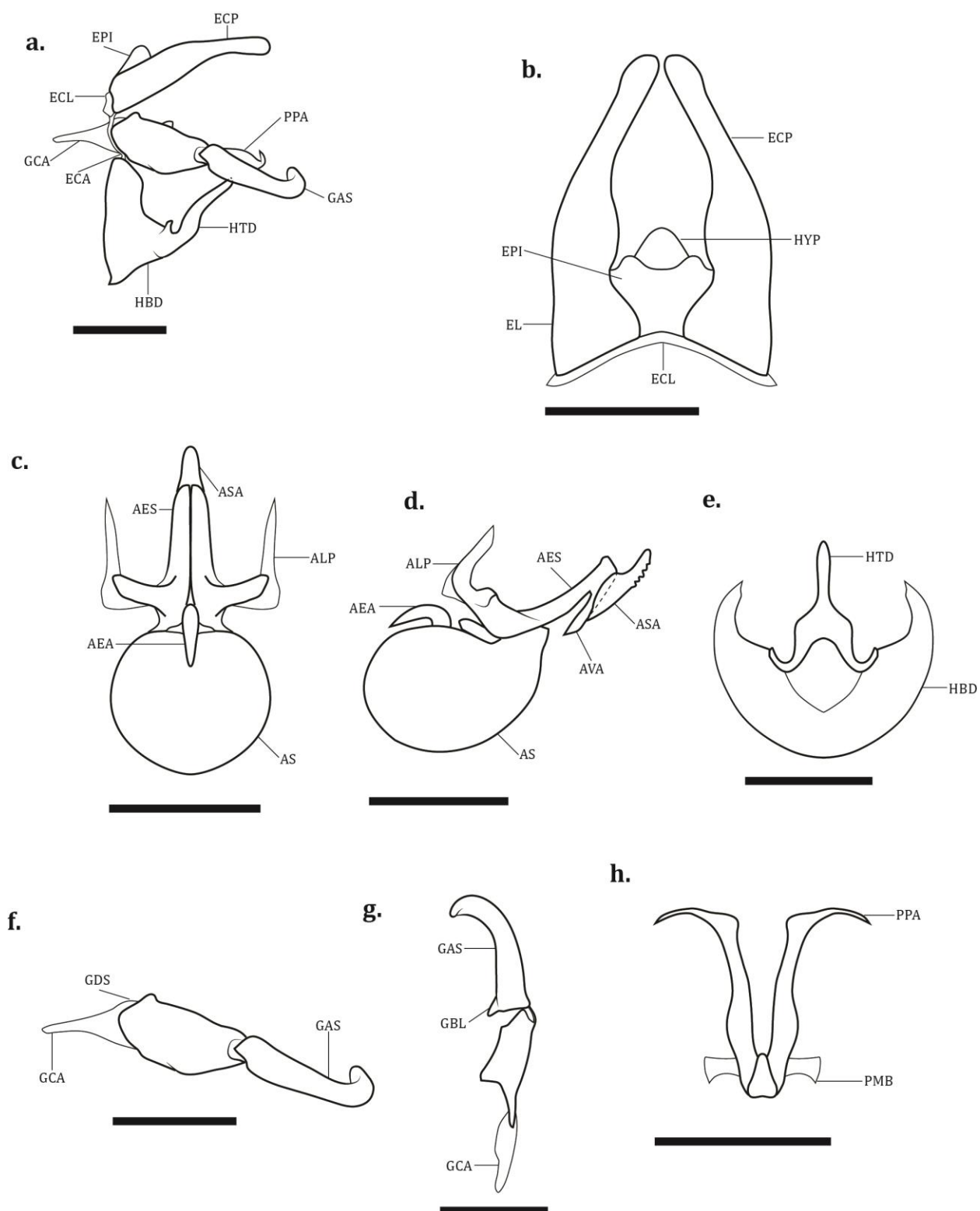


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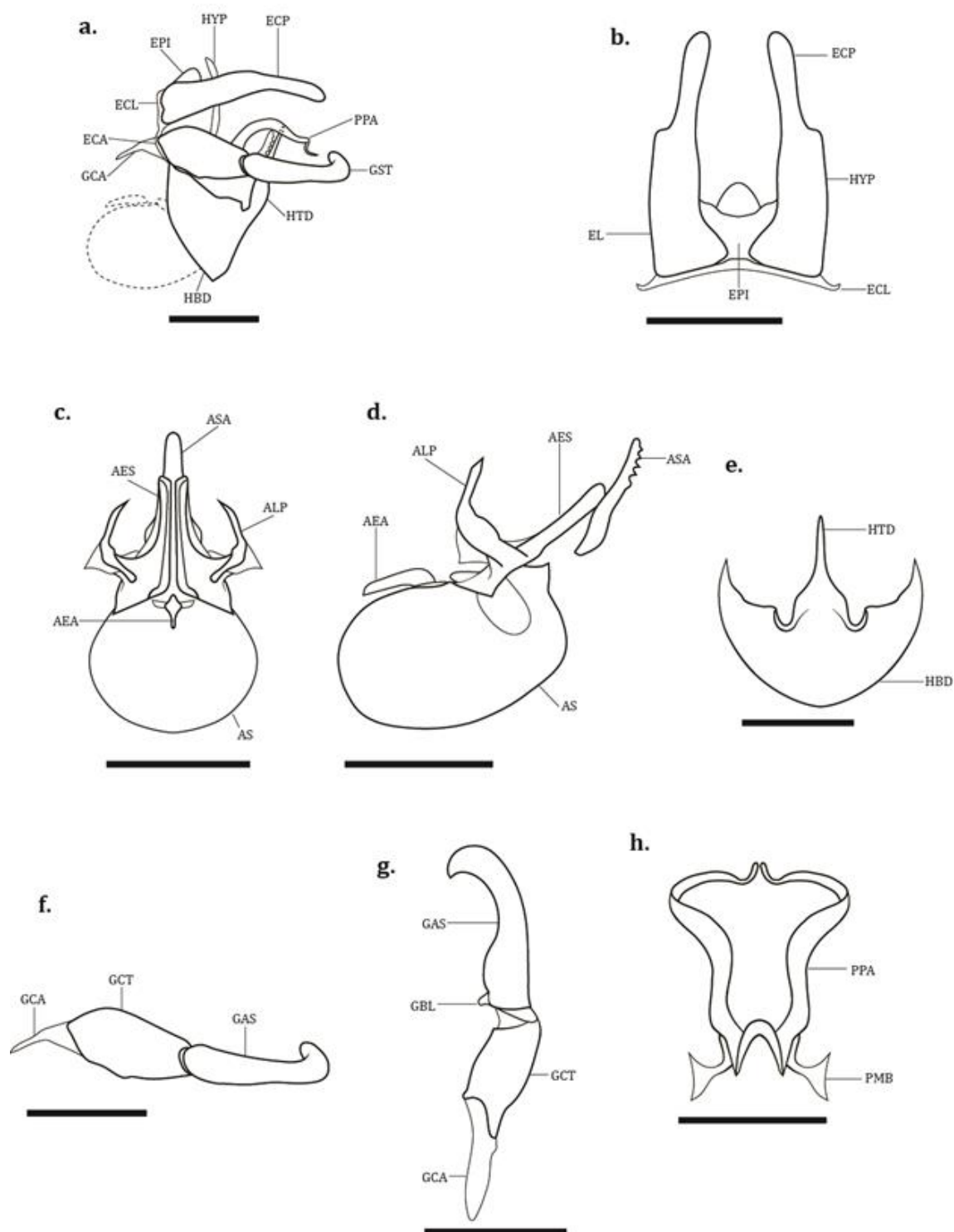


