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CHANGES IN YELLOW BASS REPRODUCTION ASSOCIATED WITH ENVIRONMENTAL CONDITIONS

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ABSTRACT. Gillnet collections of yellow bass, Morone mississippiensis, were made from April 1967 to September 1968 at Clear Lake, Iowa, to determine the normal reproductive cycle and variations in fecundity that could be related to changes in food supply and water temperatures. A major mortality from Aeromonas salmonicida occurred in May 1968 and allowed documentation of changes in body condition, fecundity and success of reproduction during the year preceding a mass mortality from furunculosis.

Spawning was initiated during mid-May in 1967 and late April in 1968 when water temperatures approached 15°C after a rapid temperature rise of 3.5 to 4.5°C over several days. At spawning time, ovaries of adult bass constituted up to 16 percent body weight and testes up to 8 percent body weight. Maturing ova had a mean diameter of 0.4 mm in the preserved state when fish commenced spawning. Fresh ovulated ova averaged 0.8 ± 0.11 mm in diameter.

Wide variation in effective fecundity was evident among mature females of similar length. Although 50 percent of the variation in fecundity could be attributed to body length in 1967, the relation was not significant in 1968 ($r = 0.32$). In 1967, mature females contained an average of 560 mature ova per mm total body length in contrast to 276 ova in 1968. In terms of body weight, the average female produced 835 ova per gram body weight in 1967 but only 350 in 1968. The reduction in fecundity was attributed to poor body condition in 1968. Females measuring 200 mm total body length weighed approximately 137 g in 1967 at spawning time but only 115 g in 1968.

Atresia of developing ova was estimated at 20 percent during the period from December to May and was

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attributed to poor nutrition. Ova retention after spawning in 1967 was approximately 34 percent of total ova production. In 1968 most fish died shortly after initiation of spawning, with a minimum number of ova shed. Reproduction success in 1968 determined by standardized seining of young-of-the-year bass was 1 percent of the 1967 level (77 vs 7015).

Young-of-the-year yellow bass were a major food item of adult bass during late summer and autumn when gonadal development was initiated. At other times adult bass ate invertebrate food similar to that of young bass.

Mesenteric fat decreased steadily with gonadal development in both sexes from March to May 1968 and reached zero levels at spawning time.

Insufficient food, as reflected by poor body condition, coupled with fluctuating spring water temperatures seemingly allowed furunculosis to reach epizootic proportions when spawning commenced in 1968. The yellow bass population was decimated by the disease, but mortality of other species was not observed. Catch per gillnet hour decreased from 2.158 bass in mid-May to 0.025 in mid-June and 0 by the end of July.

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INTRODUCTION

For many years, the yellow bass, Morone mississippiensis, has been the dominant species of fish in Clear Lake, Iowa. Clear Lake is a natural eutrophic lake of 1,474 hectares located in north-central Iowa and contains 23 species of warmwater fish (Bailey and Harrison, 1945). Food habit studies have suggested that competition for food occurs between yellow bass and most other fishes in the lake at some time in their life cycle (Ridenhour, 1960; Buchholz, 1960; Welker, 1963). Yellow bass also serve as food for piscivorous species such as walleye and northern pike. Hence, the abundance of yellow bass in Clear Lake profoundly influences other species, some of which are highly desirable sport fish. Wide annual variations in abundance of young yellow bass suggest that reproduction success is determined either before or shortly after spawning.

The current study, initiated in April 1967, was designed to obtain information on the normal reproductive cycle of male and female yellow bass and variations in fecundity and egg deposition that might be related to environmental factors such as water temperature and food supply. On a broader basis, the study sought insight into variations in reproduction potential in fish populations restricted in growth by limited food supply. Originally the study was designed for a 3-year period, but in May 1968, a furnculosis epizootic caused by Aeromonas salmonicida decimated the adult population of yellow bass (Bulkley, 1969) and forced termination of the project.

METHODS

Sampling sites selected in Clear Lake were located in the major yellow bass spawning area (Atchison, 1967) and in deep water where yellow bass have been captured regularly in annual gillnetting operations. One collecting station was established at the Island in 1-2 m of water which is also a major walleye spawning area. The area is windswept, and the bottom consists of coarse gravel and boulders. An additional station was located approximately 400 m northeast of the Island in depths of 5-6 m.

Yellow bass larger than young-of-the-year were collected with 125-foot experimental gillnets having the following mesh sizes: 3/4, 1, 1 1/4, 1 1/2 and 2-inches bar measure. Weekly gillnet samples were collected from April to June, and monthly samples from July to March.

After young yellow bass moved into shallow water, they were sampled weekly during the summer by using a 25-foot bag seine (1/4-inch square mesh bag with 1/2-inch mesh wings).

Fish utilized for fecundity and fat measurements and for determining maturity indexes were preserved in 10-percent formalin upon capture and then measured. Total body length was measured to the nearest millimeter. Body weight and weight of mesenteric fat and gonads were measured to the nearest 0.01 g. Mesenteric fat was stripped from the digestive tract and internal organs with dissecting forceps for weighing. The fat separated from the internal organs with little difficulty. Gonads were stored in 85 percent alcohol after weighing. Stomachs were collected from all specimens when body measurements were completed and combined for analysis (Borgeson, 1963). The total volume of each major group of organisms within the combined sample was determined by using a 10-ml burette accurate to 0.05 ml. Results were presented by monthly intervals to indicate seasonal changes.

Examination of yellow bass during the 1967 spawning season indicated that all female fish larger than 180 mm total length had extensive gondal development. Some females from 170 to 180 mm were mature, but many were not. All male yellow bass larger than 170 mm total length were functionally mature during the spawning season. Thus, only female yellow bass 180 mm or longer and male fish 170 mm and longer were utilized in computing the maturity index (LeCren, 1952). According to yellow bass age determinations by Atchison (1967), males of the size used in my study were 3 years of age or older; females were at least 4 years old.

Fecundity terms used here are equivalent to the relative and total fecundity of Henderson (1963) and Vladykov (1956). Potential fecundity is the number of maturing ova in the ovaries at any stage of secondary ova development. Effective fecundity refers to the number of mature or fully developed ova produced. The term functional maturity is defined as that stage of maturation when sex products can be expressed from the fish by gentle massage of the abdomen. In the yellow bass, functional maturity may or may not indicate that ova expressed are fully mature because abortion of ova is not uncommon.

Both ovaries were used in estimating fecundity. Ovaries were removed from the preservative, and the outer membrane was detached with forceps. The ova were placed in a plastic test tube containing alcohol and vigorously massaged with a pair of large forceps to separate

individual ova. Ova collected earlier than December were firmly attached to the ovarian membrane and were not satisfactorily separated by this method without considerable breakage. Ovaries from samples taken from September to November were separated by immersing an ultrasonic probe at low frequency into the test tube for 30-60 seconds. Ovaries collected in September were not entirely separated by either method because the alcohol excessively hardened the tissues.

After separation, the ova from a fish were placed in a cylindrical museum jar, and sufficient water was added to make a total volume of 400 cc. The jar was inverted several times, and a 1.5-cc aliquot was immediately extracted from the center of the jar. The aliquot was placed in a circular counting cell under a binocular microscope for determining number of ova present. Four aliquots were taken from each sample, and fecundity estimates were thus based on counts of 1.5 percent of the total ova present. Differences in the 4 counts indicated the amount of variability inherent in the sampling method. Only ova in which vitellogenesis was evident were counted.

Mean ova size at successive stages in the maturation cycle was determined from ova of 10 fish selected over the range in body length in each collection. A small sample of ova from the center of the ovary was placed upon a microscope slide and teased apart (MacGregor, 1957). The slide was then inserted in a micro-projector and magnified 85 diameters. The projected image of 20 to 30 maturing ova selected at random was measured. In ova of normal shape, length of the long axis was considered the diameter. Slightly distorted ova were measured through both the long and short axis, and the mean value was used as the ova diameter. Mean ova diameter for each date was thus based on a minimum of 200 measurements.

The percentage body weight consisting of gonads was used as an index of the stage of maturity (Braekevelt and McMillan, 1967). The maturity index for each sample of fish was determined by averaging individual gonad-body weight ratios for all fish of a given sex in a sample. When possible, 30 fish of each sex were used to determine the mean maturation index for each collection date.

Water temperature data were obtained from the City of Clear Lake water-treatment plant. Water is withdrawn from the lake at a depth of 3 m. where maximum depth is approximately 4 m. Temperature of the water is recorded at 1 pm daily. Rainfall data were obtained from published U.S. Weather Bureau Climatological Records for Mason City airport, 7 miles east of Clear Lake.

THE SPAWNING PERIOD

Sex Ratios

In 1967 and 1968, collections were made over the spawning area and in deeper water to determine if yellow bass form unisexual schools during the spawning period as reported for white bass. Male white bass mature and move to the spawning grounds earlier than the females. When ready to spawn, the females travel to the spawning area, release their eggs, and return promptly to the deeper water (Riggs, 1958). Thus, the sex ratio during spawning favors males over the spawning area and female white bass in deep water.

Sex ratios of adult yellow bass in samples obtained from Clear Lake indicated a definite movement of male fish into the spawning area during April and May (Figure 1). Females were predominant in the deep water at this time. Movement of males into the spawning area appeared to be about 2 weeks later in 1967 than in 1968. Males were most abundant in shallow-water samples in late May 1967 and early May 1968. The timing difference was attributed to temperature.

The uneven sex distribution at certain times of year can lead to erroneous conclusions on the actual sex ratio of adult fish in the population. Pooling of samples collected in different areas of the lake and over a period of time provided a more accurate estimate of the actual sex ratio of the adult population. The sex ratio in the catch of 1,093 bass collected from April 6 to June 29, 1967, was 1 male to 1.112 females. The probability of a chi-square value larger than the computed value of 3.404 was greater than 0.05, supporting the conclusion that an equal sex ratio existed. For 631 fish captured from Feb. 27 to May 21, 1968, the ratio of males to females was 1:0.997, also indicating that an equal number of fish of both sexes were present in the population (chi square = 0.002, $p = 0.95$).

The most biased sex ratio during the study was obtained in midwinter. Of 69 adult bass captured by bait fishing at several places in the lake from Jan. 30 to Feb. 7, 1968, only 14 fish were males. The large excess of females in the sample suggested a differential feeding intensity between the sexes in early February. Gillnetting through the ice on Feb. 27 produced 29 female and 26 male yellow bass, indicating that the angling sample was not representative of the actual sex ratio of the population.

Time of Spawning

Yellow bass have been reported to spawn during April and May when water temperatures in the spawning area approach 20-22°C, usually from midmorning to noon on calm days (Burnham, 1909; Harlan and Speaker, 1951; Atchison, 1967). Spawning normally occurs in water about 1 m. deep. Atchison failed to observe spawning of yellow bass at Clear Lake in 1966 but found schools of male fish over the spawning area on May 23 and captured two ripe females. He successfully fertilized and incubated ova from the two females, indicating that spawning was occurring in the lake at that time.

Functional maturity in male yellow bass occurred before their movement inshore to the spawning area. Adult males were functionally mature April 6, the earliest collection date in 1967. In a sample of 56 males collected March 19,1968, 49 fish were functionally mature. All males collected April 2, 1968, were mature. Spent males were first observed in 1967 on June 8 and on May 7 in 1968.

Functionally mature females were first collected on May 12 in 1967 when 19 of 27 females contained mature transparent ova. Fishermen reported schooling and surface agitation by yellow bass presumably spawning at the Island on May 17. Collections on May 24 contained 12 females with partly evacuated ovaries, 6 females with mature transparent ova, and 5 smaller females that had not spawned. The decision

that partial spawning had occurred was based on a wrinkled flabby appearance of the ovary wall and a sharp ventral edge of the ovary in contrast to the well-rounded appearance earlier. Venation was closer together, and the ovary itself was obviously shrinking. The ovaries were not much smaller on the average than those observed previously, however, indicating that only a small portion of the ova had been released. On June 2, only 2 fish among 57 females examined were functionally mature. Internal examination revealed that ovaries of the 2 fish contained transparent ova. Ovaries of 55 females were still large but were in an obvious state of resorption. Hence, in 1967, major spawning occurred between May 12 and May 24 with spawning essentially over by June 2.

In 1968, ovaries of 1 female among 15 captured on April 30 contained mature ova. The collection of 38 females on May 7 contained 2 fish with many transparent ova and 1 fish with partly spent ovaries. Ovaries of 3 females had a few transparent ova in the lumen but showed no other evidence of having spawned. Ovaries of remaining fish in the May 7 sample were still developing. Several males of 31 captured on that date were in a spent condition. On May 14, a sample of 52 females contained 8 functionally mature specimens. Ovary examination revealed 17 females with small numbers of transparent ova. Ovaries of 35 females were being resorbed with ova amalgamated into a gelatinous mass.

Two of 30 males in the May 13, 1968, sample were still functionally mature. Testes of the remaining 28 males were in a state of resorption and appeared spent or partly spent. On May 21, 1 functionally mature female with transparent ova was captured. Ovaries of 20 other females appeared atretic. Milt of 4 males collected on May 21 was thickened, and testes indicated that spawning had ceased. Many yellow bass were observed swimming slowly on the surface in severe stress on this date and large mortality from furunculosis occurred shortly thereafter (Bulkley, 1969). Thus, spawning in 1968 apparently occurred from April 30 to May 14 but was very limited. Most fish retained their sex products and died before spawning.

Environmental Factors Associated with Spawning

Data on temperature and rainfall at Clear Lake were analyzed to determine possible influence of these factors on yellow bass spawning (Figures 2 and 3). Little rainfall occurred in 1967 during the period when functionally mature females were collected. Maximum precipitation recorded was 9.4 mm on May 28. Precipitation was slightly higher during the 1968 spawning period (59.0 versus14.0 mm in 1967), but was well distributed over the period in frequent light rains. Maximum precipitation on a single day was 16.5 mm received on May 15. Hence, precipitation did not stimulate spawning activity of yellow bass in 1967 and 1968. Rains that stimulate spawning in certain fishes are more of the torrential type occurring in the tropics (Pickford and Atz, 1957).

In 1967, the spawning activity reported on May 17 coincided with a sharp rise in Clear Lake water temperatures. From May 16 to May 18 water temperature increased from 10.5 to 14.5°C, a rise of 4°C.

Another sharp rise from 13.4 to 17.8°C occurred from May 23 to May 27. As mentioned previously, spawning was completed before June 2, even though many ova were not ovulated and released. The rapid rise in water temperature (7.8 to 14.5°C) from April 25 to May 3, 1968, coincided with the period when females with mature ovulated ova were first captured. The May 14 collection, made shortly after another rapid rise in water temperature on May 11 to May 13 (10.5 to 13.9°C), contained the highest proportion of fish with ovulated ova.

Atchison (1967) captured 2 free-flowing female yellow bass in Clear Lake on May 23, 1966, and successfully incubated their eggs. A check of Clear Lake water temperatures in 1966 revealed a 3.4°C rise from 12.8 on May 20 to 16.2°C on May 23. These data agree with findings in the current study. It appears, on the basis of ovulation and female functional maturity, that during May, a rise in water temperature of 3 to 4°C over several days when the temperature is approaching 15°C is sufficient to stimulate yellow bass to spawn.

Temperatures of 14.5-15.5°C are 5.5 degrees lower than spawning temperatures reported for yellow bass in Mississippi by Burnham (1909). It might be thought that the temperature difference was due to using records of water temperature taken at the 3-m depth in Clear Lake rather than in the shallow-water spawning area. However, surface temperatures in the spawning area were compared each collection day during April and May with water temperatures at the 3-meter depth. Surface temperature over the spawning area averaged only 0.3°C warmer.

Other species in the genus Morone have been reported to spawn at temperatures around 15°C. Sheri and Power (1968) reported that white perch, Morone americanus, spawn when temperatures are between 11.1 and 15°C. Striped bass will commence spawning on most areas at 14.5°C and reach peak activity at 15.5-18.4°C (Albrecht, 1964). Eggs hatch in two days or less at these temperatures. Riggs (1955) stated that white bass separate into unisexual schools for spawning when water temperature approaches 12.8 to 15.5°C. Eggs hatch in 46 hours at 15.5° C. Yellow bass eggs require 2 to 2 3/4 days to hatch at temperatures from 17.2 to 21.1°C (Atchison, 1967). Burnham (1909) reported an incubation period of 4-6 days at 21°C.

Mean monthly water temperatures were lower during the spawning season in 1967 than in 1968. Mean temperature for April and May were 9.0 versus 9.4 and 12.4 versus 13.1°C, respectively. More significantly, average water temperature from May 1 to May 15, 1967, was 9.8°C in contrast to 12.7 for the same period in 1968 (Figures 3 and 4). Initial collection of functionally mature females reflected the temperature difference. Female fish, functionally mature and containing mature ova, were first captured April 30 in 1968 and on May 12 in 1967. Hence, spawning commenced 2 weeks earlier in 1968 than in the previous year, although differences in the time that male fish moved into the spawning area were not as obvious (Figure 1).

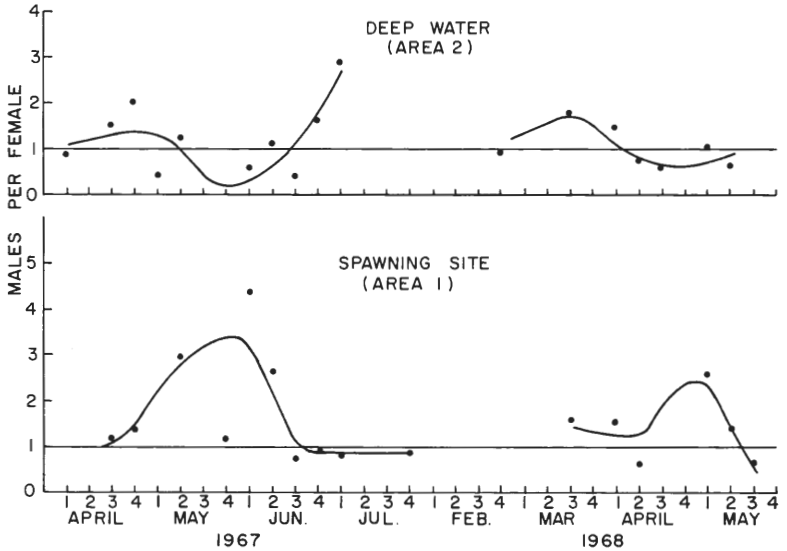

Figure 1. Sex ratios of Clear Lake yellow bass in gillnet samples exceeding 15 fish during spawning season, 1967 and 1968. Line plotted by hand.

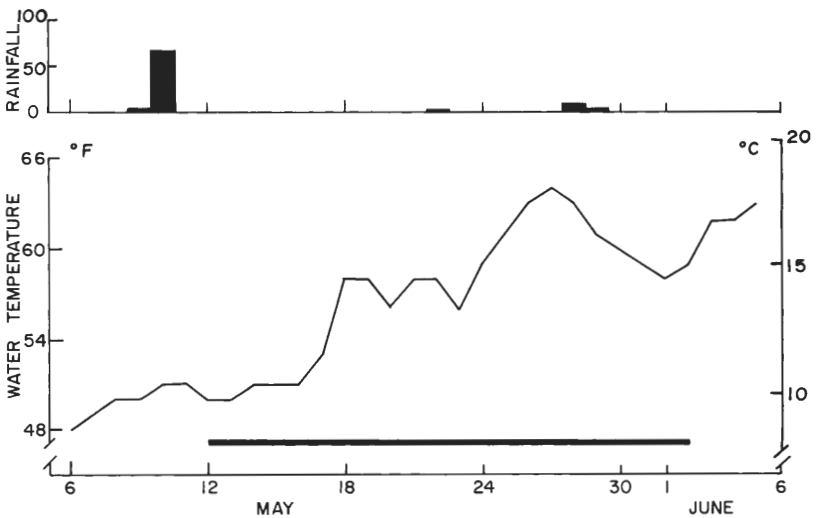

Figure 2. Spawning of yellow bass in relation to Clear Lake water temperature and rainfall (mm), 1967. Period of observed functional maturity is indicated by the broad horizontal line.

SEASONAL GONADAL CHANGES

Maturation Cycle

Further insight may be gained into fish reproduction by following the cyclical development of gonads and sex products throughout the year. A method frequently used determines the ratio of gonad weight to total body weight (Braekevelt and McMillan, 1967). This ratio, expressed as a percentage, is considered an index of stage of maturity and has been termed the gonosomatic index (GSI) by some workers (Pickford and Atz, 1957). There are weaknesses in using percentage body weight as an index of maturity. Varying fullness of the digestive tract causes body weight to fluctuate (LeCren, 1962). Fish with a full digestive tract have a lower gonad-body weight ratio than when the tract is empty. Evacuation of the entire digestive tract is not altogether practical for removing this variable. Hence, a minor portion of the sample variation in the present study was due to varying amounts of food in the digestive tract. Seasonal variations in amount of stomach contents was not excessive, except that fish collected in November and December had empty digestive tracts. However, mean weight of stomach contents did not exceed 1 percent of total body weight for any month sampled.

Another weakness in using percentage body weight is that fish may gain body weight at the same time the gonads are growing rapidly so that increase in gonad size is not reflected in the gonad-body weight ratio. LeCren (1952) found a slight but regular increase in body-minus gonad weight of European perch (Perca fluviatilis) just before spawning.

Gonads of immature yellow bass comprised less than 1 percent body weight. Gonads of mature fish also shrunk to less than 1 percent body weight shortly after spawning. Gonads of fish ready to spawn constituted up to 16 percent body weight in female bass and up to 8 percent in ripe males. Sample means of gonad weight reached peak values of 11.76 percent among females and 6.34 percent for male yellow bass (Table 1).

