

**A revision of the genus *Horaia* Tonnoir (Diptera: Blephariceridae: Blepharicerinae:
Apistomyiini)**

by

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This is to certify that the master's thesis of
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For my family.

TABLE OF CONTENTS

ABSTRACT	v
CHAPTER 1. INTRODUCTION	1
Organization of Thesis	4
CHAPTER 2. METHODS	6
Material	6
Specimen Preparation	6
Terminology	7
Descriptive Format	7
Phylogenetic Analysis	8
CHAPTER 3. KEYS TO BLEPHARICERIDAE GENERA OF NEPAL AND THAILAND AND TO THE SPECIES OF THE GENUS <i>HORAIA</i>	9
Key to Instar IV Larvae	9
Key to Pupae	11
Key to Adults	12
CHAPTER 4. TAXONOMY	14
CHAPTER 5. PHYLOGENETIC RELATIONSHIPS	41
Results	41
Discussion	41
Biogeography	48
APPENDIX A. FIGURES	51
APPENDIX B. PHYLOGENETIC CHARACTERS AND MATRIX	75
REFERENCES CITED	78
ACKNOWLEDGEMENTS	82

ABSTRACT

Net-winged midges of the family Blephariceridae display a unique biology among the Diptera. The immature stages are inhabitants of fast-flowing streams and waterfalls. Phylogenetic analysis of the blepharicerid tribe Apistomyiini, has been hampered by a lack of specimens of all life stages from all genera. Three species have been described in the genus *Horaia* Tonnoir, yet the immature stages are unknown for each of these species. Based on collections made in Nepal and northern Thailand, new data is added to the present knowledge of *Horaia*. Pupal and larval stages of *H. montana* Tonnoir are re-described. Larval descriptions for *H. manaliella* (Kaul) are also provided. Three new species, *H. barbata*, *H. namtoki*, and *H. piedmonti* are described. Dichotomous keys to the adults, pupae, and instar IV larvae of blepharicerid genera and species of the genus *Horaia* in Nepal and Thailand are provided. Phylogenetic analysis is performed on the tribe Apistomyiini. New data indicates that *Horaia* is a monophyletic genus closely related to a branch including *Apistomyia* Bigot and *Parapistomyia* Zwick. *Nothohoraia* Craig is placed as the sister-group to *Curupirina* Stuckenberg+*Nesocurupira* Stuckenberg. *Theischingeria* Zwick is identified as the sister-group to *Austrocurupira* Dumbleton. The proposed phylogeny supports Zwick's Antarctic origin hypothesis for the biogeography of the Apistomyiini in Asia and Australasia.

KEY WORDS – Nepal, Thailand, net-winged midges, systematics, phylogeny, biogeography.

CHAPTER 1. INTRODUCTION

The Blephariceridae are a highly specialized family of aquatic Diptera. Larvae and pupae inhabit cascades, waterfalls, and torrential streams throughout the world. These immature stages display a number of unique adaptations to their rheophilic lifestyles. All four larval instars have the head, thorax and first abdominal segment fused into a structure referred to as a cephalothorax. The final four abdominal segments are fused into a single anal division. This gives a general body shape consisting of a cephalothoracic division, four abdominal trunk segments, and an anal division. Respiration takes place while under water via a series of filamentous gills found on each division. Each division is also equipped with a ventral suction disc and a pair of functional prolegs. These adaptations allow the larvae to resist the constant pressure of water current and successfully inhabit torrenticolous habitats (Frutiger 1998). The larvae persist mainly on a diet of periphytous algae and form a significant proportion of the primary consumers in torrenticolous habitats (Alverson *et al.* 2001).

Blepharicerid pupae have a streamlined shape and a pair of prominent thoracic respiratory organs. Pupae are permanently attached to rocks in rapidly flowing, highly oxygenated water. The respiratory organs project up into the current. The shape of the pupa creates complex flow patterns over the body that generate negative pressure near the respiratory organs (Pommen and Craig 1995). This negative pressure allows for the creation of a plastron, or permanent air bubble, through which gas exchange takes place.

Blepharicerid adults are short-lived and rarely collected. The common name of the adults, “net-winged midges”, describes the key familial feature, a series of intercalary folds on the surface of the wings. These folds are the result of a complete development of the wings in the pupal stage and a rapid deployment upon emergence (Tillyard 1922). The overall appearance is typical of the “nematocerous” flies, with long antennae and a slender body shape. Ecology and phenology of the adults is poorly known due to the rarity of

collected adult specimens. The adults of most species of Apistomyiines are suspected to be nectar feeders spending most of their life in riparian vegetation (Zwick 1998).

Blephariceridae are a monophyletic dipteran family that originated in the Jurassic (Courtney 1991). The most recent phylogenetic work on the nematoceros Diptera (Oosterbroek and Courtney 1995) indicates that Blephariceridae is the sister-group to Deuterophlebiidae, based partly on the structure of the larval prolegs. Blephariceridae, Deuterophlebiidae, and Nymphomyiidae comprise the monophyletic infraorder Blepharicerimorpha.

Early subfamilial classification of the family Blephariceridae (eg. Alexander 1958; Hogue 1973) recognized four subfamilies: Edwardsininae, Blepharicerinae, Apistomyiinae, and Paltostominae. While recent data indicate that the family did indeed split into the Blepharicerinae and the Edwardsininae before the Cretaceous (Courtney 1991), other subfamily designations are questionable. Recent studies (eg. Zwick 1977, 1989; Courtney 2000a) recognize the two subfamilies, with Blepharicerini (s.s.), Apistomyiini, and Paltostomatini considered tribes within the Blepharicerinae (s.l.).

In early systematic research on the family, Hora (1930) separated the Blephariceridae into two groups, to which he did not give formal names. One of these groups consisted of those species having larvae with well-marked lateral appendages and constrictions between body divisions. The second group consisted of species with a chiton-like larval form and poorly defined lateral appendages. Hora suspected that the dorsoventrally flattened body of this group allowed it to withstand strong currents. He also suggested that the elongate spines present on the dorsum of some specimens further reduced the effects of strong current on the larvae. This second group corresponds well with the unique larval characteristics of the species *Horaia montana* Tonnoir. The species was formally described soon after the publication of Hora's research.

Tonnoir (1930) described the genus *Horaia* (named after Dr. S.L. Hora) and designated *H. montana* as the type species. He based his description on specimens collected in northeastern India. The initial species description was based on male and female imagoes dissected from pupae. Detailed descriptions of adult females of *H. montana* were published in a subsequent paper (Tonnoir 1932), but descriptions of immature stages were not included. This second paper also included a description of a second species, *Horaia longipes*, based on an adult female also collected in northeastern India. No descriptions of adult males, pupae, or larvae were provided for *H. longipes*.

Tonnoir (1930, 1932) noted a number of larval and pupal forms of *Horaia* present in India. He suggested that up to three other possible species of *Horaia* were present amongst the specimens examined. These other species were not named, as only larval or pupal specimens were available for each. Tonnoir also mentioned a specimen, described as “Larva K”, which he was unable to place within a genus, but which bore similarity to both *Horaia* and the genus *Apistomyia* Bigot.

Kaul (1976) described a new genus in the Blephariceridae based on specimens from northwestern India. He named the genus *Manaliella* and designated *M. manaliella* as the type species. Imagoes of both sexes dissected from pupae were described, as were larvae and pupae. The genus was similar to *Horaia* in the absence of mandibles in the adults, but differed in wing venation and genitalia.

Zwick (1990) synonymized *Manaliella* with *Horaia* based on a lack of significant difference in wing venation and the lack of a detailed description of the genitalia. He suggested that the larva described was a misidentified member of the genus *Philorus* Kellogg and was not of the same species as the described adults. Pupal descriptions are valid, because adult descriptions were based on dissected imagoes. This effectively adds a third species to the genus *Horaia*, with larval stages unknown for all species and pupal characteristics described for only one species.

Global and regional catalogues of Blephariceridae (Alexander 1958; Hogue 1973) have described *Horaia* as being restricted to the Himalayan regions of India and Nepal. Recent collections indicate a distribution extending to northern Thailand and Vietnam. Examination of recently collected Nepalese and Thai specimens suggest the presence of more species of *Horaia* than the three currently known. As well, immature stages of known species have been found.

Here, I provide complete descriptions of all life stages (four larval instars, pupae, adult males, adult females) of all current species, where possible. I describe three new species from Nepal and northern Thailand. A key for all life stages is provided. An analysis of the phylogeny of the genus *Horaia* is completed. Species and genus descriptions are used to reassess the phylogeny of genera within the Apistomyiini. The biogeography of the Apistomyiini is also addressed.

Organization of Thesis

The thesis is organized into five chapters. Chapter 1 serves as a background to the present knowledge of the family Blephariceridae as well as the history of the genus *Horaia*. Chapter 2 outlines the methods of collection and analysis used to complete my research. Chapter 3 is a key to the Blephariceridae genera of Nepal and northern Thailand and the species of the genus *Horaia*. Separate keys are provided for adults, pupae, and instar IV larvae. Chapter 4 is a taxonomic section including an updated description of the genus *Horaia* and complete descriptions of all six species mentioned previously. Chapter 5 addresses the phylogenetic relationships within the tribe Apistomyiini and the genus *Horaia*. Included are the results of cladistic analysis and sections on the phylogeny and biogeography of *Horaia* specifically and Apistomyiini in general. My study represents the most complete research on the Apistomyiinae of Thailand and Nepal.

As per Article 8.2 of the International Code of Zoological Nomenclature (1999), this document is not issued for the permanent scientific record or for purposes of zoological nomenclature. Consequently, any species names contained herein should not be considered as published (*sensu* ICZN).

CHAPTER 2. METHODS

Material

This research is based on an examination of all known species of the genus *Horaia* Tonnoir. Most specimens were collected between 1994 and 2001 by means of aerial capture and benthic sampling. Association of the larvae with pupae as well as pupae with adults was chiefly by the ontogenetic method (Hogue and Bedoya-Ortiz 1989). Pupa-adult associations were also made by rearing pupae individually to emergence (Courtney 1998). Additional specimens were borrowed from or are deposited with the following (acronyms used throughout the text): CNC, The Canadian National Insect Collection, Ottawa, Ontario, Canada; IM, the Indian Museum, Calcutta, India; ISU, Iowa State University Insect Collection, Ames, Iowa, United States; PZ, the private collection of Dr. P. Zwick, Limnologische Fluss-Station Schlitz des Max-Planck-Instituts für Limnologie, Schlitz, Germany; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Specimen Preparation

Field collected and laboratory reared specimens were fixed in 70-80% EtOH. Morphological studies were based on whole animal preparations, slide mounts, and scanning electron microscopy (SEM). Slide mounted materials were cleared in cedarwood oil and mounted in Canada Balsam. Genitalia were cleared in dilute potassium hydroxide and slide mounted temporarily in glycerin jelly. After genitalia were removed, adults were dried chemically with hexamethyldisilazane (HMDS). Specimens were observed by using an Olympus SZX-12 dissecting microscope and a Nikon E800 compound microscope, both fitted with an optical micrometer. Drawings were rendered with the aid of camera lucida. Photomicrographs were captured digitally using a SPOT RT® Color digital camera and Adobe Photoshop® 4.0. Material for SEM examination was critical point dried and sputter-

coated with gold-palladium. Scanning Electron Microscope images were captured digitally on a JEOL JSM5800LV microscope.

Terminology

Descriptions of adult morphological structures follow Merz and Haenni (2000) as well as recent papers on Blephariceridae (Zwick 1977, 1998; Courtney 2000a, 2000b). Terminology for male terminalia is that of Sinclair (2000) and Courtney (2000a, 2000b). Female postabdomen terminology of Kotrba (2000) and Courtney (2000a, 2000b) is used. Larval terminology is primarily that of Courtney et al. (2000) and Courtney (2000a, 2000b). Microsculptural terminology of the integument follows that of Harris (1979).

Descriptive Format

Diagnoses are provided for all species. Complete descriptions of adults, pupae and instar IV larvae are provided for all new species, where possible. Previously unknown life stages for described species are described, otherwise, reference is made to original descriptions. When applicable, sample sizes are provided before each description, with values presented as a mean followed by a range in parentheses. Larval body length is provided although it is highly variable within a given species and instar (Kitakami 1950; Craig 1969). Antennal shape, proleg shape, gill filament number, setal length and cranial width are consistent within an instar (Craig 1969). Larval characters given, unless otherwise noted, refer to late instar IV larvae. Larval cranial width refers to the distance between the antennal bases.

Abbreviations for life stages: L = Larva; P = Pupa; Pex = Pupal exuvia; A = Adult. Abbreviations for label and locality information include the following: coll. = collected by; E = East; Kh = Khola; N = North; NP = National Park; Rd = Road; S = South; SFR = Shivapuri Forest Reserve; trib = tributary of; W = West; Xing = crossing.

Phylogenetic Analysis

Ingroup and outgroup taxa were examined for phylogenetically informative characters. For *Horaia*, collected specimens were examined, except *H. longipes* for which original description (Tonnoir 1932) was used. Outgroup generic characters were determined from the most recent generic descriptions and re-descriptions. Outgroups included (with description source): *Peritheates* Lamb (Craig 1969), *Neocurupira* Lamb (Craig 1969), *Nothohoraia* Craig (Craig 1969), *Austrocurupira* Dumbleton (Stuckenberg 1969), *Curupirina* Stuckenberg (Stuckenberg 1969), *Nesocurupira* Stuckenberg (Stuckenberg 1969), *Theischingeria* Zwick (Zwick 1998), *Apistomyia* Bigot (Tillyard 1922, Tonnoir 1923, Zwick 1977, Zwick 1998), and *Parapistomyia* Zwick (Zwick 1977, 1998). *Edwardsina* Alexander (Zwick 1977) is included as a non-Apistomyiine outgroup to establish character polarity. Phylogenetic characters were given definitive character states and a numerical code. Each taxon was then coded for each character. Unclear, continuous, and autapomorphic characters were excluded. Cladistic analyses were performed by using PAUP 4.0b10 and MacCLADE 3.04. PAUP analyses consisted of a branch and bound search with all characters weighted equally. Multistate characters were considered as unordered. Bootstrap values were calculated for 500 replicates.

CHAPTER 3. KEYS TO BLEPHARICERIDAE GENERA OF NEPAL AND THAILAND AND TO THE SPECIES OF THE GENUS *HORAIA*.

Instar IV Larvae

Larvae of *H. piedmonti* are unknown.

1. Dorsal prolegs present (Fig. 1); antennae three-segmented *Phylorus* Kellogg
- Dorsal prolegs absent (Figs. 3, 5, 15, 16, 19, 20, 23, 24, 27, 28); antennae two- or three-segmented 2
- 2(1). Antennae two-segmented, segments separated by broad, membranous area; prolegs acutely tapered or pointed (Fig. 3) *Blepharicera* Macquart
- Antennae two- or three-segmented, segments not separated by membranous area; prolegs blunt, or slightly tapered (Figs. 5, 15, 16, 19, 20, 23, 24, 27, 28)
..... *Apistomyiini* 3
- 3(2). Body elongate and narrow, trunk segments narrower than cephalothorax; lateral margins of trunk segments tapered at insertion of prolegs; antennae two-segmented; seventh pair of prolegs present as small, setose protuberances on anal division; posterior of anal division emarginate and setose; dorsum of each abdominal segment, including posterior of cephalothorax unsclerotized except for two rows of transverse spinules or papillae (Fig. 5) *Apistomyia* Bigot
- Body anteroposteriorly compressed, trunk segments at least as broad as cephalothorax; lateral margins of trunk segments blunt at insertion of prolegs; antennae two- or three-segmented; seventh pair of prolegs present as pair of bristles or patches of setae on anal division; posterior margin of anal division heavily sclerotized and asetose; abdominal segments heavily sclerotized, never with transverse rows of spinules or papillae (Figs. 15, 16, 19, 20, 23, 24, 27, 28)
..... *Horaia* Tonnoir 4

- 4(3). Body with chiton-like shape, segments closely pressed together; antennae three-segmented; tergites heavily sclerotized throughout; dorsal spines sometimes present; lateral margins of tergites formed into comb of spinules anterior and posterior to each proleg; prolegs with pair of sclerotized prominences at base; anal division semi-circular; setae marking seventh pair of prolegs directly posterior to sixth pair of prolegs (Fig. 23, 24) *H. montana* Tonnoir
- Body segments clearly separate; antennae two-segmented; tergites with anterior and posterior transverse sclerotized ridges, and sometimes triangular sclerotized patches; dorsal spines never present; tergites emarginate laterally, with transverse rows of spinules anterior and posterior to each proleg; base of prolegs with round patch of papillae ventrally, without sclerotized prominences; anal division narrow behind sixth pair of prolegs, not semi-circular; setae marking seventh pair of prolegs at posterior corners of anal division (Figs. 15, 16, 19, 20, 27, 28) 5
- 5(4). Second antennal segment elongate, twice as long as first; anal division posterior to sixth pair of prolegs not parallel, broadening slightly to curved posterior margin; tergites without triangular sclerotization between transverse ridges; ventral surface of cephalothorax covered with elongate, dark setae (Fig. 15, 16) *H. barbata* n. sp.
- Both antennal segments quadrate, subequal in length; anal division posterior to sixth pair of prolegs parallel, posterior margin nearly straight; tergites with triangular sclerotization between transverse ridges; ventral surface of cephalothorax with setae laterally (Figs. 19, 20, 27, 28) 6
- 6(5). Lateral surfaces of genae bright white in color; patch of setae at posterior corners of anal division, no bristle present; antennal segments equal in shape; ventral cephalothoracic setae spinous; no circle of setae around mouthparts (Fig. 27, 28)
..... *H. namtoki* n. sp.

- Lateral surfaces of genae dark brown; single bristle and patch of setae at posterior corners of anal division; first antennal segment expanded apically, second segment secondarily annulated; ventral cephalothoracic setae not spinous; circle of setae around mouthparts (Fig. 19, 20) *H. manaliella* (Kaul)

Pupae

Pupae of *H. piedmonti* are unknown.

1. Ventrolateral adhesive organs present on abdominal segments III-VI
..... Blepharicerini 2
- Ventrolateral adhesive organs present on abdominal segments IV-VI
..... Apistomyiini 3
- 2(1). Inner lamellae of respiratory organs broad, short, leafy (Fig. 2) *Philorus* Kellogg
- Inner lamellae of respiratory organs elongate, triangular (Fig. 4)
..... *Blepharicera* Macquart
- 3(1). Outer lamellae of respiratory organs short, broad, fused at midline (Fig. 6)
..... *Apistomyia* Bigot
- Outer lamellae of respiratory organs elongate, triangular, separate at midline (Figs. 17, 18, 21, 22, 25, 26, 29, 30) *Horaia* Tonnoir 4
- 4(3). Anal cleft absent (Fig. 25); tergites with microsculptured papillae; all lamellae of respiratory organs closely appressed and parallel, elongate and curving posteriorly (Fig. 26); cephalic sclerite in both sexes small and triangular, never reaching base of respiratory organs *H. montana* Tonnoir
- Anal cleft present (Figs. 17, 21, 29); tergites foveolate and rugose, microsculptured papillae absent; outer lamellae of respiratory organs divergent, inner lamellae appressed and parallel (Fig. 18, 22, 30); cephalic sclerite triangular or round, but always large, reaching base of respiratory organs 5

- 5(4). Abdominal tergite I almost as wide as metatergite; abdominal tergites II, III, and IV with pair of visible, round muscle scars (Fig. 29) *H. namtoki* n. sp.
- Abdominal tergite I not more than two thirds as wide as metatergite; abdominal tergites II, III, and IV without round muscle scars (Figs. 17, 21) 4
- 6(5). Cephalic sclerite triangular; posterior outer lamellae of respiratory organs almost meeting at midline; inner lamellae narrow, one third as wide as outer lamellae (Fig. 18) *H. barbata* n. sp.
- Cephalic sclerite round; all lamellae of respiratory organs separated from midline by at least 0.05 mm; inner lamellae at least half as wide as outer lamellae (Fig. 22) *H. manaliella* (Kaul)

Adults

1. Proboscis truncate, pseudotrachae not present; vein M_2 present (Figs. 7, 8) Blepharicerini 2
- Proboscis elongate, labella with obvious pseudotracheae (Figs. 37, 38, 42, 43, 47, 48); vein M_2 absent (Figs. 9-14) Apistomyiini 3
- 2(1). R_4 and R_5 veins separate for entire length (Fig. 8) *Blepharicera* Macquart
- R_4 and R_5 joined as R_{4+5} vein for some portion (Fig. 7) *Philorus* Kellogg
- 3(1). R_{4+5} vein sinuous, reaching wing margin near distal end of R_{1+2+3} (Fig. 9); antennae with at least 8 flagellomeres; mandibles present in females *Apistomyia* Bigot
- R_{4+5} vein variable, never sinuous (Figs. 10-14); antennae variable, but always with fewer than 8 flagellomeres; mandibles absent *Horiaia* Tonnoir 4
- 4(3). R_5 vein present as vein portion at wing margin (Fig. 10); hind coxae setose; metakatepisternum setose; female tibial spur formula 0-0-0; female hind tarsal claws narrow and straight; female fore femur without distinct anterodorsal row of setae *H. manaliella* (Kaul)

- R_5 vein absent (Figs. 11-14); hind coxae variable; metakatepisternum glabrous; female tibial spur formula 0-0-2; female hind tarsal claws stout and curved; female fore femur with distinct anterodorsal row of setae 5
- 5(4). A_1 vein reduced, barely extending beyond anal angle of wing (Figs. 11, 12, 14); labrum glabrous and narrow; male pedicel variable, not expanded apically (Fig. 49); upper division of eyes in females well developed (Fig. 47) 6
- A_1 vein longer, almost reaching margin of wing (Fig. 13); labrum setose and broad; male pedicel expanded apically (Figs. 39, 44); upper division of female eyes absent or present as five or fewer rows of ommatidia (Figs. 37, 42) 7
- 6(5). Stump of R_4 vein sometimes present on R_{4+5} vein (Fig. 12); hind coxae with sparse, pale hairs; large, females approx. 6.5 mm body length, 7.0 mm wing length; male antennae glabrous *H. montana* Tonnoir
- Stump of R_4 vein never present (Fig. 14); hind coxae glabrous; females smaller, approx. 5.0 mm body length, 5.3 mm wing length; male antennae setose (Fig. 49) *H. piedmonti* n. sp.
- 7(5). Maxillary palpi one-segmented, large, spindle-shaped; female eyes not divided (Fig. 37) *H. namtoki* n. sp.
- Maxillary palpi one-segmented, small, globular; female eyes divided, upper division present as two rows of ommatidia (Fig. 42) *H. barbata* n. sp.