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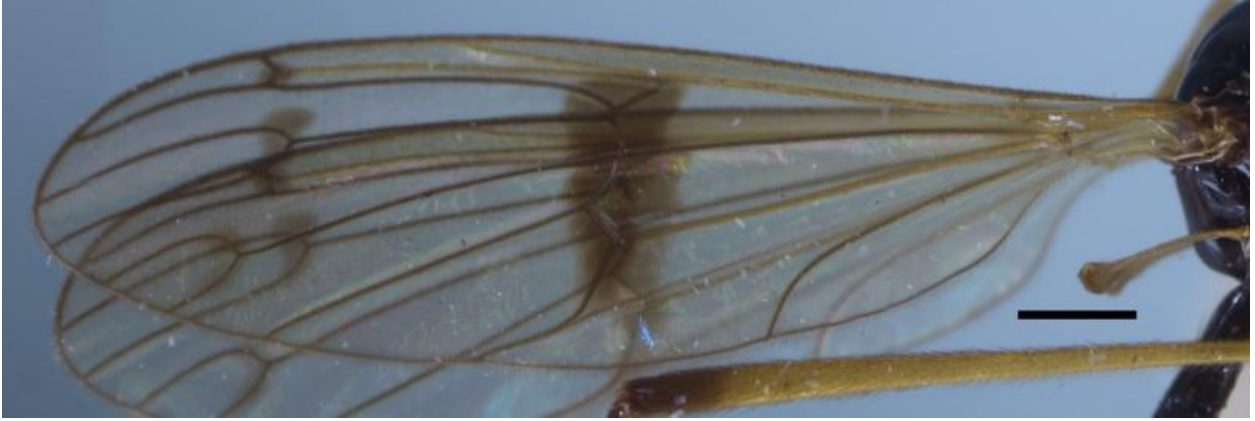


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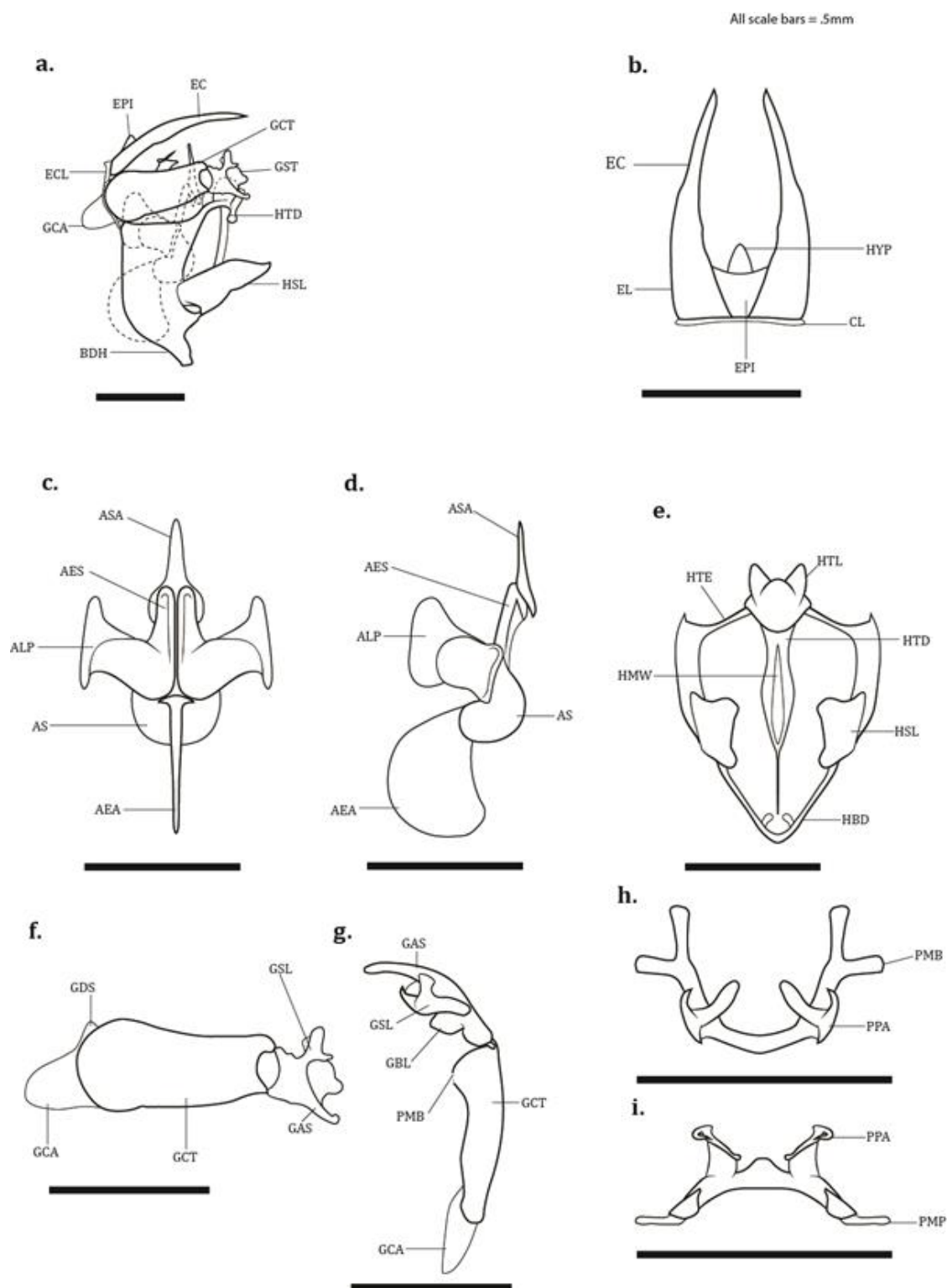


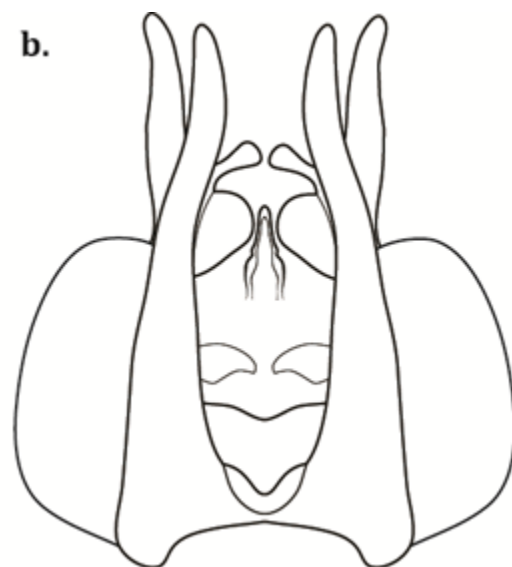
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Figure 121.



Figure 122.

a.**b.****Figure 123.**

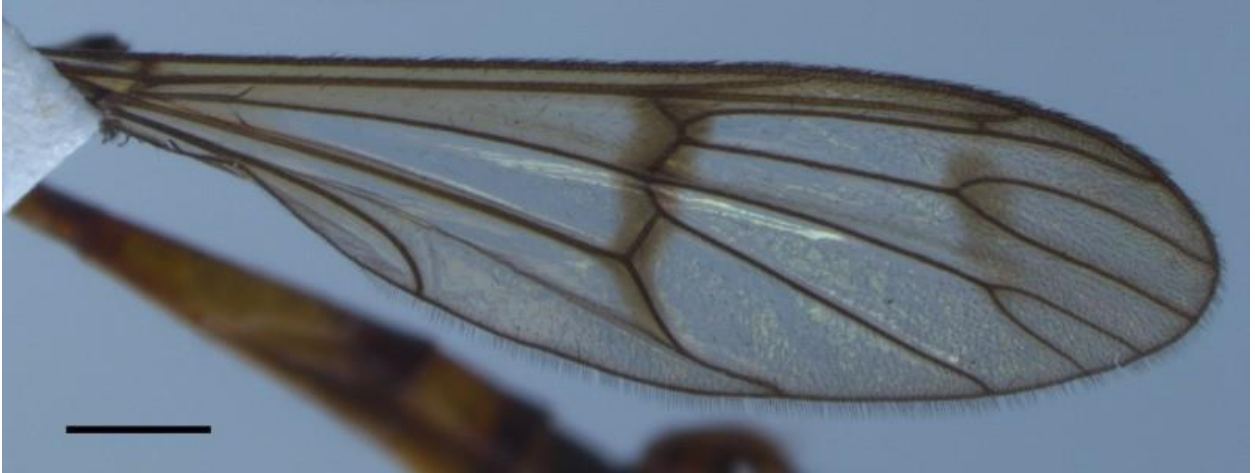


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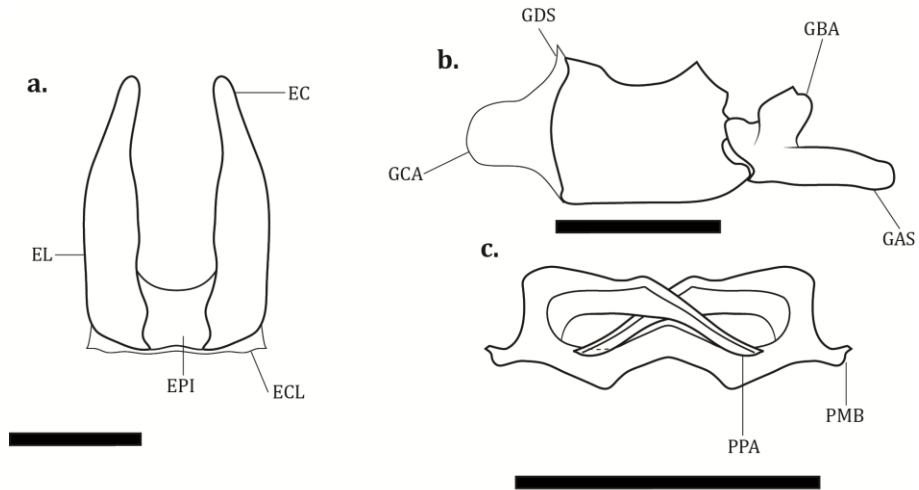