The maturity index of female yellow bass increased very rapidly during April and early May 1967 (Figure 4), reaching a peak in the sample collected May 12. The wide range in maturity index during April and May was a reflection of differences in time of reaching full maturation by individual fish as well as individual variation in amount of body energies converted to sex products. After May 12, the index dropped rapidly so that, by the end of June, ovaries constituted less than 1 percent body weight. These data on changes in gonadal size agree with observations on time of actual spawning.

From July to August, ovaries were in a quiescent state. In early August gonads of many adult females acquired a speckled appearance, suggesting that oogenesis had commenced. In late September, secondary yolk formation or vitellogenesis commenced, and by late October ovarian weight began to reflect the increase in ova size. Gonad growth from October to March proceeded at a slow pace. In early April, ovarian weight increased very rapidly, reaching a peak of 8.36 percent mean body weight on May 13, 1968. Some spawning evidentally occurred shortly before this date, as suggested by the presence of functionally

Table 1. Mean body measurements and maturity indexes of Clear Lake yellow bass collected in 1967 and 1968

Date of collection	Females				Males			
	Number of fish	Mean body length (mm)	Mean body weight (g)	Mean maturity index	Number of fish	Mean body length (mm)	Mean body weight (g)	Mean maturity index
1967								
4/6	33	204	136	4.76	29	196	116	2.89
4/20	44	203	143	6.86	41	190	112	4.34
4/27	9	203	146	6.29	20	183	92	3.45
5/4	16	201	148	8.82	8	194	124	5.72
5/12	27	201	147	11.76	66	193	122	6.34
5/24	23	201	139	8.18	25	190	111	5.34
6/2	30	202	142	6.36	42	197	124	4.81
6/8	29	196	122	5.00	33	194	121	4.37
6/14	46	195	121	3.76	21	195	120	4.17
6/22	28	196	119	1.26	33	194	119	2.54
6/29	29	196	121	0.66	29	197	124	0.96
8/3	21	193	115	0.51	10	193	108	0.12
8/28	14	200	119	0.76	14	195	108	0.20
9/25	8	199	115	0.94	12	191	100	0.33
10/23	35	202	121	1.70	34	193	104	1.38
11/22	19	196	112	1.71	23	200	113	1.41
12/18	29	202	122	1.82	17	198	120	1.25
1968								
1/30	37	200	109	2.10	14	194	101	1.40
2/26	29	199	124	2.38	26	193	111	1.70
3/18	38	196	108	2.38	32	191	97	1.60
4/1	35	197	112	3.01	29	194	106	2.42
4/15	17	194	105	4.19	21	191	98	3.45
4/29	16	196	113	5.12	15	193	108	4.69
5/6	25	193	104	6.38	30	191	97	4.62
5/10	8	192	105	7.03	18	193	105	4.91
5/13	30	195	109	8.36	30	191	96	4.81
5/20	20	196	108	6.07				

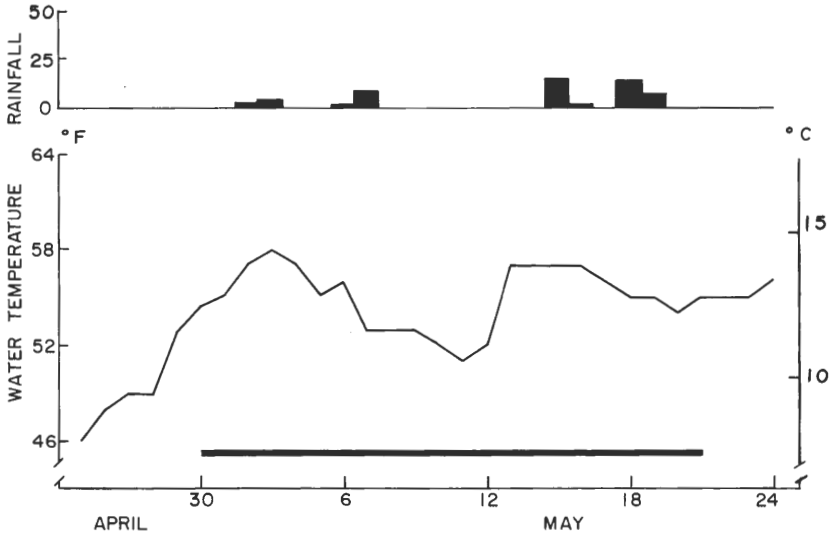

Figure 3. Spawning of yellow bass in relation to Clear Lake water temperature and rainfall (mm), 1968. Period of observed functional maturity is indicated by the broad horizontal line.

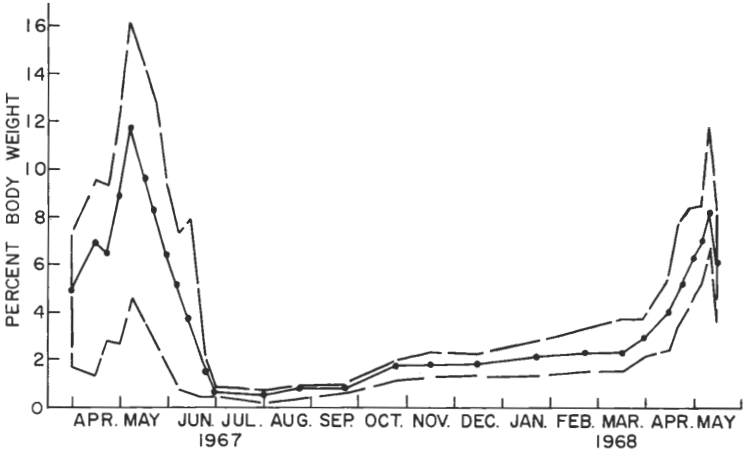

Figure 4. Maturity index of Clear Lake female yellow bass over 180 mm total length expressed as percentage of body weight consisting of ovaries, 1967-1968. Solid line connects sample means; broken lines enclose sample range.

mature fish and ovulated ova, but was very limited. The 1968 maturity index at spawning was 30 percent below that of the 1967 population. At functional maturity on May 12, 1967, ovaries of 27 females ranged from 4.3 to 16.0 percent body weight, with a mean of 11.8 percent whereas, 30 females collected May 13, 1968, had ovaries ranging from 6.9 to 11.9 percent body weight, with a mean of 8.4 percent (Figure 4).

The maturation cycle of male yellow bass paralleled in general the female cycle (Figure 5). The drop in index for April 27, 1967, was attributed to sampling variation since samples collected April 20 and 27 were not statistically different at the 0.30 probability level ($t = 0.91$). The male maturity index reached a peak in the May 12 sample similar to the female index but decreased more slowly. The mean maturation index for 65 male yellow bass on that date was 6.34 percent, with a range of 1.13 to 8.02 percent body weight. By mid-June the male index had decreased to 66 percent of its peak value, but the female index was only 32 percent of the May 12 level. By the end of June, male gonads had also entered the quiescent state, and remained below 1 percent body weight until September. Coloration changes from transparent to creamy white in conjunction with increased growth rate suggested that spermatogenesis commenced the latter part of September. By October 23, yellow bass males were functionally mature. Numerous spermatocytes and spermatids were present in the milt, but no mature spermatazoa were observed. Microscopic examination of the milt in November revealed numerous motile spermatozoa. Cooling water temperatures with resulting ice cover caused a slight regression in gonadal development by December. Testes were shrunken and no longer functionally mature. From October to March, the male index changed little, but rose in March coincident with spring turnover. Ice cover left the lake on March 17. Male yellow bass collected March 19 in 4°C water became functionally mature upon warming to room temperature. Spermatozoa were highly motile and numerous. The male maturity index peaked on May 10 in 1968 at a level 23 percent lower than the maximum measured in 1967.

Environmental factors regulating the annual cycle of gonadal development have been studied by numerous workers (Pickford and Atz, 1957). The annual cycle in day length working indirectly through the endocrine system has been proved in many instances to regulate the gonadal development cycle. Both day length and water temperatures appeared to influence the yellow bass maturation cycle (Figure 6). Gonad weight commenced rising shortly after the autumnal equinox and continued gradually through the winter months. The rapid increase in gonadal development in the spring was attributed mainly to increasing water temperature. Day length was similar in 1967 and 1968, but female yellow bass were ready to spawn some 2 weeks earlier in 1968 than in 1967.

Ovum size and development

Further indication of spawning habits and duration of spawning may be gained by measuring diameter of eggs in the ovaries (Brown, 1957). Fish that have an extended spawning period (fractional spawners) have ova of different sizes within the ovary, whereas fish that spawn only

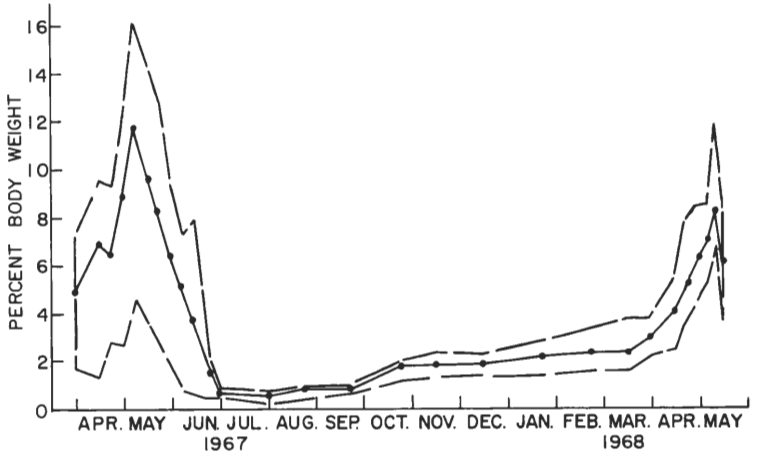

Figure 5. Maturity index of Clear Lake male yellow bass over 170 mm total length expressed as percentage of body weight consisting of gonads, 1967-1968. Solid line connects sample means; broken lines enclose sample range.

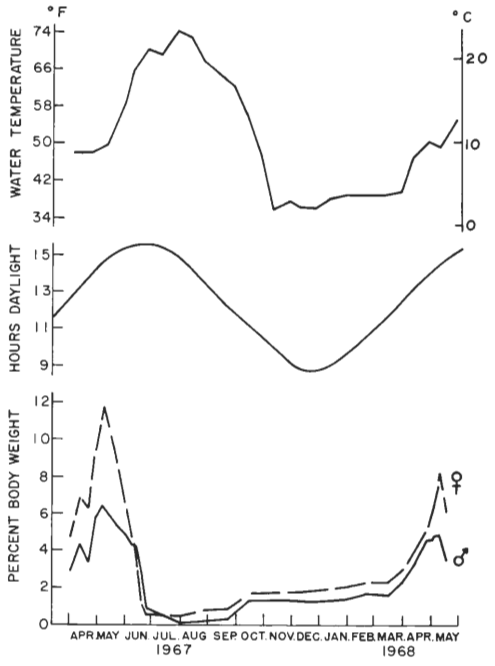

Figure 6. Relation of yellow bass maturity index to day length and Clear Lake water temperature, 1967 to 1968. Male yellow bass represented by solid line; females by dotted line. Water temperature presented as semi-monthly mean.

once contain developing ova of similar size. At spawning time in 1967 and 1968, Clear Lake yellow bass contained ova in various stages of development. Mature transparent ova along with opaque ova were readily visible in the ovary giving it a mottled appearance. The size frequency of ova was determined by measuring 20 ova selected at random from ovaries of 8 mature females collected May 14, 1967 (Figure 7). Total body length of the specimens ranged from 182 to 208 mm. Mean size of ova was directly related to size of fish. Range in ovum diameter and standard deviation about the mean size was similar for all fish except one (204 mm). The coefficient of variation about the mean ovum diameter (0.49 mm) for the combined sample was 5.5 percent. Female yellow bass had the capacity to spawn more than once within the spawning season if all ova were brought to mature size and spawned. Whether females actually spawned several times within the season was not determined. Nikolsky (1963) cautioned against concluding that a species is a fractional spawner because of the presence of small and large ova in the ovary. In many fishes, the smaller ova remain in the ovary after spawning and are gradually resorbed. Also, true fractional spawners usually have several distinct size groups of developing ova present in the ovaries which was not true of the yellow bass (Figure 7).

Variation in mean size of ova throughout the year was also determined from collected ovaries. Before measuring ovum diameter, the possibility that ovum size differed in the two ovaries was examined. Mean diameter of 30 ova each from the left and right ovaries of 27 females collected May 12, 1967, were compared. At the 0.50 level of probability ($t = 0.054$), the hypothesis could not be rejected that mean size of ova was similar in both ovaries of a given fish. Hence, center sections from either the left or right ovary were used for determining mean ovum size. Lewis (1962) also found no difference in size of maturing ova among sections of the same ovary or between left and right ovaries of striped bass. He measured ovum diameter of striped bass in North Carolina and found continuous growth from September to the May spawning period. Growth of yellow bass ova also appeared to be continuous to maturity (Figure 8). A seeming decrease in mean size of ova from October to November was not significant ($p = 0.05$; $t = 1.93$) and was attributed to sampling error.

During the last few weeks of development, ova grew rapidly and appeared to reach a certain size before ovulation occurred. Mean size of ova decreased rapidly upon spawning, indicating that the larger ova had been shed. Changes in mean ovum size closely followed the maturation index based on gonad-body weight ratio (Figure 4) although mean ovum diameter was a better indication of time when spawning occurred in the 2 years. In the 1968 sample, peak female maturity index was several percent below the 1967 level when spawning took place (8.4 versus 11.8 percent). However, mean ovum diameter reached a similar peak in size in both years coincident with spawning. Whenever mean diameter of all maturing ova exceeded 0.4 mm, ovulation with ensuing spawning appeared to be imminent. The measurements were taken from preserved ova and do not reflect the size of fresh mature ova. Most mature, ovulated ova in preserved condition measured

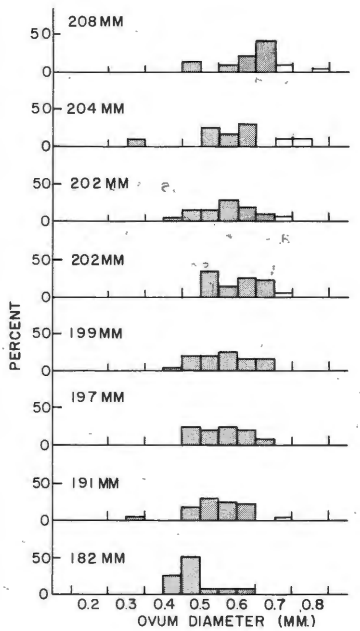

Figure 7. Size frequency of ova in samples from eight female yellow bass collected at Clear Lake, May 12, 1967. Total body length given for each fish. Clear portion of histogram represents mature transparent ova.

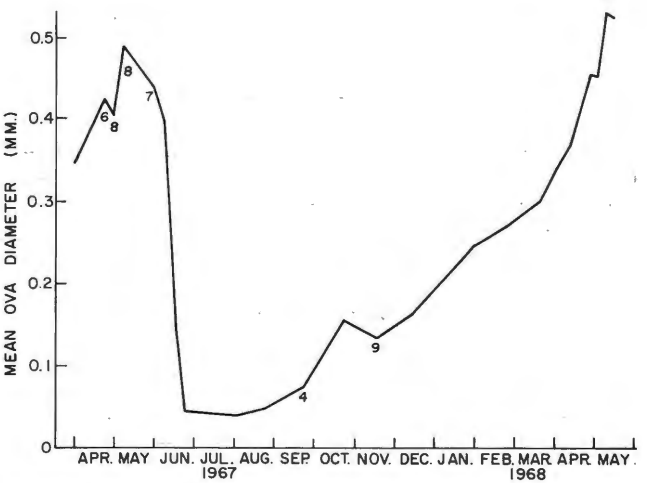

Figure 8. Seasonal change in diameter of yellow bass ova from Clear Lake collected 1967 to 1968. Solid line connects sample means of 20 to 30 ova from each of 10 fish. Samples containing less than 10 fish are noted on the figure.

0.65 mm or larger. Atchison (1967) and Burnham (1909) reported that unpreserved mature ova at spawning averaged 0.75 to 0.77 mm. Measurement of 102 mature ova in fresh condition from 4 females collected in 1967 indicated a mean size of 0.80 mm, with a standard deviation of 0.11 mm and a range from 0.66 to 1.18 mm.

Ovum Size Versus Body Length

Ovum size at maturity has frequently been found to correlate positively with fish body size (Rounsefell, 1957). Larger fish tend to produce larger eggs. Egg size within a species is important because fry hatched from large eggs may have a better chance of survival than fry hatched from small eggs (Svärdson, 1949; Privolnev, 1960). Egg size is related to nutrition according to Nikolsky (1963), but Scott (1962) found that egg size in kamloops trout, Salmo gairdneri, was genetically controlled and that only egg number was affected by nutrition.

Correlation coefficients of body length versus ovum size were computed for samples of yellow bass (Table 2). Significant increase in ovum diameter with body length was noted in the Oct. 24, 1967, and the Feb. 27, 1968 samples but not in intervening samples. The bigger fish, being repeat spawners, might start secondary ova development earlier than the smaller fish. Significant correlation were also noted on May 4 and 12, 1967, as the fish approached maturity. It is not known whether small adults spawned smaller ova than large fish or were merely slower in reaching maturity. It appeared from observations that large fish were functionally mature and ready to spawn earlier than the small adults. There was also some indication that smaller fish in the samples failed to ovulate a significant portion of their ova. In 1968, no correlation between ovum diameter and body length was evident as the fish approached maturity.

Hickling (1935) found that immature hake, Merluccius merluccius, had a seasonal variation in ovum diameter that coincided with the ovarian cycle of adult fish, but obviously no ova were brought to maturity. A similar condition was evident in yellow bass. Numerous female fish under 180 mm total length possessed enlarged ovaries at spawning time, but ova were too small to reach maturity in that year. Some fish over 180 mm also were not fully mature in the sense that only a small portion of the developing ova reached full size.

Ovarian Weight

Ovarian weight has occasionally been used as an index of reproductive capability in the sense that gonad weight estimates the ability of the female to mobilize material for reproduction (McFadden et al., 1965). Analysis of data collected in May 1967 from yellow bass revealed that, at maturity, gonad weight closely reflected mean size of ova present (Table 3). Even in 1968, when fewer ova reached maturity, the correlation between mean ovum size and ovarian weight was significant at the 0.05 level.

The reason for the declining correlation as the spawning season

Table 2. Correlation of mean ovum diameter with total body length of adult Clear Lake yellow bass collected in 1967 and 1968

Date of collection	Number of fish	Mean body length (mm)	Standard deviation (mm)	Mean ovum diameter (mm x 85)	Standard deviation (mm x 85)	r value	Significance level
1967							
4/20	6	201	9.4	35.0	4.4	0.26	NS
5/4	8	201	9.9	33.4	4.4	0.74	0.05
5/12	8	198	8.2	40.4	4.1	0.90	0.01
5/24	10	199	10.7	37.6	4.2	0.49	NS
6/2	7	201	6.1	36.4	1.1	0.27	NS
6/8	10	200	11.1	32.8	2.7	0.03	NS
9/25	4	200	7.7	6.4	0.8	0.00	NS
10/24	10	199	8.6	13.3	2.6	0.76	0.05
11/22	9	198	10.2	11.3	1.9	0.33	NS
12/19	10	200	8.9	13.5	1.6	0.00	NS
1968							
1/30	10	199	9.9	20.5	2.6	0.10	NS
2/27	10	198	7.4	21.3	1.7	0.63	0.05
3/19	10	199	7.4	25.0	2.9	0.26	NS
4/2	10	197	7.1	28.4	1.0	0.45	NS
4/16	10	196	6.7	32.6	3.8	0.20	NS
4/30	10	195	7.2	37.6	4.8	0.08	NS
5/7	10	197	8.6	37.1	4.1	0.08	NS
5/14	10	195	8.6	43.9	7.8	0.24	NS
5/21	10	195	5.9	42.8	2.7	0.12	NS

passed was evident upon plotting ovum size versus ovarian weight for each sample. At spawning, the fish with larger ovaries (usually the larger fish) had larger ova than did fish with small ovaries. As the large fish spawned, they shed the large mature ova and retained ova that were undersize. Their ovaries then shrunk to the point where they were of similar weight to ovaries of small but still unspawned females. Thus, the correlation between mean ovum size and ovary weight decreased with time. In 1968, spawning was blocked so that ovarian weight did not change. But the correlation declined because ova within smaller ovaries increased in size instead of larger ovaries decreasing in weight as the result of spawning.

OVA PRODUCTION

Fecundity Determination

The most suitable method for estimating fecundity varies among species of fish, depending upon number and size of ova produced. In certain species that produce large ova, such as some salmonids, total count of all ova present is not difficult (Henderson, 1963; Bulkley, 1967). Other more fecund species require subsampling of the numerous ova unless automatic counting devices as used by Boyer and Clifford (1967) are available. In my study, total count of yellow bass ova was precluded by the large number of minute ova produced.

A volumetric method was found most suited for measuring yellow bass fecundity. Ova numbers based on the mean of 4 aliquots provided an acceptable estimate of fecundity, although considerable sampling variation was present. Coefficients of variation ranged from 6.2 to 25.0 percent in the sample collected Oct. 24, 1967, and from 4.0 to 11.5 percent in the sample collected Feb. 27, 1968 (Table 4). The coefficient of variation in fecundity estimates for the average fish was approximately 8 percent.