CHAPTER 4. TAXONOMY

Horaia Tonnoir 1930

Horaia Tonnoir 1930: 209 [original description]. Type species *Horaia montana* Tonnoir 1930: 210. Tonnoir 1932: 275 [redescription of genus].

Manaliella Kaul 1976: 25. Type species *Manaliella manaliella* Kaul 1976 [synonymy by Zwick 1990: 254].

DIAGNOSIS - LARVA: Body broad, oval. Instar IV body length 2.5-7.0 mm; cranial width 0.5-1.2 mm. Lateral margins of abdominal segments parallel at insertion of prolegs. Body anteroposteriorly compressed, trunk segments at least as wide as cephalothorax. Antennae two- or three-segmented. Gill filaments absent in instar I; one in each tuft in instar II; three in instar III; five in instar IV, three projecting anteriorly, two projecting posteriorly. Abdominal tergites heavily sclerotized, ornamented with ridges and plates, but no setae or papillae. Dorsal prolegs absent. Seventh pair of prolegs reduced to single pair of bristles or setal patches. Segments of anal division fully fused into a single segment. Posterior margin of anal division forming heavily sclerotized, aetose margin. **PUPA:** Broad, oval. Length 2.5-5.5 mm; width 1.2-2.8 mm. Sexual dimorphism often present in shape of thoracic and cephalic sclerites. All lamellae of respiratory organs elongate and triangular, not fused at midline. Abdominal tergites either foveolate and rugose or densely papillose, never glabrous. **MALE:** Body length 3.0-6.5 mm; wing length 3.3-6.5 mm. R_{4+5} vein straight, unforked. Eyes subholoptic, divided, upper division forming hemispherical top half of head. Antennae seven- to nine-segmented; scape and pedicel expanded, twice as broad as flagellomeres; flagellomere shape and number irregular, often fused. Mandibles absent. Maxillary palpi one-segmented. Labella elongate with visible pseudotracheae. **FEMALE:** Body length 3.0-7.0 mm. Wings and antennae same as male. Eyes dichoptic; divided or

undivided. Mandibles absent. Maxillary palpi one-segmented. Labella elongate with visible pseudotracheae.

REMARKS – Wing venation similar to *Peritheates* and *Nesocurupira* with straight, unforked R_{4+5} vein; adults can be distinguished by characters of the mouthparts. Pupae unremarkable within tribe; recognized by dorsal ornamentation. Larval stages easily identified; completely fused anal division and heavily sclerotized dorsum unique to genus. Larval stages of *H. montana* superficially resemble those of *Nothohoraia* (Zwick 1977); can be distinguished by the presence of spinulose lateral margin and the absence of cephalic horns.

Horaia manaliella (Kaul 1976) (Figs. 10, 19-22, 31-33, 52)

Manaliella manaliella Kaul 1976: 25 [original description]; *Horaia manaliella* Zwick 1990: 254 [new combination].

“Larva K” Tonnoir 1930: 182.

DIAGNOSIS – **LARVA**: First antennal segment expanded apically, second segment secondarily annulated; ring of setae surrounding mouthparts; dorsal surface sclerotized and patterned; pair of bristles projecting from posterior corners of anal division; anal division narrow and square. **PUPA**: Body square anteriorly in males, parabolic in females; cephalic sclerite round, broader and with two prominences in males; outer lamellae of respiratory organ divergent; inner lamellae narrow at base; all lamellae well separated at mid-line; abdominal tergites foveolate and rugose; anal cleft prominent. **MALE**: A_1 vein almost reaching wing margin; R_{4+5} vein straight; R_5 vein present at wing margin but absent basally;

pedicel expanded apically; front femur setose apically; hind coxae and metakatepisternum setose; ventral parameres broad, blunt; dorsal paramere narrow, elongate. **FEMALE:** Hind legs extremely long; tibial spur formula 0-0-0; hind tarsal claws straight and slender; hypogynial plate broad apically; hypogynial valves with transverse rows of setiforms.

DESCRIPTION.

LARVA (Figs. 19, 20): Measurements, instar II (N = 7) body length 1.1 mm (0.9-1.8), cranial width 0.29 mm (0.28-0.33); instar III (N = 24) body length 2.5 mm (1.7-2.9), cranial width 0.45 mm (0.42-0.47); instar IV (N = 35) body length 3.5 mm (2.6-5.0), cranial width 0.62 mm (0.56-0.66). Antennae two-segmented, glabrous, dark brown to black; segments subequal in length; segment I expanded apically; segment II slender, secondarily annulated to appear as two segments. Cranial sclerites dark brown to black; ecdysial sutures with no stem line; posterior margin of frontoclypeal apotome reaches posterior cranial margin forming a broad V-shape; posterior tentorial pits narrow, dark, extending anteriorly. Trunk dark brown to black; each abdominal segment with undulate anterior ridge, curved posterior ridge and central triangular sclerotization; pair of prominent oval muscle scars lateral to each triangular sclerotization; tergites heavily sclerotized and strigate laterally. Anal division square and more narrow than base of sixth pair of prolegs; posterior margin heavily sclerotized. Prolegs stout, broad, with indefinite margin at base; first and sixth pair of prolegs smaller in size than other prolegs; ventrolateral region of each abdominal segment prominent, with round patch of tubercles at base of prolegs. Chaetotaxy: sparse, elongate setae on ventrolateral portions of cephalothorax; row of three prominent setae on each side of first organ of attachment; circle of setae surrounding mouthparts; stiff comb of setae on anterior margin of genae; three prominent, medially-directed setae posterior to genal comb; thick, broad mass of pale setae on dorsum of each proleg; spiniform setae in transverse row anterior and posterior to dorsal

base of each proleg; single stout bristle and mass of pale setae at each posterior corner of anal division.

PUPA: See Kaul 1976. Other characters, not previously noted, as follows (Figs. 21, 22). Body square anteriorly in males, parabolic in females; lateral margins of abdominal segments rounded. Cephalic sclerite round; broader in males with two protuberances. Lamellae of respiratory organs triangular in shape (height approximately 0.5 mm); outer lamellae divergent; inner lamellae close set and one half as wide at base as outer lamellae. Tergites foveolate, rugose towards lateral margins; pair of crescent-shaped muscle scars on either side of midline of each abdominal tergite. Abdominal tergite I two thirds as wide as metatergite. Color uniform light brown, respiratory organs darker. Anal cleft prominent.

ADULT MALE: See Kaul 1976. *Terminalia* (Figs. 32, 33): Epandrium simple. Cerci well-developed, parallel, densely setose; interlobular depression shallow V-shape; individual lobes broadly rounded and fused medially. Gonostyli elongate, densely setose; gonocoxal lobes short, flattened, glabrous. Genital capsule large, more than twice as long as wide. Aedeagal rods of phallus comprising three, simple, elongate rods. Base of ejaculatory apodeme broad, round; ejaculatory apodeme short and broad. Ventral parameres elongate, slightly longer than aedeagus, broad and blunt at apex; gonocoxal apodemes elongate, half as long as ventral parameres; dorsal paramere elongate, narrow, uniform; lateral parameral lobes absent.

ADULT FEMALE: See Kaul 1976. *Terminalia* (Fig. 31): Posterior margin of sternite VIII broadly bilobate, medial depression narrow, U-shaped. Genital fork V-shaped, narrow in anterior two thirds, broadening in posterior third. Hypogynial plate parallel; individual valves elongate, rounded; inner margins of valves parallel. Accessory glands not seen.

Spermathecae three in number, corpora not seen; ducts long, simple. Chaetotaxy: sternite VIII without prominent setiforms; hypogynial plate setose, each valve with eleven prominent setiforms in a transverse row on dorsal surface.

TYPE MATERIAL – Holotype [adult male]: INDIA. *Himachal Pradesh*. Left bank of Jagatsukh Nullah, near Manali, Kulu Valley, southern slope of Pir Panjal Range, 16.vi.1972, coll. B.K. Kaul. Specimen mounted on slide. Allotype [female imago dissected from pupa]: same data as holotype. Specimen mounted on slide with pupal exuvium. Holotype and allotype both possibly deposited IM.

OTHER RECORDS – INDIA. *Himachal Pradesh*. Dalhousie, Punj Pul Nallah, v-vi.1927, coll. S.L. Hora [L]; NEPAL. *Humla District*. Humane Kh above Simikot, 29°59'N 81°49'E, 28.viii.1994 [L]; Yangchu Kh near Karnali, 29°55'N 81°52'E, 25.viii.1994 [L]; *Kaski District*. “Bridal veil” falls near Nayapul, 28°23'N 83°49'E, 29.iv.2000 [LP]; Chane Kh at lower Xing, 28°21'N 83°49'E, 3.v.2000 [L]; Chhomrong Kh at Chhomrong, 28°25'N 83°49'E, 29.iv.2000 [L]; creek between Landruk and Himalpani Xing, 28°23'N 83°49'E, 29.iv.2000 [L]; creek just above Dhoban, 28°28'N 83°52'E, 30.iv.2000 [LP]; Dhoban Kh below Dhoban, 28°28'N 83°52'E, 30.iv.2000 [L]; E branch Ghirsung Kh near Tolka, 28°21'N 83°49'E, 28.iv.2000 [L]; Gandruk Kh at Himalpani, 28°22'N 83°49'E, 3.v.2000 [LP]; Ghirsung Kh above Tolka, 28°21'N 83°49'E, 28.iv.2000 [LP]; Kyumnu Kh at lower Xing, 28°24'N 83°49'E, 29.iv.2000 [LPPex]; Kyunri Kh at lower Xing, 28°23'N 83°49'E, 3.v.2000 [LPPex]; Kyunri Kh near Gandruk, 28°23'N 83°48'E, 22.viii.1992 [L]; Landruk Kh NE of Landruk, 28°22'N 83°49'E, 29.iv.2000 [LP]; Modi Kh at Nayapul, 28°23'N 83°49'E, 29.iv.2000 [LP]; Saane Kh below Gandruk, 28°21'N 83°48'E, 21.viii.1992 [LP]; W branch Landruk Kh, 28°22'N 83°49'E, 29.iv.2000 [P]; *Kathmandu District*. SFR, East trib Bagmati Kh, 2.x.1994 [L]; SFR, Jhor Kh (upper Bishnumati), 27°48'N 85°20'E, 15.iv.2000

[LPPexA]; same location, 22.iv.2000 [LPPexA]; SFR, Salmati Kh, Sundarijal, 2.x.1994 [LP]; Salmati Kh above trail Xing, 27°46'N 85°25'E, 16.iv.2000 [L]; SFR, "Bleph Falls" (upper Bagmati), 27°46'N 85°25'E, 16.iv.2000 [LA]; same location, 13.vii.1994 [LPPex], 2.x.1994 [LP], 4.ix.1994, coll Pradhan & Shrestha [L]; *Mugu District*. Jhari Kh at Rara trail, 29°29'N 82°07'E, 14.ix.1994 [L]; *Mustang District*. creek below Koiku, 28°36'N 83°38'E, 6.viii.1992 [L]; trib Chomrong Kh at Chomrong, 28°25'N 83°49'E, 23.viii.1992 [L]; trib Ghatte Kh below Larjung, 28°40'N 83°36'E, 5.viii.1992 [L]; trib Kali Gandaki below Tukche, 28°42'N 83°38'E, 5.viii.1992 [LP]; *Parbat District*. Modi Kh above Dimua, 28°16'N 83°45'E, 27.iv.2000 [L]; *Sindhupalchok District*. Bhairabkunda Kh above Xing, 27°55'N 85°55'E, 12.vii.1994 [L]; Chakhu Kh above Chakhu, 27°53'N 85°54'E, 20.iv.2000 [LPPex]; Creek between Kodari and Tatopani, 27°57'N 85°56'E, 20.iv.2000 [LP]; Lipping Kh near Kodari, 27°58'N 85°57'E, 12.vii.1994 [L]; same location, 20.iv.2000 [L]; Pangpunge Kh above Kodari Rd, 27°50'N 85°53'E, 20.iv.2000 [LPPex]; Sun Koshi R above Lamosangu, 27°45'N 85°51'E, 18.iv.2000 [P]. All collections GW Courtney unless otherwise noted.

DISTRIBUTION – (Fig. 52) Found in Himalayan India and throughout Nepal. Often found in the same locations as *H. montana*, and sometimes the same locations as *H. barbata*.

REMARKS – Adults differ in many ways from other *Horaia*, but larval and pupal form confirms the placement of *manaliella* within the genus. Shape of the cephalic sclerite is the only means of distinguishing the pupae from those of *H. barbata*. Tonnoir's (1930) original description of "Larva K" probably corresponds with the immature stages of *H. manaliella* whereas Kaul's (1976) description of larval *H. manaliella* represents a misidentification of the genus *Philorus*. Larvae of *H. manaliella* are distinguished from those of *H. namtoki* by the characteristic shape of the antennae and a circle of setae around

the mouthparts and from *H. barbata* by the presence of a dorsal sclerotized triangular plate on each abdominal segment.

***Horaia namtoki* sp. nov.** (Figs. 27-30, 37-41, 53)

DIAGNOSIS – LARVA: Lateral genae bright white; spiniform papillae on ventral surface of cephalothorax; tergites heavily sclerotized; anal division square caudally. **PUPA:** Extra muscle scar on abdominal tergites II-IV; anterior of body sexually dimorphic; cephalic sclerite sexually dimorphic; anal cleft present. **MALE:** Maxillary palpi spindle-shaped; pedicel expanded apically; cerci widely separate; dorsal paramere with bilobed opacity in basal half. **FEMALE:** Eyes not divided; maxillary palpi spindle-shaped; hypogynial valves short and stout.

DESCRIPTION.

LARVA (Figs. 27, 28): Measurements, instar II (N = 3) body length 1.9 mm (1.7–2.0), cranial width 0.28 mm (0.27–0.29); instar III (N = 25) body length 2.8 mm (2.4–3.2), cranial width 0.43 mm (0.40–0.46); instar IV (N = 33) body length 4.2 mm (2.7–5.1), cranial width 0.62 mm (0.55–0.66). Antennae two-segmented; segments black, subequal, cylindrical. Cranial sclerites dark brown, lateral genae bright white posterior to antennal sockets; ecdysial sutures with no stem line; posterior margin of frontoclypeal apotome extends to posterior cranial margin forming narrow V-shape; posterior tentorial pits darkly colored and prominent, especially in instar III. Trunk pale to dark brown; each abdominal segment with transverse, anterior, sclerotized ridge and weaker transverse, posterior sclerotized ridge; sclerotized triangular plate between transverse ridges; series of visible muscle scars lateral to central triangle; tergites strigate between sclerotized structures.

Anal division square beyond sixth pair of prolegs; posterior margin heavily sclerotized. Prolegs stout, broad, with indefinite margin at base; first pair of prolegs half the size of other prolegs; ventrolateral region of each abdominal segment prominent, with round patch of tubercles at base of prolegs. Chaetotaxy: row of elongate setae and short, spiniform papillae along lateral margin of cephalothorax; stiff comb of setae on anterior margin of genae; row of three prominent setae and row of punctures on each side of cephalothoracic suctorial disc; elongate, pale setae in rows along dorsum of each proleg; spiniform setae in transverse row anterior and posterior to dorsal base of each proleg; patch of pale setae at each posterior corner of anal division.

PUPA (Figs. 29, 30): Measurements, male (N = 16) length 3.8 mm (3.3–4.3), width 1.7 mm (1.4–2.0); female (N = 18) length 4.0 mm (3.4–4.5), width 1.9 mm (1.6–2.2). Body square anteriorly in males, parabolic in females, lateral margins of abdominal segments rounded. Abdominal tergite I three fourths as wide as metatergite. Abdominal tergites foveolate, rugose at lateral margins; pair of crescent shaped muscle scars on either side of midline of each abdominal tergite; single, circular muscle scar medial to each crescent shaped scar on abdominal segments II, III, and IV. Anal cleft prominent. Color uniform light brown, respiratory organs darker. Lamellae of respiratory organs triangular in shape (height 0.56 mm); lamellae at least 0.04 mm from midline; outer lamellae widely set and divergent (0.30 mm wide at base); inner lamellae close set and two thirds as wide at base as outer lamellae. Cephalic sclerite round; male pupae with taller cephalic sclerite and a central vertical depression; female pupae with shorter cephalic sclerite and a central prominence.

ADULT MALE: Head and terminalia only, dissected from pupa. Head (Fig. 39). Normal type, subholoptic. Clypeus rounded and bulbous, longer than wide. Eyes meet dorsally; eyes divided, upper division large, forming hemispherical top half of head; lower

division smaller, about as wide as upper division at callis oculi; callis oculi bare and narrow; upper ommatidia diameter 1.5 times as large as lower. Proboscis long, free portion 1.5 times head height, sparsely setose on basal half; mandibles absent; palpi one-segmented, elongate, spindle-shaped; labrum elongate, one third length of proboscis, densely setose. Antennae seven-segmented, any or all of flagellomeres II-V partially or fully subdivided into two segments; scape broad and quadrate; pedicel broad, elongate, expanded apically; flagellomeres slender; all segments setose.

Terminalia (Figs. 40, 41): Epandrium simple, emarginate posteriorly, with anterior row of setiform sensilla. Cerci well-developed, parallel, sparsely setose; interlobular depression deep, V-shape; individual lobes rounded. Gonostyli large, densely setose; gonocoxal lobes elongate, flattened, and glabrous. Aedeagal rods of phallus comprising three, simple, elongate rods. Base of ejaculatory apodeme broad and oval-shaped. Ventral parameres elongate, straight, longer than aedeagus; gonocoxal apodemes narrow, half as long as ventral parameres; basal half of dorsal paramere with bilobed opacity; lateral parameral lobes absent.

ADULT FEMALE: Head and terminalia only, dissected from pupa. Head (Fig. 37). Normal type, dichoptic. Clypeus rounded and bulbous, longer than wide. Eyes separate, not divided. Proboscis long, free portion 2.5 times head height, sparsely setose on basal half; mandibles absent; palpi one-segmented, elongate, spindle-shaped; labrum elongate, one third length of proboscis, densely setose. Antennae seven-segmented, pedicel broad, but not expanded apically, otherwise identical to male. Color uniform light brown.

Terminalia (Fig. 38): Posterior margin of sternite VIII broadly bilobate, medial depression broad, U-shaped. Genital fork V-shaped, narrow in anterior third, broadening in posterior two thirds. Hypogynial plate parallel sided; individual valves short, stout, rounded; inner margin of valves parallel. Accessory glands large, oval. Spermathecae three in

number, corpora ovoid, small with long, simple ducts. Chaetotaxy: sternite VIII without prominent setae; hypogynial plate glabrous, valves with ten prominent setiforms each on dorsal surface.

TYPE MATERIAL – Holotype [male dissected from pupa]: THAILAND. *Chiang Mai Province*: Doi Suthep NP, Namtok Monthatarn, 18°49'N 98°55'E, 3.xi.1994, coll. GW Courtney, deposited USNM. Specimen dissected from pupa and mounted on slide in Canada Balsam with pupal exuvium. Allotype [female dissected from pupa]: same locality and date as male, deposited USNM, slide-mounted in Canada Balsam with pupal exuvium. Paratypes: same data as holotype and allotype [1 male A (slide); 1 male A (slide); 1 female A (slide); 1 female A (slide); 5 Pex (slide); 4 Pex (slide); 1 instar II L, 1 instar III L, 1 instar IV L (slide); 2 instar II L, 2 instar III L, 2 instar IV L (slide); 2 instar IV L, 1 male P (EtOH); 3 instar II L, 25 instar III L, 107 instar IV L (EtOH)]. All paratypes deposited ISU.

OTHER MATERIAL EXAMINED – THAILAND. *Chiang Mai Province*. Doi Inthanon NP, Ban Sob Ab near Nam Mae Klang, 18°31'N 98°36'E, 11.iv.2000 [L]; Doi Inthanon NP, Nam Mae Klang near Ban Sob Ab, 18°31'N 98°36'E, 19.v.2001 [L]; Doi Inthanon NP, Namtok Mae Pan, 18°31'N 98°27'E, 4.xi.1994 [LP]; same location, 11.iv.2000 [L]; same location, 18.v.2001 [L]; Doi Inthanon NP, Namtok Siriphum, 18°32'N 98°30'E, 11.iv.2000 [LP]; same location, 18.v.2001 [L]; Doi Suthep NP, Namtok Monthatarn, 18°49'N 98°55'E, 3.xi.1994 [LP]; same location, 29.xii.1995, coll MB and MT [LP]. *Mae Hong Son Province*. Namtok Mawpang, 14.xi.1994 [L]. All specimens collected by GW Courtney unless other wise noted.

ETYMOLOGY – From the Thai word *namtok* meaning waterfall.

DISTRIBUTION – (Fig. 53) Found only in Chiang Mai and Mae Hong Son provinces of northern Thailand. Often found in same localities as *H. montana* and unidentified species of *Apistomyia* and *Philorus*.