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Figure 127



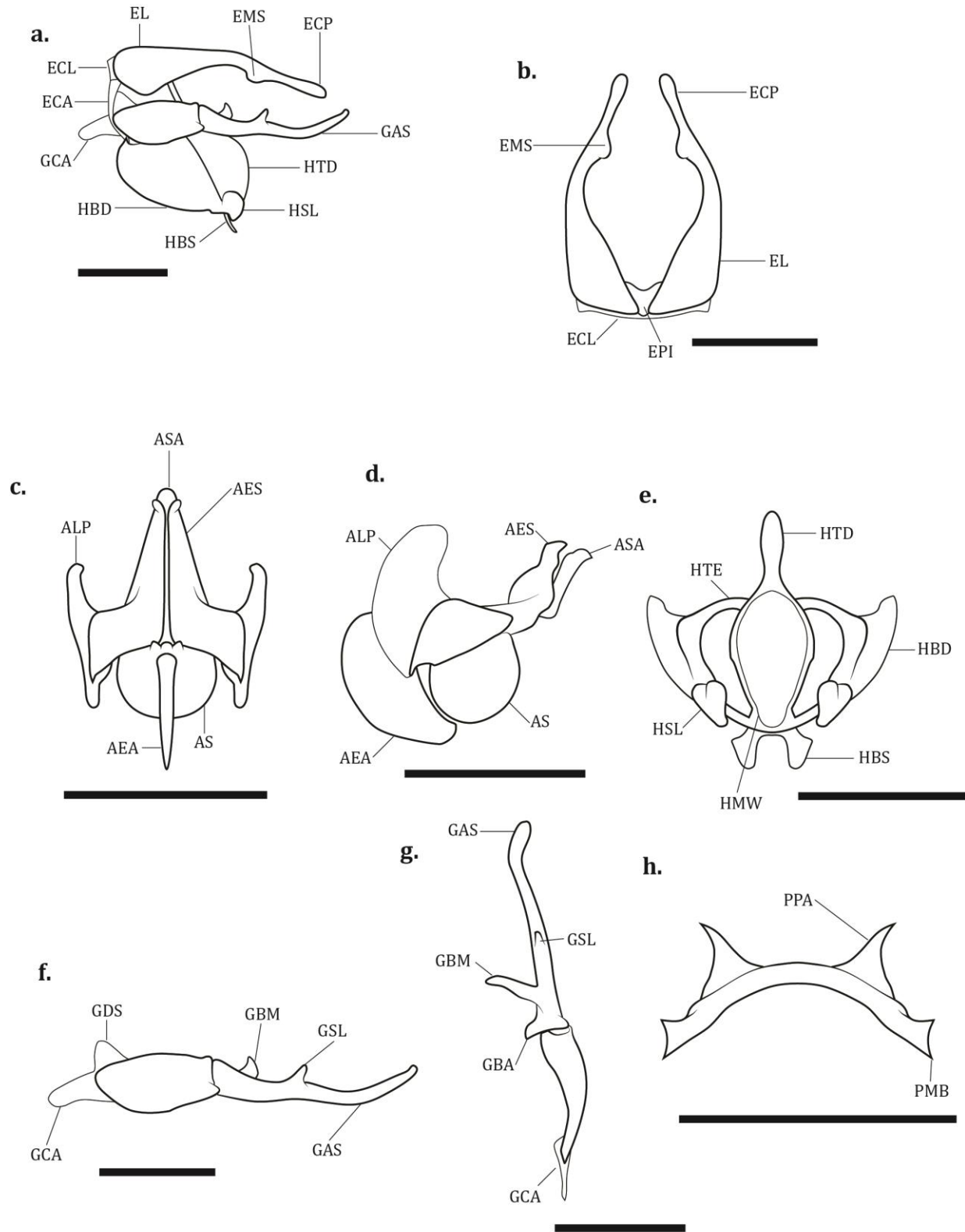


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Figure 130.



Figure 131.



Figure 132.

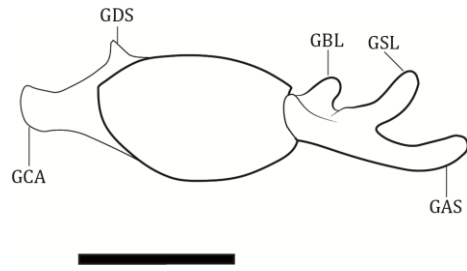


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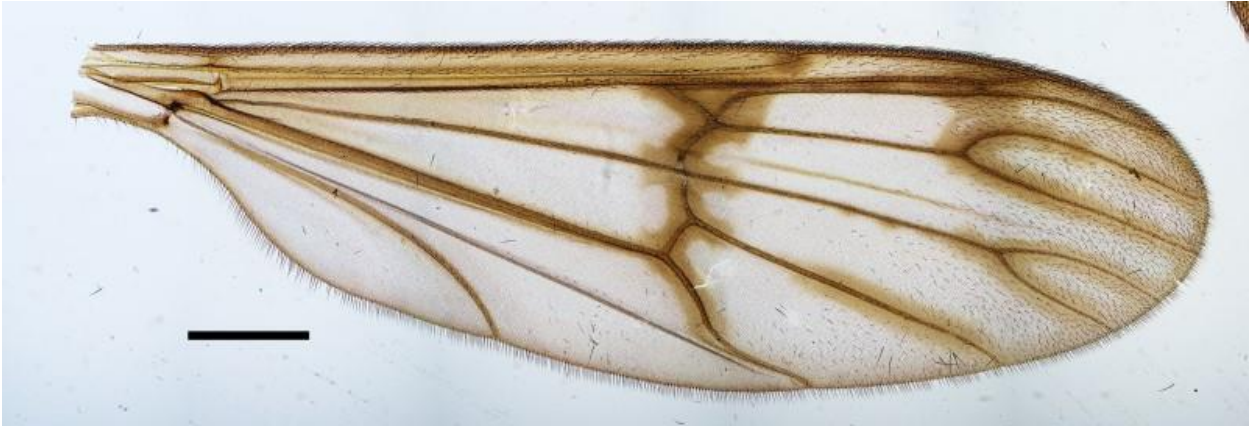


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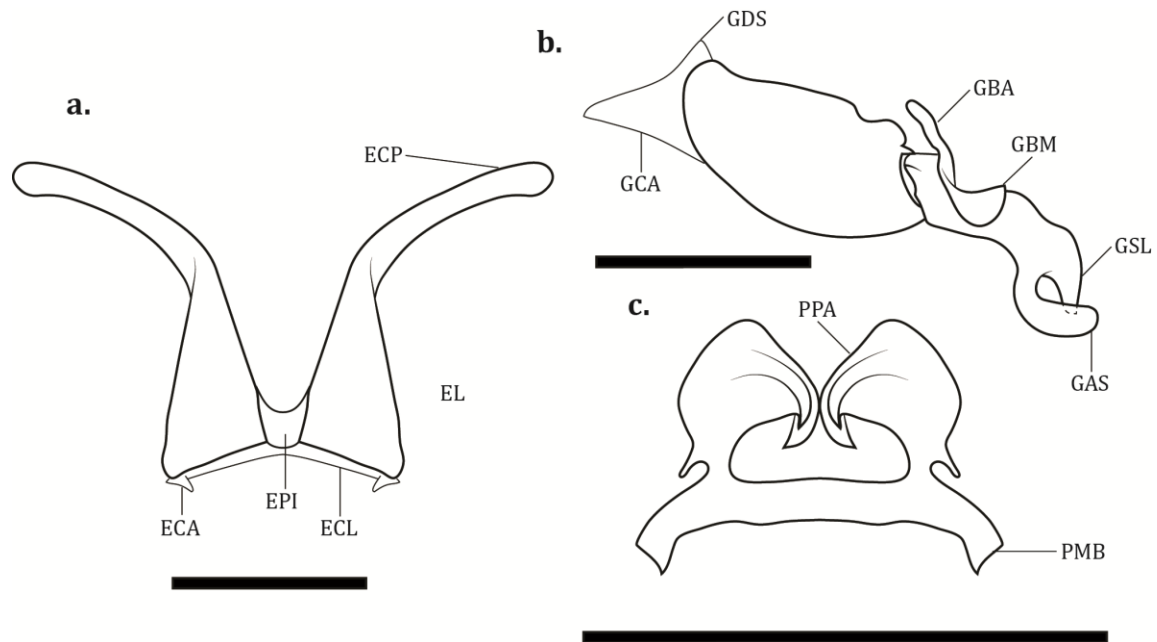