Fecundity Versus Body Length

The size range of fish selected for my study (180-230 mm) eliminated many small maturing females so that the fecundity body-length relationship was not as obvious as reported for other species. In the sample of ripe females collected May 12, 1967, the relation between ova number and body length was significant at the 0.5 probability level, but only 50 percent of the variation in fecundity could be attributed to body length (Table 5). The body length-fecundity relationship for these prespawners was expressed by the formula:

$$Y = -880,985 + 5,446\ TL$$

where Y refers to number of ova (potential fecundity) and TL is total body length in millimeters.

After the 1967 spawning season, a negative correlation ($r = -0.22$) was obvious between ova numbers and body length, agreeing with the conclusion that smaller females retained their eggs and did not spawn. Correlation was also not significant for mature fish in the sample collected April 30, 1968 when spawning was again impending.

Table 3. Correlation of mean ovum diameter[a] with ovarian weight of adult Clear Lake yellow bass collected 1967 and 1968

Date of collection	No. of fish	Ovarian weight (g)	Standard deviation (g)	r value	Significance level (p)
1967					
5/4	8	13.3	5.1	0.91	0.01
5/12	8	15.4	6.1	0.88	0.01
5/24	10	11.1	3.1	0.84	0.01
6/2	7	9.9	2.8	0.66	0.05
6/8	10	5.7	1.8	0.38	NS
1968					
5/7	10	6.7	1.1	0.66	0.05
5/14	10	10.3	2.2	0.42	NS
5/21	10	6.5	1.2	0.34	NS

[a] See Table 2 for values.

Table 4. Coefficients of variation (percent) in estimates of Clear Lake yellow bass fecundity based on four aliquots for each fish collected from 1967 to 1968. Ten fish were sampled each date.

Date of collection	Coefficient of variation	
	Mean	Range
1967		
5/12	11.5	4.4 - 17.5
6/4	7.1	3.3 - 16.7
10/24	10.4	6.2 - 25.0
12/19	8.7	3.8 - 16.0
1968		
2/27	7.0	4.0 - 11.5
4/30	7.7	3.1 - 18.1

Table 5. Potential fecundity of Clear Lake yellow bass collected 1967 to 1968 in relation to body total length. Range in fecundity and number of fish in parentheses

Date of collection	Mean body length (mm)	Mean fecundity (100's)	r value	Significance level	Mean fecundity (100's) at body length 180-189	190-199	200-209	210-219
1967								
5/12	199	203.8	0.72	0.05	51.3(1)	221.0(4) (148.2-282.4)	213.3(4) (179.0-229.4)	249.2(1)
6/14	198	72.2	-0.22	NS	94.6(2) (84.3-94.9)	49.8(3) (34.6-70.0)	79.9(3) (54.3-99.4)	80.1(2) (72.0-89.9)
10/24	203	112.6	0.26	NS	-	107.1(5) (81.7-121.1)	114.0(3) (73.2-143.1)	124.4(2) (106.1-142.6)
12/19	198	148.8	0.81	0.01	127.7(2) (106.5-148.9)	128.7(3) (102.6-147.3)	149.2(5) (139.2-173.9)	-
1968								
2/27	199	127.5	0.53	NS	-	119.3(5) (88.9-150.4)	135.7(5) (104.8-153.6)	-
4/30	195	113.6	0.32	NS	109.3(2) (108.1-110.5)	98.2(4) (82.4-104.5)	130.9(4) (99.2-156.7)	-

Potential Fecundity

The average number of ova estimated in yellow bass ovaries just before spawning time in 1967 (May 12) was 203,800 ova for a female measuring 199 mm total length and weighing 142 g (Table 5). Hence, in terms of unit measure, the average yellow bass produced 1,023 ova per millimeter of body length or 1,439 ova per gram of body weight. Ova number varied within the sample from 51,300 for a fish measuring 182 mm and weighing 101 g. to 282,400 ova in a female 197 mm long and weighing 149 g. The largest fish in the sample measured 215 mm in length and weighed 178 g. but contained only 249,000 ova.

Fecundity of yellow bass in 1967 was somewhat higher than fecundity reported for other serranids in terms of body weight. Riggs (1955) found a potential fecundity of 565,000 ova in average-sized white bass. The number of ova per gram of body weight ranged from approximately 814 to 1,138. The smallest female examined measured 254 mm (fork length) and contained 242,000 ova. Lewis and Bonner (1966) estimated average striped bass effective fecundity at approximately 176 ova per gram body weight (80,000 per pound) among fish weighing 2 to 16 lb. Counts of near-mature white perch ova ranged from 143 to 786 per gram body weight with 551 ova per gram in a female averaging 148 g body weight (Sheri and Power, 1968).

All ova in advanced secondary development were included in the fecundity estimates of yellow bass, but only a portion actually reached maturity and were ovulated. Thus, the ova estimates represented potential fecundity rather than the number of ova shed. Differences between potential and effective fecundity were evident upon comparing ovary contents before and after the spawning period. A comparison was made between ova numbers within the gonads when spawning was impending (May 12) in 1967 with the numbers of ova still present well after spawning activity had ceased (June 14). After spawning, ovaries of the average-sized female still contained over 70,000 unspawned ova or approximately 34 percent of the total number present when spawning commenced (Figure 9). In the post-spawning period, the relationship between fecundity and body length assumed a negative slope:

$$Y = 135,518 - 320\ TL.$$

Thus, fewer ova remained in the large fish than in the small fish.

The large proportion of unshed ova emphasizes the importance of differentiating between potential and effective fecundity when discussing yellow bass reproduction.

It was evident that large females spawned a higher percentage of the ova present in their ovaries than did the small females. Weekly comparisons from May to June not shown here supported this observation. The large amount of ova retention agreed also with observations reported previously that gonads of the larger females soon shrank after spawning to a size equal to the ovaries of small fish, and remaining ova were of equal size to ova present in the smaller females.

Few ova over 0.6 mm diameter were present in gonads of 15 females collected June 14, 1969. If it is assumed that all ova over 0.6 mm, or over 0.5 mm, on May 12 were shed, we may make additional estimates of the effective fecundity (Table 6).

Ova growth was very rapid just before spawning (Figure 8), and growth probably continued as long as factors stimulating gonadal development were present. Hence, many ova which were under 0.5 mm one week before spawning could easily have grown large enough to be ovulated before spawning ceased. The number of ova measuring 0.5 mm and larger in the May sample agreed closely with estimates of effective fecundity based on numbers of shed ova (Table 6). A common regression line fitted both sets of date ($p = 0.01$).

Annual Differences in Fecundity

Potential fecundity was considerably lower in 1968 than in 1967. Ova estimates just before spawning in 1967 ranged from 51,300 in a 182 mm female to 282,400 ova in a fish 197 mm total length. The 1968 estimates ranged from 82,400 ova in a fish 196 mm long to 156,000 ova in a female measuring 202 mm in length (Figure 10). Potential fecundity in 1968 was expressed by the formula $Y = -88,383 + 1035TL$, in contrast to the 1967 formula $Y = -880,985 + 5446TL$. A yellow bass measuring 199 mm total length produced 203,400 secondary ova in 1967 and 117,600 in 1968. Females in the 180 mm length range contained similar numbers of ova in both years indicating that whatever factor influenced the larger fish to produce fewer ova in 1968 did not affect fish 180 mm in length.

Mean weight for a fish measuring 199 mm at spawning time was 142 g in 1967 and 114 g in 1968. Evidence that the lowered potential fecundity in 1968 was due to reduction in body weight was obtained by comparing fecundity in 1967 and 1968 with body-minus-ovary weight (Figure 11). A single regression line adequately described the relationship ($F = 1.48$; $p = 0.05$) for the 2 years. Approximately 58 percent of the variation in fecundity in 1967 and 1968 could be explained by differences in body-minus-ovary weight ($r = 0.77$; $p = 0.05$). Differences in body length only accounted for 50 percent of the variation in 1967 fecundity and 36 percent of the variation in 1967 and 1968 combined. Fecundity estimates adjusted to a common body-weight without ovaries were also similar ($F = 3.81$; $p = 0.05$). Females produced as many ova per unit of body weight without ovaries in 1968 as in 1967. But they were much lighter for their length in 1968 so that total fecundity was reduced considerably.

The decrease from 1967 to 1968 in estimated effective fecundity was similar to the 40 percent decrease in potential fecundity. By using the method of calculating effective fecundity based on the assumption that all ova 0.5 mm and larger will be spawned, effective fecundity was computed for 1968 (Table 7). There was no obvious relation between body length and the percentage of ova larger than 0.5 mm in diameter in the 1968 sample. Females near the mean length of fish in the sample (195 mm) contained most ova presumably large enough to be spawned.

Mean effective fecundity was estimated at 53,900 ova for the average size female. In terms of body size, effective fecundity in 1968 averaged approximately 276 ova per millimeter body length (versus 560 for 1967) or 350 ova per gram body weight (versus 835 for 1967). Hence, the

Table 6. Data used for estimating effective fecundity of Clear Lake yellow bass based on number of ova larger than 0.5 and 0.6 mm present in ovaries collected May 12, 1967.

Total length (mm)	Percent of ova larger than 0.6 mm	Percent of ova larger than 0.5 mm[a]	Potential fecundity[b]	Number of ova larger than 0.6 mm	Number of ova larger than 0.5 mm	Estimated effective fecundity[c]
182	0	16	111,200	0	17,680	32,900
191	5	50	159,200	8,000	79,600	81,900
197	10	55	191,900	19,200	105,500	119,400
199	15	55	202,800	30,400	111,500	130,900
202	17	65	219,100	43,800	142,400	148,400
204	20	65	230,000	46,000	149,500	159,800
208	55	85	251,800	138,500	214,000	182,800

[a] From Figure 8.

[b] Computed from formula: $Y = -880,985 + 5446\ TL$.

[c] Difference between ova counts before and after spawning: $Y = (-880,985 + 5446\ TL) - (135,518 - 320\ TL)$, from Figure 9.

Table 7. Data for estimating effective fecundity of Clear Lake yellow bass based on number of ova larger than 0.5 mm present in ovaries collected May 12, 1968

Total length (mm)	Percent of ova larger than 0.5 mm	Potential fecundity[a]	Estimated effective fecundity
182	70	100,000	70,000
187	35	105,200	36,800
190	60	108,300	65,000
192	10	110,300	11,000
196	75	114,500	85,900
196	85	118,600	97,300
200	20	118,600	23,700
200	20	120,700	23,700
202	70	120,700	84,500
205	33	123,800	40,900

[a] Computed from formula $Y = -88,383 + 1,035\ TL$.

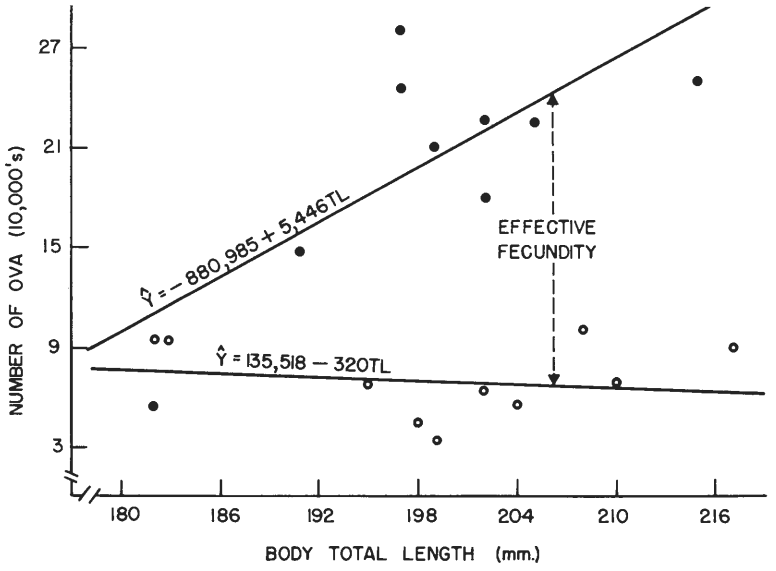

Figure 9. Estimated number of ova in female Clear Lake yellow bass collected May 12 (upper line) and June 14, 1967 (lower line). Difference between the two lines represents the estimated number of ova .

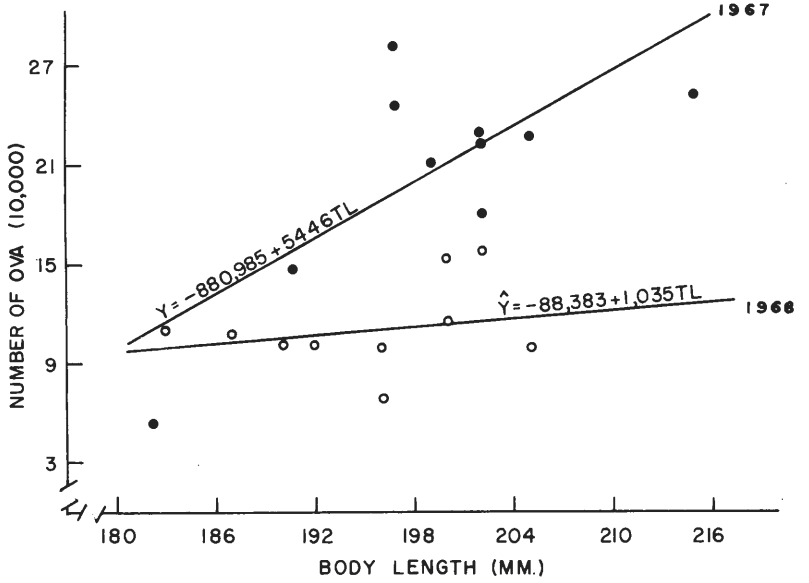

Figure 10. Potential fecundity of female Clear Lake yellow bass collected the week prior to spawning in 1967 (solid circles, upper line) and 1968 (open circles, lower line) in relation to body length.

number of ova large enough to be ovulated as well as the number of secondary ova produced in 1968 was 40 to 50 percent less than in 1967.

FACTORS INFLUENCING OVA PRODUCTION

Source of Fecundity Variations

The large reduction in ova numbers and in gonad size from 1967 to 1968 justified a review of factors regulating fecundity. Within species fecundity may be regulated by age, body size, and growth rate plus factors such as nutrition. Increased fecundity by faster growing individuals reflects an adaptive response to environmental changes mainly because of a change in food supply (Nikolsky, 1963). When food is abundant, more ova are brought to maturity, and thus, more young are produced to utilize the extra food if still available. Scott (1962) found that fecundity of rainbow trout, Salmo gairdneri, could be altered by manipulating the food supply of maturing fish. McFadden et al. (1965) related brown trout fecundity to fertility of the aquatic environment. Wydoski and Cooper (1966) found that an infertile stream environment could reduce brook trout fecundity up to 50 percent in females of similar size. Krumholz (1948) found that better feeding increased brood size of the mosquitofish. Woodhead (1960) summarized the relation between nutrition and reproductive capacity of fish and reported that feeding can alter the frequency of spawning as well as the number of eggs produced. Seemingly, when feeding conditions improve sufficiently, carp, which normally resorb up to 35 percent of their eggs, will bring all ova to maturity and release them. Failure of yellow bass in my study to spawn all secondary ova in 1967 and 1968 could well be related to limited food supply. The Clear Lake population has been stunted for some years because of overabundance and interspecific competition for food.

Developmental Atresia

The number of developing ova present in yellow bass during the maturation period was checked at 2-month intervals from October 1967 to May 1968 (Table 5). A common regression line of fecundity to body length fitted all samples at the 0.01 level of probability ($F = 1.95$). But, numbers of ova present in fish of similar size collected October, December, February and April were not equal ($p = 0.01$; $F = 7.56$). The October and December samples indicated differences in fecundity for similar length fish at the 0.01 level, but no difference was suggested between February and April samples ($p = 0.05$; $F = 0.61$).

Comparison of adjusted mean ova numbers (Figure 12) suggested that atresia of approximately 15 percent occurred from December to March and an additional 5 percent from March to April 30. In December ovaries of a female measuring 199 mm total length contained approximately 149,000 ova. By spawning time only 113,500 secondary ova were still present. Few atretic ova were detected in the samples but small immature ova are readily resorbed and are rarely seen (Braekevelt and McMillan, 1967). The seeming increase in ova numbers from October to December suggested that additional ova commenced vitellogenesis after the October sample was taken.

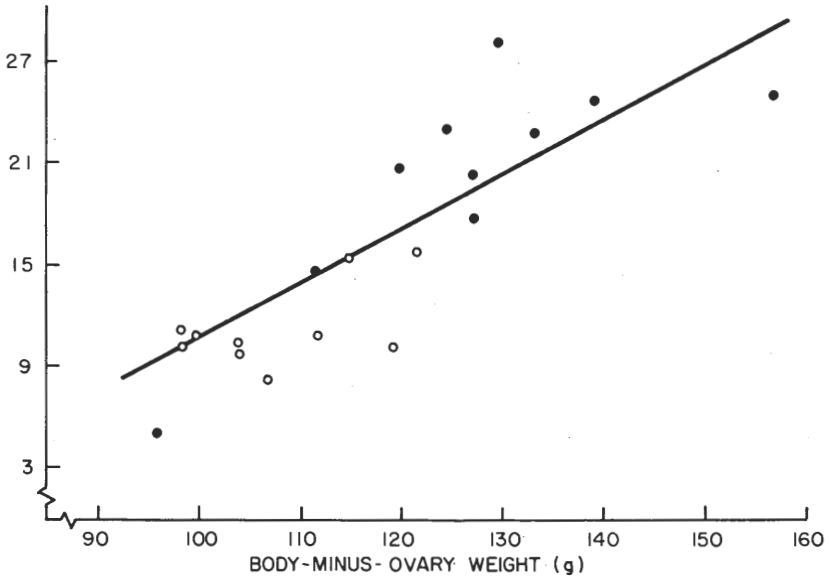

Figure 11. Potential fecundity of female Clear Lake yellow bass collected the week prior to spawning in 1967 (solid circles) and 1968 (open circles) in relation to body minus ovary weight.

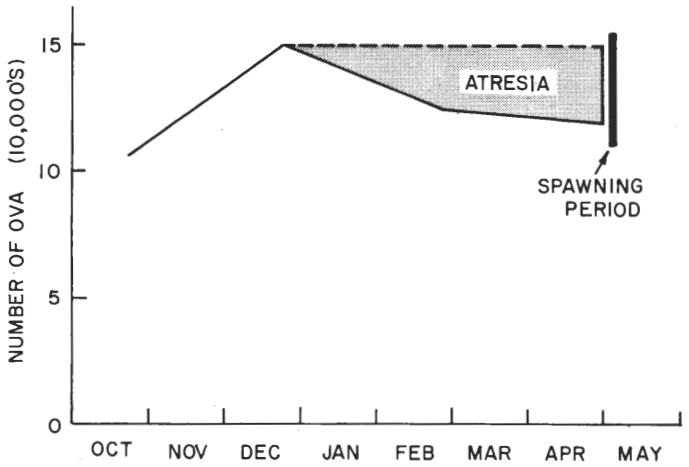

Figure 12. Adjusted mean numbers of ova from Clear Lake yellow bass with a mean body length of 199 mm by two-month intervals during the maturation period, 1967 to 1968.

Henderson (1963) commented on the need to consider body growth when measuring developmental atresia in brook trout ova, which Vladykov (1956) evidently failed to do. In contrast to brook trout, which spawn in the fall, yellow bass body growth occurs at a different time of year than gonadal maturation. Also, adult yellow bass were growing very slowly in Clear Lake so that increase in body size during maturation could be disregarded when estimating developmental atresia.

Numerous studies have been conducted in recent years to determine factors causing reduction in ova numbers during maturation. Atresia of developing ova has been attributed to several factors besides nutrition. Ball (1969) stated that atresia can result from any form of stress induced by the environment, such as cold, shock, etc. He believes that the ease with which atresia occurs suggests that the corpora atretica produced may be a normal source of estrogens to enhance development of remaining ova as is found in higher vertebrates. Ingram (1962) presented evidence that, in higher vertebrates, oocytes, particularly those having started development, are very sensitive of ischemia, possibly as a result of oxygen or gonadotropin deprivation. In my study complete atresia in mature ovaries was easily induced in yellow bass by capture but could be averted by increasing oxygen content of the holding water.

Seasonal Food Selection

Although numerous studies on the food habits of Clear Lake yellow bass have been reported, most information is restricted to the summer months (Bailey and Harrison, 1945; Ridenhour, 1960; Buchholz, 1960; Welker, 1963; Kraus, 1963; and Atchison 1967). My study, conducted over the full year, provided new information on the diet of yellow bass during the colder months of the year. One disadvantage was that collections of yellow bass were made primarily for information on reproduction. When an adequate sample of fish was obtained for the reproduction study, the collecting was terminated regardless of the time of day. Hence, stomachs were not always collected during the same portion of a 24-hour period. Helm (1958) found that yellow bass had a diurnal variation in the type of food eaten. During the late evening when feeding was maximal, chironomids were the major item ingested, whereas in the daylight hours, zooplankton were selected for food. To the extent that Clear Lake yellow bass exhibit a diurnal variation in food preference, conclusions based on data presented here may not be entirely accurate. However, a relatively large number of fish collected at different times of the day was examined each month so that any bias due to difference in time of feeding would appear to be negligible.

Mean volume of stomach contents never exceeded 1 cc (Table 8), but volume was higher in April 1967 than in any other month. Stomach contents were greater in both April and May 1967 than in those months in 1968. Chironomid larvae were present in all but one of the monthly samples containing food. Pupae and emerging adults were sporadically present during the warmer months. Planktonic crustacea were composed mostly of Daphnia in the spring and autumn, with Leptodora becoming more common in late spring and early summer. All fish remains that could be identified were young yellow bass.