REMARKS - Adults and pupae are typical of *Horaia*. Adults can be distinguished from *H. barbata* by the shape of the maxillary palpi and the undivided female eye. Pupae are separated from other members of the genus by a wide abdominal tergite I and round muscle scars on abdominal tergites II, III, and IV. Larvae have the following unique characters: the lateral surface of the genae bright white and the ventral surface of the cephalothorax with spinous setae.

***Horaia barbata* sp. nov.** (Figs. 13, 15-18, 42-46, 52)

DIAGNOSIS – A small *Horaia*. **LARVA**: Cephalothorax markedly hirsute ventrally; second antennal second twice as long as first; abdomen dorsally marked with transverse, sclerotized ridges on each segment; Anal division square posteriorly. **PUPA**: Body anteriorly square in males, parabolic in females; cephalic sclerite large and triangular, not sexually dimorphic; outer lamellae of respiratory organ divergent; inner lamellae narrow at base; posterior lamellae almost meeting at midline; abdominal tergites foveolate and rugose; anal cleft prominent. **MALE**: Pedicel expanded apically; flagellomere I elongate; lower eye division triangular; cercal lobes almost completely fused; gonocoxal lobes expanded apically; ventral parameres cross at apices; dorsal paramere with bilobate opacity on basal half. **FEMALE**: Pedicel broad; flagellomere I elongate; eyes not divided; sternite VIII fused; hypogynial plate broad apically; hypogynial valves fused; necks of spermathecae with characteristic bulge

DESCRIPTION.

LARVA (Figs. 15, 16): Measurements, instar III (N = 19) body length 2.3 mm (2.0–2.6), cranial width 0.40 mm (0.33–0.43); instar IV (N = 21) body length 3.1 mm (2.6–3.7), cranial width 0.53 mm (0.50–0.56). Antennae two-segmented, black, glabrous, cylindrical; second antennal segment twice as long as first. Cranial sclerites dark brown; ecdysial sutures with no stem line; posterior margin of frontoclypeal apotome extends to posterior cranial margin forming a narrow V-shape; posterior tentorial pits darkly colored and prominent. Trunk medium to dark brown; dark, heavily sclerotized ridge at anterior and posterior margin of each abdominal segment; two pairs of oval muscle scars present lateral to midline of each trunk segment, tergites strigate between ridges. Prolegs stout, broad, with indefinite margin at base; first and sixth pair of prolegs smaller than other prolegs; ventrolateral region of each abdominal segment prominent, with round patch of tubercles at base of prolegs. Anal division narrow posterior to sixth pair of prolegs, broadening slightly to a wide, heavily sclerotized posterior margin. Chaetotaxy: elongate, dark setae distributed across lateral portions of ventral surface of cephalothorax; stiff comb of setae along anterior edge of genae; elongate, pale setae in rows along dorsum of each proleg; prominent, stout seta extending from each posterior corner of anal division; small, spiniform setae in transverse row anterior and posterior to dorsal base of each proleg.

PUPA (Figs. 17, 18): Measurements, male (N = 28) length 2.8 mm (2.7–3.2), width 1.4 mm (1.2–1.7); female (N = 4) length 2.9 mm (2.8–3.2), width 1.4 mm (1.3–1.4). Body square anteriorly in males, parabolic in females; lateral margins of abdominal segments rounded. Cephalic sclerite triangular; no sexual dimorphism in cephalic sclerite. Lamellae of respiratory organs triangular in shape (height approximately 0.4 mm); outer lamellae divergent and 0.3 mm wide at base; posterior outer lamellae almost meeting at midline; inner lamellae close set and one third as wide at base as outer lamellae. Tergites foveolate, rugose

towards lateral margins; pair of crescent-shaped muscle scars on either side of midline of each abdominal tergite. Abdominal tergite I two thirds as wide as metatergite. Color uniform light brown, respiratory organs darker. Anal cleft prominent.

ADULT MALE: Body (N = 3) length 3.3 mm (3.0-3.7). Head (Fig. 44) Normal type, subholoptic; uniform light brown color. Clypeus rounded, bulbous, about as long as wide. Eyes meet dorsally; divided, upper division large, forming hemispherical top half of head; lower division triangular, 0.75 times as wide as upper division at callis oculi; callis oculi bare, not as wide as one upper ommatidium; upper ommatidia twice as large as lower. Proboscis long; free portion twice height of head; mandibles absent; palpi small, one-segmented, globular; labrum elongate, densely setose, one fourth of length of proboscis. Antennae seven-segmented, penultimate flagellomere elongate or divided into two subequal flagellomeres; scape short and quadrate; pedicel expanded apically; flagellomere I elongate, as long as scape and pedicel together; remaining flagellomeres cylindrical with varying length; scape with long setae, remaining segments sparsely setose; all antennal segments concolorous, light brown. Thorax: medium brown color; dorsum dark brown, almost black; mesothorax with distinct triangular marking on posterior margin; all thoracic sclerites glabrous. Wing (Fig. 13) length 3.5 mm (3.3-3.7). Venation: A_1 almost reaching wing margin; R_{4+5} straight, reaching margin near wing tip. Legs not fully sclerotized, characters unclear.

Terminalia (Figs. 45, 46): Epandrium simple, sparsely setose in lateral regions. Cerci well-developed, parallel, densely setose; interlobular depression slight concave; individual lobes rounded, fused medially. Gonostyli elongate, narrow, densely setose; gonocoxal lobes elongate, flattened, glabrous, expanded apically. Genital capsule large, twice as long as wide. Aedeagal rods of phallus comprising three, simple, elongate rods. Base of ejaculatory apodeme small, round; ejaculatory apodeme short, broad. Ventral

parameres elongate, narrow, longer than aedeagus, apices cross beyond apex of aedeagus; gonocoxal apodemes elongate, broad, half as long as ventral parameres; dorsal paramere with bilobate opacity in basal half; lateral parameral lobes absent.

ADULT FEMALE: Body (N= 1) length 3.2 mm. Head (Fig. 42) Normal type, dichoptic; uniform light brown color. Clypeus bulbous and rounded, as long as wide. Eyes separate, divided, upper division present as two rows of small ommatidia, callis oculi narrow. Proboscis elongate, free portion 2.3 times height of head; mandibles absent; palpi small, one-segmented, globular; labrum elongate, one fifth the length of the proboscis, setose. Antennae seven-segmented, pedicel broad, not expanded apically, otherwise antennae identical to male. Thorax and Wing identical to male. Legs not fully sclerotized, most characters unclear; anterodorsal row of hairs present on fore femur, hind tarsal claws broad, curved.

Terminalia (Fig. 43): Posterior margin of sternite VIII slightly bilobate, medial depression slight concave. Genital fork shallow U-shaped. Hypogynial plate narrow basally, broadening apically; individual valves rounded, fused; medial depression shallow V-shape. Accessory glands not seen. Spermathecae three in number; corpora not seen; necks with characteristic bulge; ducts simple, long. Chaetotaxy: sternite VIII without prominent setiforms; hypogynial plate setose, each valve with eleven prominent setiforms in transverse row on dorsal surface.

TYPE MATERIAL – Holotype [reared male with pupal exuvium]: NEPAL. *Dolkha District*: Rojenaagee Kh above Jiri Rd, 27°41'N 85°59'E, 19.iv.2000, emerged 21.iv.2000, coll. GW Courtney, deposited USNM. Specimen pinned with pupal exuvium, genitalia in glycerin microvial. Allotype [reared female with pupal exuvium]: same locality and date as male, emerged 19.iv.2000, deposited USNM. Specimen pinned with pupal exuvium, genitalia in glycerin microvial. Paratypes: same date and location as holotype and allotype [1

male A, reared (pinned); 1 male A, reared (EtOH); 121 instar III L (EtOH); 115 instar IV L (EtOH); 14 male P, 1 female P, Pex (EtOH)]. All paratypes deposited ISU.

OTHER MATERIAL EXAMINED – NEPAL. *Dolkha District*. Charnewati Kh above Jiri Rd, 27°42'N 85°59'E, 19.iv.2000 [LP]; Yanmara Kh above Jiri Rd, 27°42'N 85°57'E, 19.iv.2000 [LPPex]; *Sindhupalchok District*. Bhairabkunda Kh above Xing, 27°55'N 85°55'E, 12.vii.1994 [L]; Bulgate Kh above Kodari Rd, 27°52'N 85°53'E, 12.vii.1994 [L]; Chakhu Kh above Chakhu, 27°53'N 85°54'E, 12.vii.1994 [L]; Ghatte Kh at Lamosanga, 11.vii.1994 [L]; Kupre Kh above Lamosanga, 11.vii.1994 [L]; all material coll. GW Courtney.

ETYMOLOGY – From the Latin *barbatus* meaning beard, in reference to the elongate, dark setae on the ventral surface of the cephalothorax of the instar IV larvae.

DISTRIBUTION – (Fig. 52) Found only in Dolkha and Sindhupalchok districts of central Nepal. Some locations contain both *H. barbata* and *H. montana*.

REMARKS – Adults and pupae are typical of *Horaia*. Adults can be distinguished from *H. namtoki* by the shape of the maxillary palpi and the presence of a small upper eye division in the females. Pupae similar to *H. manaliella*. Respiratory organs are closer to meeting at the midline than in the rest of the genus. Larvae distinct from *H. montana* and *H. manaliella* in having the dorsal surface much less sclerotized. It is difficult to distinguish *H. barbata* from *H. manaliella* in early instar larvae.

Horaia longipes Tonnoir 1932

Horaia longipes Tonnoir 1932: 273 [original description].

DIAGNOSIS – FEMALE: A₁ vein almost reaching wing margin; R₄₊₅ vein straight; front femur with anterodorsal row of setae; hind legs long, femora thin; tibial spur formula 0-0-2.

DESCRIPTION

LARVA: Unknown.

PUPA: Unknown.

MALE: Unknown.

FEMALE: See Tonnoir 1932.

TYPE MATERIAL – Holotype [adult female]: INDIA. *Sikkim*. Pashoke Jhora near Tista bridge, date unknown, coll. S. L. Hora. Possibly deposited IM.

DISTRIBUTION – Known only from type location in northeastern India.

REMARKS – *H. longipes* may be synonymous with another species of *Horaia*, but until types can be examined, it will remain as a species with a single collected specimen.

Horaia piedmonti sp. nov. (Figs. 14, 47-51, 53)

DIAGNOSIS – MALE: A₁ vein reduced, barely extending beyond anal angle of wing; labrum short, narrow, and glabrous; antennae nine-segmented and setose; dorsal paramere with bilobed opacity in basal half. **FEMALE:** Dorsal eye division with five rows of ommatidia; accessory gland elongate, tapered.

DESCRIPTION.

LARVA: Unknown.

PUPA: Unknown.

ADULT MALE: Body (N = 2) length 4.4 mm (4.1–4.7). Head (Fig. 49). Normal type, subholoptic; uniformly light brown. Clypeus rounded, bulbous, about as long as wide. Eyes meet dorsally; eyes divided, upper division large, forming hemispherical top half of head; lower division triangular, nearly as wide as upper division at callis oculi; callis oculi narrow and bare; upper ommatidia twice as large as lower; upper division pale, lower division darker. Proboscis long, setose, free portion 1.8 times head height; mandibles absent; palpi small, one-segmented, globular; labrum narrow, glabrous, short, one seventh length of proboscis. Antennae nine-segmented, flagellomere VII fully or partially subdivided into two subequal flagellomeres; scape and pedicel expanded, twice as wide as flagellomeres; flagellomeres slender; all antennal segments setose. Thorax: uniformly light brown, sutures lighter; bare, except for small patch of setae on lateral margin of scutellum; posterior margin of scutellum heavily sclerotized. All legs with uniform, sparse setal covering; tibial spur formula 0-0-2, spurs stout, black, elongate, anterior spur half as long as posterior; tarsal claws simple, elongate.

Leg segment measurements (in mm):

	Femur	Tibia	t1	t2	t3	t4	t5	Claw
I	1.0	1.5	0.6	0.4	0.3	0.3	0.3	0.1
II	1.1	0.9	0.4	0.3	0.3	0.2	0.2	0.1
III	2.8	3.4	1.1	0.5	0.4	0.4	0.3	0.2

Wing (Fig. 14). Length 5.3 mm (4.8–5.7); An barely extending beyond anal angle; R_{4+5} straight, reaching margin near wing tip; r-m twice as long as base of R.

Terminalia (Figs. 50, 51): Epandrium simple, sparsely setose. Cerci well-developed, densely set with elongate setiforms; interlobular depression broad V-shape; individual lobes rounded. Gonostyli elongate, setose; gonocoxal lobes elongate, flattened, glabrous. Aedeagal rods of phallus comprising three, simple, elongate rods. Base of ejaculatory apodeme small, indistinct. Ventral parameres elongate, parallel, slender, slightly longer than aedeagus; gonocoxal apodemes broad, half as long as ventral parameres, dorsal paramere with bilobed opacity in basal half; lateral parameral lobes absent.

ADULT FEMALE: Body (N = 2) length 5.1 mm (4.8–5.3). Head (Fig. 47). Normal type, dichoptic; uniformly light brown. Clypeus bulbous, rounded. Eyes separate, divided; upper division smaller, approximately five rows of ommatidia at meridian; callis oculi narrow and bare. Proboscis elongate, free portion twice the height of the head; mandibles absent; palpi small, one-segmented, globular; labrum short, narrow, glabrous, one fourth the length of the proboscis; setae present on basal half of proboscis. Antennae nine-segmented; any or all of flagellomeres V-VII fully or partially subdivided into two segments; scape and pedicel broad; flagellomeres slender. Thorax identical to male. Front and mid leg with prominent anterodorsal row of setae on femur; joints of hind tarsal segments oblique; tibial

spur formula 0-0-2, tarsal spurs short, stout, and black, anterior spur half as long as posterior; claws simple, elongate, curved.

Leg segment measurements (in mm):

	Femur	Tibia	t1	t2	t3	t4	t5	Claw
I	1.0	1.3	0.2	0.1	0.1	0.1	0.2	0.1
II	0.9	1.4	0.2	0.1	0.1	0.1	0.2	0.1
III	2.0	2.6	0.7	0.3	0.2	0.2	0.5	0.1

Wing length 5.3 mm (5.0–5.5); identical to male.

Terminalia (Fig. 48): Posterior margin of sternite VIII broadly bilobate, medial depression broad, U-shaped. Genital fork V-shaped. Hypogynial plate parallel sided; individual valves elongate, rounded; inner margin of valves parallel. Accessory gland elongate, tapering to a point at anterior end. Spermathecae not seen. Chaetotaxy: sternite VIII without prominent setiforms; hypogynial plate densely setose; valves with eleven prominent setiforms each on dorsal surface.

TYPE MATERIAL – Holotype [adult male]: THAILAND. *Chiang Mai Province*: Doi Inthanon NP, Nam Mae Klang near Ban Sob Ab, 18°31'N 98°36'E, 11.iv.2000, coll. G.W. Courtney, deposited USNM. Specimen pinned, genitalia in glycerin microvial. Allotype [adult female]: THAILAND. *Chiang Mai Province* Doi Inthanon NP, Namtok Mae Pan, 18°31'N 98°27'E, 4.x.1994, coll. G.W. Courtney, deposited USNM. Specimen pinned, genitalia in glycerin microvial [ISU]. Paratypes: same data as holotype [1 male A, pinned]; same data as allotype [1 female A, pinned]. All paratypes deposited ISU.

ETYMOLOGY – From the French *piedmont* meaning foothill, in reference to the species being similar to *H. montana*, except for the much smaller size.

DISTRIBUTION – (Fig. 53) Found only in Chiang Mai Province of northern Thailand.

REMARKS – Adults are similar to *H. montana* in body shape and wing venation. Adults of both sexes are much smaller in body and wing size. Adults can be distinguished from *H. montana* by the absence of setae on the hind coxae and the setose male antennae. Larvae and pupae are unknown. Owing to similarities in appearance to *H. montana* in the adult stage, immature stages may be, as yet, indistinguishable from *H. montana* immatures.

Horaia montana Tonnoir 1930 (Figs. 11, 12, 23-26, 34-36, 52, 53)

Horaia montana Tonnoir 1930: 210 [original description]; Tonnoir 1932: 271 [redescription of adult females].

“Larva R1, R2, R3, R4” Tonnoir 1930: 193.

“Pupa R1” Tonnoir 1930: 193.

Horaia sp. Tonnoir 1932: 274.

DIAGNOSIS – **LARVA**: Chiton-shaped, most specimens with two, elongate, submedian dorsal spines on cephalothorax and a single, elongate, median dorsal spine on each subsequent division; antennae three-segmented; abdominal tergites with comb of spinules at lateral margin; prolegs stout, with anterior and posterior prominences at base; anal division fused, semi-circular. **PUPA**: Cephalic sclerite small and triangular, two prominences present in males; respiratory organs elongate, close-set and curved towards posterior; outer gill lamellae transversely corrugated; dorsal surface covered with finely microsculptured tubercles. **MALE**: A_1 vein reduced, barely extending beyond anal angle of wing; stump of R_4

sometimes present; labrum short, narrow, and glabrous; hind coxae setose; dorsal paramere with bilobed opacity in basal half. **Female:** Front and mid tibiae tapered apically; spermathecae large, spherical; accessory gland elongate, tapered.

DESCRIPTION.

LARVA (Figs. 23, 24): Instar I (N = 14) body length 1.0 mm (0.8-1.3), cranial width 0.20 mm (0.17-0.21); antennae one-segmented, black; prolegs small, conical, weakly sclerotized; no gill filaments; cranial sclerite dark brown almost black; egg burster pale, nearly as long as frontoclypeal apotome; trunk pale, with a pair of dark, transverse sclerotized ridges on each abdominal segment. Instar II (N = 16) body length 2.0 mm (1.4-2.3), cranial width 0.38 mm (0.34-0.42); antennae three-segmented; prolegs pale, weakly sclerotized, sparsely setose; one gill filament; trunk pale, each abdominal segment with three dark, transverse ridges. Instar III (N = 25) body length 3.2 mm (2.5-4.0), cranial width 0.63 mm (0.59-0.66); three gill filaments, two directed anteriorly, one directed posteriorly; trunk pale to medium brown; cranial sclerites light reddish to dark brown; dorsal spines sometimes present; prolegs abruptly broadened at base; lateral margin of tergites with ridge of spinules anterior and posterior to base of each proleg. Instar IV (N = 44) body length 5.3 mm (3.6-7.1) cranial width 1.10 mm (0.90-1.22). Antennae three-segmented; all segments black, glabrous, cylindrical; first segment short, broad; third segment elongate, as long as first two segments combined. Cranial sclerites pale to reddish to almost black, darker in larger specimens; ecdysial sutures with no stem line; posterior margin of frontoclypeal apotome extends to posterior cranial margin forming U-shape. Trunk pale to dark brown; each segment with three transverse dark ridges; a pair of oval muscle scars on each side of each segment directly behind the anterior ridges; five gill filaments, three directed anteriorly, two directed posteriorly. Anal division semi-circular with heavily sclerotized posterior margin. Prolegs stout with anterior and posterior prominence at base; comb of spinules at lateral

margin of tergites anterior and posterior to each proleg; first pair of prolegs slightly smaller than others. Dorsal spines present in some specimens; spines arising from midline at posterior transverse ridge on abdominal segments II-VI; spines long (approximately 0.8 mm, regardless of size of specimen), dark, and undulate; two spines also arising from submedian dorsal region of cephalothorax. Chaetotaxy: row of three prominent setae on either side of cephalothoracic suctorial disc; prominent seta on lateral base of each maxillary cardo; row of pale, elongate setae on dorsum of each proleg; single, stout seta posterior to each of sixth pair of prolegs.

PUPA (Figs. 25, 26): Measurements, male (N = 10) length 5.2 mm (4.8–5.6), width 2.6 mm (2.2–2.8); female (N = 1) length 5.1 mm, width 2.5 mm. Body rounded and irregular anteriorly; lateral margins of abdominal segments rounded. Abdominal tergites papillate with evident oval muscle scars. Abdominal tergite I nearly as wide as metatergite. Cephalic sclerite small and triangular; males with a pair of prominences. Color uniform dark brown, respiratory organs darker, almost black. Lamellae of respiratory organs triangular in shape (length 1.7 mm, width at base 0.8 mm); all lamellae separated medially by at least 0.18 mm; lamellae arise anteriorly and curve back posteriorly; all lamellae close set and parallel; outer lamellae transversely corrugated on outer surface, corrugation not evident in mature pupae. No anal cleft.

ADULT MALE: See Tonnoir 1930. *Terminalia* (Figs. 35, 36): Epandrium simple. Cerci well-developed, large, parallel, densely setose at apices; interlobular depression broad, U-shaped; individual lobes rounded laterally and fused medially. Gonostyli elongate, sparsely setose; gonocoxal lobes elongate, flattened, glabrous. Genital capsule large, 1.5 times longer than wide. Aedeagal rods of phallus comprising three, simple, elongate rods. Base of ejaculatory apodeme round. Ventral parameres elongate, slightly longer than

aedeagus, parallel; gonocoxal apodemes elongate, broad, half as long as ventral parameres; dorsal paramere with bilobed opacity in basal half; lateral parameral lobes absent.

ADULT FEMALE: See Tonnoir 1930, 1932. *Terminalia* (Fig. 34): Posterior margin of sternite VIII broadly bilobate, medial depression broad, U-shaped. Genital fork V-shaped; narrow in anterior quarter, broadening widely in posterior three-quarters. Lateral margins of hypogynial plate parallel; individual valves elongate, rounded; inner margins of valves parallel. Accessory gland large, elongate, tapering to a point anteriorly. Spermathecae three in number, corpora large, spherical, irregular; ducts long and simple. Chaetotaxy: sternite VIII without prominent setiforms; hypogynial plate densely setose, valves with ten prominent setiforms each on dorsal surface.

TYPE MATERIAL – Holotype [male imago dissected from pupa]: INDIA.