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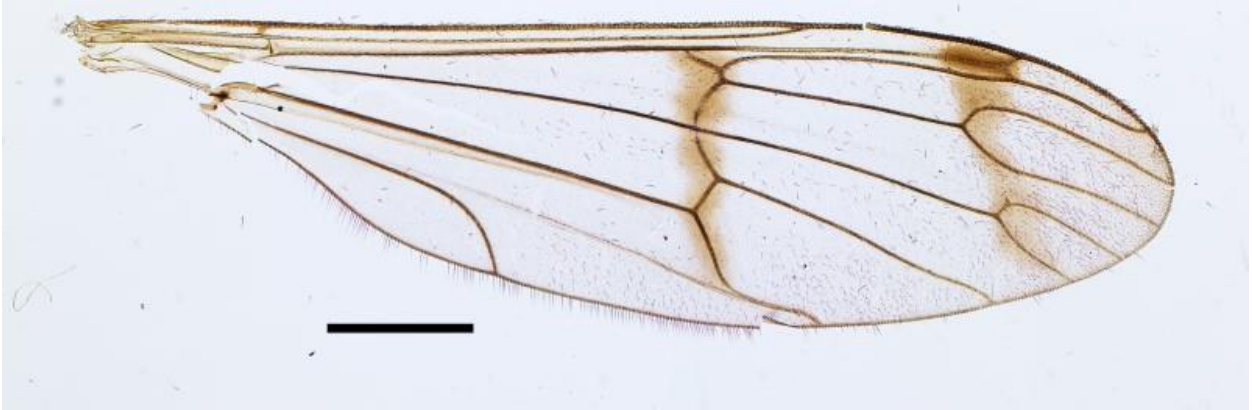


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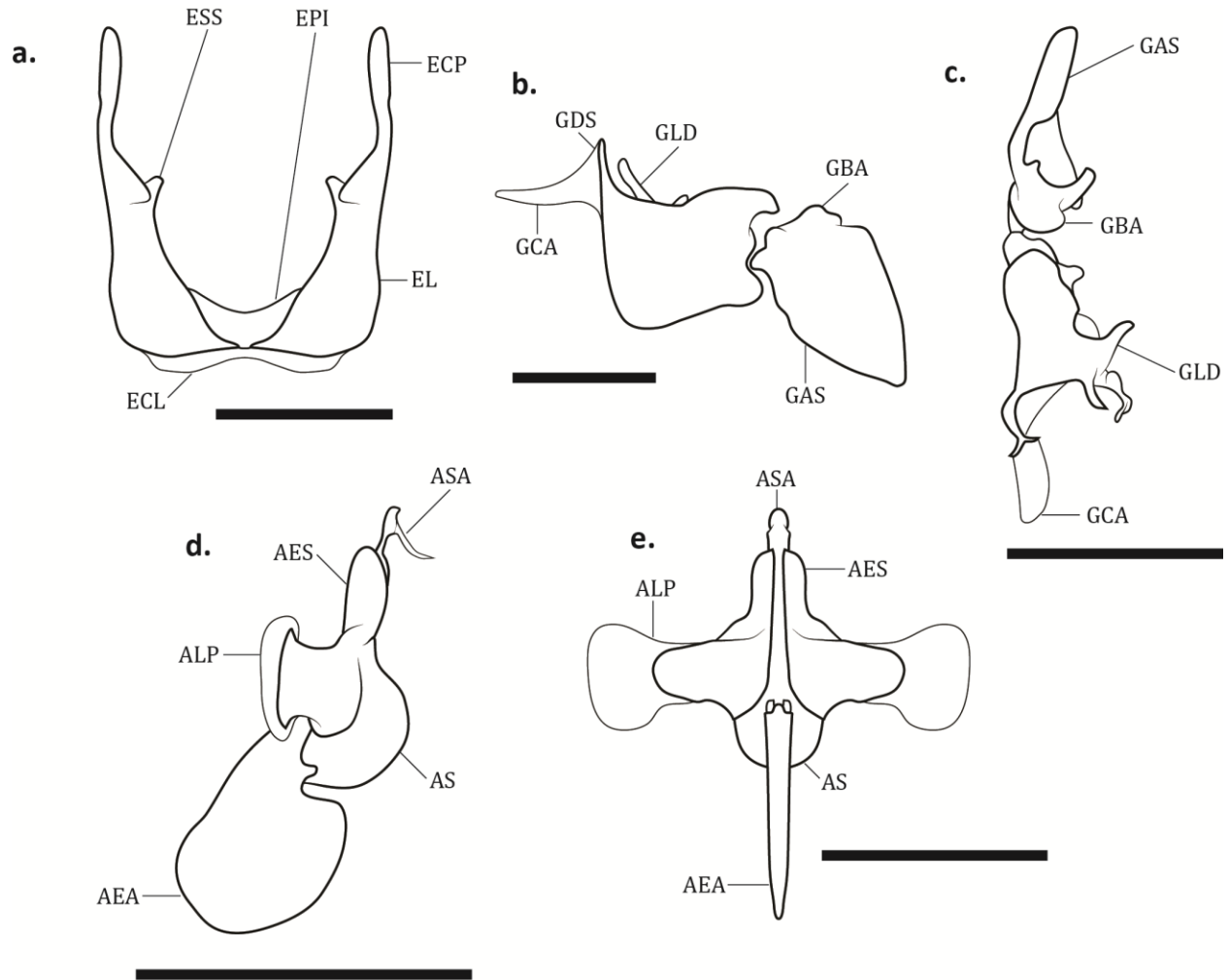


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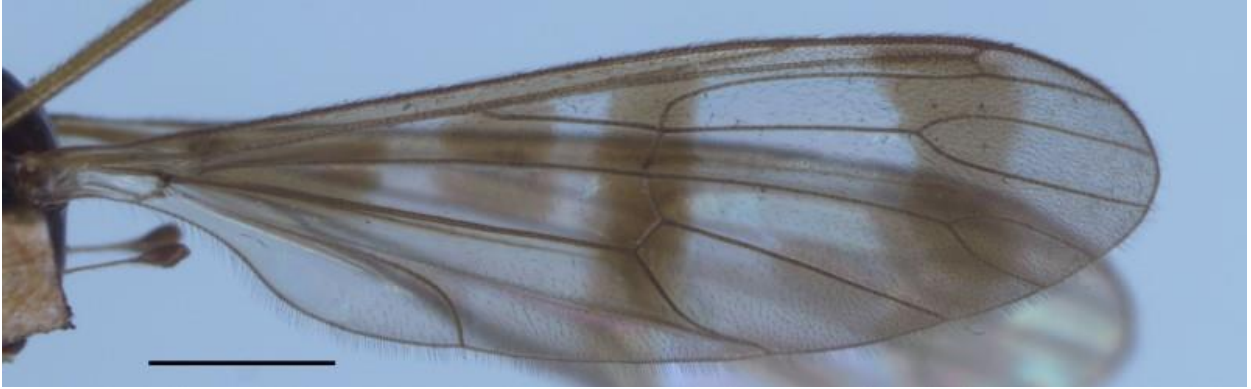


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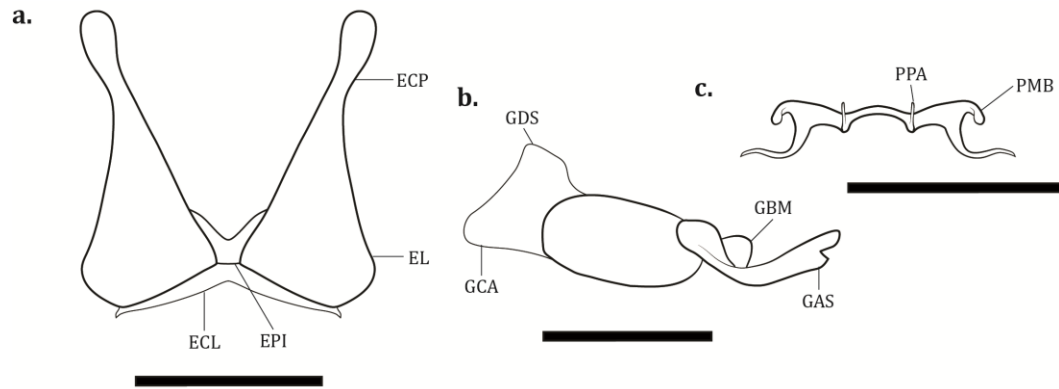


Figure 145.