Table 8. Number of stomachs examined and mean volume (cc) of major food items of 881 adult Clear Lake yellow bass collected 1967 to 1968

Month of capture	Number of stomachs	Stomachs with food	Mean volume of stomach contents[a]			
			Chironomids	Fish	Zooplankton	Total[b]
1967						
April	89	83	0.28	0.00	0.42	0.74
May	82	69	0.39	0.00	0.05	0.44
June	140	117	0.19	Tr.[d]	0.04	0.24
July	30	10	0.18	0.15	0.06	0.39
August	69	58	0.07	0.28	0.01	0.37
September	26	19	0.02	0.31	0.01	0.37
October	47	41	0.01	0.37	0.09	0.49
November	42	0	0.00	0.00	0.00	0.00
December	49	0	0.00	0.00	0.00	0.00
1968						
January	50	--[c]	0.03	0.01	0.06	0.16
February	55	--	0.00	0.00	0.18	0.18
March	32	23	0.01	0.00	0.02	0.03
April	90	--	0.07	0.00	0.28	0.43
May	80	--	0.10	0.00	0.17	0.30

a The mean volumes are based upon fish with and without food.
b Total includes miscellaneous items and unidentified food remains.
c Number not recorded.
d Trace = <0.01

In April and May 1967, chironomid larvae were utilized heavily, whereas in 1968, Daphnia made up the major portion of the identified food in both months (Table 8). Chironomids continued as a major food item until midsummer in 1967 when replaced by young yellow bass. From August to October, fish was the major food item, and the volume eaten increased steadily from July to October. Average size of ingested yellow bass was consistently smaller than the mean size of fish in the Age 0 population, as determined from seining samples, indicating that the smaller fish were being selected. In August, there were usually 3 to 4 yellow bass averaging 46 mm total length in each stomach containing fish. In September, mean size of ingested bass was 57 mm. By October yellow bass in adult stomachs ranged from 48 to 76 mm in length and each stomach usually contained a single fish.

The large percentage of fish in the yellow bass diet during late summer and autumn in 1967 differed considerably from previous studies on food habits of Clear Lake yellow bass. Kraus (1963) summarized information on yellow bass feeding from 1957 to 1963 and reported that from 1 to 5 percent of stomachs examined contained fish.

An explanation for the seemingly uncommon utilization of young yellow bass for food may lie in the large number of offspring produced in 1967. Since young yellow bass shortly after hatching start eating invertebrate foods similar to those eaten by adults (Ridenhour, 1960; Kraus, 1963), the abundant 1967 year class undoubtedly utilized large amounts of food suitable for the adult bass. Hence, the adult fish presumably turned on their own offspring for sustenance when other food became more difficult to obtain. Another possibility was that limited food restricted growth of the young fish so that their small size exposed them to predation for a longer time.

The transition to a fish diet in late summer and autumn suggested that yellow bass exhibit the autumn feeding spree characteristic of several species of warm water fish. The actual volume of stomach contents did not increase from July to Sept. (0.39 to 0.37 cc), but mean volume of stomach contents in Oct. (0.49 cc) was surpassed only by the April sample. The high angling success for yellow bass in Sept. and Oct. reported by Harlan and Speaker (1951) is a reflection of this increased feeding intensity.

Maximum utilization of fish for food coincided with the period of the year when gonadal development was initiated. It is postulated that release of hormones for yellow bass gonadal development and vitellogenesis also resulted in appetite increase. In turn, the hunger caused a transition to larger food items such as fish. Change in availability of forage fish in late summer was evidentally not a major factor because fish were found in only 1 yellow bass stomach in June when young of the year were most abundant. Heavier feeding in Autumn would allow storage of sufficient energy for continuation of gonadal development through the winter period of semi-fasting. Investigation into the hormone production in domestic chickens provides a possible explanation for the appetite increase in yellow bass. As hens approach sexual maturity, food intake increases (van Tienhoven, 1968). Estrogen secretions associated with ovarian maturation stimulates the appetite so that sufficient energy is ingested for deposition of the large amount of yolk material needed in the egg. Hence the hen has an endocrine mechanism for achieving maximum reproductive efficiency. By increasing food intake, egg production is maximized. Available information suggests that a similar mechanism might operate in yellow bass. Teleost production of estrogen needs additional documentation (Pickford and Atz, 1957), but appetite stimulation coincidentally with initiation of gonadal development would certainly be an effective mechanism for assuring successful reproduction in a species that must store much of the energy needed for gonadal maturation several months before spawning.

Body Condition

Adequate measurement of food supply available to maturing yellow bass is difficult to obtain. Competition for available food in Clear Lake exists, not only between individual adult yellow bass, but also between adults and juveniles and with other species of fish in the lake. Black bullheads were particularly abundant and competed directly with yellow

bass for food in 1967 and 1968. A fairly reliable index of food adequacy in the recent past may be obtained by examining body condition as reflected by the length-weight relationship. Within the same species, sex and stage of maturity, the heavier a fish is for a given length, generally the larger are its nutritional reserves. These nutritional reserves indicate, in part, the amount and quality of food ingested previously.

The length-weight relationship was computed by sex for each sample of yellow bass collected in 1967 and 1968 by using the formula:

$$\text{Log } W = \text{Log } a + b \text{ Log } L$$

where W is body weight in grams, L is total body length in millimeters, a is a constant and b an exponent. Mean body weight and length and values of a and b for each sample are presented in Tables 9 and 10.

Fish tend to increase in body weight approximately in proportion to the cube of their length (i.e., $b = 3$). If values for the exponent b are larger than 3, the longer fish are proportionally heavier for their length than are the small fish. In the current study, it was evident that, during the 1967 prespawning period, the longer fish of both sexes were proportionally heavier for their length than were the small adults. One exception was the sample of female fish collected May 4, which had a b value not statistically different from 3 ($p = < 0.50$).

Values of b during the 1968 prespawning period from April 1 to May 15 were much lower for both sexes than during the same period in 1967. Thus, larger females were proportionally lighter for their length than were small fish of the same sex ($b < 3.0$; $p = 0.01$; $t = 1.18$). There was no change in plumpness of males with length in 1968. During the summer of 1967, large and small adult bass of both sexes showed no change in plumpness with length. At this time of year, the gonad-body weight ratio is similar in both mature and immature fish so that this possible source of variation in plumpness was not present.

These comparisons of length-weight differences within samples as indicated by the slope for the length-weight formula provide some insight into growth conditions within the population. But, more information is gained by comparing weights of fish of similar length collected from the population at different times. Such comparisons are most valid if fish are collected by the same type of gear, are of similar stage of maturity, etc. The requirements were best met in comparisons of fish during the 1967 and 1968 prespawning period. There were no major shifts in length frequency of the samples in the 2 years and change in girth due to weight difference was not thought to seriously alter gillnet selectivity. Combined samples of yellow bass were compared by sex for the period from April 1 to May 15 for the 2 years (Table 11). A common regression line would not fit the length-weight relationship for both years ($p = 0.01$) for either sex. Slope of the regression line was also different at the 0.01 level. Hence, comparison of mean weights adjusted for length differences for the 2 years was not completely justified. Since the ranges in length and mean lengths of the samples were quite similar, however, adjusted mean weights near the mean length of both samples were thought to be sufficiently valid for comparison. The large difference in weight of females for a given length was evident from

Table 9. Values of a and b in the length-weight relationship of female Clear Lake yellow bass collected in 1967 and 1968

Date of collection	Number of fish	Mean length (mm)	Length range (mm)	Mean weight (g)	Log a	b value
1967						
4/5	33	204	182-221	136	-5.770	3.420
4/20	44	203	182-220	143	-5.980	3.526
4/27	9	203	196-208	146	-6.863	3.912
5/4	16	201	183-216	148	-4.863	3.037
5/12	27	201	182-215	147	-5.890	3.498
5/24	23	201	182-214	139	-5.115	3.152
6/2	30	202	181-213	142	-5.689	3.400
6/8	29	196	181-210	122	-4.928	3.058
6/14	46	195	180-217	121	-4.502	2.875
6/22	28	196	180-212	119	-5.001	3.088
6/28	29	196	182-217	121	-5.638	3.364
8/3	21	193	184-212	115	-4.711	2.963
8/28	14	200	181-214	119	-4.687	2.939
9/25	8	199	190-208	115	-4.719	2.948
10/23	35	202	188-218	121	-3.981	2.630
11/22	19	196	186-217	112	-4.055	2.663
12/19	29	202	188-207	122	-4.636	2.922
1968						
1/30	37	200	187-217	109	-3.866	2.566
2/26	29	199	184-207	124	-3.434	2.403
3/18	38	196	181-211	108	-3.573	2.446
4/1	36	197	186-210	112	-3.066	2.463
4/15	17	194	184-203	105	-4.717	2.943
4/30	16	196	182-205	113	-2.279	1.891
5/6	25	193	185-215	104	-4.384	2.800
5/10	8	192	185-200	105	-2.375	1.926
5/13	30	195	180-209	109	-3.113	2.249
5/20	20	196	185-219	108	-4.299	2.760

Table 10. Values of a and b in the length-weight relationship of male Clear Lake yellow bass collected in 1967 and 1968

Date of collection	Number of fish	Mean length (mm)	Length range (mm)	Mean weight (g)	Log a	b value
1967						
4/5	29	196	171-211	116	-6.403	3.693
4/20	41	190	170-223	112	-5.883	3.483
4/27	20	183	170-203	92	-6.175	3.598
5/4	8	194	175-210	124	-6.051	3.559
5/12	66	193	171-211	122	-5.937	3.510
5/24	25	190	172-210	111	-5.127	3.149
6/2	42	197	175-211	124	-4.656	2.941
6/8	33	194	171-211	121	-4.848	3.028
6/14	21	195	172-211	120	-5.015	3.099
6/22	33	194	178-206	119	-5.388	3.260
6/29	29	197	179-223	124	-4.833	3.019
8/3	10	193	176-212	108	-4.837	3.005
8/28	14	195	178-208	108	-4.771	2.970
9/25	12	191	173-202	100	-4.622	2.904
10/23	34	193	177-207	104	-5.296	3.200
11/22	23	200	188-212	113	-4.327	2.774
12/19	20	197	182-207	116	-5.579	3.330
1968						
1/30	14	194	176-208	101	-5.392	3.229
2/26	26	193	176-210	111	-3.240	2.305
3/18	32	191	183-213	97	-4.238	2.729
4/1	29	194	183-214	106	-5.312	3.204
4/15	21	191	176-210	98	-4.667	2.916
4/30	15	193	178-209	108	-4.707	2.947
5/6	30	191	178-206	97	-5.526	3.292
5/10	18	193	179-210	105	-3.633	2.473
5/13	30	191	175-207	96	-4.984	3.052

Table 11, Length-weight data of adult Clear Lake yellow bass collected from April 1 to May 15 in 1967 and 1968.

Sex	Year	Number of fish	Mean length (mm)	Length range (mm)	Mean weight (g)	Log a	b value
Female	1967	129	203	182-220	143	-5.240	3.205
	1968	132	195	180-215	108	-3.638	2.477
Male	1967	164	192	170-223	114	-6.048	3.552
	1968	143	192	175-214	99	-5.053	3.088

plotted curves based on the calculated length-weight relationship (Figure 13). The average female measuring 200 mm had a calculated weight of 137 g in 1967 but only 115 g in 1968, a 16-percent decrease in mean weight.

Males could be compared directly for 1967 and 1968 because mean body lengths were similar (Table 11). A sample of 164 males collected in 1967 from April 1 to May 15 measured 192 mm mean total length and 115 g mean weight. In 1968, the sample of 143 adult males measured 192 mm total length but averaged only 99 g in weight. Thus, the average spawning male was approximately 13 percent lighter in 1968 than in the previous year.

The change in mean weight of adult bass between 1967 and 1968 was more evident when computed weight of fish was plotted at a selected length (200 mm) for each collection date (Figures 14 and 15). Fortunately, length distribution of fish within the various samples was fairly restricted so that no sample mean length varied more than 6 mm from the mean of all samples.

Net body weight, as well as total body weight and gonad weight, increased in both sexes during the 1967 prespawning period. LeCren (1952) found a similar increase in body-minus-gonad weight for European perch from 1944 to 1947. The weight increase could have resulted from increased food intake or from increased efficiency of energy conversion due to hormonal activity associated with sexual maturation (Hervey and Hervey, 1967).

In my study no increase was noted in body-minus-gonad weight of bass during April 1968, when gonads were again increasing. On the contrary, mean female weight decreased almost continuously from May 1967 until termination of the study in May 1968. Male bass showed a regular downward trend, with only a slight swing upward in body weight during April 1968, but mean values were well below April 1967 values. A slight but temporary increase in body condition in both sexes during

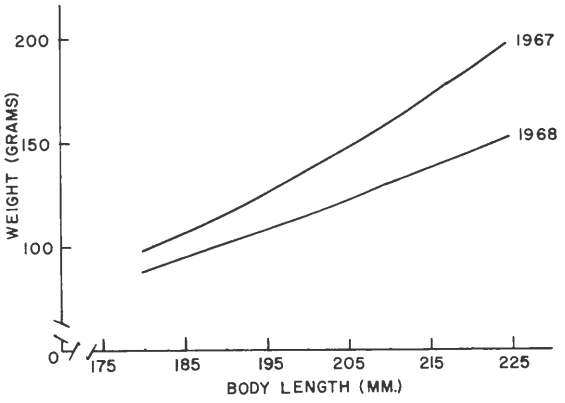

Figure 13. Length-weight relationship of adult female yellow bass collected in Clear Lake April 1 to May 15, 1967 and 1968.

late autumn was attributed to the increased food intake during that period.

An additional index of fish body condition can be obtained by measuring fat content. Fat is the most labile form of stored energy in fish, accumulating when energy is in excess and decreasing during periods of reduced energy intake (Shul'man, 1960). If energy reserves are inadequate, reproduction may be depressed either through lowered fecundity (Bekker, 1958), reduced frequency of spawning or increased egg mortality (Fontaneand Olivereau, 1962). The mesenteric fat is a reliable index of well-being in some fishes and is first utilized for gonadal development in both "fat" and "lean" species of fish (Shul'man, 1960).

A negative correlation ($r = -0.92$), significant at the 0.01 level, existed between weight of mesenteric fat and ovarian weight from March to May (Figure 16). There was a suggestion that mesenteric fat actually increased from January to February, but by mid-May, fat reserves had dropped to negligible levels. The amount of mesenteric fat lost during the period was much less than the gain in ovarian weight. Energy other than that drawn from mesenteric fat was obtained either from other storage sites or through feeding. The continual decrease in body-minus gonad weight during the 1968 maturation period (Figure 14) suggested that much of the energy for gonadal development was obtained at the expense of other body tissue. Feeding seemingly failed to provide adequate energy during the period. In 1967, however, body-minus gonad weight actually increased during late maturation.

Males contained only half the amount of mesenteric fat found in females during January, February, and March 1968, but a similar rise in gonadal weight coincided with decrease in fat levels during the pre-spawning period (Figure 17). Negative correlation between fat level and gonad weight from March to May was significant at the 0.01 level ($r = -0.93$). As with females, more mesenteric fat was found in fish during

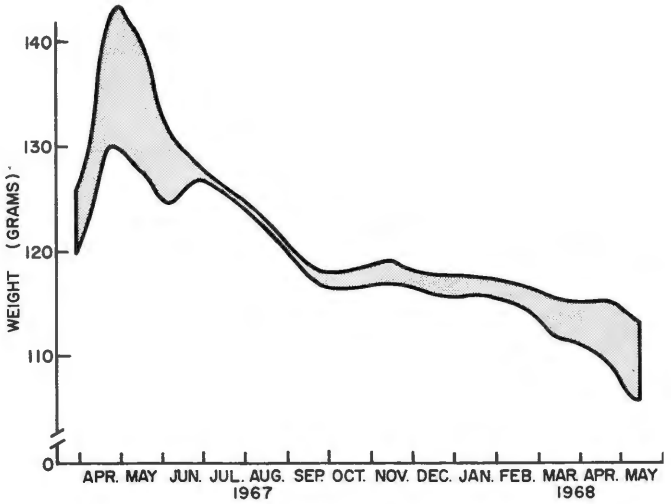

Figure 14. Seasonal changes in computed body weight of a 200-mm female yellow bass with and without ovaries. The upper line represents total body weight. The weights were computed from the formulae in Table 9 and the curves are based on rolling averages of three sample values. The lower edge represents weight minus the ovaries, derived by multiplying body weight by the mean maturity index for that sample.

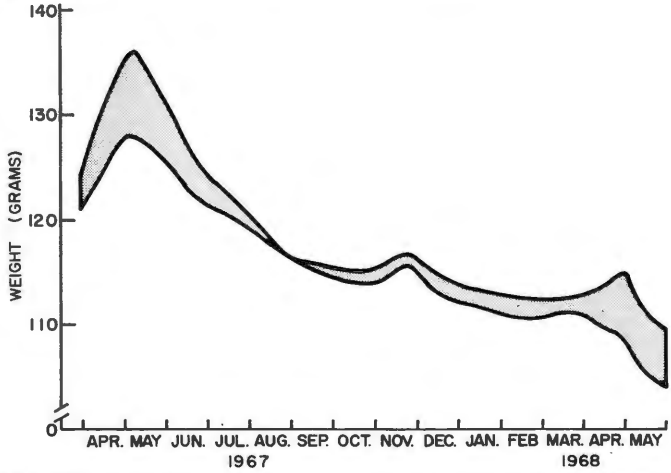

Figure 15. Seasonal changes in computed body weight of a 200-mm male yellow bass with and without testes. The upper line represents total body weight. The weights were computed from the formulae in Table 10 and the curves are based on rolling averages of three sample values. The lower edge represents weight minus the testes, derived by multiplying body weight by the mean maturity index for that sample.

March than in February. Mean weight of mesenteric fat of 358 mg dropped to 6 mg by May 14. Testicular weight almost tripled during the same period from 1.7 to 4.6 g.

Additional information on the relationship among available food, mesenteric fat, and gonadal development was sought by feeding adult female bass in the laboratory. Fish were obtained from Clear Lake on April 16, 1968, and maintained for 20 days in two 145-gallon aquaria. Ten fish were placed in each aquarium; all but 3 fish completed the experiment. Water temperature was maintained at 16 $\pm$ 1°C. Light from cool white fluorescent lamps was provided equally to both groups for 15 hr. per day, which approximated natural day length during the spawning period. Intensity of light at the water surface was 18 ft.-c.

Fish were fed bluntnose minnows (Pimephales notatus) at two feeding levels. The low level group was fed approximately 1-percent body weight 6 days weekly. Live minnows were available to the second group at all times so they could feed to satiation. At termination of the experiment, the second group had consumed an average of 3.1 percent body weight (18.4 percent body weight per week). Daily food intake when forage minnows were always present varied from 0.6 to 5.2 percent body weight. Since feeding levels were computed on the basis of final body weight of the bass, the levels were not exactly as given. Handling was kept at a minimum until termination of the experiment because previous tests indicated that yellow bass readily undergo atresia if stressed.

At the end of 20 days, fish fed to satiation contained mesenteric fat with a mean weight of 0.53g. Fish fed at the 1-percent level had an mesenteric fat content of 0.24 g (Table 12). A common line fit the relation of body weight to mesenteric fat for both groups ($p = 0.01$; $f = 14.66$). The fish fed to satiation had 135 percent more fat than the group fed at the lower level.

Amounts of mesenteric fat of laboratory-fed bass were compared with bass captured at the beginning and end of the feeding trial. Fish held in the laboratory, particularly those fed at a high level, seemingly increased in fat during the feeding trial, if samples were representative. Fish in the lake remained essentially unchanged in body weight, but experienced a decrease in mesenteric fat as reported earlier.

Gonadal development appeared blocked in fish brought into the laboratory. Evidently, certain stimuli necessary for continued ovarian maturation were lacking. Ovaries of fish fed at the 1-percent level decreased in weight. Weight of ovaries of bass fed at the higher level remained unchanged, whereas females of similar length in the wild increased gonadal weight by approximately 50 percent during the 3-week period.

Hence, the additional food provided the laboratory fish seemingly decreased mobilization of mesenteric fat for ovarian development and actually increased fat stores. However, the desired effect of increasing the number of ova brought to maturity was not realized.

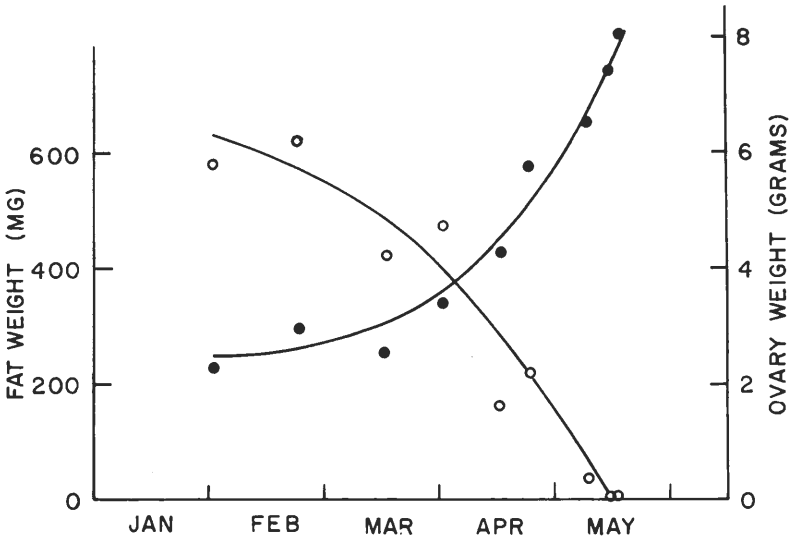

Figure 16. Relation of mean ovarian weight (solid circles) of female Clear Lake yellow bass to mean weight of mesenteric fat (open circles) during late stages of sexual maturation, 1968. Curves drawn in by eye Sample size ranged from 14 to 38 fish (mean, 26) except that the May 10 sample included only 8 fish.