Meghalaya. Khasi Hills, Lashdat stream, 10.x.1929, coll. S. L. Hora. Allotype [female imago dissected from pupa]: same data as holotype. Holotype and allotype both possibly deposited at IM.

OTHER RECORDS – INDIA: *Himachal Pradesh*. Chamba, stream below Power House, v.1927, coll. S.L. Hora [LP]; Dalhousie, Punj Pul Nallah, v-vi.1927, coll. S.L. Hora [L]; Dalhousie, Krelnu Giri Nullah, v-vi.1927, coll. S.L. Hora [L]; *Meghalaya*. Khasi Hills, Lashdat stream below Chirrapunji Road, 10.x.1929, coll. S.L. Hora [LP]; Khasi Hills, Um-Daung, falls below Dumpep, x.1929, coll. S.L.Hora [L]; Khasi Hills, Dumpep, Pun-Wa-Sherra stream, 21.xi.1926, coll. S.L. Hora [L]; Shillong stream below power house station 16, 6.x.1929, coll. S.L. Hora [L]; Khasi Hills, Dumpep, Pun-Wa-Sherra stream, 1.iv.1930, coll. J. Bhaduri [LPA]; *Sikkim*. Pashok, date unknown, coll. F.H. Gravely [L]; Jhora stream, Tista bridge, 21.xii.1926, coll. S.L. Hora [L]; Reo Jhora stream, 18.xii.1926, coll. S.L. Hora

[L]; NEPAL: *Chitawan District*. trib Trisuli Kh, 7km below Mugling, 27°49'N 84°31'E, 28.viii.1992 [L]; *Dolkha District*. Charnewati Kh above Jiri Rd, 27°42'N 85°59'E, 19.iv.2000 [LPA]; Tama Koshi Kh at Nayapul, 27°37'N 86°04'E, 19.iv.2000 [L]; *Humla District*. Shamne Kh below Simikot, 29°57'N 81°50'E, 25.viii.1994 [L]; Yangchu Kh near Karnali, 29°55'N 81°52'E, 25.viii.1994 [L]; *Jumla District*. Chaudabise Kh above Jumla, 29°17'N 82°13'E, 28.ix.1994 [L]; Chaudabise Kh at Tila, 29°16'N 82°12'E, 25.ix.1994 [L]; Chaudabise Kh at Uthagon, 29°18'N 82°13'E, 25.ix.1994 [L]; Jugau Kh at Jumla, 29°16'N 82°11'E, 10.ix.1994 [L]; Jugau Kh below Ghumurti, 29°17'N 82°11'E, 10.ix.1994 [L]; Sinja Kh at Sinja, 29°24'N 82°01'E, 18.ix.1994 [L]; *Kaski District*. Bhichok Kh above Bhichok, 28°20'N 83°49'E, 28.iv.2000 [LPPex]; Chane Kh at lower Xing, 28°21'N 83°49'E, 3.v.2000 [L]; creek between Landruk and Himalpani Xing, 28°23'N 83°49'E, 29.iv.2000 [L]; Dhorti Khola above Baglung Rd, 15.viii.1992 [L]; same location, 27.iv.2000 [LPA]; E branch Ghirsung Kh near Tolka, 28°21'N 83°49'E, 28.iv.2000 [L]; Furshe Kh at Thuldunga, 28°11'N 83°54'E, 26.iv.2000 [LP]; Gandruk Kh at Himalpani, 28°22'N 83°49'E, 3.v.2000 [L]; Ghirsung Kh above Tolka, 28°21'N 83°49'E, 28.iv.2000 [L]; Kyunri Kh at lower Xing, 28°23'N 83°49'E, 3.v.2000 [L]; Kyunri Kh near Gandruk, 28°23'N 83°48'E, 22.viii.1992 [L]; Kyumnu Kh at lower Xing, 28°24'N 83°49'E, 29.iv.2000 [A]; Landruk Kh NE of Landruk, 28°22'N 83°49'E, 29.iv.2000 [L]; Modi Kh at Nayapul, 28°23'N 83°49'E, 29.iv.2000 [P]; Phus Kh above Xing, 28°11'N 83°54'E, 28.viii.1992 [LP]; Saane Kh below Gandruk, 28°21'N 83°48'E, 21.viii.1992 [LP]; S branch Phus Kh, 28°11'N 83°54'E, 28.viii.1992 [LP]; Seti River near confluence of Yamdi Kh, 28°15'N 83°57'E, 26.iv.2000 [LPAPex]; small creek between Lumle and Kaare, 28°17'N 83°48'E, 15.viii.1992 [L]; small creek N Tamijung, 28°19'N 83°48'E, 21.viii.1992 [LPPex]; small creek S Tamijung, 28°19'N 83°48'E, 21.viii.1992 [LP]; Suikhet Kh at Phedi, 28°17'N 83°52'E, 13.viii.1992 [LPPex], same location, 16.viii.1992 [LP]; same location, 31.viii.1992 [LPPex]; same location, 27.ix.1992 [L]; same location, 26.iv.2000 [LA]; Syauli Kh at Syauli Bazar, 28°20'N

83°48'E, 3.v.2000 [L]; trib Kaare Kh, 28°17'N 83°48'E, 15.viii.1992 [L]; Yamdi Kh above Ghatte, 28°17'N 83°51'E, 13.viii.1992 [LPPex]; same location, 31.viii.1992 [L]; same location, 26.iv.2000 [L]; Yamdi Kh at lower Xing, 28°15'N 83°57'E, 31.viii.1992 [L]; *Kathmandu District*. SFR, "Bleph Falls" upper Bagmati Kh, 27°46'N 85°25'E, 13.vii.1994 [L]; same location, 4.ix.1994, coll Pradhan & Shrestha [L]; same location, 2.x.1994 [LP]; same location, 16.iv.2000 [LP]; SFR, Chharchhare Kh, 27°47'N 85°22'E, 15.iv.2000 [LP]; same location, 22.iv.2000 [LP]; SFR, Dhobi Kh, 9.vii.1994 [L]; SFR, "E trib" upper Bagmati Kh, 27°46'N 85°25'E, 13.vii.1994 [LP]; same location, 2.x.1994 [LP]; same location, 16.iv.2000 [LP]; SFR, "Mica trib" Nagmati Kh, 27°46'N 85°26'E, 13.vii.1994 [L]; SFR, Nagmati Kh at Shivapuri Rd, 13.vii.1994 [L]; SFR, Salmati Kh above trail Xing, 27°46'N 85°25'E, 2.x.1994 [LP]; same location, 16.iv.2000 [L]; SFR, upper Bagmati Kh, 2.x.1994 [LP]; *Mugu District*. Jhari Kh at Rara trail, 29°29'N 82°07'E, 14.ix.1994 [L]; *Parbat District*. Ambot Kh above Ambot, 28°15'N 83°43'E, 27.iv.2000 [LPPex]; falls above Saharadhara, 28°14'N 83°37'E, 27.iv.2000 [L]; Kali Gandaki near Saharadhara, 28°14'N 83°37'E, 27.iv.2000 [LP]; Kanthe Kh near Kali Gandaki, 28°15'N 83°37'E, 27.iv.2000 [L]; Kewadi Kh (mainstem), 28°14'N 83°39'E, 27.iv.2000 [L]; Modi Kh above Dimua, 28°16'N 83°45'E, 27.iv.2000 [LP]; Pati Kh above Patichaur, 28°16'N 83°44'E, 27.iv.2000 [LPPex]; trib Kewadi Kh, 28°14'N 83°39'E, 27.iv.2000 [L]; *Sindhupalchok District*. Belaphi Kh above Belaphi, 27°44'N 85°46'E, 18.iv.2000 [LP]; Bhairabkunda Kh above Xing, 27°55'N 85°55'E, 12.vii.1994 [L]; Bulgate Kh above Kodari Rd, 27°52'N 85°53'E, 12.vii.1994 [L]; same location, 20.iv.2000 [LPPexA]; Chakhu Kh above Chakhu, 27°53'N 85°54'E, 12.vii.1994 [LPPex]; same location, 20.iv.2000 [PPex]; Dhad Kh above "Lhasa" Rd, 11.vii.1994 [L]; Ghatte Kh at Lamosanga, 11.vii.1994 [L]; Itabare Kh above Barabise, 12.vii.1994 [LPPex]; Kupre Kh above Lamosanga, 11.vii.1994 [L]; Lipping Kh near Kodari, 27°58'N 85°57'E, 12.vii.1994 [L]; Pangpunge Kh above Kodari Rd, 27°50'N 85°53'E, 20.iv.2000 [LP]; Sun Koshi Kh above Lamosangu, 27°45'N 85°51'E, 18.iv.2000 [LPA]; Sun

Koshi Kh below Barabise, 27°46'N 85°54'E, 18.iv.2000 [LPA]; Takdel Kh above Kodari Rd, 27°49'N 85°53'E, 20.iv.2000 [LP]. THAILAND. *Chiang Mai Province*. Doi Inthanon NP, Nam Mae Klang near Ban Sob Ab, 18°31'N 98°36'E, 11.iv.2000 [LP]; same location, 19.v.2001 [L]; Doi Inthanon NP, Namtok Huai Sai Leung, 18°31'N 98°27'E, 4.xi.1994 [LPPex]; same location, 11.iv.2000 [LPPex]; same location 18.v.2001 [L]; Doi Inthanon NP, Namtok Mae Klang, 18°31'N 98°27'E, 4.xi.1994 [L]; Doi Inthanon NP, Namtok Mae Pan, 18°31'N 98°27'E, 4.xi.1994 [LPPexA]; same location 11.iv.2000 [LPPex]; same location, 18.v.2001 [L]; Doi Inthanon NP, Namtok Siriphum, 18°32'N 98°30'E, 4.xi.1994 [LP]; same location, 11.iv.2000 [P]; same location, 18.v.2001 [L]; *Chiang Rai Province*. Huai Mae Korn, 19°51'N 99°38'E, 5.xi.1994 [L]; Huai Phrong Phrabat, 19°59'N 99°48'E, 5.xi.1994 [L]; Namtok Pha Noi, 19°51'N 99°38'E, 5.xi.1994 [L]; *Lampang Province*. Namtok Chae Son, 18°48'N 99°29'E, 6.xi.1994 [LPPex]. *Mae Hong Son Province*. Nam Mae Surin, 18°55'N 98°05'E, 15.xi.1994 [LP]; Namtok Mawpang, 14.xi.1994 [LPPex]; Namtok Phasua, 14.xi.1994 [P]. *Nan Province*. Namtok Silapet, 19°07'N 100°58'E, 11.xi.1994 [LPPex]; *Phrae Province*. Huai Mae Keung, 17°58'N 99°35'E, 13.xi.1994 [L]; Namtok Mae Kung, 17°58'N 99°35'E, 13.xi.1994 [LPPex]. All specimens coll GW Courtney unless otherwise noted.

DISTRIBUTION – (Figs. 52, 53) Found throughout the Himalayan region of Nepal and northern India. Also found in the northern provinces of Thailand, most likely found in mountainous regions between. Often found in same location as other members of *Horaia* as well as other genera.

REMARKS – Adults are distinctive from most other *Horaia* in their large size and reduced A₁ vein. Adults can be distinguished from *H. piedmonti* by the larger size, setose hind coxae, and glabrous male antennae. In some specimens, both male and female, a

segment of the R_4 vein is seen on the R_{4+5} vein (Tonnoir 1930). Pupae are unique in a number of features including the shape of the respiratory organs and the presence of microsculptured papillae on the tergites. Larvae are also unique amongst the *Horaia* with a characteristic chiton-like shape and spinulose lateral margin. A number of different larval forms of *H. montana* are known (Tonnoir 1930, Zwick pers. comm.). Differences between these forms are slight and inconsistent, with intermediate morphs plentiful. The perceived differences in forms are likely due to morphological changes associated with growth and molting. Coloration and relative body size can change greatly in the course of a single instar, but sclerotized structures (i.e., suctorial discs, cephalic sclerites, antennae, mouthparts) are invariant (Craig 1969). The presence or absence of dorsal spines is also not a species-defining character (Tonnoir 1930).

CHAPTER 5. PHYLOGENETIC RELATIONSHIPS

Results

Characters used in the phylogenetic analysis are summarized in Appendix B. 22 characters and 16 taxa are used in the analysis. Of the characters, twelve are adult characters, three are pupal characters, and seven are larval characters. All multistate characters are considered as unordered. Parsimony analysis produced two trees of length 29 steps. A strict consensus of these trees (Fig. 55) has a Consistency Index (CI) of 0.862, a Retention Index (RI) of 0.926, and a Rescaled Consistency Index (RC) of 0.798. Bootstrap values strongly support nearly all nodes of the consensus tree.

Discussion

Within the Blepharicerinae, Apistomyiini is a monophyletic group. All Apistomyiine genera are characterized by the following synapomorphies: (1) adult maxillary palps reduced to one or two segments (Zwick 1977), (2) elongate labella (in those cases where it is reduced, the pupal sheath reveals past presence) (Alexander 1958), (3) four pairs of adhesive organs in the pupae (Zwick 1977), and (4) larvae without intercalary abdominal segments (Kitakami 1950). While some of these characters are seen in some members of the Paltostomatini (eg. *Hapalothrix* Loew), this is a product of convergence (Zwick 1977).

Genus-level classification of the Apistomyiini has been hampered by a lack of specimens of all life stages from all genera (Tonnoir 1932). Fossil records, essential for establishing ancestral character states, are completely lacking for the family (Alexander 1958). Edwards (1929) suggests that the unique life history and habitat of members of the family makes it unlikely that fossil Blepharicerids will ever be found. For these reasons, attempts at phylogenetic analysis have been based exclusively on incomplete descriptions of extant species. An overwhelming factor in any attempt to analyze the Apistomyiini is the frequency of convergence among the genera (Stuckenberg 1958; Zwick 1977).

Early phylogenetic analyses of the Apistomyiini relied heavily on characters of wing venation. The guiding principle of these studies has been a progression from ancestral states with a full complement of veins (eg. *Edwardsina* Alexander) to a derived reduction in venation (eg. *Hammatorrhina* Loew) (eg. Kitakami 1950; Alexander 1958; Dumbleton 1963). Within the Apistomyiini, the presence of a forked R_{4+5} vein, with R_4 and R_5 separate at the tip (eg. *Neocurupira*) is the ancestral condition (Craig 1969). An unforked R_{4+5} vein is common to *Horaia*, *Apistomyia*, *Parapistomyia*, *Nesocurupira*, *Theischingeria*, and *Peritheates*. This change in venation is likely to have arisen independently many times. The exact nature of the change (i.e. whether the R_4 or the R_5 vein was lost) is impossible to determine. Even amongst genera with the ancestral, forked condition, it is likely that the presence of a forked R_{4+5} vein is convergent (Zwick 1977). For this reason, the use of the radial veins for phylogenetic analysis is discouraged. At most, the only character useful for analysis is the sinuous shape of the R_{4+5} vein synapomorphic to *Apistomyia* and *Parapistomyia*. An extra vein fragment in the radial sector of *H. manaliella* is of an uncertain origin. The condition of the A_1 vein is another ambiguous character. The ancestral condition, seen in *Peritheates* and *Neocurupira*, is a complete or nearly complete A_1 vein. The degree of vein reduction from the ancestral state varies inter- and intragenetically. An extreme in reduction is present in one case and indicates relationships within *Horaia*. Both *H. montana* and *H. piedmonti* have the A_1 vein greatly reduced.

Adult mouthparts are usually consistent within a genus (Kitakami 1950). The presence of mandibles in adult females is plesiomorphic for the Blephariceridae (Zwick 1977). Absence of mandibles is common to nearly all members of the Apistomyiini, yet this condition may have arisen due to convergence (Stuckenberg 1958; Zwick 1977). Mandibles have been regained in the *Apistomyia* due to character reversal (Zwick 1998) and the presence of weak mandibles in members of the *Parapistomyia* may represent a transitional state. The reduction of other mouthparts, notably the labella, has arisen independently

several times in the family (Stuckenberg 1969). A characteristic reduction of the labrum, producing a slender, asetose condition is a synapomorphy of *H. montana* and *H. piedmonti*. The plesiomorphic condition of the maxillary palpi in Apistomyiini is two segments, a quadrate palpiger and an elongate distal segment (Zwick 1977). The two-segmented condition is seen in *Neocurupira*, *Peritheates*, *Curupirina*, and *Austrocurupira*, although the general reduction of mouthparts in *Nesocurupira*, *Theischingeria* and *Nothohoraia* obscures this character. The presence of a characteristic sense-organ on the second palpal segment is a synapomorphy of *Neocurupira* and *Peritheates* (Stuckenberg 1969). Fusion of the two segments of the maxillary palpi is a synapomorphy of *Apistomyia*, *Parapistomyia*, and *Horaia*. Further reduction of the maxillary palpi to a small, globular shape has taken place in all species of *Horaia*, except *H. manaliella* and *H. namtoki*.

The eyes in adult Apistomyiini display a wide range of conditions including dichoptism, holoptism, and sexual dimorphism. While excellent key characters, the variability of the condition of the eyes, even within genera, makes this suite of characters of questionable phylogenetic value (Stuckenberg 1958; Craig 1969).

Informative antennal characters are two-fold in the Apistomyiini. Reduction of flagellomere number is a common derived character (Kitakami 1950). From an ancestral condition of as many as 12 flagellomeres (eg. *Nothohoraia*; Zwick 1977) there is reduction to as few as five (eg. *H. barbata*). Genera, species, and individual specimens can display a range of flagellomere number. Because reduction in flagellomere number is due to fusion, determining definite character states is impossible. When flagellomere number can be accurately determined, similar character states between species are likely to be due to convergence (Zwick 1977). The condition of the scape and pedicel is easier to determine. The plesiomorphic state, present in *Neocurupira*, *Nothohoraia*, *Curupirina*, *Nesocurupira*, and *Peritheates*, is a scape and pedicel subequal to the flagellomeres in width. The remaining

genera of the Apistomyiini are synapomorphic in having a scape and pedicel greatly expanded to at least twice the width of the flagellomeres (Zwick 1977).

Phylogenetically informative characters of the leg are few. Tibial spur formula, often useful in other groups proves to be convergent in the Apistomyiini (Kitakami 1950). Tarsal claw shape and size also varies greatly amongst genera and species. The only leg character used in the present analysis is an anterodorsal row of dark setae on the front femora of females (Tonnoir 1930). This character is synapomorphic to all *Horaia* except *H. manaliella*. A number of characteristic conditions exist in the hind legs of female *H. manaliella*, including an absence of tibial spurs, straight joints between the tarsal segments, and slender tarsal claws. These characters are autapomorphies of the species and are most likely associated with the extreme lengthening of the hind legs.

Until recently, complete genitalic characters have not been included in species descriptions. Many early descriptions neglected to mention the terminalia or provided only crude drawings. For this reason, only the genitalic characters of the presently examined species can be analyzed for insight into evolutionary relationships. Within *Horaia*, a few conclusions can be drawn from genitalic characters. In the females, an elongate, tapered accessory gland is a synapomorphy of *H. montana* and *H. piedmonti*. In the males, the presence of a notched or completely bilobate opacity on the basal half of the dorsal paramere is a synapomorphy of the *Horaia* excluding *H. manaliella*.

Another reproductive character of phylogenetic interest is the development of the eggs within the adult female. In the ancestral condition, the female emerges from the pupa with an abdomen replete with chorionated eggs. In *Apistomyia*, the females emerge with no or only slightly developed eggs (Zwick 1998). This character is an autoapomorphy of the genus.

Characters of the immature stages have been used in blepharicerid systematics far more often than in other dipteran taxa. This could be due to the morphological adaptations

evident in many species. The biology of the larval and pupal stages of Blephariceridae makes it likely that phylogenetically significant adaptations will be more evident in immature life stages than in the adult stages (Hora 1930).

The Apistomyiini share an oval pupal shape common to most blepharicerids. Variations in gross morphology are few. *Curupirina* and *Nesocurupira* share a synapomorphic medial fusion of abdominal tergites VII and VIII (Zwick 1977). Finely microsculptured papillae are present in *H. montana* and may be of importance for current avoidance (Hora 1930). They are an autapomorphy of the species, but may be homologous to the foveolae seen in the rest of the *Horaia*.

Analyses of flow patterns indicate that vortices and areas of negative pressure are created around the lamellae of the respiratory organs regardless of their shape. This would eliminate any evolutionary pressure towards a more efficient lamellar shape (Pommen and Craig 1995). The ancestral form for Apistomyiine respiratory organs is likely that of *Neocurupira* (Craig 1969). The plesiomorphies of the Apistomyiini thus include elongate, triangular outer gill lamellae; all lamellae well removed from the mid-line; outer lamellae divergent; and the tracheal opening present as a U-shaped slit. *Parapistomyia*, *Apistomyia*, *Nothohoraia*, and *H. barbata* all show a shift in the positioning of the respiratory organs towards the midline. This variability in the location of the respiratory organs is likely a convergent character. Only the extreme displacement and fusion of the outer lamellae at the midline, seen in *Apistomyia*, is of importance as it is the defining autapomorphy of that genus (Zwick 1998). *Apistomyia* also shows an extreme reduction in the outer lamellae resulting in low, blunt ridges. This is an autapomorphy for the genus that may be linked to the fusion of the outer lamellae along the midline. Within the *Horaia*, there appears to be little divergence from the apistomyiine groundplan. In *H. montana* the outer lamellae are not divergent, but closely set and heavily sclerotized. This is an autapomorphy of the species, but would be

expected to be present in the pupal stages of *H. piedmonti*. This same, heavily-sclerotized condition is seen in *Austrocurupira*, but is convergent.