Figure 146.



Figure 147.



Figure 148.



Figure 149.



Figure 150.



Figure 151.

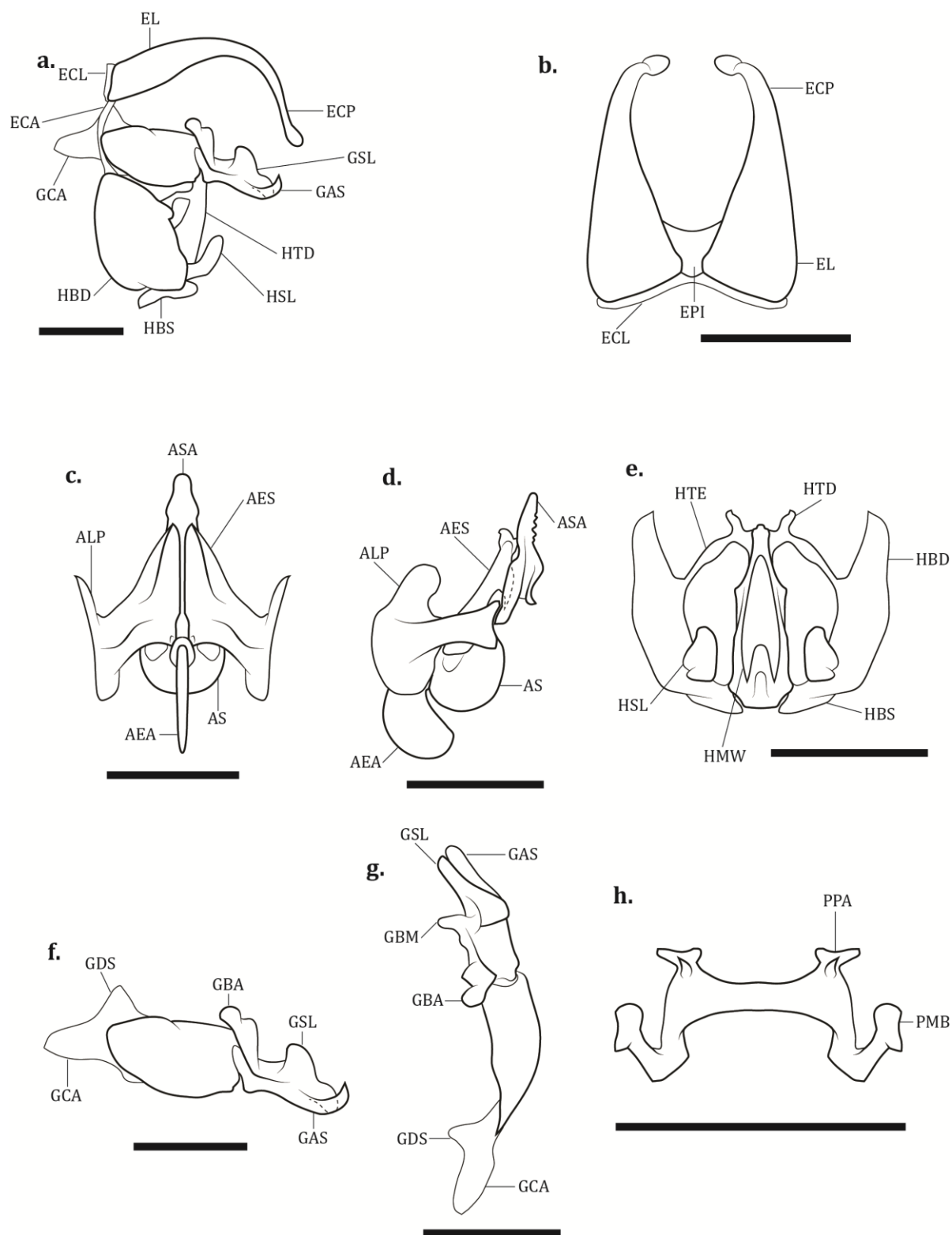


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Figure 153.



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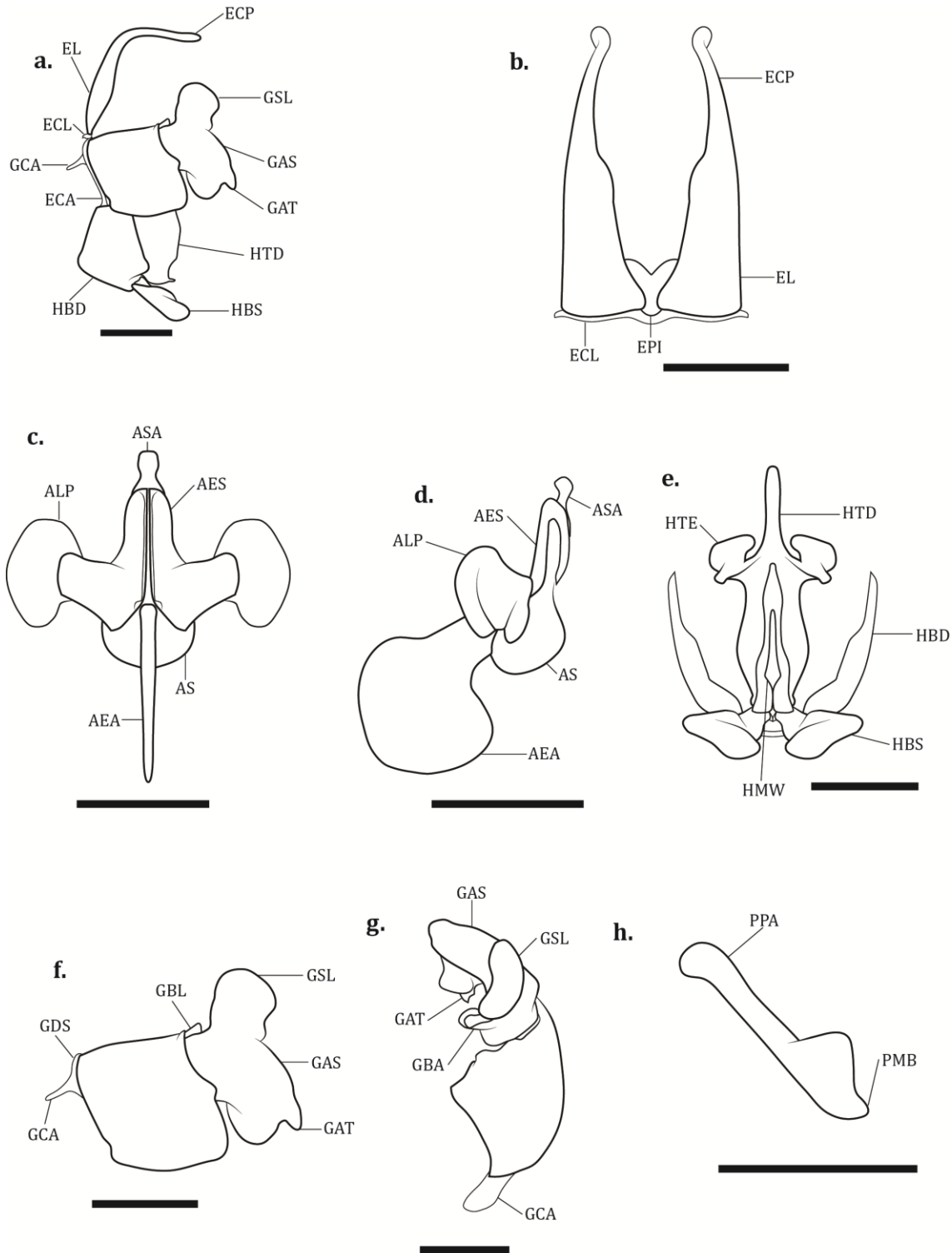