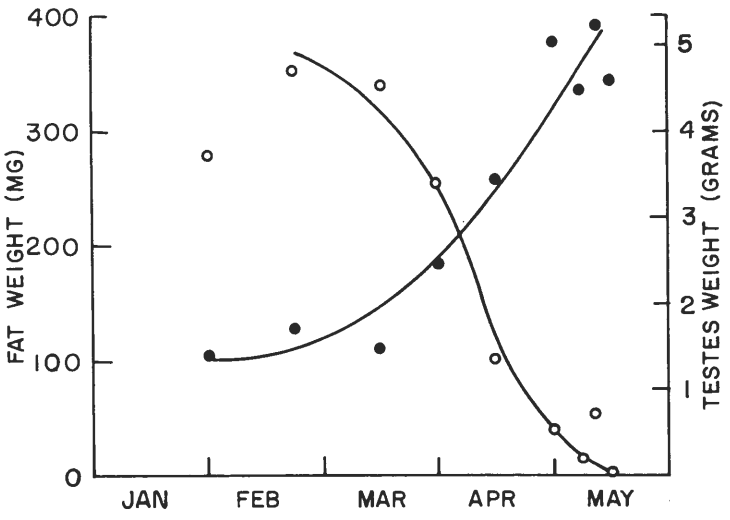

Figure 17. Relation of mean testicular weight (solid circles) of male Clear Lake yellow bass to mean weight of mesenteric fat (open circles) during late stages of sexual maturation, 1968. Curves drawn in by eye. Sample size ranged from 14 to 32 fish (mean, 24).

CHANGES IN POPULATION ABUNDANCE

Mass Mortality

On May 21, 1968, numerous dead yellow bass were found in gillnets. Fish still living appeared in a moribund condition with extensive growth of fungus over the body surface. Large schools of bass in severe stress were observed in shallow water along the lake shore. The epizootic reached a peak during the week of May 20, and mortality was essentially over by May 29. U. S. Fish and Wildlife Service biologists at the Genoa National Fish Hatchery identified the causative organism as Aeromonas salmonicida, the agent involved in fish furunculosis. Yellow bass of all age groups were affected, but mortality was not evident in other fish species.

Hansen (1943) described a similar mortality of yellow bass at Lake Chautauqua, Ill., but the causative organism was not identified. Periodic mass mortality of yellow bass is not uncommon in Clear lake and had usually occurred in the autumn or early spring when temperatures were changing rapidly. Atchison (1967) summarized reports of mass mortality of yellow bass during the past 2 decades. A die off in 1965 also was attributed to A. salmonicida. The 1968 mortality was unique in that a major portion of the yellow bass population was removed from the lake (Table 13). Only one adult and two yearling yellow bass were caught from 119 hr. of gillnetting effort on June 11. No bass were captured on July 29. Previous catches exceeded one fish per hour per 125-foot experimental gillnet.

The decrease in catch was not related to any change in distribution with the onset of warmer weather since a comparison of summer gillnet catches from 1965 to 1968 also indicated a major decrease in relative abundance. Weekly gillnet sampling is conducted on a systematic basis at Clear Lake during July and August each year to obtain an index of relative fish abundance. Values of catch-per-gillnet hour of yellow bass during the 4-year period were 1965, 2.633; 1966, 1.032; 1967, 2.009, and 1968, 0.029. With similar effort, 703 yellow bass were netted in the summer of 1967 in contrast to 8 fish in 1968. Hence, the population was sufficiently depleted in 1968 to force termination of collections for studying reproduction.

Success of Reproduction

Young-of-the-year fish in Clear Lake have been seined annually since 1946 (Ridenhour 1960) to obtain estimates of growth rate and reproduction success. During a 6-week period before Aug. 31, 1967,

Table 12. Measurements of Clear Lake yellow bass at beginning and end of feeding trials, April–May, 1968.

Date	Source of sample	No. of fish	Mean body length (mm)	Mean weight (g)		
				Body	Ovaries	Mesenteric fat
4/16	Directly from lake	17	194.5	105.06	4.48	0.16
5/7	Low feeding level	7	196.7	109.86	3.43	0.24
5/7	High feeding level	10	194.3	108.60	4.33	0.53
5/7	Directly from lake	25	193.1	104.48	6.64	0.09

Table 13. Catch of Clear Lake yellow bass per gillnet hour, April to July, 1968. Mass mortality was observed May 20 to 29.

Date	Hours of effort	Catch per gillnet hour
4/29	45	0.967
5/6	64	1.219
5/13	73	2.158
5/21	67	0.735
5/28	73	0.108
6/11	119	0.025
7/29	36	0.000

7,015 young-of-the-year yellow bass were captured. In 1968, with a similar amount of seining effort by the same personnel, 77 young-of-the-year yellow bass were captured.

DISCUSSION

A fish population restricted in growth to the point of stunting by limited food supply offers an interesting study of the influence of environmental conditions such as food supply on reproduction. A commonly observed phenomenon in nature is that, other factors being equal, an organism will respond to increased food supply with additional reproduction. In turn, increase in population density to the point where food supply or some other factor is limited eventually has an adverse effect, not only on reproduction, but also on body growth. Bekker (1958) found that a sharp increase in population density of goldfish, Carassius auratus, with its attendant decrease of food per individual, caused a suspension of vitellogenesis, resorption of oocytes close to maturity, and consequently, a disturbance in the intensity of spawning and reduction in number of offspring produced. Clemens and Grant (1964) reported that goldfish showed weekly gains in body weight for 7 months on a 3-percent diet, but lost weight as spawning time approached until the feeding level was increased. They agreed that fish such as the goldfish require more food during the spawning period for successful reproduction.

Nutrition as reflected by body condition and fat reserves appears to influence ova production in yellow bass also. Food reserves in the autumn, when yolk deposition is initiated, evidently regulate the number of ova commencing vitellogenesis as well as the amount of atresia during ova development. It also seems that sufficient energy may be stored in late summer and fall for successful reproduction but that the number of ova actually released can be increased by the presence of abundant food during the spring prespawning period. If adult bass enter winter in poor condition with low energy reserves, and additional food is not available during the prespawning period, low fecundity is almost assured.

The premise that yellow bass reproduction is controlled at times by its food supply does not preclude the influence of other factors on successful spawning. Rapid fluctuations in spring water temperature are common at Clear Lake and could easily cause sufficient physiological stress for mass atresia or termination of spawning. In both 1967 and 1968, a significant decrease in temperature occurred shortly after spawning was initiated (Figures 2 and 3). In 1967, the temperature dropped from 18 to 14.5°C over a 5-day period and in 1968 a similar drop from 14.5 to 10.5°C occurred over an 8-day period. Butler, as quoted by Pickford and Atz (1967), concluded that large mature ova of goldfish will remain intact only as long as temperature remains at a level where normal spawning and development are possible. Once the temperature drops and remains at a low level, atresia of the mature ova occurs. On the other hand, Faleeva (1966) observed ovarian atresia in fish kept above spawning temperatures. Hypophysial hormones administered after the start of atresia led to normal spawning.

Temperature influence in my study appeared highly probable because yellow bass are notably sensitive to environmental changes, as indicated by the high mortality and atresia induced by capture. Stress from temperature fluctuations also is suggested by the frequency of mass mortality of yellow bass in Clear Lake during periods of the year when temperature is changing most rapidly (Atchison, 1967). The additional stress presumably weakens the fish so that disease organisms can become established. However, nutrition cannot be ruled out as the cause of mature ova resorption as well as the cause of developmental atresia. Yellow bass appeared to have adequate nutritional reserves in 1967 to ovulate more ova than were actually released, but the 34 percent ova resorption was very close to that reported for carp when feeding was below optimum (Woodhead, 1960).

It is unfortunate that mass mortality forced premature termination of the current project, but from another standpoint, the population depletion provided information not otherwise available. The fecundity estimates for 1967 and 1968 must represent somewhat the extremes for yellow bass of the size and status found in Clear Lake. Fecundity was high in 1967, and a good year class was produced, even with the high ova resorption that occurred. In 1968 reproduction was low from the standpoint of fecundity and from the number of ova actually shed in spawning. Because the disease organism A. salmonicida was presumably still present in 1967 and from the 1955 epizootic, the reduced 1968 potential fecundity was attributed to lack of food, not to disease. The low body condition and extensive utilization of fat stores during the 1968 prespawning period presumably weakened the fish to the point where conditions were ideal for disease outbreak. Disease resistance in fish is at its lowest ebb in early spring because of depleted plasma proteins needed for antibody production (Snieszko, 1958). When water temperatures reached levels optimum for growth of A. salmonicida (10-20°C), stress from spawning and fluctuating water temperature, along with lowered resistance, evidently allowed furunculosis to rapidly attain epizootic proportions. The disease probably exerted its influence on reproduction by aborting spawning activity so that mature ova were never released. In any event, reproduction was relatively unsuccessful in 1968, and contributing factors appeared to be poor nutrition, adverse water temperatures, and disease. Further study is needed on the influence of nutrition and temperature fluctuations in a population where disease is not a factor.

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EFFECT OF SUPPLEMENTAL POLLEN, GROWTH REGULANTS AND MODIFIED PRUNING ON YIELD OF TOMATO, LYCOPERSICON ESCULENTUM

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ABSTRACT. Tomato plants pollinated with supplemental stored pollen set more fruits on lower clusters and had more early production than did control plants. Gibberellic acid (GA) applied as a post-set fruit spray russeted fruits. A pre-transplanting foliar application of GA delayed fruit production and caused misshapen and russeted fruits. NIA 8198 foliar sprays and a modified single stem pruning system had no effect on yield.

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INTRODUCTION

Two major problems of tomato production in greenhouses and in the field are poor fruit set, and "button" fruits which do not develop into marketable size. Unfavorable temperature, light intensity and duration, nutrition, and soil and air-water relations cause poor fruit set by hindering pollen production, pollination, pollen tube growth or fertilization (9). Gibberellin (GA) has induced tomato fruit set, increased early and total yield, and has overcome arrested tomato fruit development (1, 3, 6, 8, 10).

The research reported herein was conducted to investigate the effect of supplemental pollen, GA and NIA 8198[3] on tomato fruit set and yield, and the effect of a modified single stem pruning system on yield.

MATERIALS AND METHODS

Greenhouse experiment

Treatments were: a) control, b) stored pollen, c) GA 10 ppm post-set cluster spray, d) GA 100 ppm post-set cluster spray, and e) NIA 8198 10 ppm foliar spray. Tomato pollen used in treatment 2 was collected about 3 months before use and was dried in tear bulbs for 30 minutes with a Model 10-145 VirTis freeze drier. Tear bulbs were sealed while still under vacuum and stored at room temperature. Dried pollen was rehydrated by 24-hour exposure to air inside a refrigerator. Rehydrated pollen was refrigerated and was used within 1 week of rehydration. Stored pollen was applied with a camel hair brush to stigmas at 3-day intervals.

Potassium salt of gibberellic acid was applied as an aqueous spray to the fruit clusters of the GA treatments. The first application was made when 3 fruits had set. Subsequent applications were made at 7 to 10-day

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[3] Experimental chemical of the Niagara Chemical Co., Middleport, N.Y.

intervals until harvest. A 5% water miscible concentrate of NIA 8198 was used to prepare the 10 ppm solution which was applied as a foliar spray when the plants had 8–10 leaves.

A 5 x 5 Latin square design with 4 plants per plot was used with 'Manapal' plants spaced 13 x 36 inches in a plastic greenhouse. Plants were pruned to a single stem and flower clusters of all plants were vibrated daily to facilitate natural pollination. Night temperature was 65–70°F and day temperature was 70–75°F except when outside temperatures were so high that this temperature could not be maintained by fan ventilation. Weekly harvests were from January 23 to April 21. The first 5 harvests were considered early production in data analysis. Soluble solids were measured with a refractometer on 4 randomly selected fruits from each treatment on each of 4 harvest dates. The Firm-O-Meter (5) was used to measure firmness of 3 fruits of each treatment for each of 3 harvest dates.

Field experiment

Treatments were: a) GA 50 ppm foliar spray, b) GA 10 ppm blossom spray, c) modified pruning, d) control, e) NIA 8198 50 ppm foliar spray (4-leaf stage) and f) NIA 8198 (4 and 6-leaf stages). The GA source was 85% active gibberellic acid. In the foliar GA and NIA 8198 treatments, the aqueous sprays were applied to plants before they were transplanted to the field. The GA floral spray was applied to a cluster when several flowers were open. The modified pruning treatment consisted of decapitating each axillary shoot after 2 leaves had formed, as opposed to removing the entire shoot as is usually done in the single stem pruning system.

A randomized complete block design with 6 replications and 4 'Floralou' plants per plot was used. Plants were spaced 18 x 70 inches and were staked and pruned to a single stem. Weekly harvests were made from May 29 to June 30. The first 3 harvests were considered early production in the data analysis. Soluble solids were measured on 4 fruits on each treatment on each of 3 harvest dates.

RESULTS

Greenhouse experiment

Early fruit production and fruit set were greater in the stored pollen treatment than in the other treatments (Table 1). However, total fruit set and total production were similar to the other treatments.

Many fruits in the GA treatments had russeted peels. Some fruits were unmarketable, and the problem was worse in the higher GA concentration. GA did not increase size of fruits or stimulate growth of "dormant" or "button" fruits. NIA 8198 did not affect yield. Soluble solids, firmness, and number of seeds per fruit (Table 1) were not significantly different (.05).

Field experiment

No treatments significantly increased production, and the GA foliar treatment reduced the amount of marketable fruit, causing misshapen, russeted fruits (Table 2). Plants receiving the GA foliar spray exhibited an increased vegetative growth for a few days after application. Plants

Table 1. Effect of stored pollen, GA and NIA 8198 on fruit set, yield, firmness, soluble solids, and seeds per fruit of greenhouse tomatoes.

	Early Production[2]		Total Production[3]				
Treatment[1]	No. lbs. Per Plant	Mean No. Per Plant	No. lbs. Per Plant	Mean No. Per Plant	Percent Soluble Solids	Firmness[4]	Mean No. Seed Per Fruit
Control	1.3b[5]	3.4b	7.2	23.5	4.4	6.4	137
Stored Pollen	2.8a	9.0a	7.9	25.3	4.3	5.3	132
GA 10 ppm	1.6b	5.7b	7.3	28.0	4.6	6.7	158
GA 100 ppm	1.7b	4.4b	7.0	26.0	4.3	7.0	122
NIA 8198	1.7b	4.8b	8.2	27.8	4.3	6.1	129
					N.S.	N.S.	N.S.

[1] All treatments were in addition to self-pollination

[2] First 5 weekly harvests.

[3] Fourteen weekly harvests.

[4] Lower numbers indicate firmer fruits.

[5] Means followed by a letter in common are not significantly different (.05, Duncan's Multiple Range).

became spindly and foliage yellowed. Few fruits were harvested from this treatment in the first harvest, and most of these were catfaced and/or russeted. Soluble solids were appreciably higher in the modified pruning treatment, but the difference was not statistically significant (.05).

DISCUSSION AND CONCLUSIONS

Results of this research indicate that the use of supplemental pollen may offer promise in overcoming fruit set problems with greenhouse tomatoes. Increased early set and early yield of greenhouse tomatoes resulted when freeze-dried pollen was used to supplement natural pollination. Supplemental pollen is advantageous, compared to fruit set chemicals, in that it does not cause adverse effects. Fruit set can occur in response to pollen which is incapable of effecting sexual fertilization (7). Further research on the use of supplemental pollen under different environmental conditions, on pollen pre-storage and storage requirements, and on methods of applying pollen would be beneficial.

GA in these experiments had adverse effects. Applied as a post-set fruit spray on greenhouse tomatoes, it russeted fruits. Both russeted and misshapen fruits were produced by field tomato plants which received a pre-transplant GA foliar spaay. GA has previously caused russeted and misshapen fruits (2, 6). Neither a GA blossom spray, NIA 8198 foliar sprays, or a modified single stem pruning system produced any noticeable effects on yield or quality of tomatoes in these experiments. A similar modified pruning system has increased yields in a different environment (4).

Table 2. Effect of GA, NIA 8198 and axillary foliage on yield and soluble solids of field tomatoes.

Treatment	U.S. No. 1 Early[1] lbs per Plant	U.S. No. 1 Total[2] lbs per Plant	U.S. No. 1 Mean No. Fr. per Plant	U.S. No. 2 Early lbs per Plant	U.S. No. 2 Total lbs per Plant	U.S. No. 2 Mean No. Fr. per Plant	Percent Soluble Solids
NIA 8198 4 Leaf Stage	1.9a[3]	2.4a	6.3	1.3	1.7	6.5	5.0
NIA 8198 4 & 6 Leaf Stages	1.0a	2.8a	7.1	1.2	1.5	6.6	5.0
GA 4 Leaf Stage	.9b	1.6b	3.9	.8	1.1	3.9	5.0
GA Blossom Spray	2.0a	2.6a	6.7	1.1	1.5	6.0	5.0
Axillary Foliage	1.5a	2.6a	6.7	1.1	1.6	6.6	5.5
Control	1.8a	2.4a	6.4	1.1	1.7	7.0	5.1
							N.S.

[1] First 3 weekly harvests.

[2] Five weekly harvests.

[3] Means followed by a letter in common are not significantly different (.05, Duncan's Multiple Range).

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FURTHER STUDIES ON THE PROTEIN AND ENERGY REQUIREMENTS OF DAIRY CALVES[1]

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ABSTRACT. Two experiments were conducted to evaluate soy flour as a substitute for dried skimmilk in milk replacers and to obtain further information on nitrogen and energy requirements of young calves. In the first experiment substitution was on the basis of total nitrogen. Nitrogen digestibility, nitrogen retention, fatty acid digestibility, energy digestibility and weight gains showed a significant ($P < 0.01$) linear decrease with increasing levels of soy flour. In the second experiment, when substitution was on the basis of digestible nitrogen (as determined in the first experiment), only slight differences in growth rate were observed. The energy requirement for maintenance was 41.3 kcal digestible energy daily per kilogram of body weight; for growth the requirement was 3.82 kcal/gram of weight gain. Nitrogen retention was 2.17g/100 g body weight gain.

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Although extensive work has been done with milk replacers in an attempt to replace whole milk at an early stage in the feeding of young dairy calves, definitive data on the value of many ingredients still is lacking. The digestible energy and protein in corn distillers dried solubles were critically evaluated in recent studies (3). The present study was designed to obtain information on soy flour similar to that obtained with corn distillers dried solubles.

The main objectives of this experiment were to determine the replacement value of soy flour and lactose for dried skimmilk and to study further the nitrogen and energy requirements of the young calf.

EXPERIMENTAL PROCEDURE

Ninety-six three-day-old Holstein calves from the Iowa State University herd were used in two experiments. In Experiment I, 32 male calves

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were allotted to four 17% protein milk replacer diets (8 replications) in a randomized block design. The allotment of animals covered a period from December 1962 through July 1963. Soy flour[4] and lactose were substituted for dried skimmilk[5] to provide 0, 20, 35, and 50% of the total nitrogen. The four replacers (Table 1) were fed for a 56-day period at the daily rate of 10% body weight during the first period (from 4-32 days of age) and 13.3% of body weight during the second (from 32-60 days of age), respectively. The milk replacers, reconstituted by mixing one part dry replacer with six parts water, readily dispersed to form a relatively stable suspension. They were mixed immediately before each feeding and were fed twice daily by nipple pail. Adjustments of feeding to body weight were made at the end of weeks 1, 2, 4, 5, 6 and at the completion of each digestion trial. The feeding level was changed after the morning feeding of the 32nd day. Data from Blaxter and Wood (1) and Brisson et al. (2) were used to calculate diets sufficient to provide weight gains of .33 and .55 kg per day in Periods 1 and 2, respectively.

Two 5-day digestion trials were conducted with each calf, starting at 21 and 49 days of age. In each trial total collections of urine and feces were made.

The care, feeding and management of the animals, collection and preservation of urine and feces, and analytical procedures were the same as those described in a previous report by Bryant et al. (3); the only exception was that the fecal lipid and milk replacer lipid were determined by the method of Van de Kamer et al. (4).

In Experiment II the diets were adjusted from data in Experiment I to an iso basis for digestible protein and for energy. Four diets were used: the 0-level was the same as in Experiment I; in the 20, 35, and 50 levels, respectively, 20, 35 and 50% of the digestible nitrogen (instead of crude protein as in Experiment I) was supplied by soy flour[6]. Thirty-two male and thirty-two female Holstein calves were assigned to a randomized block experiment with 16 replications. The period of assignment for animals on this experiment was August 1964 through January 1965. The composition of the diets is shown in Table 2. Digestible protein was calculated using the digestibility coefficients of dried skimmilk obtained in Experiment I and the digestibility coefficients for soy flour that were determined by difference. The lengths of feeding periods were identical to those in Experiment I. The milk replacers were fed at the daily rate of 10.0, 10.2, 10.5 and 11.2% of the calves' body weight for the 0, 20, 35 and 50 levels, respectively, during the first period. The comparable levels for the second period were 13.0, 13.5, 14.0 and 14.9%. The different levels of feeding were necessary to provide equal digestible protein and energy intakes.

Since the diets used in Experiment II, as well as in Experiment I,

[4] A dehulled, defatted, fully cooked flour ground so that at least 90% passed through a 100 mesh screen; it was provided by The Borden Company (Feed Division), Elgin, Illinois.