Within the respiratory organs, a straight tracheal opening, without an operculum, is plesiomorphic for the Blephariceridae (Zwick 1977). The plesiomorphic condition for the Apistomyiini, seen in *Neocurupira*, *Peritheates*, *Austrocurupira* and *Theischingeria*, is the presence of an operculum and a U-shaped tracheal opening. In *Nothohoraia*, *Curupirina*, and *Nesocurupira*, the tracheal opening is modified into a Y-shape (Zwick 1998; Stuckenberg pers. comm.). In *Parapistomyia*, *Apistomyia*, and *Horaia* character reversal has resulted in a loss of the operculum and straight tracheal opening (Stuckenberg pers. comm.). The closely set lamellae of *H. montana* make the tracheal opening appear to have an irregular pattern, yet this is only a slight variation on the simple slit seen in the rest of the genus.

The groundplan for the larvae of Blephariceridae includes a proleg on abdominal segment VII and eversible, crochet-tipped prolegs in the first instar (Courtney 1990, 1991). The groundplan for the Apistomyiini is the same as this condition and is seen in the ancestral genera *Neocurupira* and *Peritheates* (Zwick 1981). Other plesiomorphic larval conditions for the Apistomyiini (as seen in *Neocurupira* and *Peritheates*) include dorsal tergites without sclerotized ornamentation; anal division incompletely fused into a single segment; and posterior margin of anal segment emarginate and setose. While used in past phylogenetic analyses, an increased number of gill filaments is a convergent character (Zwick 1977).

Modification of the crochet-tipped prolegs of the first instar larva into seta-tipped prolegs is a synapomorphy of all Apistomyiini excluding *Neocurupira* and *Peritheates*. In *Austrocurupira* and *Theischingeria* the modification is carried further and the prolegs are modified into asetose, sclerotized plates (Zwick 1998). Synapomorphic of the genera excluding *Neocurupira* and *Peritheates* is the reduction of the seventh pair of prolegs to a pair of small protuberances or setae. Increased dorsal sclerotization is synapomorphic to all *Horaia*. A convergent condition is seen in *Nothohoraia*. The formation of the posterior

margin of the anal division into a sclerotized, asetose margin is synapomorphic of the Apistomyiini exclusive of *Neocurupira* and *Peritheates*. This character is lost in *Apistomyia* and *Parapistomyia* through character reversal. The complete fusion of the anal division into a single segment, without any clear demarcation between abdominal segments VI and VII, is synapomorphic of the members of the genus *Horaia*. The anal division is further modified in *H. montana* into a semi-circular shape. This autapomorphy of *H. montana* is related to a number of other adaptations in the species leading to a chiton-like, sharply-margined larval form. *Nothohoraia* also have this larval shape, but any similarity is convergent (Zwick 1977).

Larval mouthparts, particularly the maxillary palpi, indicate a close, possibly sister-group, relationship between *Apistomyia* and *Horaia* (Courtney 2000a). The plesiomorphic condition for Blephariceridae is palpi with 10-11 distinct sensillae each, with the “F” sensillae comprising one or two broad plates. In both *Apistomyia* and *Horaia* the “F” sensillae are subdivided into a series of sensillae.

Other potentially informative phylogenetic characters include the structure of the plastron on the respiratory organs and microsculpture of the pupal integument. Once these characters are known for all genera, more characters can be added to improve the resolution of the proposed phylogeny.

Zwick (1977) has proposed the only previous phylogeny for the Apistomyiine genera (Fig. 54). He states that, while *Apistomyia* and *Horaia* have morphological characters in common, the closest sister-group to *Horaia* is most likely to be *Austrocurupira*. This conclusion was based on the condition of the labium in adults. In *Horaia* and *Austrocurupira*, the base of the labium is split for over half of its length. In light of the present data, this character must be convergent. My proposed phylogeny (Fig. 56) is based on the characters discussed above and summarized in Appendix B.

Horaia is clearly a monophyletic genus with *Apistomyia*+*Parapistomyia* the closest sister-group. In light of recent synonymization (Zwick 1998), the species of the genus *Hammatorrhina* are included with *Apistomyia*. Other differences from Zwick's (1977) phylogeny include the establishment of *Nothohoraia* as the sister group to *Nesocurupira* +*Curupirina* based on the shape of the tracheal opening in the pupal respiratory organs. I propose *Theischingeria* as the sister-group to *Austrocurupira* based on the modification of the first instar prolegs. The *Theischingeria*+*Austrocurupira* clade is the sister-group to the (*Apistomyia*+*Parapistomyia*)+*Horaia* clade with all five genera sharing a synapomorphically expanded scape and pedicel. An additional character uniting the Apistomyiini exclusive of *Neocurupira*+*Peritheates* is the presence of a sclerotized, asetose posterior margin in the larval anal division.

The genus *Horaia* is a valid, monophyletic taxon characterized by a fully fused anal division and heavily sclerotized dorsal integument in the larvae. Within the genus, relationships are not fully resolved because of a lack of all life stages for some species. Three adult characters serve as synapomorphies of *H. montana* and *H. piedmonti*. Synapomorphic reduction of the maxillary palpi groups the *Horaia* exclusive of *H. namtoki* and *H. manaliella*. The placement of *H. longipes* within the genus is uncertain due to a lack of knowledge about genitalia, larval, and pupal characters.

Biogeography

The distribution and life history of Blephariceridae has presented a challenge to systematists seeking to draw conclusions about the biogeography of the family.

Blephariceridae are limited to specific habitats and do not survive for long when removed from torrenticolous waterways. Local geographic distribution can only be explained by past movement along land routes. More specifically, the family could only have ever existed in areas of mountainous streams (Tillyard 1922). A single example exists of a species present

on non-continental islands; *Paltostoma schineri* Williston, present on the islands of the Caribbean (Scott, 1915; Stuckenberg 1969). It is a poor capacity for dispersal that makes Blephariceridae particularly useful in studies of the biogeography of a region (Zwick 1981).

Blephariceridae likely originated in the Southern Hemisphere and moved north (Tillyard 1922). Alexander's (1958) analysis of the distribution of Blephariceridae indicates that Edwardsininae is limited to Australia, southern South America, and Madagascar. This is a relictual Gondwanan distribution (Zwick 1977). The Blepharicerinae are more widespread with each tribe in the subfamily endemic to specific zoogeographical zones. The Blepharicerini are Holarctic and Oriental in distribution. The Paltostomatini are found in South Africa and the Neotropics. The Apistomyiini are restricted to the Palearctic, Oriental, and Australasian regions.

The presence of plesiomorphic endemics in New Zealand is not uncommon amongst the Diptera (Brundin 1967). The most basal members of the Apistomyiini (*Neocurupira*, *Peritheates*, *Curupirina*, *Nesocurupira*, and *Nothohoraia*) are confined to New Zealand and New Caledonia (Zwick 1977, 1981), while derived genera are found in Asia, Europe, New Guinea, and Australia.

Stuckenberg (1969) and Craig (1969) have suggested that the Apistomyiini originated in Asia. Within this hypothesis, the present distribution of the Apistomyiini is the product of radiation in Asia and subsequent waves of colonization into the Australasian region via land bridges. The Asian origin hypothesis corresponds with Ross's (1956, 1967) conclusions about the radiation of Trichoptera into Australia.

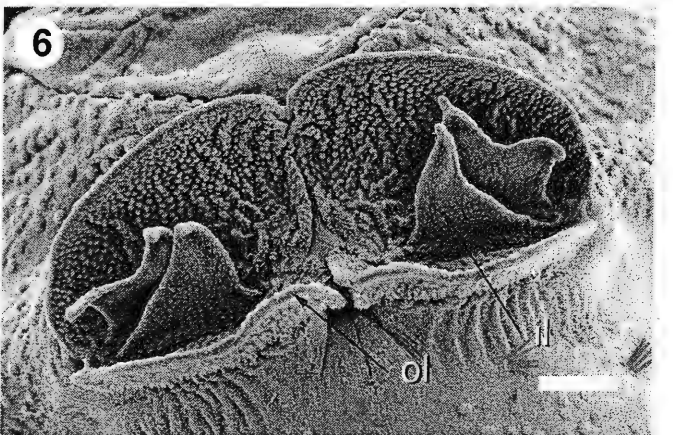
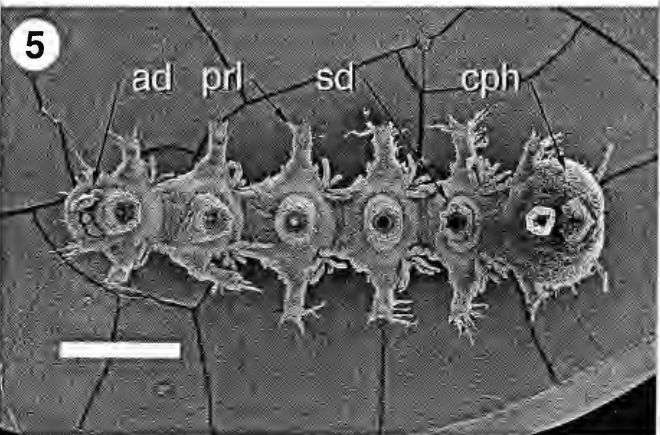
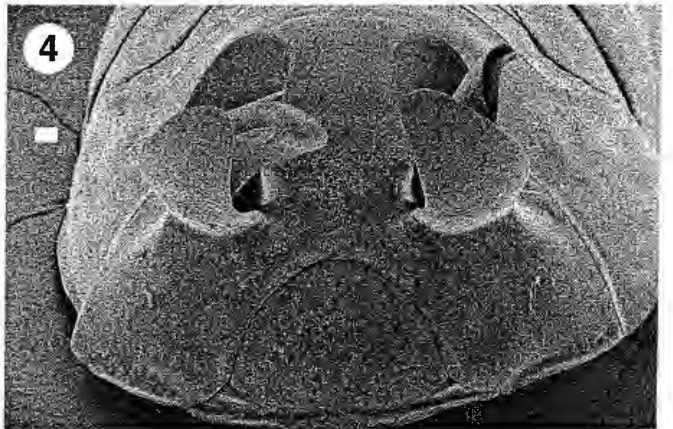
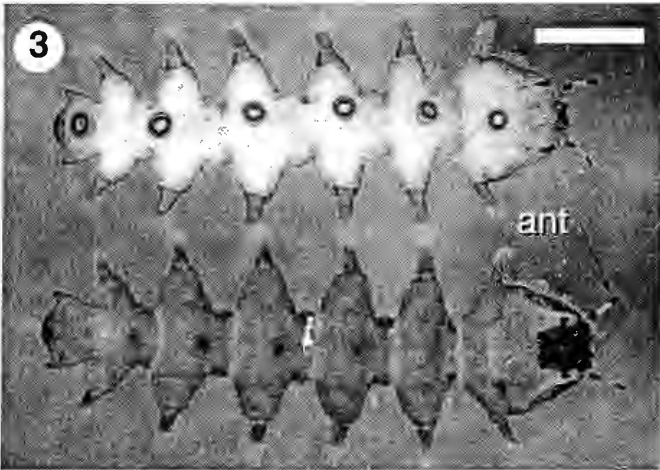
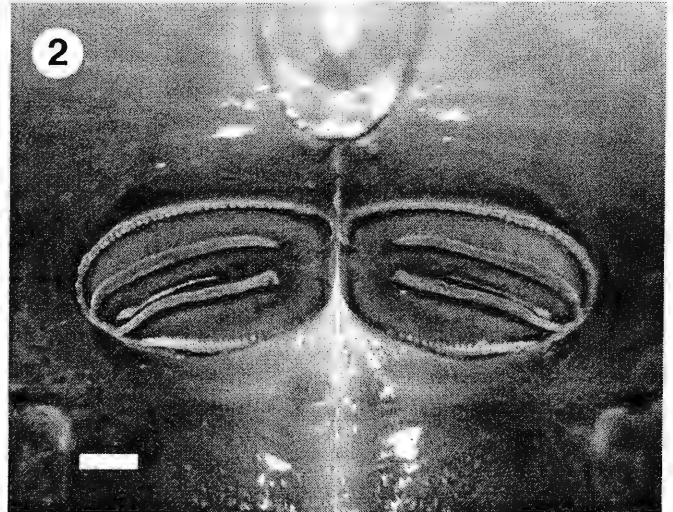
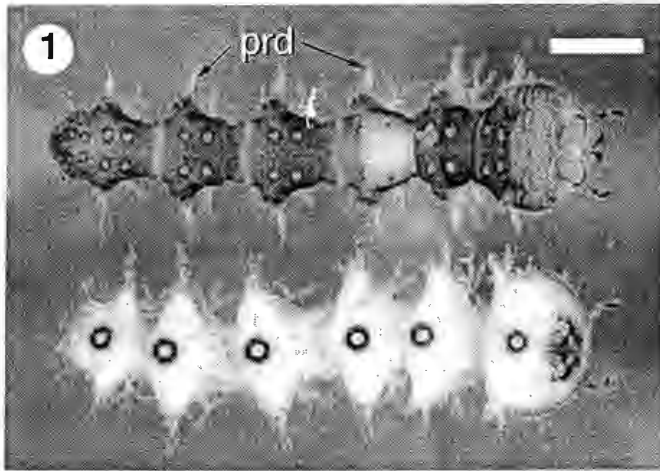
The present research is in close accordance with the Antarctic origin hypothesis of Zwick (1977, 1981). Apistomyiini is a subgroup of a Neotropical branch of Paltostomatini. This branch split with Paltostomatini while South America and New Zealand were still connected via Antarctica. Apistomyiini then spread into Asia via New Caledonia. As this continuous landmass was split up, ancestral genera were isolated (Zwick 1977). The new

placement of *Nothohoraia* as sister-group to *Curupira*+*Nesocurupira*, adds strength to this argument. Within Asia, an adaptive radiation into the present genera *Apistomyia*, *Parapistomyia*, and *Horaia* took place. Whether *Theischingeria*+*Austrocurupira* represent isolated ancestral genera or a product of radiation in Asia is unclear. Subsequent to adaptive radiation, *Horaia* remained within Asia, while *Apistomyia* spread West to Europe, East to Japan, and South to New Guinea and Australia. *Parapistomyia* is present only in New Guinea and Australia, making it likely that the split with *Apistomyia* took place after departure from Asia.

Biogeography of the *Horaia* is difficult to ascertain. The most widespread species is *H. montana*, but it is also the most derived and its present distribution may be a product of extreme range expansion. Basal species, *H. manaliella*, and *H. namtoki*, are limited to Nepal and Thailand respectively, but these may be relict populations. Certainly, a lack of specimens of all species and genera, particularly from the mountainous regions of south and southeast Asia, hampers any attempts at drawing conclusions about species range.

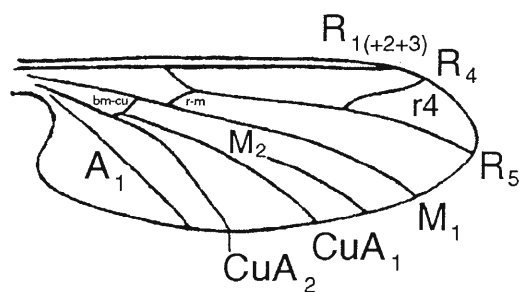
APPENDIX A. FIGURES

Figures 1-6. Larval and pupal Blephariceridae. **1-2:** *Philorus* sp.: **1:** larva, dorsal and ventral views. **2:** pupal respiratory organs, dorsal view. **3-4:** *Blepharicera* sp.: **3:** larva, dorsal and ventral views. **4:** pupal respiratory organs, dorsal view. **5-6:** *Apistomyia* sp.: **5:** larva, ventral view. **6:** pupal respiratory organs, dorsal view (abbreviations: ad – anal division; ant – antennae; cph – cephalothorax; il – inner lamellae of respiratory organs; ol – outer lamellae of respiratory organs; prd - dorsal prolegs; prv – ventral prolegs; sd – suctorial discs). Scale bars: 1mm (Figs. 1, 3, 5); 100µm (Figs. 2, 4, 6).

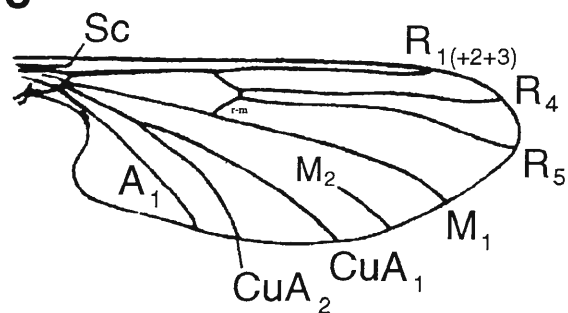


Figures 7-14. Wings of Blephariceridae. **7:** *Philorus horai* Tonnoir. **8:** *Blepharicera fasciata* (Westwood). **9:** *Apistomyia elegans* Bigot. **10:** *Horaia manaliella* (Kaul). **11:** *H. montana* Tonnoir. **12:** *H. montana* Tonnoir, variation with stump of R₄ vein. **13:** *H. barbata* sp.n. **14:** *H. piedmonti* sp.n. (adapted from Courtney 2000a).

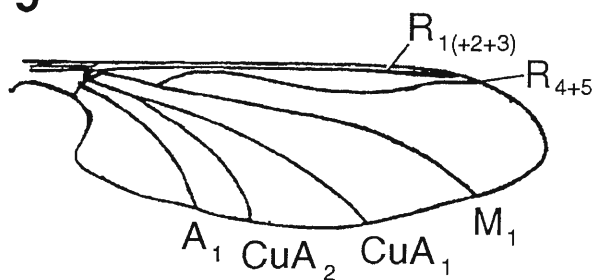
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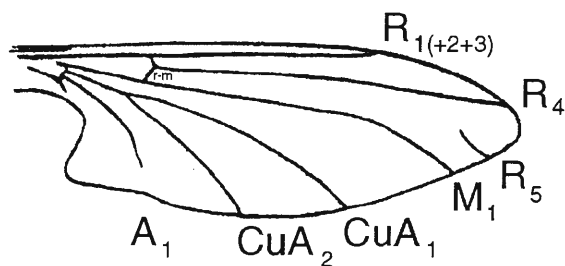
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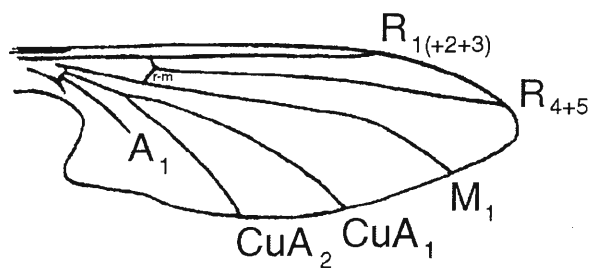
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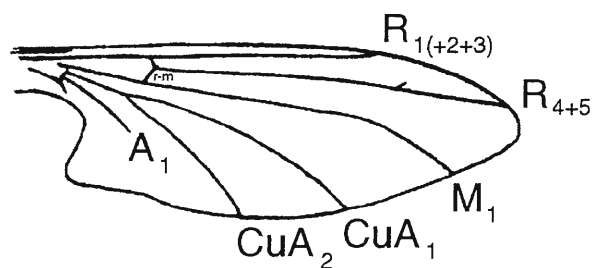
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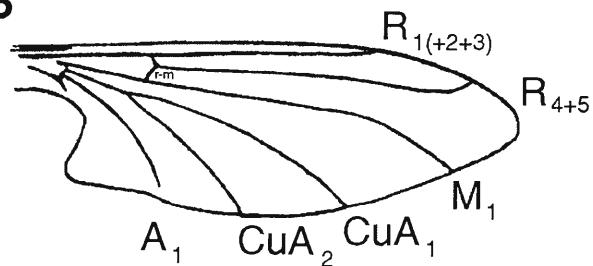
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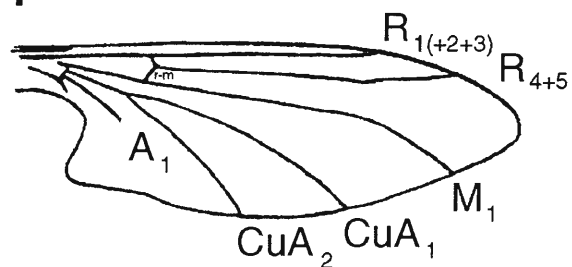
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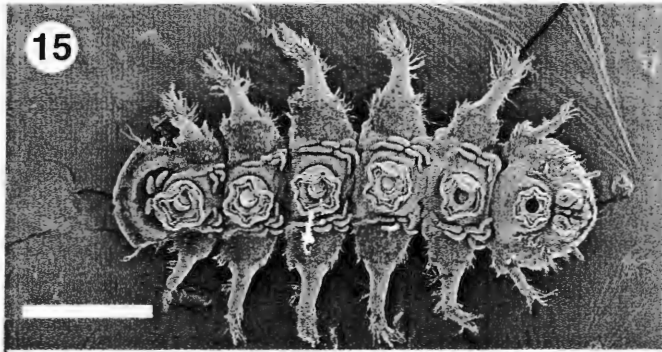
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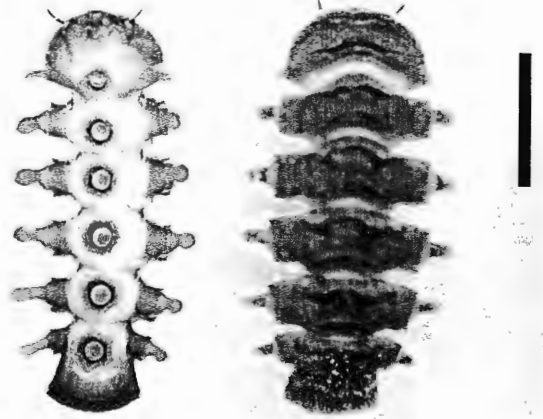
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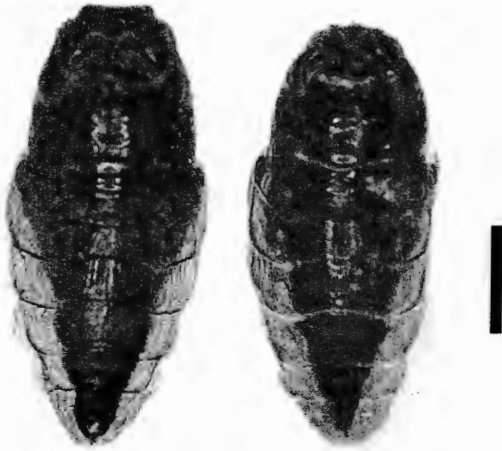
Figures 15-22. Scanning electron and light micrographs of larvae and pupae of *Horaia barbata* sp.n. and *H. manaliella* (Kaul). **15-18: *H. barbata*:** **15:** Instar IV larva, ventral view. **16:** Instar IV larva, ventral (left) and dorsal (right) views. **17:** male (left) and female (right) pupae, dorsal view. **18:** pupal respiratory organs, dorsal view. **19-22: *H. manaliella*:** **19:** Instar IV larva, ventral view. **20:** Instar IV larva, ventral (left) and dorsal (right) views. **21:** male (left) and female (right) pupae, dorsal view. **22:** pupal respiratory organs, dorsal view (abbreviations: ac – anal cleft). Scale bars: 1mm (Figs. 15-17, 19-21); 100µm (Figs. 18, 22).