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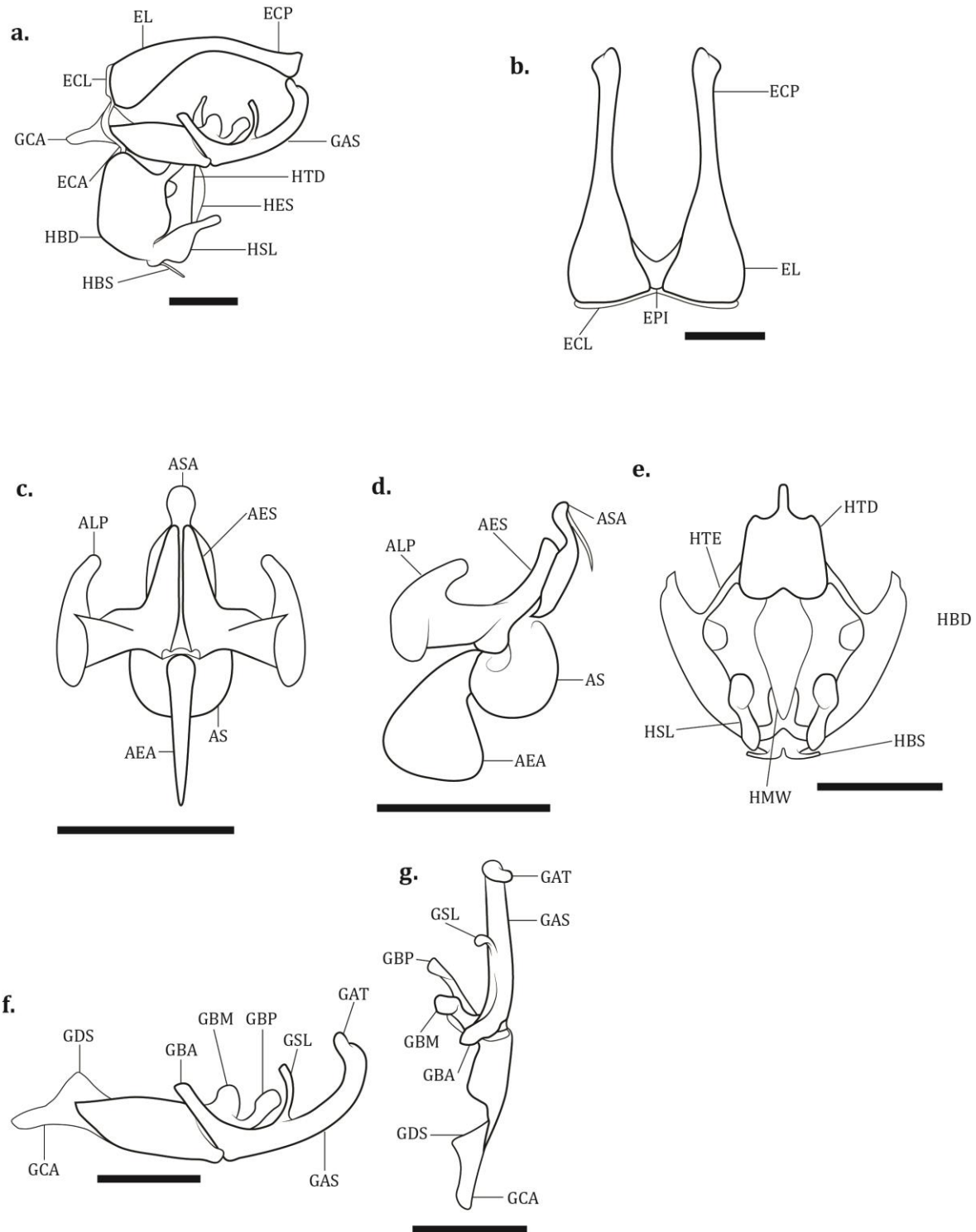


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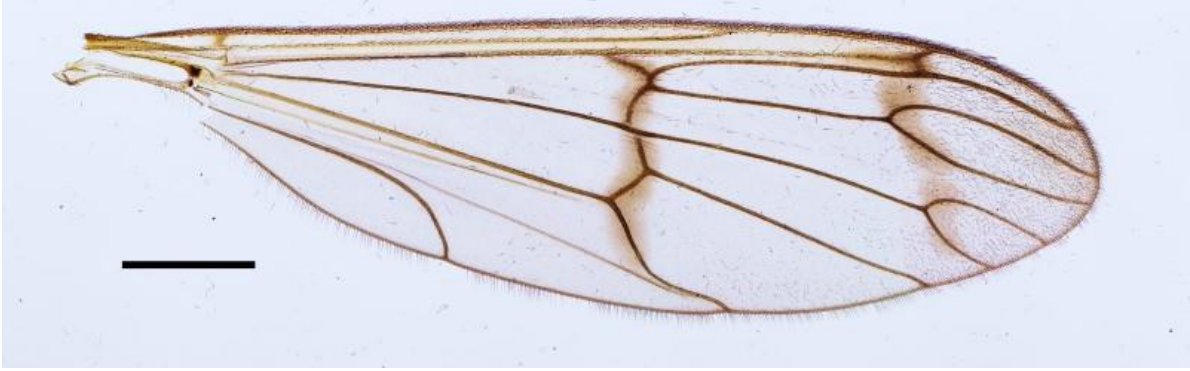


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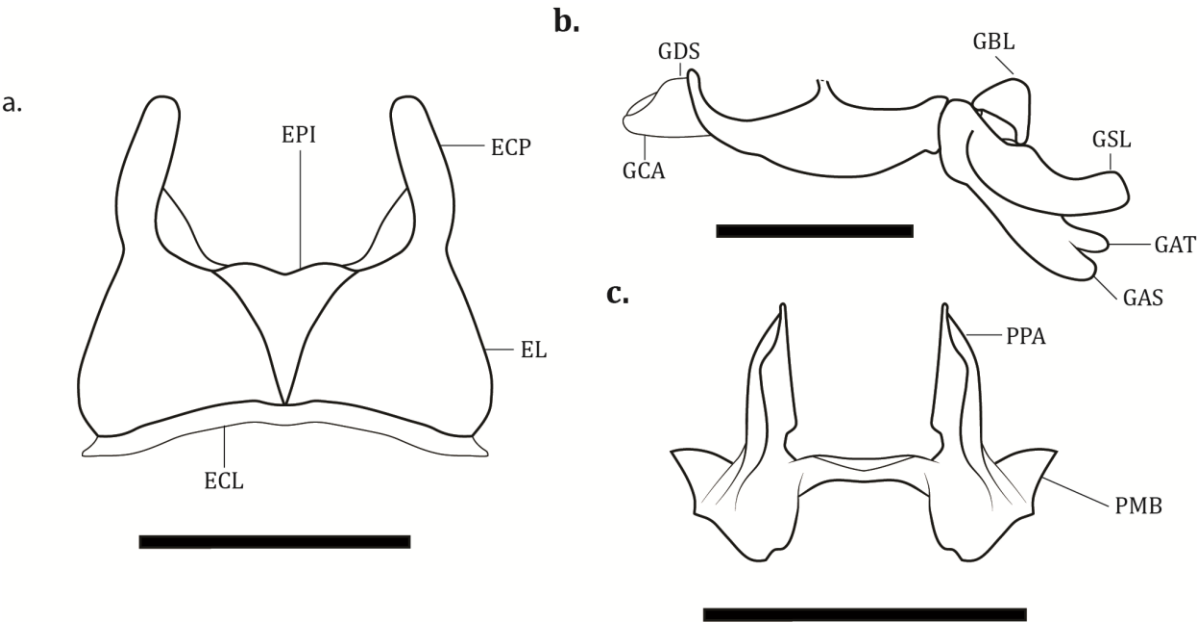