[5] A low heat, spray dried skimmilk obtained from Des Moines Milk Marketing Coop., Des Moines, Iowa.

[6] A dehulled, defatted, fully cooked 200-mesh flour obtained from Archer Daniels Midland Co., Minneapolis, Minnesota.

Table 1. Percentage of ingredients in diets fed in Experiment I[a]

Ingredient	Percentage of crude protein supplied in diets by soy flour			
	0	20	35	50
	%air-dry weight			
Dried skimmilk	51.4	41.1	35.5	25.7
Soy flour	00.0	6.7	11.7	16.9
Lactose	30.6	34.2	36.8	39.4
Lard oil[b]	18.0	18.0	18.0	18.0
Total	100.0	100.0	100.0	100.0

[a]Each calf received the following supplements daily: 10,000 I.U. vitamin A, 960 I.U. vitamin D, 50 mg chlortetracycline, and a trace mineral mix containing Mn, Cu, Co, Zn, I and Fe.

[b]94% lard oil, 6% emulsifier (polyethylene glycol mono-and dioleate). Milk Specialties, Inc., Dundee, Illinois.

Table 2. Composition and intake of diets fed in Experiment II

	Percentage of crude protein supplied in diets by soy flour			
	0	20	35	50
Ingredients of replacers, air-dry basis (%)				
Dried skimmilk	51.4	40.4	31.9	23.0
Lactose	30.6	33.6	35.1	35.2
Soy flour	0.0	8.3	15.8	25.7
Lard oil	18.0	17.7	17.2	16.1
Composition of air-dry replacers				
Total protein (%)	17.6	18.0	19.0	20.7
Digestible protein (%)	15.5	15.2	14.8	13.9
Gross energy (kcal/g)	4.9	4.9	4.9	4.8
Digestible energy (kcal/g)	4.5	4.4	4.3	4.0
Air-dry ingredients in liquid replacer (%)	14.3	14.3	14.3	14.3
Rate of feeding liquid replacer (g/kg body weight daily)				
4-32 days	100.0	102.0	105.0	112.0
32-60 days	130.0	135.0	140.0	149.0
Intake/kg body weight				
Digestible protein (g)				
4-32 days	2.2	2.2	2.2	2.2
32-60 days	2.9	2.9	2.9	2.9
Digestible energy (kcal)				
4-32 days	64.4	64.2	64.5	64.0
32-60 days	83.7	84.9	86.0	85.2

appeared to be marginal or low in Ca and P, particularly when any flour was included, one-half of the males and one-half of the females on each treatment in Experiment II received supplemental Ca and P in the form of dicalcium phosphate. The intakes of Ca and P from the diet and from the supplemental dicalcium phosphate are shown in Table 3. The supplemental dicalcium phosphate was added to the diet at each feeding.

Table 3. Daily intake of Ca and P in Experiment II

	Percentage of crude protein supplied in diets by soy flour							
	0		20		35		50	
	Ca	P	Ca	P	Ca	P	Ca	P
	g.							
4-32 days								
Diet	4.3	3.4	3.6	3.2	3.1	3.0	2.7	3.0
Di Cal.	1.4	1.1	2.4	1.8	2.9	2.2	3.4	2.5
Total[b]	5.7	4.5	6.0	5.0	6.0	5.2	6.1	5.5
32-60 days								
Diet[a]	5.7	4.6	4.8	4.2	4.1	4.0	3.6	4.0
Di Cal.	1.4	1.1	2.4	1.8	2.9	2.2	3.4	2.5
Total[b]	7.1	5.7	7.2	6.0	7.0	6.2	7.0	6.5

[a] Ca and P intake of unsupplemented calves.
[b] Ca and P intake of supplemented calves.

Feeding levels of the replacers were adjusted to body weight at the end of each weekly interval on experiment. Feeding and recording procedures were similar to those described in Experiment I.

RESULTS AND DISCUSSION

The mean digestion coefficients and weight gains obtained in Experiment I are summarized in Table 4 and Figure 1, respectively. The digestibilities of nitrogen in dried skimmilk were 84.5 and 90.8% at three and seven weeks of age, respectively; these values are similar to those of Blaxter and Wood (1), Brisson et al. (2), and Bryant et al. (3). The energy digestibility for the 0-level diet was 91.4 and 93.6% at three and seven weeks of age, respectively, which also was similar to the results of Bryant et al. (3).

As the content of soy flour in the diet increased, there was a significant ($P < 0.01$) linear decrease in nitrogen digestibility, nitrogen retention (NR), fatty acid digestibility and energy digestibility at three and seven weeks of age. The large improvement in NR from three to seven weeks of age on the 20 and 35 levels indicates the calf can utilize soy flour to a greater extent at seven weeks of age. The NR on the 0, 20 and 35 levels were nearly alike at seven weeks of age.

The decrease in energy digestibility was due to the combined decrease in digestible nitrogen and fat.

The consistency of the feces was recorded daily; a scale from zero

Table 4. Summary of results of digestibility studies in Experiment I

	Age (weeks)	Percentage of crude protein supplied in diet by soy flour			
		0	20	35	50
		%			
Apparent nitrogen digestibility	3	84.5	82.8	75.6	68.3
	7	90.8	86.9	84.6	74.1
Nitrogen retention	3	50.5	45.2	40.9	30.4
	7	56.3	56.9	57.3	42.4
Apparent "fatty acid" digestibility	3	89.2	86.7	84.8	77.6
	7	91.6	90.3	88.6	78.4
Apparent energy digestibility	3	91.4	89.8	87.0	82.9
	7	93.6	92.0	90.7	85.2

(normal) to four (watery diarrhea) was employed. Diarrhea was not a problem with any of the treatments. The differences in the incidence of diarrhea were not significant between treatments, and no trend could be determined from the data.

Body weight gains (BWG) exhibited a significant ($P < 0.01$) linear decrease with increased levels of soy flour (Fig. 1). This is supported by the digestibility data previously discussed. The feed conversion or feed required to produce a kilogram of BWG increased with increasing levels of soy flour. With the exception of the excellent response obtained on the 35-level diet at seven weeks of age, digestion coefficients and linear trends are quite similar to the results obtained with corn distillers dried solubles as the source of nitrogen (Bryant et al. (3)). However, the overall mean digestion coefficient as calculated by difference was 64% for soy flour and 54% for corn distillers dried solubles.

The results of Experiment II are shown in Figure 2. No differences within treatments were observed between the animals which received supplemental Ca and P and those which did not. Therefore, the data for the supplemented and nonsupplemented calves for each treatment were combined and any response differences between treatments were assumed to be exclusive of the levels of Ca and P. When the substitution of soy flour for dried skimmilk was on a digestible basis, the differences between treatments were greatly decreased as seen by comparing Figures 1 and 2. It was necessary to use two sources of soy flour—Borden, 100 mesh in Experiment I and Archer Daniels, 200 mesh in Experiment II. (As far as can be determined these flours were processed similarly with the exception of mesh size.) Thus, the source of soy flour may have had some effect on response.

The energy requirements for growth and maintenance may be estimated from the results of Experiment I using a linear regression of body weight gain (BWG) in grams/kilogram of body weight/day on digestible energy (DE) intake in kilocalories/kilogram body weight/day (Fig. 3). At the intercept with X axis, or when BWG equals 0, DE equals 41.3 for the total regression including three and seven weeks digestibility data. DE equals 47.9 and 46.4 for the separate regressions at three and seven weeks of age, respectively. These values are close to those reported by Bryant et al. (3) and also fall within the range of those reported by Blaxter and Wood (1) and Brisson et al. (2). The BWG data used in these regressions included the following age periods: 18-32 and 46-60 days inclusive for the three and seven weeks, respectively. The regression line indicates the energy required for growth. One kilocalorie DE above maintenance resulted in 0.26 g of BWG or 100 g of BWG requires 382 kcal DE. This is quite close to the value reported by Bryant et al. (3) and intermediate between the values reported by Blaxter and Wood (1) and Brisson et al. (2).

The protein requirements were calculated using a linear regression of NR on DE as shown in Figure 4. The regression line indicates that 5.68 mg of nitrogen were retained for each digestible kilocalorie consumed. One kilocalorie of DE produced 0.26 g of BWG, and it can be calculated that 2.17 g of nitrogen was retained per 100 g of BWG. This value is slightly lower than those reported by Blaxter and Wood (1), Brisson et al. (2), and Bryant et al. (3). The nitrogen and energy requirements are summarized in Table 5. The maintenance requirements for the NR

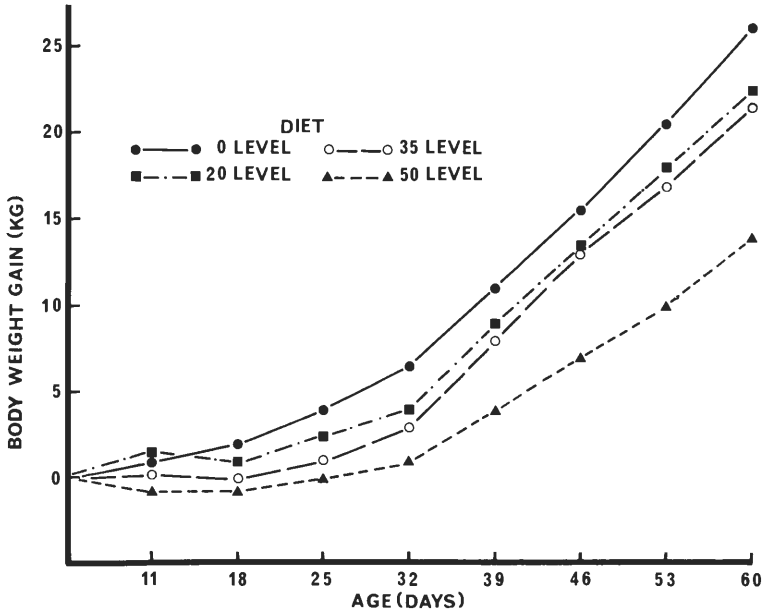

Figure 1. Weight gain from 4 to 60 days of age for 0, 20, 35 and 50% levels of dietary protein from soy flour in Experiment I.

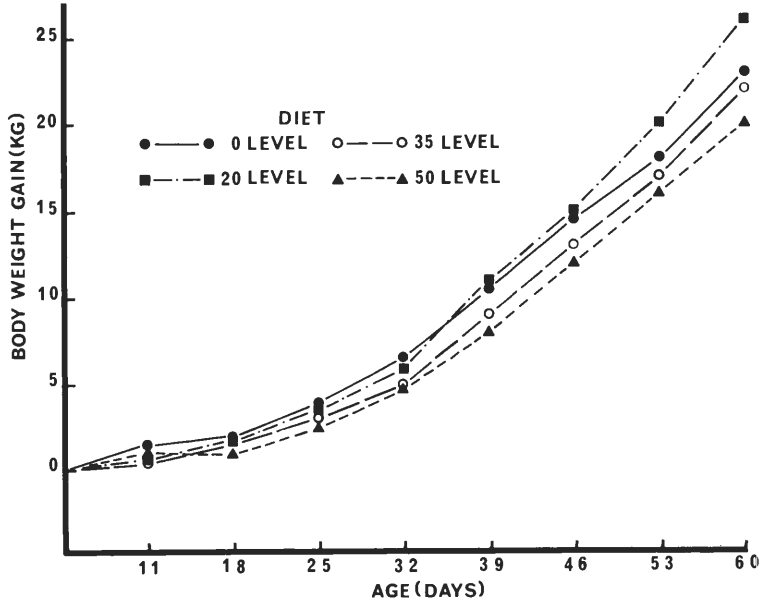

Figure 2. Weight gain from 4 to 60 days of age for the 0, 20, 35 and 50% levels of digestible protein from soy flour in Experiment II.

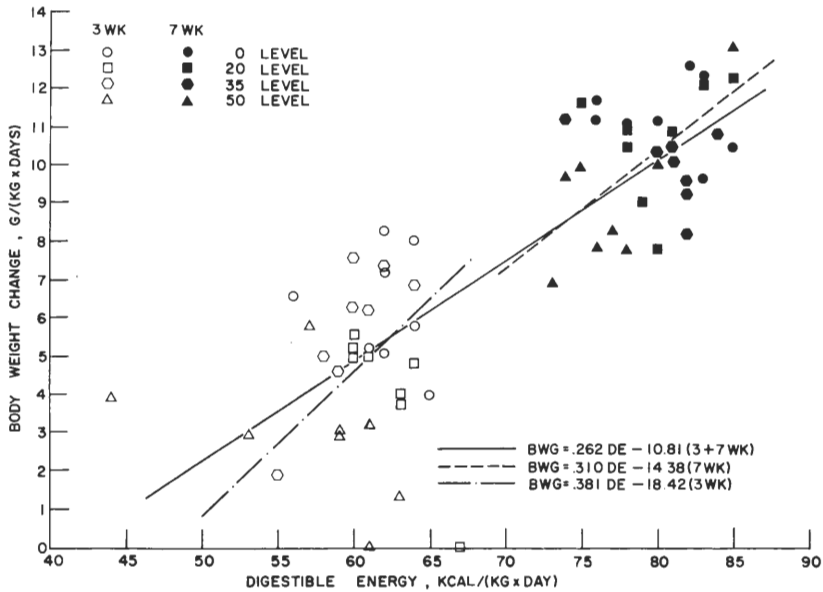

Figure 3. The linear regression of body weight gain (BWG) on digestible energy (DE).

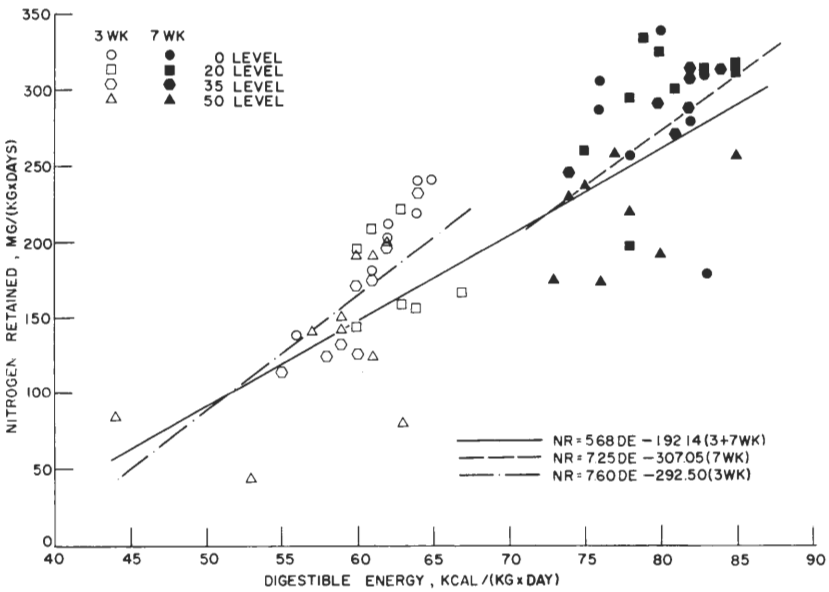

Figure 4. The linear regression of nitrogen retained (NR) on digestible energy (DE).

Table 5. Calculated requirements of calves for digestible energy and digestible protein[a]

	Kilograms gain per day for a 45.4 kg calf							
	0	.09	.18	.27	.36	.45	.55	.64
Digestible protein, kg								
Blaxter and Wood (2) (B&W)	.029	.044	.058	.074	.088	.100	.118	.132
Brisson et al. (3) (BC&H)	.019	.037	.055	.073	.092	.108	.127	.145
Present Study								
Regression of NR on BWG								
Using B&W value[b]	.049	.059	.068	.077	.086	.095	.106	.115
Using BC&H value[c]	.045	.054	.064	.073	.082	.091	.102	.111
Regression of NR on DE								
Using B&W value[b]	.035	.047	.059	.071	.083	.096	.109	.121
Using BC&H value[c]	.031	.043	.055	.067	.079	.091	.105	.117
Digestible energy, kcal								
B&W	2,379	2,655	2,932	3,208	3,484	3,773	4,052	4,330
BC&H	2,029	2,275	2,515	2,760	3,001	3,246	3,491	3,732
Bryant et al. (3)	2,188	2,523	2,857	3,192	3,526	3,862	4,234	4,469
Present study	1,875	2,219	2,562	2,906	3,249	3,593	3,975	4,319
Digestible protein required as a percent of the digestible energy								
B&W	6.9	9.3	11.1	13.0	14.2	15.0	16.4	17.2
BC&H	5.5	9.5	12.8	15.5	17.9	19.5	21.3	22.8
Bryant et al. (3)	8.4	9.1	11.4	12.6	13.5	14.2	14.8	15.2
Present study	10.6	11.9	12.8	13.3	13.9	14.4	14.7	15.0

[a] Assuming a Biological Value of 100

[b] Blaxter and Wood endogenous nitrogen 80 mg/kg/day

[c] Brisson et al. endogenous nitrogen 65.3 mg/kg/day

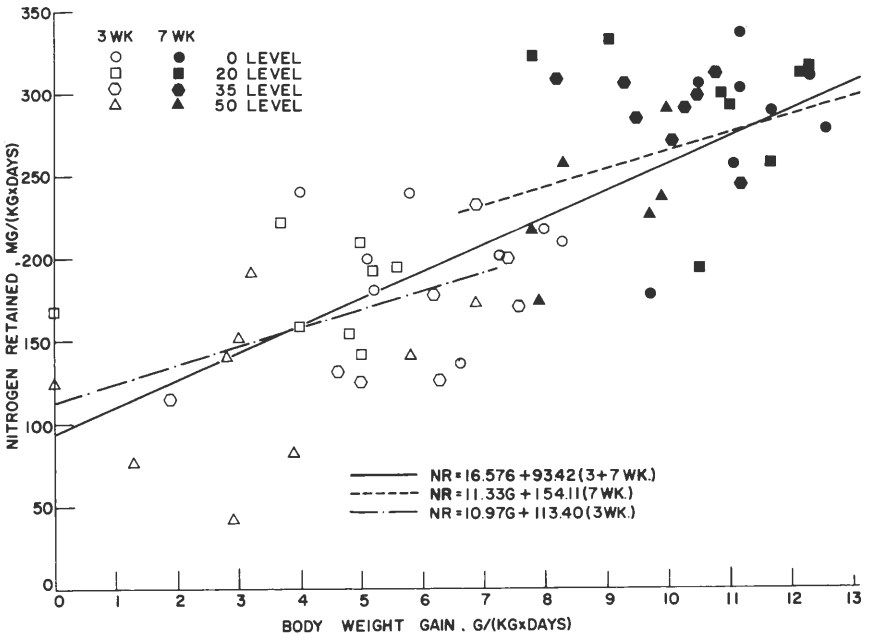

Figure 5. The regression of nitrogen retained (NR) on body weight gain. (BWG).

regressions are slightly lower than those for the BWG regressions. This is explained in Figure 5, which shows a positive NR at zero BWG. Therefore, zero NR does not coincide with zero BWG, and with a positive NR at zero BWG, the DE value calculated for zero NR would be lower than the value calculated for zero BWG. Bryant et al. (3) show data that agree with this and discuss some of the contributing factors.

The protein and energy requirements shown in Table 5 compare quite closely with those of Blaxter and Wood (1), Brisson et al. (2) and Bryant et al. (3). The protein requirements were calculated using endogenous nitrogen (EN) values from both Blaxter and Wood (1) and Brisson et al. (2) and using both regressions (the regression of NR on BWG and NR on DE). The two methods gave comparable results.

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INTERRELATIONSHIPS AMONG SEVERAL STALK CHARACTERISTICS IN MAIZE AND THEIR SIGNIFICANCE IN RESISTANCE TO NATURAL STALK BREAKAGE[1]

D.A. Sleper and W.A. Russell[2]

ABSTRACT. The purpose of this research was to compare stalk characters among inbred lines of maize, Zea mays L., as selection criteria to use in developing inbred lines that will contribute to field stalk-lodging resistance when used in hybrid combinations.

Characters measured in inbred lines and their testcrosses were: rating for Diplodia stalk rot, mechanical breaking strength of the first elongated internode above ground level, weight of a 5.2-cm stalk cross section, crushing strength of a 5.2-cm stalk cross section, rind thickness, date for 50% silk emergence, and natural stalk lodging.

Inbreds included were 43 S_7 random lines from Stiff Stalk Synthetic and seven checks selected for their known reaction to Diplodia stalk rot. The testers were single crosses Os420x187-2 (susceptible to Diplodia stalk rot) and WF9xHy (intermediate in resistance to Diplodia stalk rot).

Correlations involving the seven check lines were usually high but not significant. Mechanical strength, rind thickness, and natural stalk lodging of the random lines were correlated ($P < .01$) with natural stalk lodging of the testcrosses with values of -0.46, -0.47 and -0.57, respectively. Heritability values for the random lines were 90% for mechanical strength, 74% for rind thickness, and 49% for natural stalk lodging. Selecting among the inbreds for stalks with high mechanical strength, thick rinds, and low natural stalk lodging will contribute to high resistance to natural stalk lodging in hybrid combinations. These, however, are not satisfactory methods for evaluation within segregating progenies.

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Stalk lodging is one of the most serious production problems in maize, Zea mays L., in the United States. Breeders have made much progress in developing hybrids with better stalk strength, but the gains have been partly offset by cultural practices, such as increased nitrogen fertilization and higher plant densities. Breeding for resistance to stalk lodging is difficult because stalk strength results from many factors interacting complexly. If more precise measures of stalk strength were available, significant progress could be made more rapidly.