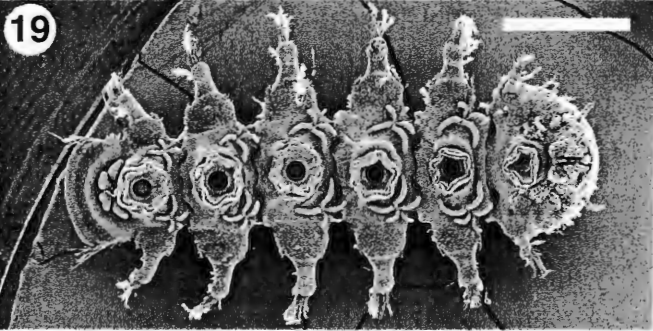
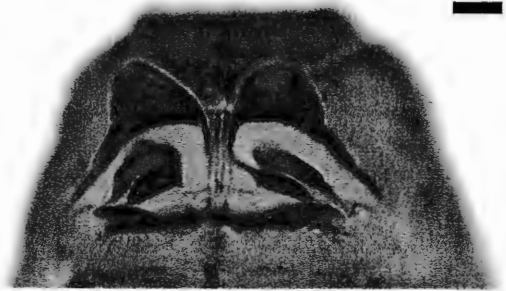
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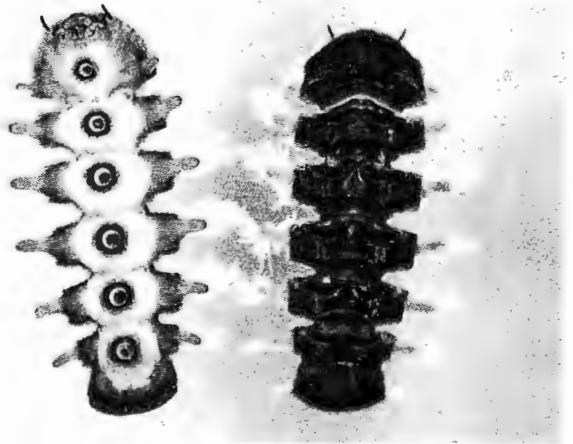
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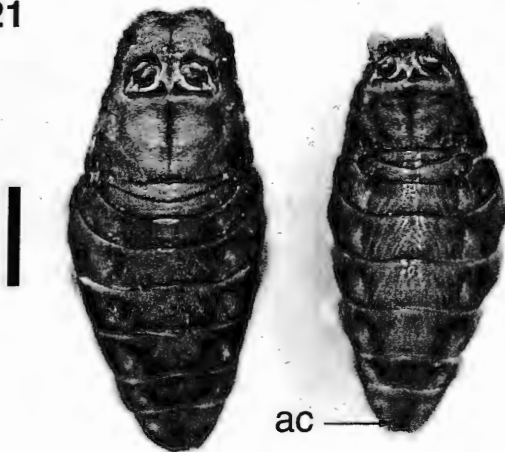
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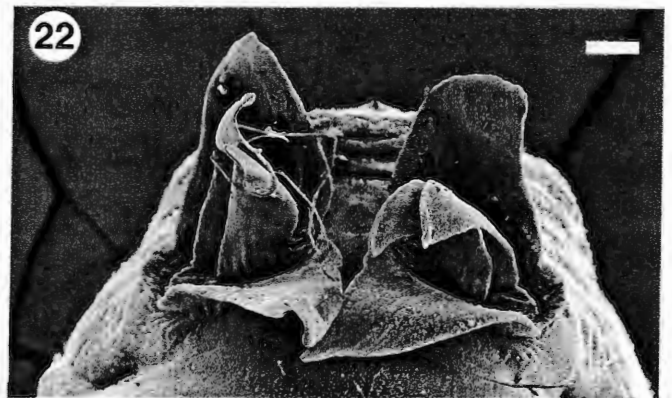
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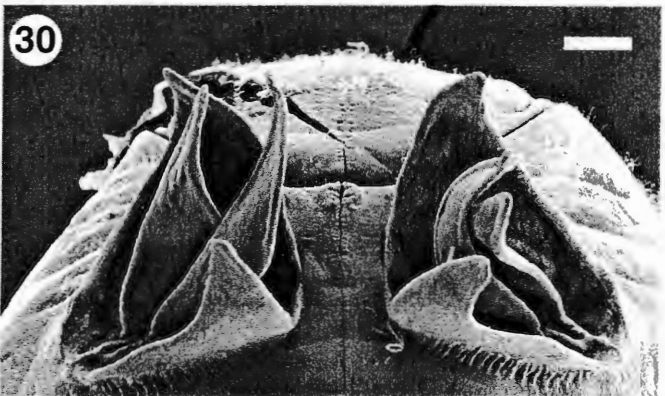
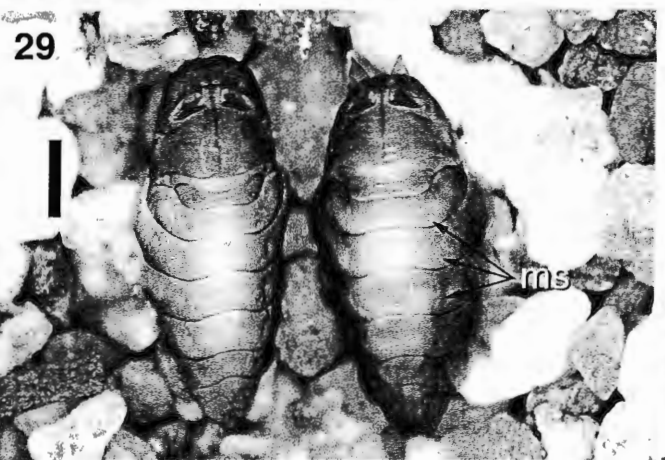
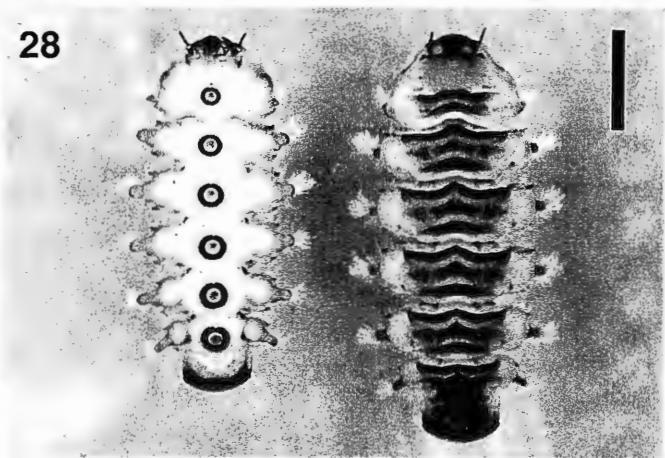
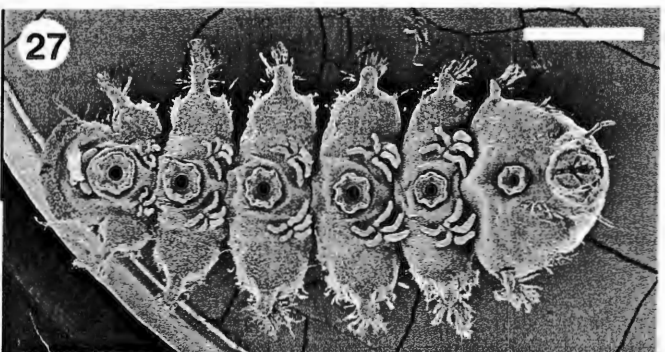
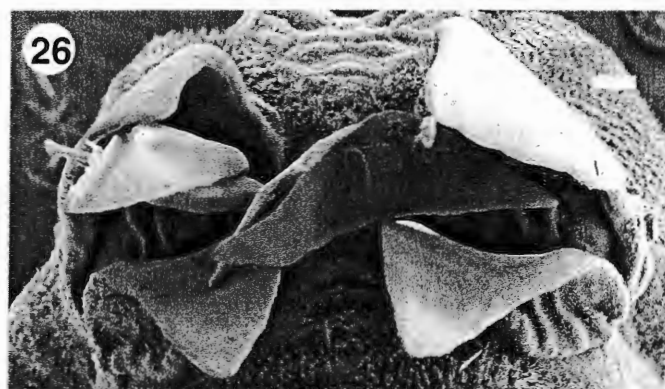
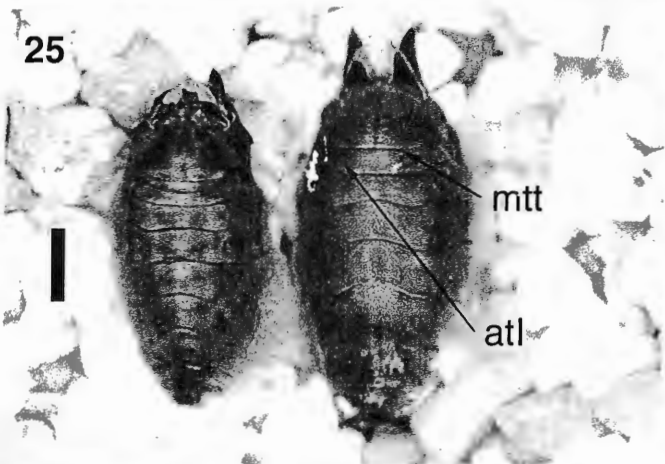
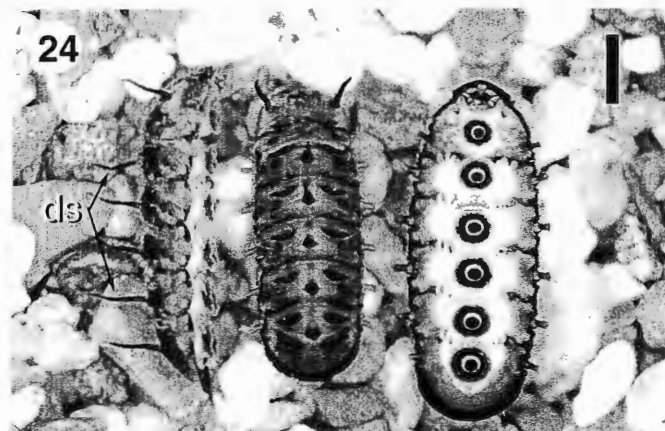
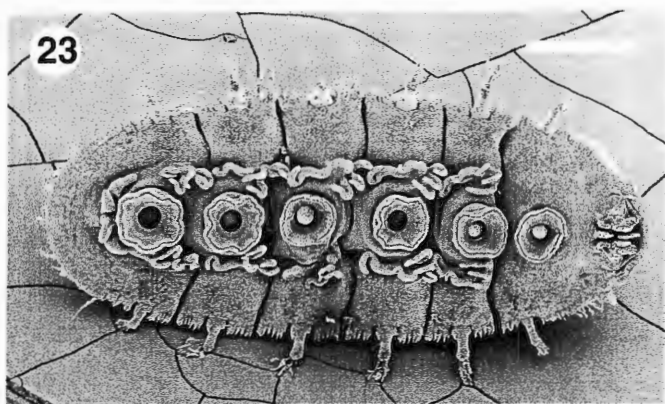
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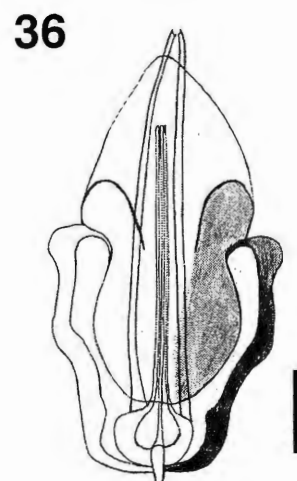
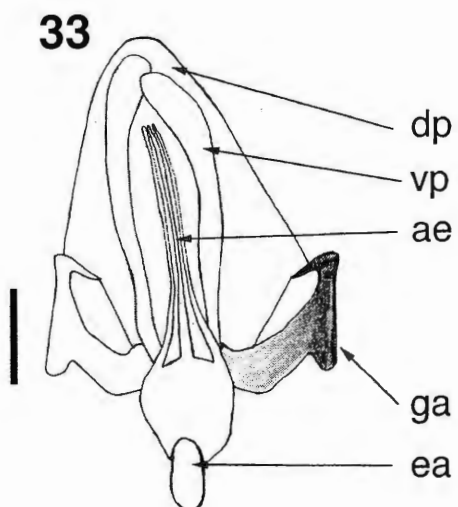
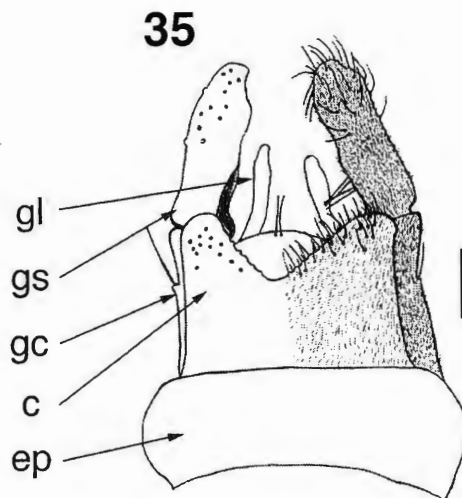
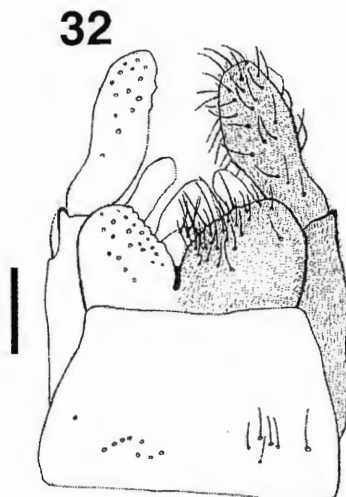
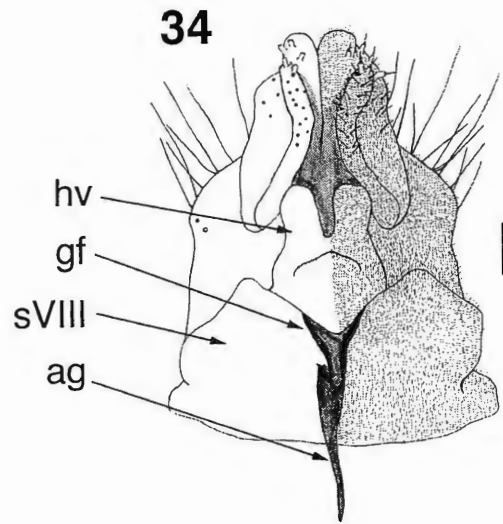
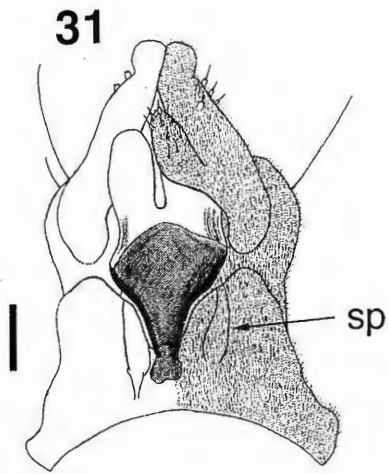
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Figures 23-30. Scanning electron and light micrographs of larvae and pupae of *Horaia montana* Tonnoir and *H. namtoki* sp.n. **23-26: *H. montana*:** **23:** Instar IV larva, ventral view. **24:** Instar IV larva, lateral (left) dorsal (center), and ventral (right) views. **25:** male (left) and female (right) pupae, dorsal view. **26:** pupal respiratory organs, dorsal view. **27-30: *H. namtoki*:** **27:** Instar IV larva, ventral view. **28:** Instar IV larva, ventral (left) and dorsal (right) views. **29:** male (left) and female (right) pupae, dorsal view. **30:** pupal respiratory organs, dorsal view (abbreviations: atI – abdominal tergite I; ds – dorsal spines; ms – muscle scars; mtt - metatergite). Scale bars: 1mm (Figs. 23-25, 27-29); 100µm (Figs. 26, 30).

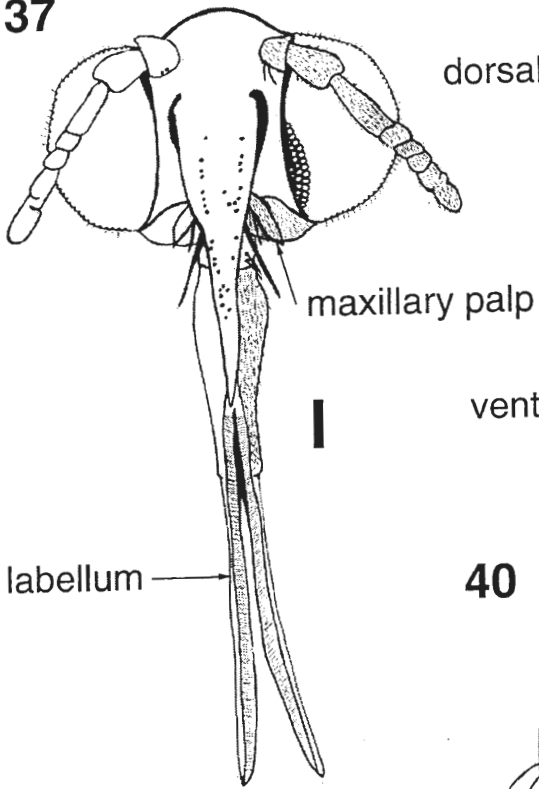


Figures 31-36. Adults of *Horaia manaliella* (Kaul) and *H. montana* Tonnoir. **31-33:** *H. manaliella*: **31:** female terminalia, ventral view. **32:** male terminalia, dorsal view. **33:** male terminalia (phallic structures), dorsal view. **34-36:** *H. montana*: **34:** female terminalia, ventral view. **35:** male terminalia, dorsal view. **36:** male terminalia (phallic structures), dorsal view (abbreviations: ae – aedeagus; ag – accessory gland; c – cercus; dp – dorsal paramere; ea – ejaculatory apodeme; ep – epandrium; ga – gonocoxal apodeme; gc – gonocoxite; gf – genital fork; gl – gonocoxal lobe; gs – gonostylus; hv – hypogynial valves; sVIII – sternite VIII; sp – spermathecal ducts; vp – ventral parameres). Scale bars: 100µm.

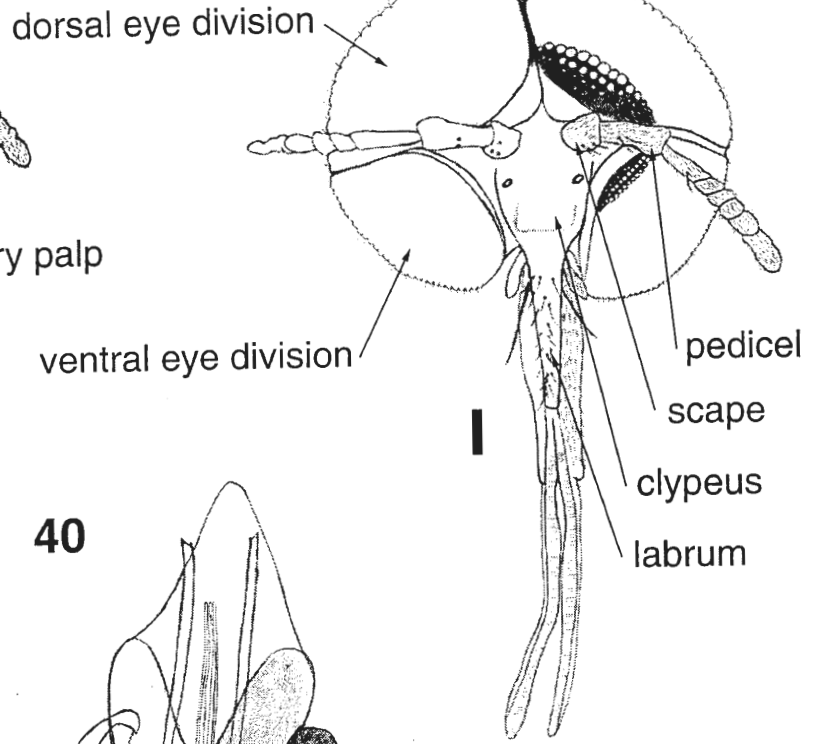


Figures 37-41. Adults of *Horaia namtoki* sp.n. **37**: female head, frontal view. **38**: female terminalia, ventral view. **39**: male head, frontal view. **40**: male terminalia (phallic structures), dorsal view. **41**: male terminalia, dorsal view. Scale bars: 100µm.