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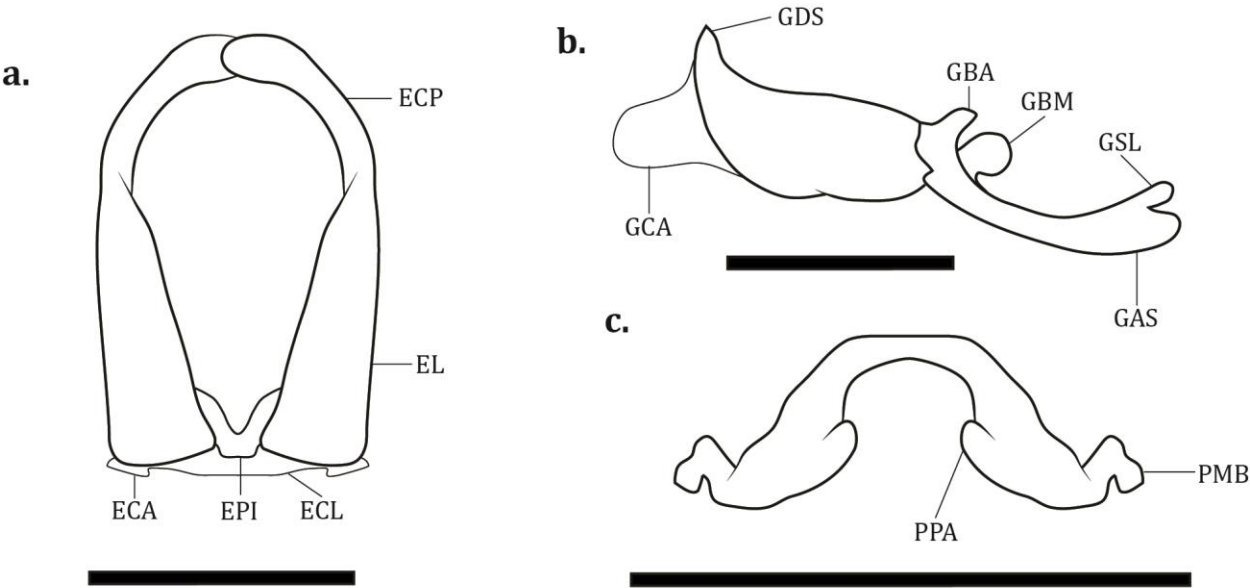


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Figure 165.



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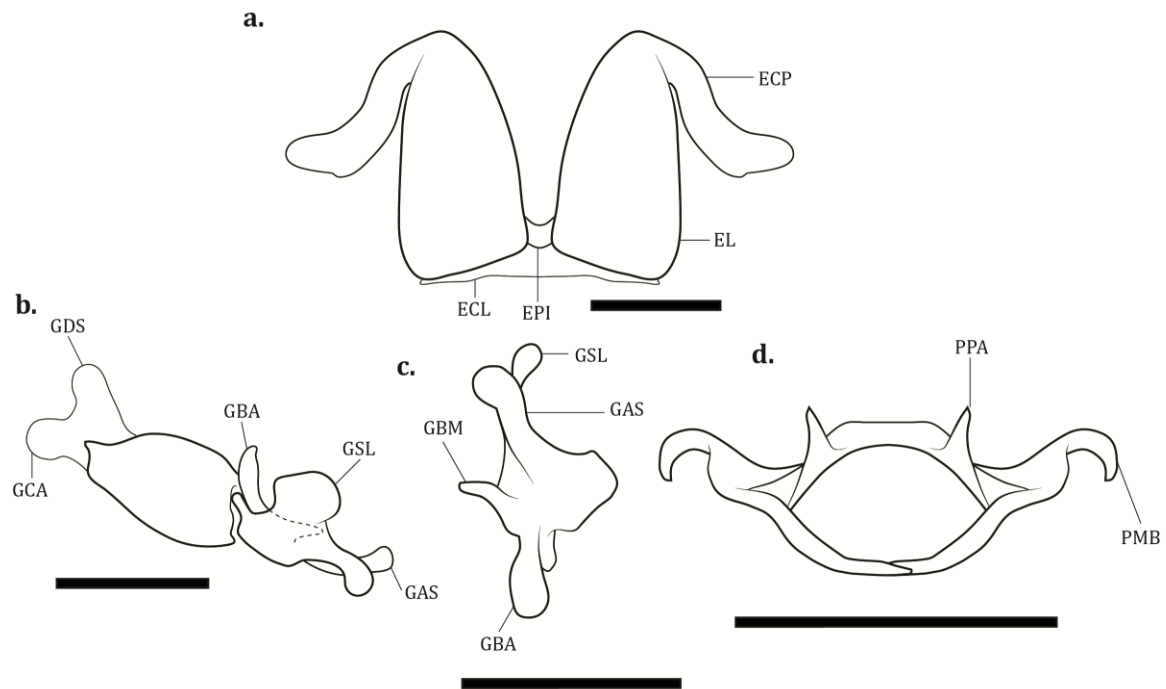


Figure 167.



Figure 168.



Figure 169.

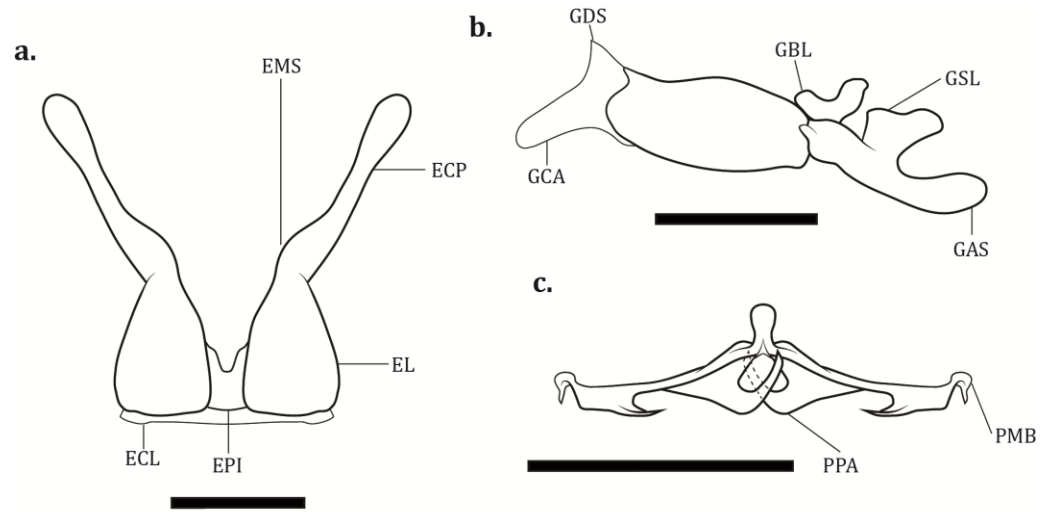


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Figure 171.



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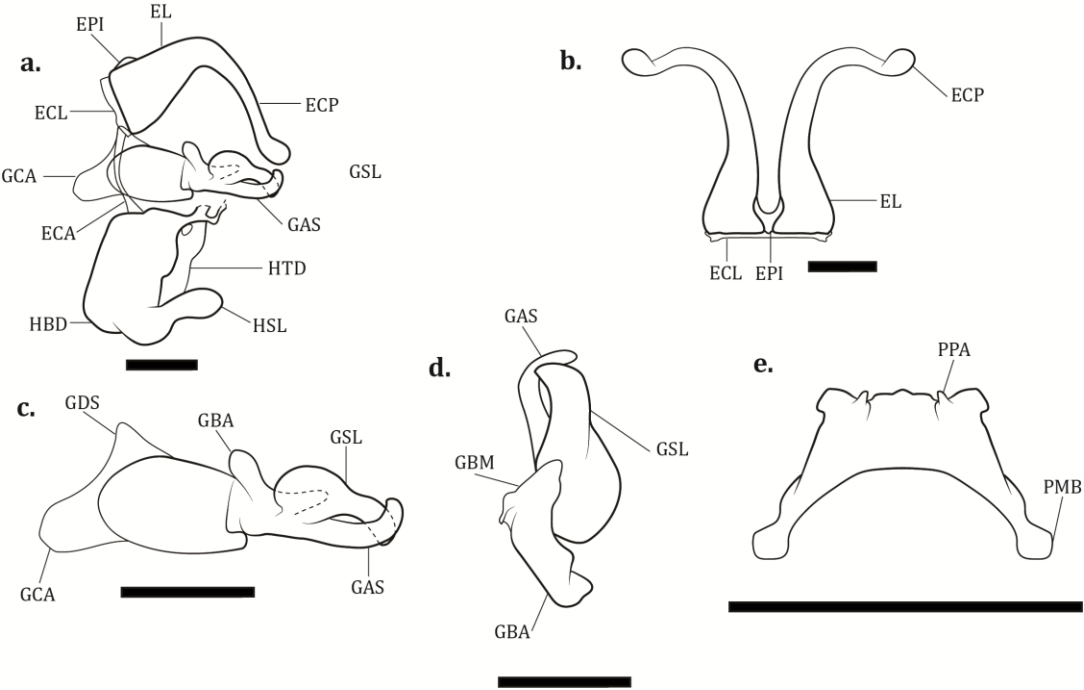


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Figure 174.