Several methods of measuring stalk strength have been evaluated. Jenkins (1) obtained a correlation of -0.58 between the breaking strength of the lowest internode tested and percentage of broken plants in the field. Zuber and Grogan (6) found highly significant correlations of -0.57 and -0.53, respectively, for the relationship of stalk strength with rind thickness and crushing strength of a 5.2-cm internode section. Thompson (5) found that the coefficient of variation for rind thickness was approximately one-third of that for crushing strength. Jinahyon and Russell (3) obtained a crushing strength coefficient of variation of 10.2% and of 7.8% for rind thickness.

Advantages attributed to the use of rind thickness and crushing strength measurements are that selection for resistance to stalk lodging is possible under a variety of environmental conditions. It is not necessary to wait for the influence of wind, insects, or pathogens to cause broken plants. Also, if these measurements are more precise than actual counts of field stalk lodging, smaller populations and less testing can be used to obtain the required data.

Most studies of the relationship between stalk quality characteristics and field stalk lodging have used selected materials characterized previously for some attributes. The primary purpose of our investigation was to evaluate the relationship of several physical stalk traits of random inbred lines with stalk strength of these inbreds in hybrid combinations.

MATERIALS AND METHODS

We included check inbred lines of two types based on their known stalk rot when artificial inoculations of Diplodia zeae (Schw.) Lev. are used: (a) B14A, Mo17, and R101, which are resistant and (b) four numbered selections that are susceptible.

We used 43 S_7 inbred lines taken from a larger group of 250 random lines developed from Iowa Stiff Stalk Synthetic. These 43 lines were selected for a narrow range of silk emergence dates so that maturity would not be a confounding factor. Also, they were chosen for stalk-rot ratings representative of the distribution from highly resistant to highly susceptible. Although the lines were selected for a narrow maturity range, we are treating them as a random sample under the assumption that they represent a complete distribution in Iowa Stiff Stalk Synthetic for reaction to stalk rot.

In 1967, the random lines and checks were self-pollinated and crossed to Os420 x 187-2, considered susceptible to stalk rot, and to WF9 x Hy, considered intermediate in resistance to stalk rot. Consequently, we had available 86 testcrosses of the random lines, 14 testcrosses of the check lines, 43 random S_7 inbred lines, and 7 inbred lines as checks.

Evaluations of inbreds and testcrosses for stalk quality traits were made in nine field experiments in 1968: five experiments of testcrosses and four of inbreds. We used these experiments to obtain data as follows:

(a) Diplodia stalk-rot ratings;
(b) mechanical breaking strength of the stalk;
(c) data for date of silk emergence, stalk weight, rind thickness, and crushing strength;
(d) natural field stalk lodging, one location for the inbreds and two locations for the testcrosses.

All experiments were grown at the Agronomy and Agricultural Engineering Research Center, Ames, except one testcross experiment which was grown on the Ankeny University Farm as a second location for natural field stalk lodging.

All testcross experiments were split-plot designs, with tester parents randomized as whole plots and inbred lines as subplots. We used randomized complete block designs for the inbred experiments. Testcross and inbred experiments (a), (b), and (c) had four and three replications, respectively, except for hybrid experiment (c) which had three replications. We used single-row plots in experiments (a), (b), and (c), 102 cm between rows, and 17 single-plant hills spaced 25 cm. The final plant density after thinning in these experiments was approximately 38,750 plants/ha.

In the stalk-rot tests all plants were inoculated with a spore suspension of Diplodia zeae approximately one week after the date for 50% silk emergence in the experiment. Seven weeks after inoculation, 15 competitive plants per plot were split longitudinally through the inoculation point, and the amount of decaying tissue relative to the cross-section area of the internode was rated on a scale of 0.5 (highly resistant) to 6.0 (highly susceptible).

The breaking-strength data were obtained approximately eight weeks after the 50% silk emergence date for the experiment. The first elongated internodes of 15 competitive plants per plot were placed individually in a machine designed to measure the force required to break the internode. The machine applied a gradually increasing lateral force against the center of the stalk until breakage occurred. Breaking was done immediately after the stalk was cut in the field. The force required to break the stalk was recorded in pounds from a maximum-value indicator on a spring scale.

Data for 50% silk emergence were taken on only two replications for the testcrosses and three replications for the inbreds. Nine weeks after 50% silk emergence for the experiment, stalk samples containing the first elongated internode were taken from 10 competitive plants per plot, placed in mesh bags, and dried for one week at 40°C. A saw with blades mounted 5.2 cm apart was used to extract a section from the center of the internode. Weight of the ten 5.2-cm stalk samples was recorded in grams. The stalk sections were crushed individually in a hydraulic press, with the pressure recorded in pounds. The rind usually broke free in the crushing process, and a portion of it was used to measure the thickness in mm with a micrometer caliper. (These data were obtained in Dr. M.S. Zuber's laboratory at the University of Missouri.)

The inbred and testcross experiments for natural field stalk lodging

had two-row plots and three replications. At Ames, plot rows were 102 cm apart, and rows had nine hills spaced at 25 cm. At Ankeny, plot rows were 91 cm apart, and rows had nine hills spaced at 24 cm. At both sites, there were 40 plants per plot after thinning. Plant densities after thinning were approximately 38,750 plants/ha at Ames and 43,055 plants/ha at Ankeny. A plant was considered stalk lodged if broken at or below the ear node. Counts of broken plants were made in mid-October at Ankeny and in early November at Ames. Broken plants were expressed as percentage per plot and converted to the angle = arcsin $\sqrt{\text{percentage}}$ for statistical treatments.

In the statistical analyses of the testcross data in the split-plot designs, testers were considered as fixed effects and inbred lines as random effects. In a combined analysis of variance for both locations involving stalk lodging, locations were treated as random effects. Variance components were estimated to obtain information pertinent to an evaluation of the data. Variance due to lines in the experiments of testcrosses and lines *per se* was subdivided into among random lines, among checks, and random lines vs. checks. Simple correlations were made among all characters within the testcross progenies and inbreds *per se*, as well as between testcross progenies and inbreds *per se*.

RESULTS

Summaries of F tests and coefficients of variation in the experiments of testcross progenies and inbred lines *per se* for all characters are presented in Table 1. Results of only line and line x tester source of variation are shown for testcross progenies; testers differed, however, at the 5% level for breaking strength, *Diplodia* rating, and rind thickness. Combined data and analysis for two locations were used to calculate F values and coefficients of variation for natural stalk lodging of the testcrosses.

Highly significant differences among progenies are evident in all sets of evaluations, except for rind thickness and silking date for testcrosses of the inbred checks. Line x tester interactions are of greater relative importance for the random lines than for the check lines. In all sets of data, silking date has the lowest coefficient of variation, and natural stalk lodging has the highest. This shows one reason for seeking other stalk characters that give more precision in studies of stalk quality.

Simple correlations of the mean values for the same characters between Os420 x 187-2 and WF9 x Hy testcrosses are shown in Table 2. Except for silking date, the values are higher for the check lines than for the random lines. For some characters, the magnitude of the correlations indicates that either tester would give similar information for the lines, whereas for other characters, such as rind thickness and crushing strength for the random lines, the testers did not rate the lines similarly. The higher correlation values when stalk lodging is combined over locations show the desirability of obtaining this kind of data from more than one location.

All simple correlation coefficients among the characters calculated on mean values over testers are presented in Table 3. As in Table 2, the

Table 1. F tests and coefficients of variation for seven characters in tests of testcross progenies and inbreds per se.

Characters	Testcross progenies [†]			Inbreds per se [†]	
	Lines	Lines x Testers	C.V. (%)	Lines	C.V. (%)
	Random inbred lines				
Mechanical strength	**	**	14.5	**	12.7
Diplodia rating	**	NS	19.5	**	16.5
Crushing strength	**	**	13.8	**	19.9
Rind thickness	**	**	11.6	**	10.1
Weight/5.2-cm section	**	**	9.3	**	11.4
Silking date	**	NS	4.6	**	3.5
Natural stalk lodging	**	**	24.5	**	54.5
	Inbred checks				
Mechanical strength	**	*	15.4	**	17.8
Diplodia rating	**	NS	20.5	**	19.0
Crushing strength	**	NS	13.7	**	26.4
Rind thickness	NS	NS	18.0	**	11.7
Weight/5.2-cm section	**	NS	11.8	**	18.3
Silking date	NS	NS	7.9	**	3.8
Natural stalk lodging	**	NS	24.2	**	37.2

[†] C.V., coefficient of variation
* significant at the 5% level of probability
** significant at the 1% level of probability
NS nonsignificant

Table 2. Simple correlation coefficients between the Os420 x 187-2 and WF9 x Hy testcrosses of the random and check inbred lines.

Characters	Random lines [1]	Check lines [1]
Mechanical strength	.53	.49
Diplodia rating	.72	.84
Crushing strength	.25	.71
Rind thickness	.14	.82
Wt./5.2-cm stalk section	.48	.90
Silking date	.44	.38
Natural stalk lodging (Ames)	.56	.69
Natural stalk lodging (Ankeny)	.69	.77
Natural stalk lodging (combined)	.72	.81

[1] Values necessary for significance

.30 for P = .05 (Random lines)

.39 for P = .01 (Random lines)

.75 for P = .05 (Checks)

.87 for P = .01 (Checks)

correlation values are usually higher for the check lines than for the random lines. The correlation values between the five stalk characters and natural stalk lodging are the most important. For the combined lodging data, the r values are significant, or highly significant, in all cases except for crushing strength and weight for the checks and rind thickness for the random lines. Usually, the correlations are higher with the Ankeny data than with the Ames data. Correlations of greatest magnitude with the random lines for the relationship between stalk characters and to natural lodging are for mechanical breakage, *Diplodia* rating, and stalk weight, but these values do not have much predictive value. Most correlations involving silking date are low, which can be expected because the extremes of maturity were eliminated in selecting lines.

All simple correlation coefficients among seven characters evaluated in experiments of random and check inbred lines *per se* are shown in Table 4. High correlations are evident among mechanical strength, crushing strength, rind thickness, and weight, indicating that selection for any one of these characters would effect improvement in the other

Table 3. Simple correlation coefficients among seven characters of the testcrosses using mean values combined over testers.

	Correlation values [1]								
	Diplodia rating	Crushing strength	Rind thickness	Wt/5.2cm stalk section	Silking date	Natural stalk lodging (Ames)	Natural stalk lodging (Ankeny)	Natural stalk lodging (combined)	
Mechanical strength	-.51	.47	.59	.76	.13	-.33	-.44	-.42	Random lines
	-.77	.63	.75	.97	.07	-.70	-.89	-.83	Checks
Diplodia rating		-.28	-.18	-.47	.03	.43	.47	.48	Random lines
		-.51	-.94	-.70	.21	.73	.94	.87	Checks
Crushing strength			.60	.59	.32	-.31	-.38	-.38	Random lines
			.38	.55	-.62	-.74	-.58	-.70	Checks
Rind thickness				.61	.30	-.08	-.26	-.20	Random lines
				.65	-.04	-.73	-.96	-.88	Checks
Wt/5.2-cm stalk section					.05	-.39	-.48	-.47	Random lines
					.18	-.58	-.79	-.71	Checks
Silking date						.28	.10	.18	Random lines
						.50	.11	.33	Checks
Natural stalk lodging (Ames)							.77	.91	Random lines
							.81	.96	Checks
Natural stalk lodging (Ankeny)								.96	Random lines
								.95	Checks

[1] Values necessary for significance, .30 at 5% level (Random lines). .75 at 5% level (Checks).
.39 at 1% level (Random lines). .87 at 1% level (Checks).

Table 4. Simple correlation coefficients among seven characters of inbreds *per se*.

	Correlation values [1]						
	Diplodia rating	Crushing strength	Rind thickness	Wt/5.2cm stalk section	Silking date	Natural stalk lodging	
Mechanical strength	-.44	.81	.78	.87	-.12	-.45	Random lines
	-.77	.88	.93	.76	.24	-.59	Checks
Diplodia rating		-.21	-.27	-.32	.08	.18	Random lines
		-.48	-.68	-.53	-.09	.71	Checks
Crushing strength			.87	.89	.07	-.34	Random lines
			.97	.90	.35	-.43	Checks
Rind thickness				.86	.03	-.28	Random lines
				.89	.44	-.56	Checks
Wt/5.2-cm stalk section					.03	-.39	Random lines
					.52	-.49	Checks
Silking date						.09	Random lines
						-.01	Checks

[1] Values necessary for significance, .30 at 5% level (Random lines).
.39 at 1% level (Random lines).
.75 at 5% level (Checks).
.87 at 1% level (Checks).

characters. Correlations involving stalk rot are lower and, in all except mechanical strength, crushing strength, and weight, have significant correlations with natural stalk lodging, and these values are too low to be of predictive value.

Correlation coefficients of the same characters in the inbreds per se and their testcrosses and of all characters in the inbreds with natural stalk lodging of their testcrosses are given in Table 5. Only the mean

Table 5. Simple correlation coefficients between the same character for inbreds and testcrosses and between stalk characters of the inbreds and natural stalk lodging of the testcrosses †/

		Same testcross character	Natural stalk lodging		
			Ames	Ankeny	Combined
Mechanical strength	Random lines	.56	-.43	-.43	-.46
	Checks	.88	-.67	-.79	-.76
Diplodia rating	Random lines	.48	.14	.19	.18
	Checks	.96	.64	.92	.81
Crushing strength	Random lines	.61	-.29	-.35	-.34
	Checks	.65	-.41	-.50	-.47
Rind thickness	Random lines	.44	-.38	-.48	-.47
	Checks	.49	-.51	-.64	-.60
Wt/5.2-cm stalk section	Random lines	.32	-.30	-.36	-.36
	Checks	.65	-.17	-.40	-.29
Silking date	Random lines	.54	.15	.06	.10
	Checks	.74	.27	.00	.15
Natural stalk lodging	Random lines		.61	.49	.57
	Checks		.76	.68	.76

†/ Values necessary for significance:

.30 for P = 0.05 (Random lines)
.39 for P = 0.01 (Random lines)
.75 for P = 0.05 (Check lines)
.87 for P = 0.01 (Check lines)

values over both testers were used in these calculations. Correlations of the same characters in the random lines and testcrosses are significant at the 5% level for weight and at the 1% level for all other characters. Correlations for the check lines are higher, but few are significant because of lower degrees of freedom. Selection for any one of these characters at the inbred level should be reflected by improvement of the same character in hybrids of the lines.

The primary purpose of our study was to determine the relationship of several physical traits of maize inbred lines with natural stalk lodging of these inbreds in testcross combinations. Mechanical strength, rind thickness, and natural stalk lodging of the random lines are highly correlated with natural stalk lodging of the testcrosses (combined over locations, Table 5). Crushing strength and weight of the random lines are correlated ($P < .05$) with natural stalk lodging of the testcrosses. Selection among the random lines for those genotypes that have high breaking strength, thick rinds, and low natural stalk lodging should give lines with above-average resistance to stalk lodging in hybrid combinations. Our data indicate a nonsignificant relationship between stalk-rot ratings of the random lines with natural stalk lodging of their testcrosses. Mechanical strength, *Diplodia* ratings, and natural stalk lodging of the check lines correlated at the 5% level with natural stalk lodging of their testcrosses (combined over locations). Silking date shows no relationship with testcross stalk lodging, but this is probably a reflection of the lines used rather than a true effect.

Heritability values for the inbred lines were calculated by the variance component method using plot means. These values give heritability in the narrow sense since the lines are nearly homozygous and mainly additive genetic variance is present. Highest values (Table 6) in the random lines are for mechanical strength and weight, indicating that selection for these traits should be very effective. Highest heritability values for the check lines are for mechanical strength, rind thickness, and silking date.

Table 6. Heritability values for seven characters evaluated in the inbreds *per se*.

Character	Heritability (%)	
	Random lines	Check lines
Mechanical strength	90	87
Diplodia rating	73	68
Crushing strength	61	73
Rind thickness	74	80
Wt/5.2-cm section	88	72
Silking date	74	83
Natural stalk lodging	59	74

DISCUSSION

When maize inbred lines are evaluated in testcross progenies, the contribution of the tester parent may be an important factor in the information obtained. We included two testers differing in reaction to Diplodia stalk rot to see if this difference affected line evaluation. Tester Os420 x 187-2 is known to be more susceptible to stalk rot and stalk lodging than is WF9 x Hy. In all characters of the random line testcrosses, except mechanical breakage, estimated line components for Os420 x 187-2 were greater than for WF9 x Hy. Estimated variance components for lines were greater than for lines x testers in all characters, except for rind thickness. Thus, the more susceptible tester is more effective for discrimination among lines, and the line contribution to the total variance is of greater importance than the use of different testers. When values of the stalk characteristics were correlated with the natural stalk lodging in the two series of testcrosses separately, the results relative to significance were similar. Consequently, either tester gave near equal information for the relationship between inbred stalk characters and lodging in the testcrosses. Since the $\bar{r}$ values between the same characters of the two series of random line testcrosses were relatively low in most traits, however, and since the line x tester interactions were highly significant for all except Diplodia rating and silking date, the ranking of the lines with the two testers would not be the same. Consequently, lines selected on the basis of testcross performance would not be the same between the two testers.

Inbred line checks, whose stalk-rot reactions were known, were included to give information on the extent of stalk-rot development from artificial inoculations. Because they are not a random sample of the complete distribution for stalk rot, comparisons of correlations involving the checks and random lines probably have little value. Frequently, correlations involving the checks were high, and higher than the random lines, but not significant because of a low number of degrees of freedom.

Corn breeders need a more effective and efficient method of obtaining resistance to natural stalk lodging than has been used in past years. Environmental influences need to be minimized. Mechanical strength, rind thickness, and natural stalk lodging of the random lines were highly correlated with natural stalk lodging of these lines in testcrosses. The $\bar{r}$ values were relatively small, however, and a correlation of -0.46 between mechanical strength of the random lines and stalk lodging of the testcrosses accounts for only 21% of the variability in the testcross stalk lodging.

Selecting those inbreds that have high resistance to natural stalk lodging seems an easy procedure to obtain the stalk strength needed in hybrids. Frequently, however, stalk lodging of individual trials is affected by environment to an extent that results are not reliable. For example, it is not possible to control external forces such as insects and diseases that may affect stalk quality. Or, it may be necessary to harvest the materials before field conditions conducive to stalk breakage have occurred. In this study we counted broken stalks when differences among progenies were believed to be greatest. Since it is not always possible to make counts at the optimum time, our correlations may have been

higher than could be normally expected between stalk lodging of the inbreds and topcrosses. The coefficient of variation for natural stalk lodging of the inbreds was 55%, whereas mechanical strength and rind thickness had coefficients of 13% and 10%, respectively. The larger coefficient of variation for natural stalk lodging resulted from the failure of the lines to behave relatively the same among the replications and is probably a reflection of environmental effects.

Considering all correlations for random and check lines of stalk quality traits with natural stalk lodging of the testcrosses, as well as heritability values of the random and check lines, selection among lines for high mechanical breaking strength should be the most effective in obtaining lines that give high resistance to field stalk lodging in hybrids. Furthermore, recurrent selection among inbred lines, probably at the S_1 level, should be an effective procedure to improve stalk quality of a heterogeneous population.

None of the mechanical procedures used in this study is satisfactory for screening of stalk quality among plants in a heterogeneous population. The methods are too cumbersome and too time-consuming. Also, the extreme nonheritable plant-to-plant variability rules out these methods for individual plant selection.

Selection within segregating progenies for stalk-rot resistance, induced by artificial inoculations, is an easy and relatively effective procedure. Although the correlation of stalk-rot rating of the random lines with stalk lodging of their testcrosses was not significant, the same correlation for the check lines was highly significant. Development of stalk rot in some of the random lines probably was not normal because of barrenness caused by slow silk emergence and destruction of silks by the western corn rootworm beetle. Barren plants have high levels of sugars within the stalks, and stalk-rotting organisms do not flourish under these conditions (4). Selection among and within segregating progenies for stalk-rot resistance in the S_1 and S_2 generations, followed by selection among surviving progenies for mechanical breaking strength should be an effective method to obtain strong-stalked inbred lines. Jinahyon and Russell (2, 3) found that recurrent selection for stalk-rot resistance in the Lancaster variety was effective for three cycles but that correlated resistance to mechanical breakage showed no improvement from the second to third cycles.

We have shown significant relationships between physical stalk traits of inbred lines and resistance to stalk lodging in hybrids. However, since evaluation for these characters is not feasible for individual plants and is too time-consuming and costly at the progeny level, further research is needed to find an acceptable method.

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GROWTH AND SYNNEMATA DEVELOPMENT OF *CEPHALOSPORIUM GREGATUM* AT VARIOUS PH LEVELS[1]

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ABSTRACT. Isolates of *Cephalosporium gregatum*, the causal organism of soybean brown stem rot, from Mexico, Illinois, and Iowa were grown on a medium ranging in pH from 6.0 to 10.0. The pH was adjusted with 1M KOH and 1M NH_4OH (bases), and with 0.01M carbonate and 0.01M phosphate buffers. Growth of all isolates was obtained when the pH was adjusted to 10.0 with KOH. The Mexico isolate grew best at all pH values tested when compared with the Illinois and Iowa isolates. With NH_4OH there was no growth of the Iowa isolate at pH 9.0 and of the Iowa and Illinois isolates at pH 10.0. Only the Mexico isolate developed synnemata at pH levels ranging from 7.0 to 10.0, irrespective of bases or buffers used to adjust pH.