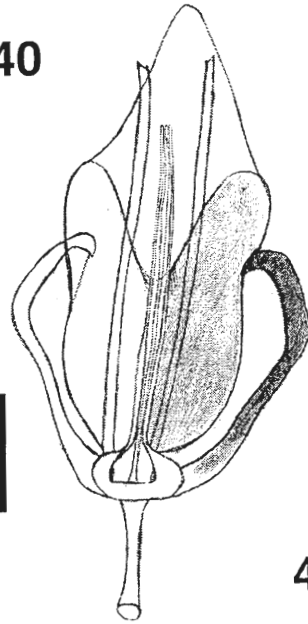
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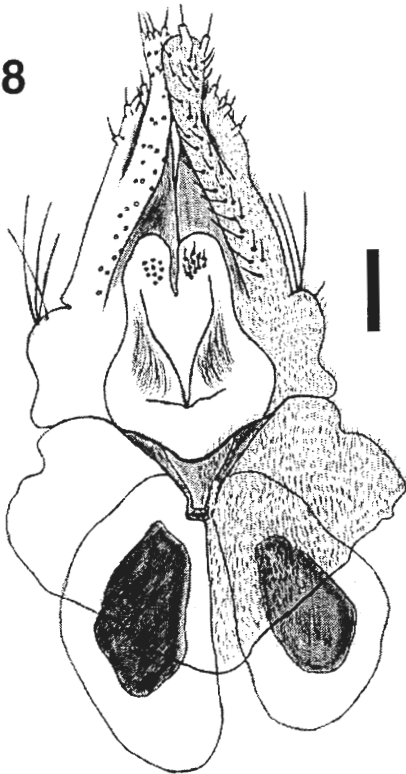
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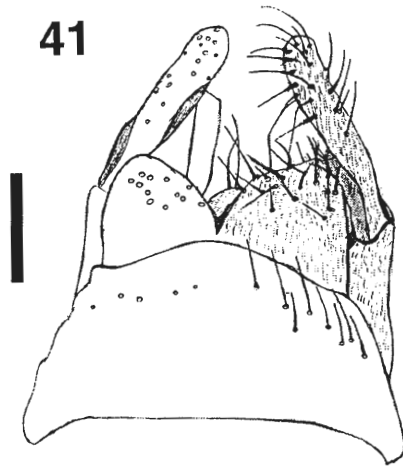
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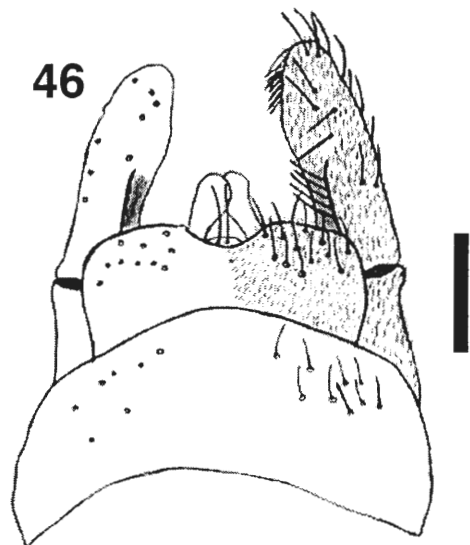
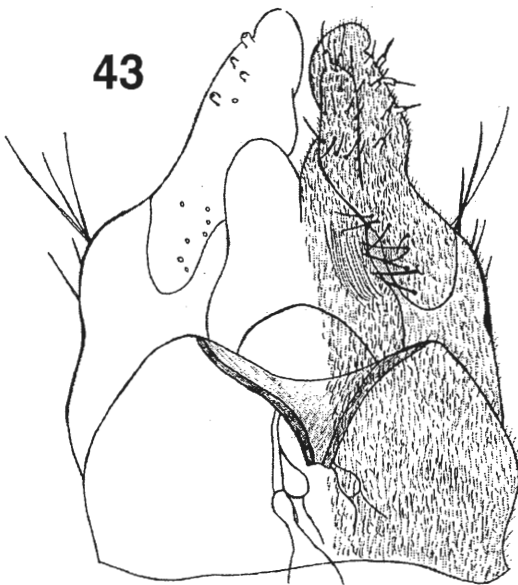
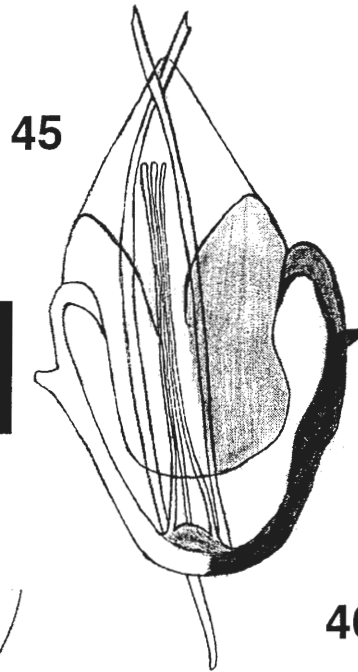
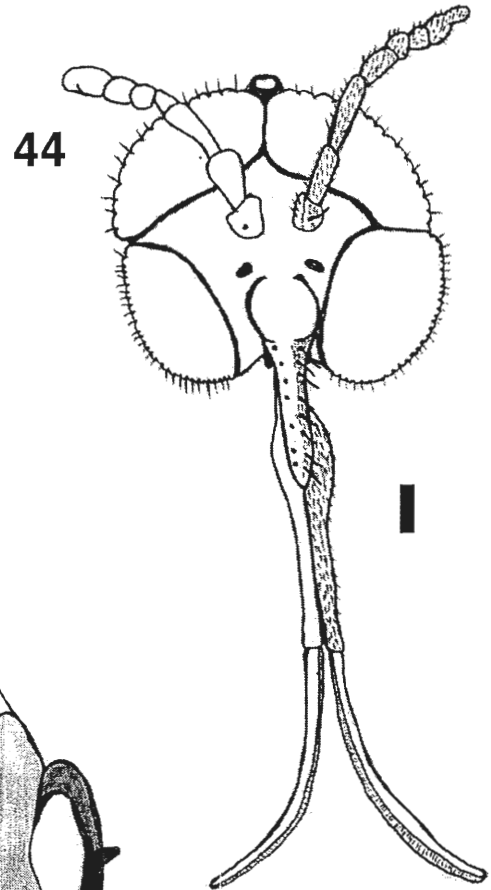
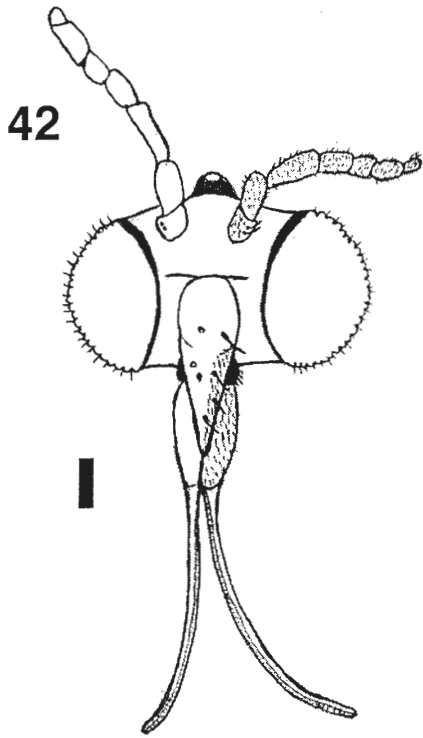
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Figures 42-46. Adults of *Horaia barbata* sp.n. **42:** female head, frontal view. **43:** female terminalia, ventral view. **44:** male head, frontal view. **45:** male terminalia (phallic structures), dorsal view. **46:** male terminalia, dorsal view. Scale bars: 100µm.



Figures 47-51. Adults of *Horaia piedmonti* sp.n. **47:** female head, frontal view. **48:** female terminalia, ventral view. **49:** male head, frontal view. **50:** male terminalia (phallic structures), dorsal view. **51:** male terminalia, dorsal view. Scale bars: 100µm.

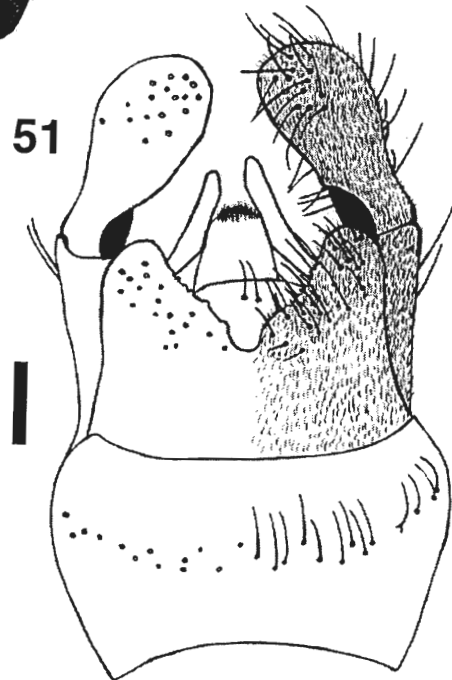
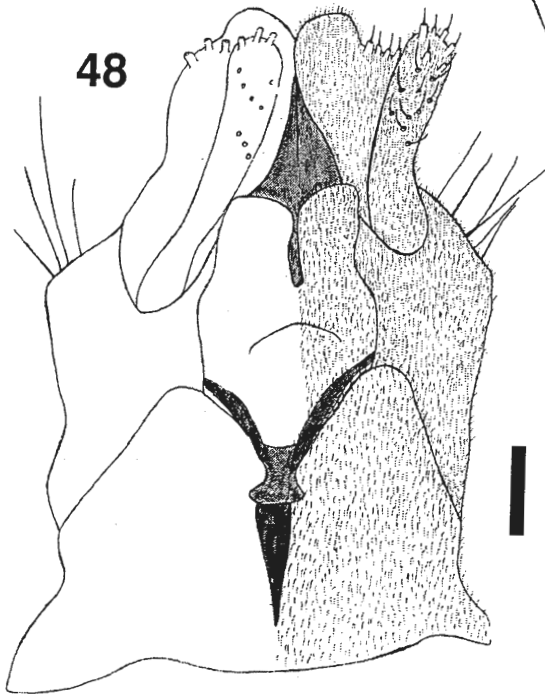
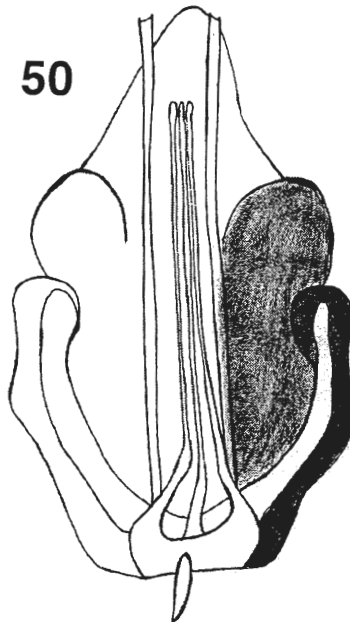
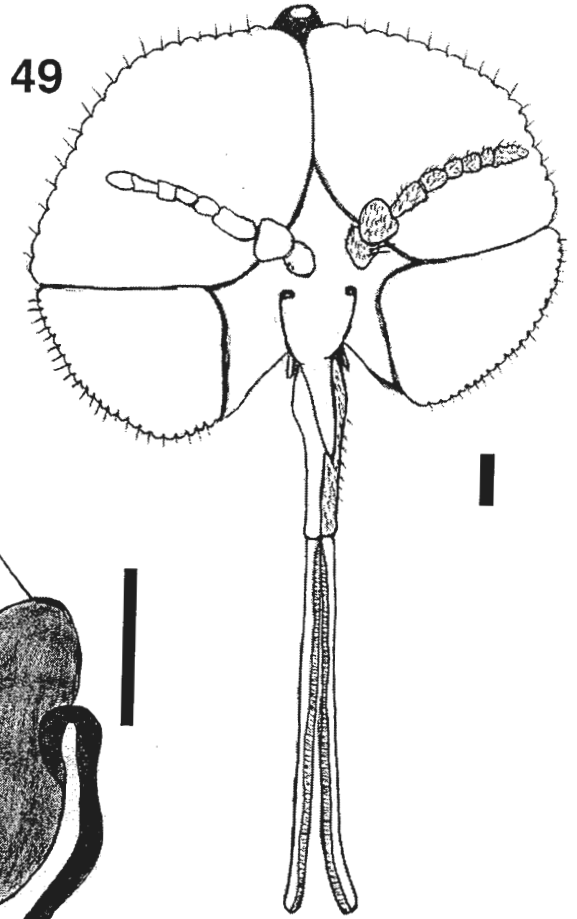
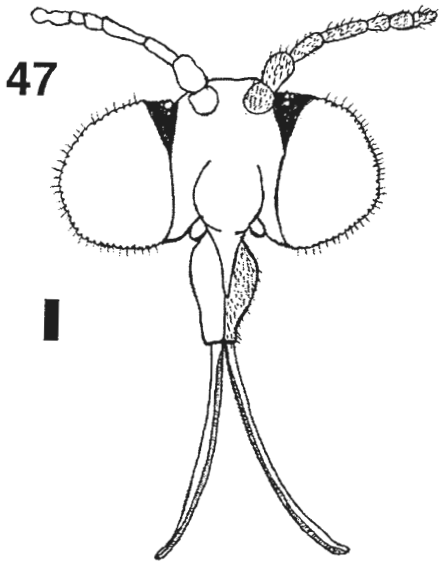


Figure 52. Distribution of *Horaia* species in Nepal.

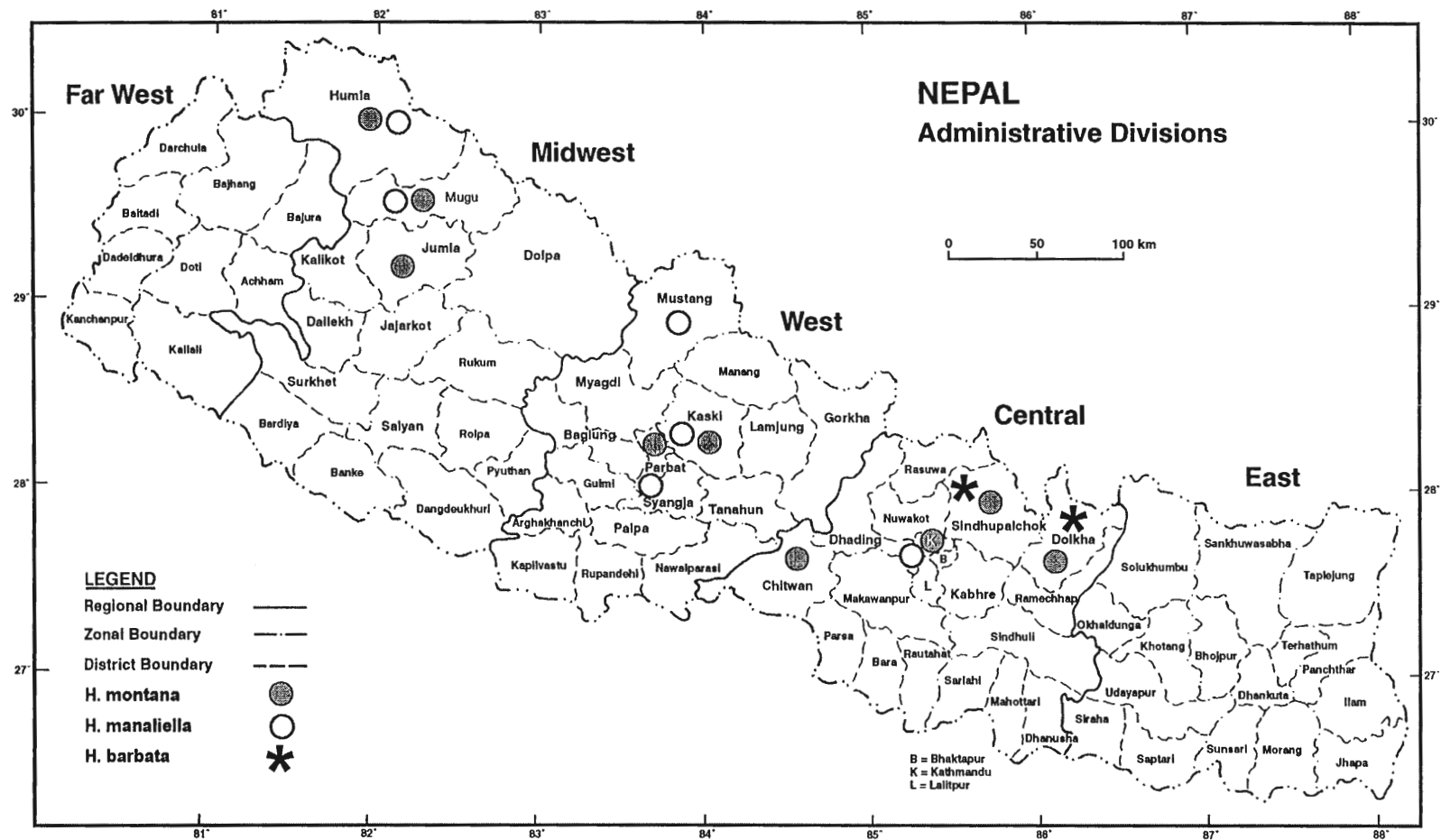
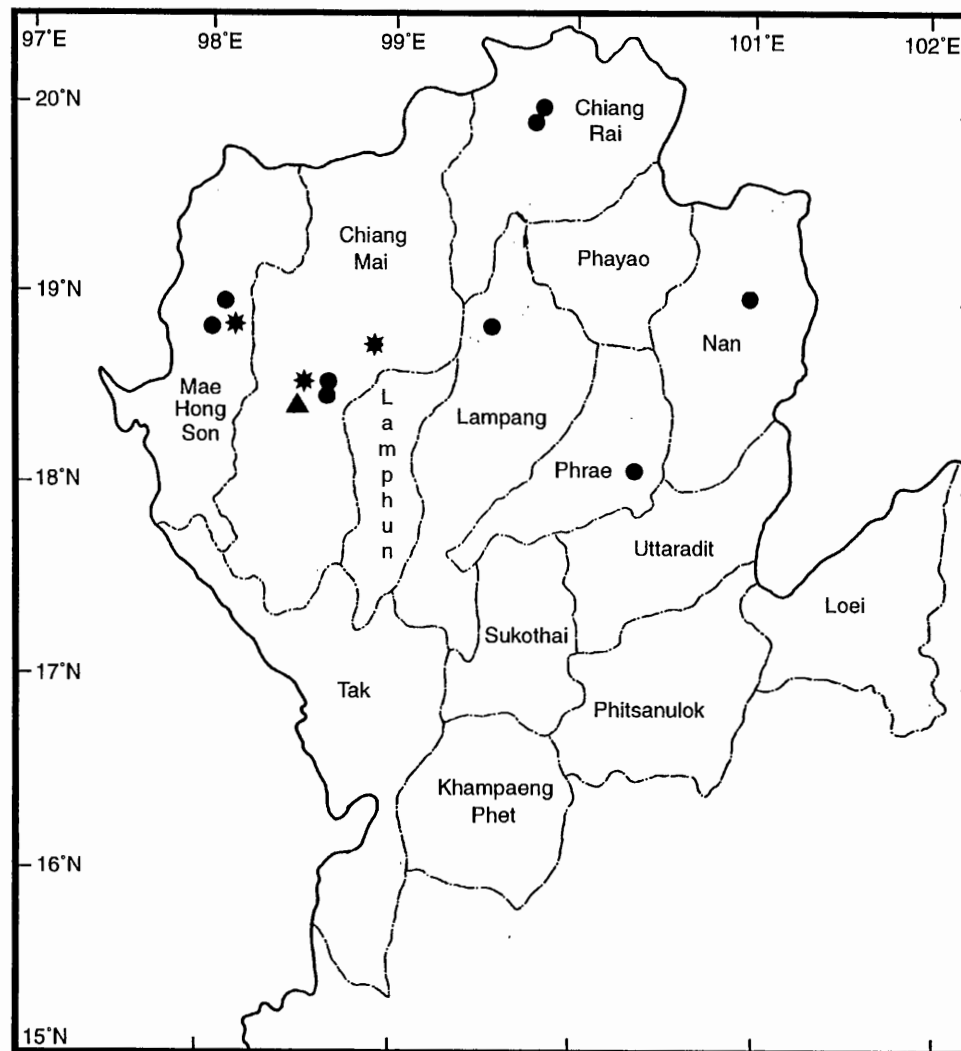


Figure 53. Distribution of *Horaia* species in Thailand.