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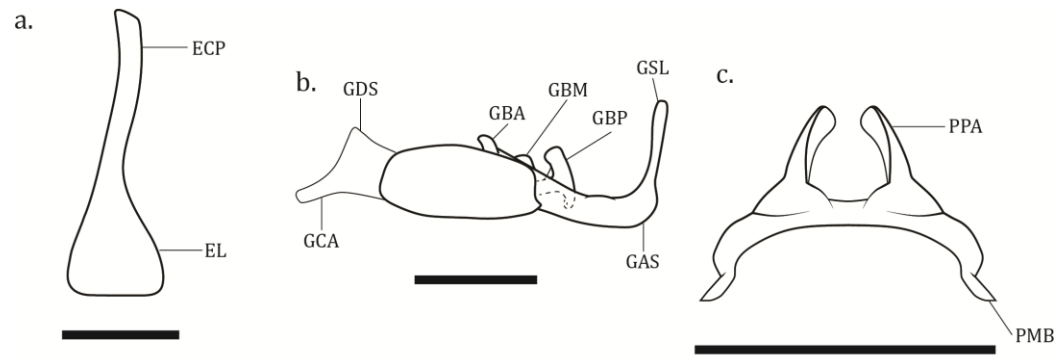


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Figure 177.



Figure 178.

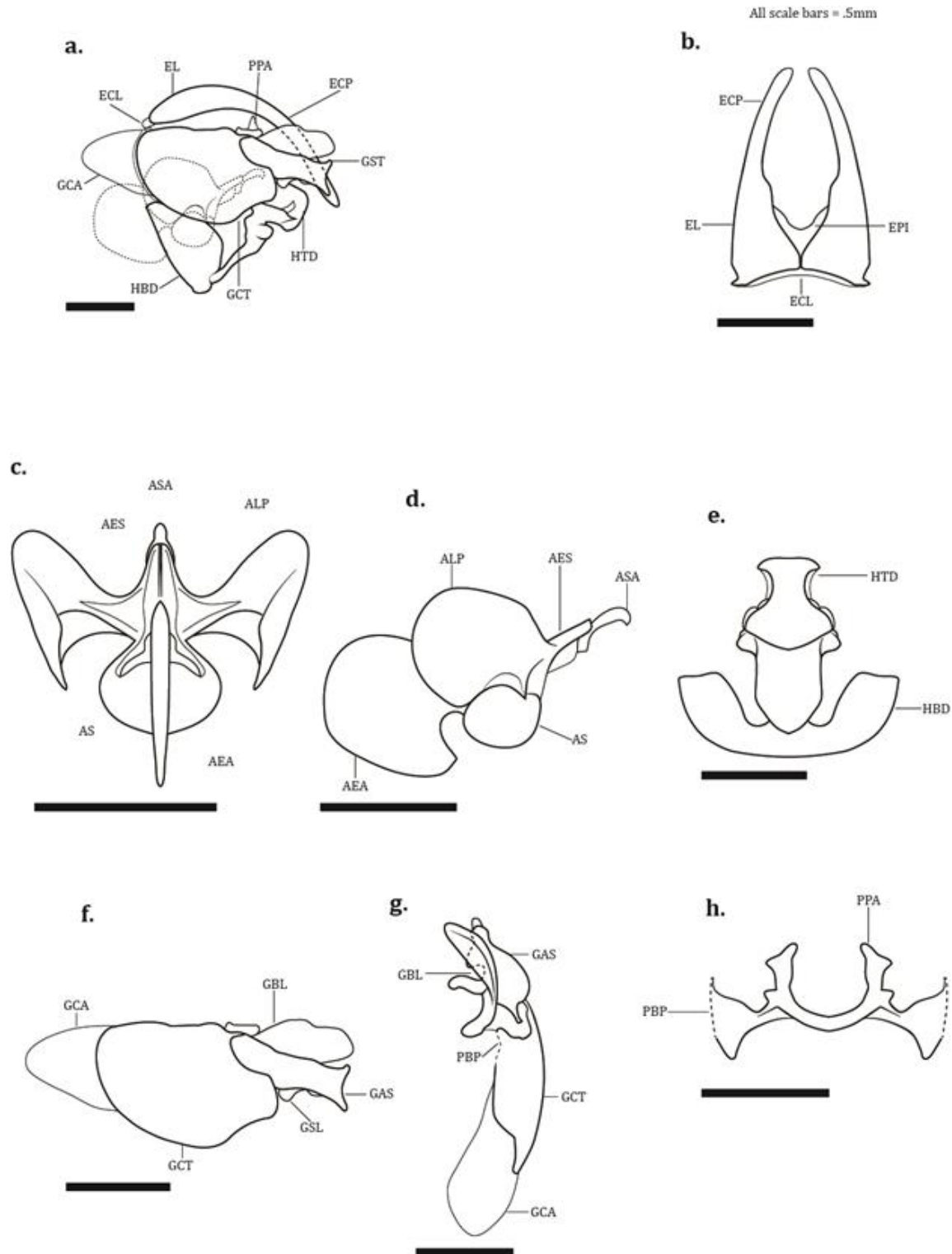


Figure 179.



Figure 180.



Figure 181.

CHAPTER EIGHT: OUTCOMES

In 2009 most species of Ptychopteridae were unidentifiable to anyone but specialists, and even for a specialist many species required references to type specimens. The relationships within the family were understood only to the extent that *Bittacomorpha* Westwood and *Bittacomorphella* Alexander were considered sister groups, and *Ptychoptera* Meigen was considered sister to Bittacomorphinae. The monophyly of the families or genera was never tested. The evolutionary structure of *Ptychoptera* was known only to the extent that *P. (Parapteroptera)* Tonnoir was considered a distinctive group of species in a sea of incertae sedis species (Zwick & Starý 2003). No comprehensive study of the morphological diversity of the group was ever conducted.

The works completed as part of this dissertation will change our understanding of Ptychopteridae, and helped facilitate additional work by specialists and promote broader understanding of the group in evolutionary and ecological contexts. Basic outcomes include: The name *Ptychoptera contaminata* and the usage of *Ptychoptera* and Ptychopteridae were stabilized through designation of a neotype. The previously unexplored complex male genital morphology was cataloged and placed in a coherent and predictive organization scheme. Phylogenies were recovered that answer questions about evolution within the group, and illustrated broader concepts such as allopatric speciation and ecological specialization. New subgenera were erected to recognize well supported clades that corresponded to radiations and specializations within Ptychopteridae. Identification materials were created to facilitate the determination of species without resorting to minimalist original descriptions or type specimens.

There remains extensive regions of ptychopterid taxonomy and phylogeny that merit investigation. The molecular phylogeny included here is but dipping a foot in the ocean, representing only a fraction of the extant fauna based on sampling from a single region. Additionally, while using molecular techniques to solve species level taxonomic problems was not a focus of this study, even this

cursory examination has shown at least three cryptic species complexes in the Nearctic taxa (*Bittacomorpha clavipes*, *Ptychoptera (Tigrimyia) quadrifasciata*, and *Ptychoptera (Unguiptycha) coloradensis*. Species diversity in many regions remain poorly sampled, with the Afrotropics and Asia having only cursory studies at a limited number of sample sites.

Although the structure and homologies of the sclerotized structures of the male genitalia have been explored here, the soft tissue male genital tract was not examined in this study. Furthermore, due to time constraints examination of female and larval character sets was cursory, and there remains much to be discovered in these morphology of the structures associated with these life stages. Natural history and ecology was also only briefly examined during this work, and there remain many interesting questions about speciation sympatry, phenology, and ecological specialization.

The knowledge compiled during this study will ideally serve as a springboard for broader investigations of Ptychopteridae by non-specialists as well as other Dipterists.

Work Cited

Zwick P., Starý J. 2003. *Ptychoptera delmastroi* sp. n. (Diptera: Ptychopteridae) from Italy. *Aquatic Insects* 25(3), 241–246.