Legend

- H. montana* ●
H. namtoki ★
H. piedmonti ▲



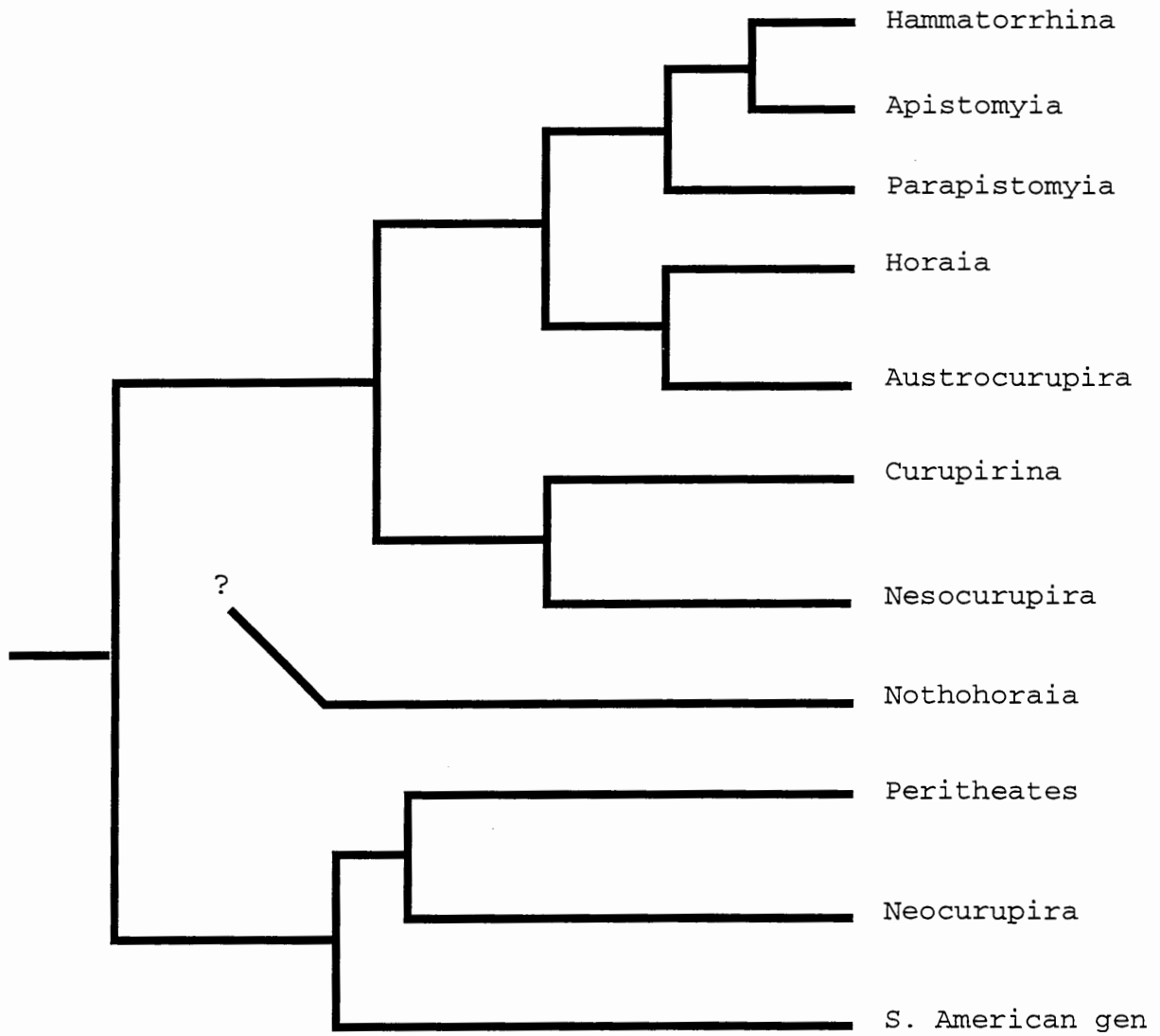


Fig. 54. Hypothesized phylogenetic relationships of Apistomyiini after Zwick 1977.

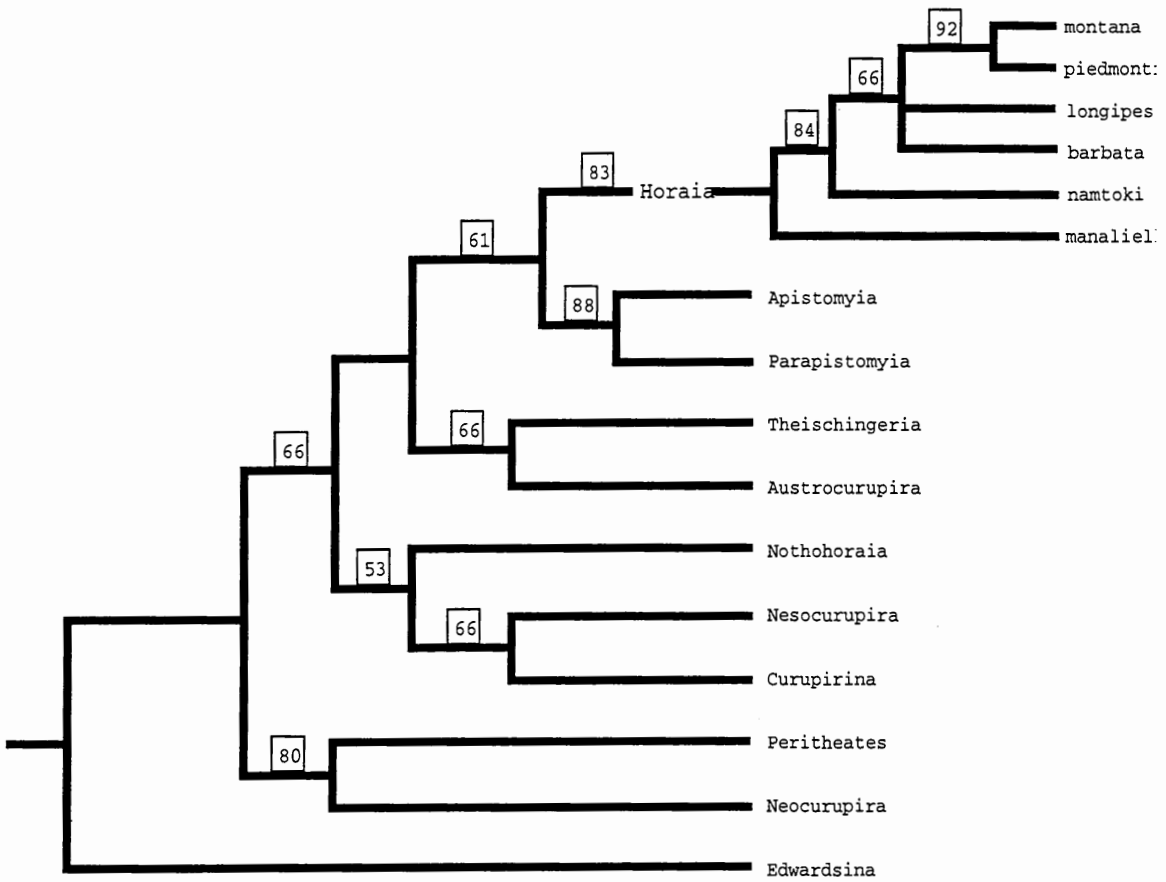


Fig. 55. Hypothesized phylogenetic relationships of Apistomyiini, including relationships within *Horaia* Tonnoir. *Edwardsina* Alexander is included as an outgroup. Numbers in boxes refer to bootstrap values for percentages above 50%. Tree length – 29; consistency index (CI) – 0.862; rescaled consistency index (RC) – 0.798; retention index (RI) – 0.926.

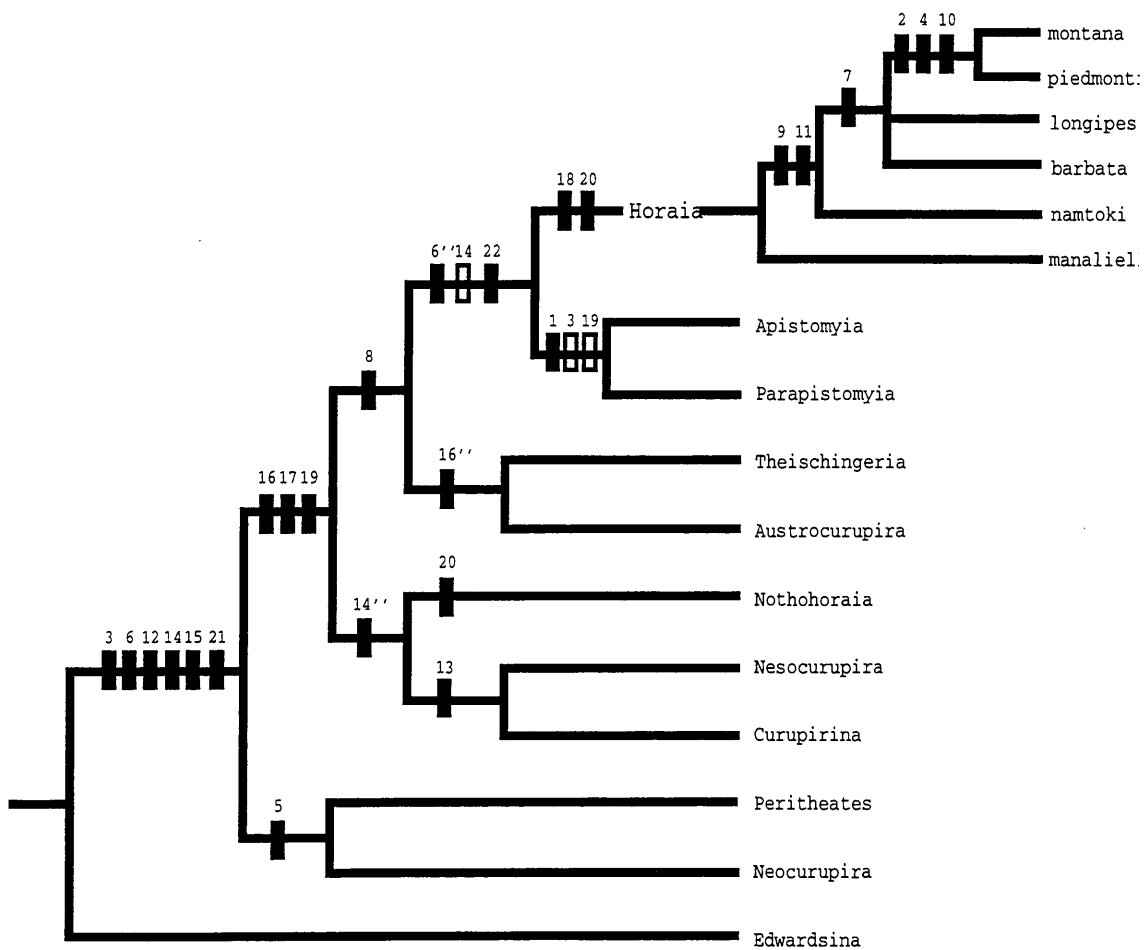


Fig. 56. Hypothesized phylogenetic relationships of Apistomyiini, including relationships within *Horaia* Tonnoir. *Edwardsina* Alexander is included as an outgroup. Numbers 1-22 refer to character states as explained in text and listed in Appendix B. Black rectangles refer to character state 1, double accents refer to character state 2, white rectangles refer to character reversal.

APPENDIX B. PHYLOGENETIC CHARACTERS AND MATRIX

See text for full descriptions of characters and states.

Adult

1. R_{4+5} vein: straight basally (0); sinuous throughout length (1).
2. A_1 vein: extending well beyond anal angle (0); ending at anal angle (1).
3. Mandibles: present in females (0); absent (1).
4. Labrum: normal, broad (0); reduced, slender (1).
5. Maxillary palpi: normal (0); with sense organs (1).
6. Maxillary palpi: three or more segments (0); two segments (1); one segment (2).
7. Maxillary palpi: elongate, cylindrical (0); short, globular (1).
8. Scape and pedicel: slender, subequal in width to flagellomeres (0); expanded, twice as broad as flagellomeres (1).
9. Female front femora: normal (0); with anterodorsal row of dark setae (1).
10. Female accessory glands: globular, indistinct (0); distinct, elongate, tapered (1).
11. Male dorsal paramere: uniform plate (0); basal half with bilobate opacity (0).
12. Labella: truncate, without pseudotracheae (0); elongate, with pseudotracheae (1).

Pupa

13. Abdominal tergites VII and VIII: separate (0); fused medially (1).
14. Tracheal opening of respiratory organ: straight line, no operculum (0); U-shaped, operculate (1); Y-shaped, operculate (2).
15. Pair of adhesive organs on abdominal segment III: absent (0); present (1).

Larva (Instar IV unless otherwise noted)

16. Prolegs of instar I: tipped with crochets (0); tipped with elongate setae (1); tipped with sclerotized plate (2).
17. Seventh pair of abdominal prolegs: vestigial, but present (0); replaced with sclerotized plates or setae (1).
18. Anal division: divided between abdominal segments VI and VII (0); fully fused into single segment (1).
19. Posterior margin of anal division: emarginate, setose (0); sclerotized, asetose (1).
20. Dorsal tergites: weakly sclerotized (0); heavily sclerotized (1).
21. Larval intercalary segments: present (0); absent (1).
22. Maxillary palpi: with eleven distinct sensillae each (0); posterior two sensillae subdivided into lobes (1).

Taxon	Character Number																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
<i>Edwardsina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Peritheates</i>	0	0	1	0	1	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0
<i>Neocurupira</i>	0	0	1	0	1	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0
<i>Nesocurupira</i>	0	0	1	0	0	1	0	0	0	0	0	1	1	2	1	1	1	0	1	0	1	?
<i>Curupirina</i>	0	0	1	0	0	1	0	0	0	0	0	1	1	2	1	1	1	0	1	0	1	?
<i>Austrocurupira</i>	0	0	1	0	0	1	0	1	0	0	0	1	0	1	1	2	1	0	1	0	1	0
<i>Nothohoraia</i>	0	0	1	0	0	1	0	0	0	0	0	1	0	2	1	1	1	0	1	1	1	0
<i>Theischingeria</i>	0	0	1	0	0	1	0	1	0	0	0	1	0	1	1	2	1	0	1	0	1	?
<i>Apistomyia</i>	1	0	0	0	0	2	0	1	0	0	0	1	0	0	1	1	1	0	0	0	1	1
<i>Parapistomyia</i>	1	0	0	0	0	2	0	1	0	0	0	1	0	0	1	1	1	0	0	0	1	1
<i>H. manaliella</i>	0	0	1	0	0	2	0	1	0	0	0	1	0	0	1	?	1	1	1	1	1	1
<i>H. barbata</i>	0	0	1	0	0	2	1	1	1	0	1	1	0	0	1	?	1	1	1	1	1	1
<i>H. longipes</i>	0	0	1	0	0	2	1	1	1	?	?	1	?	?	?	?	?	?	?	?	?	?
<i>H. namtoki</i>	0	0	1	0	0	2	0	1	1	0	1	1	0	0	1	?	1	1	1	1	1	1
<i>H. piedmonti</i>	0	1	1	1	0	2	1	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?
<i>H. montana</i>	0	1	1	1	0	2	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1

REFERENCES CITED

- Alexander, C.P. 1958.** Geographical distribution of the net-winged midges (Blepharoceridae, Diptera). *Proceedings of the Tenth International Congress of Entomology*. **1**: 813-828.
- Alverson, A.J., Courtney, G.W., and Luttenton, M.R. 2001.** Niche overlap of sympatric *Blepharicera* larvae (Diptera: Blephariceridae) from the southern Appalachian Mountains. *Journal of the North American Benthological Society*. **20**: 564-581.
- Brundin, L. 1967.** Insects and the problem of Austral disjunctive distribution. *Annual Review of Entomology*. **12**: 149-168.
- Courtney, G.W. 1990.** Cuticular morphology of larval mountain midges (Diptera: Deuterophlebiidae): implications for the phylogenetic relationships of Nematocera. *Canadian Journal of Zoology*. **68**: 556-578.
- Courtney, G.W. 1991.** Phylogenetic analysis of the Blepharicerimorpha, with special reference to the mountain midges (Diptera: Deuterophlebiidae). *Systematic Entomology*. **16**: 137-172.
- Courtney, G.W. 1998.** A method for rearing pupae of net-winged midges (Diptera: Blephariceridae) and other torrenticolous flies. *Proceedings of the Entomological Society of Washington*. **100**: 742-745.
- Courtney, G.W. 2000a.** Family Blephariceridae. In Contributions to a Manual of Palearctic Diptera. Appendix. Papp, L. and Darvas, B. (eds.). Budapest: Science Herald. pp 7-30.
- Courtney, G.W. 2000b.** Revision of the net-winged midges of the genus *Blepharicera* Macquart (Diptera: Blephariceridae) of eastern North America. *Memoirs of the Entomological Society of Washington*. **23**: 1-99.
- Courtney, G.W., Sinclair, B.J., and Meier, R. 2000.** Morphology and terminology of Diptera larva. In Contributions to a Manual of Palearctic Diptera. Vol. 1. Papp, L. and Darvas, B. (eds.). Budapest: Science Herald. pp. 85-161.
- Craig, D.A. 1969.** A taxonomic revision of New Zealand Blepharoceridae and the origin and evolution of the Australasian Blepharoceridae (Diptera: Nematocera). *Transactions of the Royal Society of New Zealand, Biological Sciences*. **11**: 101-151.
- Dumbleton, L.J. 1963.** New Zealand Blepharoceridae (Diptera: Nematocera). *New Zealand Journal of Science*. **6**: 234-258.

- Edwards, F.W. 1929.** Blepharoceridae. *In* Diptera of Patagonia and South Chile based mainly on material in the British Museum (Natural History). Part II, Fascicle II. London: British Museum. pp. 33-75.
- Frutiger, A. 1998.** Walking on suckers – new insights into the locomotory behavior of larval net-winged midges (Diptera: Blephariceridae). *Journal of the North American Benthological Society*. **17**: 104-120.
- Harris, R.A. 1979.** A glossary of surface sculpturing. *Occasional Papers in Entomology*. **28**: 1-31.
- Hogue, C.L. 1973.** Family Blephariceridae. *In* A catalog of the Diptera of the Oriental region. Vol. I. Delfinado, M.D. and Hardy, D.F. (eds.). Honolulu: The University Press of Hawaii. pp. 258-260.
- Hogue, C.L. and Bedoya-Ortiz, I. 1989.** The net-winged midge fauna (Diptera: Blephariceridae) of Antioquia Department, Colombia. *Contributions in Science, Natural History Museum of Los Angeles County*. **413**: 1-57.
- Hora, S.L. 1930.** Ecology, bionomics and evolution of the torrential fauna, with special reference to the organs of attachment. *Philosophical Transactions of the Royal Society of London*. **218**: 171-282.
- International Code of Zoological Nomenclature. 1999.** Fourth edition. International Trust for Zoological Nomenclature, c/o Natural History Museum, London.
- Kaul, B.K. 1976.** Torrenticole insects of the Himalaya VII. A new genus of Blepharoceridae (Diptera). *Oriental Insects*. **10**: 25-31.
- Kitakami, S. 1950.** The revision of the Blepharoceridae of Japan and adjacent territories. *Journal of the Kumamoto Women's University*. **2**: 15-80.
- Kotrba, M. 2000.** Morphology and terminology of the female postabdomen. *In* Contributions to a Manual of Palaearctic Diptera. Vol. 1. Papp, L. and Darvas, B. (eds.). Budapest: Science Herald. pp. 75-84.
- Merz, B. and Haenni, J-P. 2000.** Morphology and terminology of adult Diptera (other than terminalia). *In* Contributions to a Manual of Palaearctic Diptera. Vol. 1. Papp, L. and Darvas, B. (eds.). Budapest: Science Herald. pp. 21-51.
- Oosterbroek, P. and Courtney, G. 1995.** Phylogeny of the nematoceros families of Diptera (Insecta). *Zoological Journal of the Linnean Society*. **115**: 267-311.

- Pommen, G.D.W., and Craig, D.A. 1995.** Flow patterns around gills of pupal net-winged midges (Diptera: Blephariceridae): possible implications for respiration. *Canadian Journal of Zoology*. **73**: 373-382.
- Ross, H.H. 1956.** Evolution and classification of the mountain caddisflies. Urbana: University of Illinois Press. 213pp.
- Ross, H.H. 1967.** The evolution and past dispersal of the Trichoptera. *Annual Review of Entomology*. **12**: 167-206.
- Scott, H. 1915.** The early stages of *Paltostoma schineri*, Williston (Diptera, Blepharoceridae). *The Annals and Magazine of Natural History, Series 8*. **15**: 181-202.
- Sinclair, B.J. 2000.** Morphology and terminology of Diptera male genitalia. In Contributions to a Manual of Palaearctic Diptera. Vol. 1. Papp, L. and Darvas, B. (eds.). Budapest: Science Herald. pp. 53-74.
- Stuckenberg, B.R. 1958.** Taxonomic and morphological studies on the genus *Paulianina* Alexander (Diptera: Blepharoceridae). *Mémoires de l'Institut Scientifique de Madagascar, Series E*. **10**: 97-198.
- Stuckenberg, B.R. 1969.** Ergebnisse der Österreichischen Neukaledonien-Expedition: The Blepharoceridae (Diptera) of New Caledonia. *Annals of the Natal Museum*. **20**: 217-256.
- Tillyard, R.J. 1922.** Australian Blepharoceridae (Order: Diptera). Part 1: Description of new species. *Australian Zoologist*. **2**: 159-172.
- Tonnoir, A.L. 1923.** Australian Blepharoceridae. Part II: Larvae and pupae. *Australian Zoologist*. **3**: 47-59
- Tonnoir, A.L. 1930.** Notes on Indian Blepharocerid larvae and pupae with remarks on the morphology of Blepharocerid larvae and pupae in general. *Records of the Indian Museum*. **32**: 161-124.
- Tonnoir, A.L. 1932.** Notes on Indian Blephariceridae III. *Records of the Indian Museum*. **34**: 269-275.
- Zwick, P. 1977.** Australian Blephariceridae (Diptera). *Australian Journal of Zoology Supplementary Series*. **46**: 1-121.
- Zwick, P. 1981.** Blephariceridae. In Ecological Biogeography of Australia. Keast, A. (ed.). The Hague: Junk. pp. 1185-1193.

- Zwick, P. 1989.** Family Blephariceridae. *In* Catalog of the Diptera of the Australasian and Oceanian regions. Evenhuis, N.L. (ed.). Honolulu: Bishop Museum Press. pp . 119-121.
- Zwick, P. 1990.** Systematic notes on the Holarctic Blephariceridae (Diptera). *Bonn Zoologische Beitrang.* **41**: 231-257.
- Zwick, P. 1998.** Australian net-winged midges of the tribe Apistomyiini (Diptera: Blephariceridae). *Australian Journal of Entomology.* **37**: 298-311.
- Zwick, P. and Hortle, K.G. 1989.** First records of net-winged midges (Diptera: Blephariceridae) from Papua New Guinea, with a description of a new species. *Australian Journal of Marine and Freshwater Research.* **40**: 361-367.

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