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INTRODUCTION

Cephalosporium gregatum Allington and Chamberlin, causes brown stem rot of soybeans (*Glycine max* (L.) Merr.) in the United States. There has been some confusion on the taxonomy of sporulating stages within the genus *Cephalosporium*. Bruehl (1) established *Hymenula cerealis* as a saprophytic sporulating stage of *Cephalosporium gramineum* Nisikadao and Ikata. Morgan and Dunleavy (5) reported the occurrence of synnemata of *C. gregatum* on the stems and pods of soybeans. Turian (8) has reviewed the factors influencing morphogenesis of synnemata on other imperfect fungi in culture, based on results obtained by Taber (7), Lougheed (4), and Hejtmanek and Hejtmankova-Uhrova (2).

In one instance, we observed signs of synnemata development when the pH was increased. This suggested that pH might be involved in the development of synnemata. This study was initiated to determine the effect

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of pH on growth and development of synnemata in three isolates of Cephalosporium gregatum.

MATERIALS AND METHODS

Isolates of Cephalosporium gregatum obtained from diseased soybeans grown in Mexico, Illinois, and Iowa were grown on Ramachandran's (6) M_2 medium (glycerine 10 ml, glucose 10 g, yeast extract 5 g, sodium chloride 5 g, potassium phosphate (monobasic) 2 g, agar 20 g, water 1000 ml). The pH of the medium was adjusted to 6.0, 7.0, 8.0, 9.0, and 10.0 with either buffer (0.01 M phosphate or 0.01 M carbonate) or base (1 m KOH or 1 M NH_4OH) after autoclaving. Growth of the fungus was measured by increase in diameter of the colony. Data are the means of three replications. The medium in pH control plates was pH 5.8, and no buffers or bases were added.

RESULTS

The Iowa isolate of C. gregatum was slow-growing compared with the Illinois and Mexico isolates, even on the control plates. Growth of the Iowa isolate decreased as pH was increased. At pH 9.0 and 10.0, however, the Iowa isolate grew only when KOH was used to adjust pH (Table 1). There was no growth when NH_4OH, carbonate, or phosphate buffers were used. There was no development of synnemata at any pH level.

The Illinois isolate grown on control medium was intermediate in growth compared with the Iowa and Mexico isolates. Its growth was unaffected from pH 6.0-9.0 when the medium was buffered with KOH. When the medium was buffered with NH_4OH, there was marked reduction in the growth rate at pH 8.0 and 9.0, and no growth at pH 10.0. No synnemata developed at any pH level.

The Mexico isolate was fast-growing, compared with the Illinois and Iowa isolates. Growth of the Mexico isolate increased with increase in pH above 7.0, irrespective of bases or buffers used. Synnemata were observed from pH 7.0 to pH 10.0 on all the plates regardless of base or buffers used.

All three isolates produced conidia on short conidiophores. Conidia were cut off in succession and were held together by a drop of mucus, forming a globose, glistening head (Fig. 1; A, B). The Mexico isolate also produced conidia on synnemata. Synnemata of the Mexico isolate were white, elongated, red-headed spore-bearing structures, which looked like bristles, and bore conidia at the tip (Fig. 1; C, D). This is the first report of production of synnemata in culture by C. gregatum.

DISCUSSION

Growth and development of C. gregatum on media such as soybean stem agar, or potato dextrose agar, has been reported to be very slow (3). Our observations with M_2 medium indicate that growth of the Mexico isolate increases with an increase in pH from 7.0. Even though all isolates tested were pathogenic to soybeans, there was great variability among them, not only in their reaction to various pH levels, but also to different

Table 1. Effect of pH on growth of Cephalosporium gregatum on M_2 medium at 28C for 14 days.

Base or buffer	Growth (mm)[a/]					
	pH					
	5.8	6.0	7.0	8.0	9.0	10.0
			Iowa isolate			
None	22					
KOH		18	17	13	12	10
NH_4OH		20	23	15	None	None
0.01M PO_4				21		
0.01M CO_3				12		
			Illinois isolate			
None	31					
KOH		30	32	31	30	23
NH_4OH		30	31	10	11	None
0.01M PO_4				29		
0.01M CO_3				23		
			Mexico isolate			
None	49					
KOH		56	59	72	80	80
NH_4OH		43	55	68	60	46
0.01M PO_4				54		
0.01M CO_3				80		

[a/] Mean of 3 replications

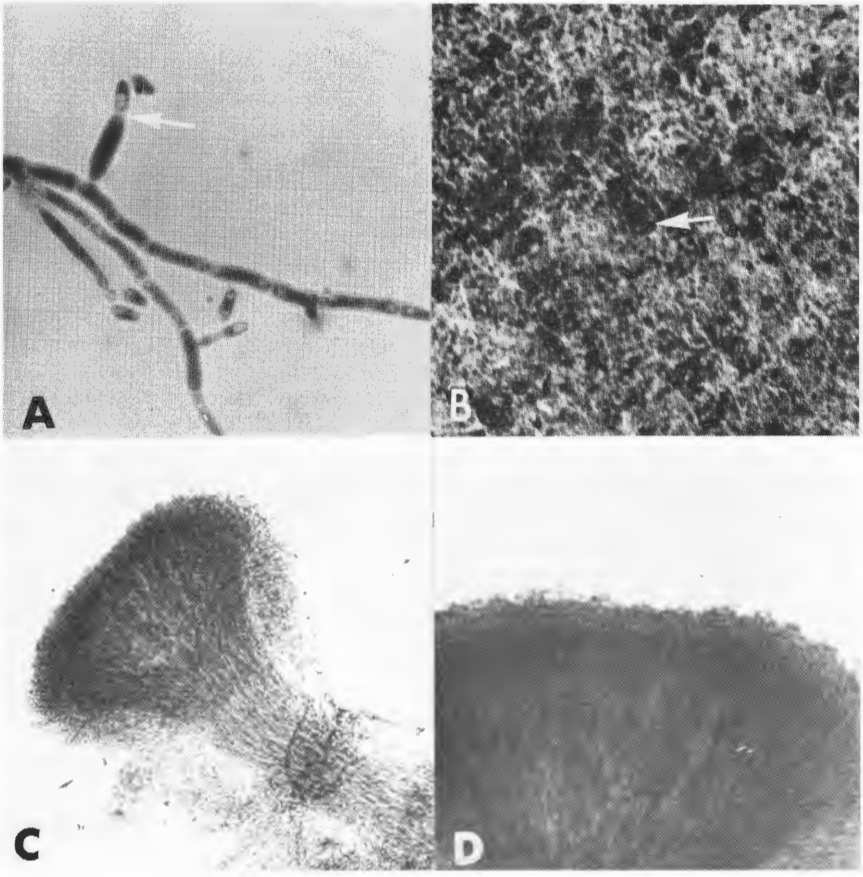

Figure 1. Spore-bearing structures of Cephalosporium gregatum.
A. Region of conidiophore producing conidium (arrow) (1050X).
B. Production of synnemata in culture (arrow).
C. Fully developed synnema (340X).
D. Conidial head of synnema enlarged (450X).

buffers or bases. The Mexico isolate differed from the Iowa and the Illinois isolates in the form of asexual reproduction. The Mexico isolate reproduced both by endoconidia and synnemata, whereas the Iowa and Illinois isolates reproduced only by endoconidia.

Taber (7) has shown that morphogenesis of synnemata is under genetic control in Isaria cretacea. Lougheed (4) made the observation that phosphoglyceric and gibberellic acid are effective stimulants of synnemata formation in Hirsutella gigantia. Hejtmanek and Hejtmankova-Uhrova (2) have also observed that change in ion concentration influences the synnemata formation in Trichophyton mentagrophytes. Our results indicate that changes in ion concentration of the medium alone will influence the development of synnemata of Cephalosporium gregatum (Mexico isolate), regardless of bases or buffers used to adjust the pH.

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MASS SELECTION FOR CROWN RUST RESISTANCE IN AN OAT POPULATION[1]

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ABSTRACT. The "fan-mass method" plant breeding selection procedure was tested for increasing the gene frequency of crown rust (*Puccinia coronata* Cda. var. *avenae* Frasier and Led.) resistance alleles in a genetically heterogeneous population of oat plants (*Avena sativa* L.). The method entailed 2 parts: (a) the population of oat plants was subjected to a crown rust epiphytotic, and (b) the seeds produced from the oat plants were divided into high and low density classes by threshing or by threshing plus additional winnowing. The high density seeds were planted and the process was repeated.

A mass selection procedure of threshing with a plot thresher only increased the gene frequency of crown rust resistance from 0.21 in the F_3 to about 0.35 in the F_{10}. Additional winnowing of the seeds after threshing did not increase the frequency of the resistant allele(s) further. Most of the increase in the frequency of the resistance allele(s) occurred in the first three cycles of selection. The gene frequency in the check population remained at about 0.20 through 7 cycles of propagation.

The mean heading dates of F_{10} oat plants in rusted and rusted-winnowed lines of descent were earlier than that of the check by 2 to 3 days. Similarly, the mean plant height of rusted and rusted-winnowed lines of descent were shorter. Evidently, 2 selection forces, one possibly due to linkage of maturity and plant height loci with rust reaction loci and one unknown, were causing the rusted and rusted-winnowed populations to become earlier and shorter.

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INTRODUCTION

Since crown rust (Puccinia coronata Cda. var. avenae Frazier and Led.) is a destructive disease of oats in many countries of the world, a primary objective in oat breeding is the development of crown rust resistant cultivars. Usually, selection for resistance is practiced via the pedigree system of plant breeding or some modification of it, but the fan-mass-sselection method (6) should be useful in selecting for this trait.

With mass selection, the frequency of a desirable gene(s) in a genetically heterogeneous population of plants is gradually increased. Thus, mass selection for crown rust resistance in an oat plant population would use a technique that would increase the frequency of resistance genes.

The mass selection technique we used had 2 parts: (a) heterogeneous populations of plants were subjected to epiphytotics of crown rust; (b) the seeds produced on these oat plants were separated into 2 density classes, light and heavy, by threshing and winnowing. Supposedly, crown rust susceptible plants would produce seeds in the low-density fraction and by eliminating this portion, the frequency of resistance genes in the remnant population would be increased.

Specifically, the objectives of our experiment were to study the efficiency of the fan-mass method of selection for increasing crown rust resistance in successive generations of a hybrid oat population and to observe whether a change in crown rust resistance of the population would be accompanied by associated changes in heading date and plant height.

REVIEW OF LITERATURE

The fan-mass method was first used by McFadden (6) on a hybrid population from a cross of Yaroslav emmer (resistant to stem rust) and Marquis hard red spring wheat (susceptible to stem rust). The bulk population of F_3 plants was subjected to severe epiphytotics of rust and other diseases, and the susceptible plants produced shrunken grain. The fan-mass method was described by McFadden as follows:

> Threshed grain was run through a clipper seed cleaner using an upper screen of the proper mesh to run off most of the seeds to which the hull had adhered in threshing. A rather coarse rectangular mesh screen was used beneath to separate the plump seed from the naturally slender types and seed that had been shrunken as a result of disease injury. A strong air blast was used to blow out practically all of the light weight seed that the grading process had failed to remove. The resulting plump, heavy seed which presented in large measure, the disease resistant type was next run through an Emerson kicker which removed the long-kerneled types and left only the short, plump types. After the seed had passed through the various mechanical elimination processes described, only a fraction of 1 percent by bulk of original seed remained.

MATERIALS AND METHODS

Selection Procedures

The experimental material we used came from a composite of F_2 seeds obtained by mixing 5-g samples from 250 oat single crosses made between pure-line parents. No attempt was made to categorize the exact resistance genes put into the composite, but the crosses composited were remnants from the crossing program of the Iowa oat improvement project during 1952-56. The crown rust resistance genes most in use then were derived from 'Landhafer' (Pc-5), 'Santa Fe' (Pc-6), "Acencao' (Pc-14), 'Victoria' (Pc-2) and 'Trispernia' (Pc-6d), all of which are dominant to susceptibility and monogenically inherited. Insofar as records for 1952-56 are available, they show the single crosses were made at random with respect to alleles at the crown rust reaction loci. F_2 plants of the composite were grown in a bulk planting to increase the seed supply prior to the application of various methods of mass selection.

One sample from the F_3 composite was carried as a check. The F_3 generation seed for the check was sown at the rate of 100 kg per ha with a grain drill, and the resultant plants were protected from foliar diseases by spraying with a fungicide at weekly intervals between anthesis and maturity to preclude rust infection from natural sources. The plot contained about 90,000 plants and occupied 300 m^2. At maturity the plants were harvested en masse and threshed, producing about 90 kg of seed. To obtain F_4 material for planting, the 90 kg of seed was divided into 10 lots of 9 kg each. Equal size samples were taken from each lot to make a 3-kg composite for planting and a 1-kg composite for storage for future use. We sampled each of the 10 seed lots by extracting several random samples with a small beaker. The F_4 composite was planted, sprayed and harvested, as was the F_3. This procedure of sampling, sowing and harvesting was repeated each generation through F_9.

A second F_3 seed sample was sown and the resultant plants were subjected to artificially induced crown rust infections, races 202, 203 and 216 in F_3 through F_7 and races 203, 216 and 290 in F_8 and F_9. Inoculum from the spreader rows was sufficient to cause an epiphytotic shortly after anthesis as evidenced by the fact that severe epiphytotics resulted in adjacent head-row nurseries each year. At maturity plants were harvested, dried and threshed en masse. No records were kept of the air settings on the thresher, but each year the machine was adjusted for the whole threshing season to give samples of threshed grain from non-rusted plots that were free from chaff, straw and light-weight seeds. The same adjustments were used for threshing the plants from check and rusted plots.

After threshing, the F_4 seed from the F_3 generation rusted plot was subdivided into 2 parts. One part was given no further treatment, but the second was winnowed by running the seed through a "Clipper Cleaner" adjusted to maximum air blast. This treatment winnowed out some seeds not removed during threshing. Hereinafter, these 2 "lines of descent" are called "rusted" and "rusted-winnowed."

Successive generations of rusted and rusted-winnowed lines of descent were sampled for propagation and storage in the same way as the check. Crown rust was spread in the plots of the rusted and rusted-winnowed

lines of descent in each generation, and the resulting seed lots were treated in the same ways as the F_3.

After the 1964 season, 23 seed lots were available, 8 representing the F_3 through F_{10} seed of the check, 8 representing the F_3 through F_{10} seed of the rusted line of descent (a second sample of unselected F_3 seed of the composite was included in the rusted line of descent) and 7 representing the F_4 through F_{10} seed of the rusted-winnowed line of descent. From each seed lot 1200 seeds were taken for determining the percentage of crown rust resistance.

From each line of descent 200 F_{10} plants were grown in a nursery space planted in the field at Ames, Iowa in 1965. Heading date and plant height were recorded on each plant. A plant was considered headed when the first panicle was completely emerged from the boot, and height of a plant was the number of centimeters from ground level to the primary panicle tip. At maturity, one panicle from each plant was harvested and threshed separately. Two 20-seed lots from each F_{11} progeny were used for additional rust tests.

Testing for Crown Rust Reaction

The 23 "generation-line of descent" entries were assayed for percentage of crown rust resistance in 2 experiments, 1 with race 203 and 1 with race 216, conducted in the greenhouse. The 1200 seeds from an entry were divided into 12 subsamples of 100 seeds each, and the subsamples were used for 6 replicates in each of 2 randomized block experiments. The replicates of an experiment were planted at successive 5-day intervals, and corresponding replicates of the 2 experiments were grown simultaneously. A plot consisted of 100 seeds sown in a 33-cm row across a flat, and 5 plots were sown per flat.

When the seedlings were in the first-leaf stage, they were inoculated with urediospores of the appropriate crown rust races. We inoculated by spraying seedlings with a mild detergent solution and dusting the moist leaves with a urediospore-talc mixture. Flats of inoculated plants were placed in a moist chamber for 15 hours after which they were kept on greenhouse benches (temperature range from 27° to 35°C). Ten days after inoculation, seedlings were classified for rust reaction according to the system of Murphy (7). Seedlings with a 0-, 1- or 2-type reaction were classed as resistant, whereas those with a 3- or 4-type were classed as susceptible. The data obtained were used to calculate percentage of resistant seedlings in a population.

The 200 F_{11} progenies in each line of descent were also tested for reaction to races 203 and 216 of crown rust. From each progeny, 20 seedlings were tested with race 203 and 20 with race 216, using the same techniques of propagation, inoculation and reading as described for the bulk progeny tests. These data were used to study the association between crown rust resistance, heading date and plant height.

Calculating Gene Frequencies and Selective Values

Inheritance of reaction to crown rust in our oat populations probably can be assumed to be monogenic with resistance completely dominant to susceptibility (8). Also, we assumed the oat varieties used in making the 250 hybrids, the F_2's of which were composited, were crossed at random with respect to crown rust reaction loci.

Since oats are self fertilizing (4) few generations after hybridization are needed for the heterozygosity at a locus to virtually disappear. The expected frequencies of homozygous and heterozygous genotypes in a population propagated without selection, such as the check, can be calculated by the following formula (11, 12):

Genotype	Frequency
AA (R)	$p^2 + pqF$
Aa (R)	$2pq - 2pqF$
aa (S)	$q^2 + pqF$

where: F = coefficient of inbreeding, R and S designate resistance and susceptibility to rust, respectively, p and q represent the frequencies of genes A and a, respectively, and $p + q = 1$.

The formula for calculating selective value, "s" of a gene is as follows:

Genotype	AA	Aa	aa	Total
Initial frequencies	P	H	Q	1
Relative fitness	1	1	1-s	
Gametic contribution (after selection)	P	H	Q (1-s)	1-Qs

After selection the total gametic contribution is no longer unity since there has been a loss of Qs due to selection. This is reflected in the next generation. When a heterozygote is selfed, the offspring are $\frac{1}{4}$AA:$\frac{1}{2}$Aa:$\frac{1}{4}$aa. Thus, in the subsequent generation the genotypic frequencies following selection are:

AA	Aa	aa
$\frac{P}{1-Qs} + \frac{1}{4} \cdot \frac{H}{1-Qs}$	$\frac{1}{2} \cdot \frac{H}{1-Qs}$	$\frac{Q(1-s)}{1-Qs} + \frac{1}{4} \cdot \frac{H}{1-Qs}$

The frequency of resistant genotypes is:

$$AA + Aa = \frac{P}{1-Qs} + \left(\frac{1}{4} \cdot \frac{H}{1-Qs}\right) + \left(\frac{1}{2} \cdot \frac{H}{1-Qs}\right)$$

By substituting known values for P, H and Q from the previous generation and equating the formula to the observed proportion of resistant plants in the immediate generation, the selective value, s, can be estimated.

EXPERIMENTAL RESULTS

When the data from the 200 F_{11} progenies tested with races 203 and 216 were compared, the reactions to the two races were identical in each progeny regardless of the line of descent, which suggested the same genes controlled the reaction to both crown rust races in this oat population. Perhaps this would be expected since the primary crown rust resistance genes used in the mid 1950's (when the crosses used in our composite were made) were Pc-2, Pc-5, Pc-5, Pc-6d and Pc-14 and these genes give identical reactions to race 203 and 216.

Since the 2 races seemed to be assaying alleles at the same loci, the

two experiments conducted upon the 23 "generation-line of descent" entries, 1 with race 203 and the other with 216, were analyzed as a single experiment with 12 replicates.

There was a highly significant mean square among entries for percent resistant plants (Table 1). When the entries mean square was partitioned, the mean square for each subdivision, i.e., lines of descent and among generations within the check, the rusted and rusted-winnowed, was highly significant.

Table 1. Pertinent mean squares from the analysis of variance of the percent resistant plants in 23 oat populations.

Source of variation	Degrees of freedom		Mean squares
Entries	22		406.7**
Lines of descent	2		3411.9**
Among generations/check	7		127.8**
Linear		1	694.5**
Quadratic		1	88.2
Cubic		1	0.0
Deviation		4	27.9
Among generations/rusted	7		62.4*
Linear		1	278.9**
Quadratic		1	5.4
Cubic		1	34.9
Deviation		4	29.4
Among generations/winnowed	6		132.0**
Linear		1	424.6**
Quadratic		1	49.1
Cubic		1	0.1
Deviation		3	79.6
Error	242		29.3

* Significant at the 5 percent level.
** Significant at the 1 percent level.

Population Means

The percentage of resistant plants in the check line of descent gradually decreased from F_3 to F_{10}, whereas it increased in the rusted and rusted-winnowed lines of descent (Figure 1). The only significant source of regression among generations within the check was linear (Table 1) with a regression of -1.2% per generation (Table 2). The decrease in percent resistant plants was due to the segregation that accompanied selfing. With resistance to crown rust being dominant, heterozygotes and homozygotes were resistant, but with selfing, half of the offspring

from the heterozygotes were shifted irrevocably into the homozygous classes in each generation. This would cause an increase in percentage of susceptible plants in successive generations.

The percentages of resistant plants in the rusted and rusted-winnowed lines of descent increased in successive generations. In the rusted line of descent it increased from 29.3 in the F_3 to 34.3 in the F_6, after which it fluctuated between 31.1 and 35.5 (Figure 1).

In the rusted-winnowed line of descent, the percentage of resistant plants was increased from 29.3 in the F_3 to 36.2 in the F_6, after which it fluctuated between 33.1 and 36.6 (Figure 1). As with the check, the only significant sources of regression among generations within the rusted and rusted-winnowed lines of descent were the linear portions (Table 1). The mean increases in percentage rust-resistant plants of 0.7 and 1.2 per generation in the rusted and rusted-winnowed lines of descent, respectively, were both highly significant (Table 2).

Table 2. Linear regressions of percent crown rust resistant plants per generation in the check, rusted and rusted-winnowed lines of descent.

Line of descent	Linear regression (%) per generation
Check	- 1.2**
Rusted	+ 0.7**
Rusted-winnowed	+ 1.2**

** Significant at the 1 percent level.

Gene Frequency and Selective Value

As shown previously, the percentage of crown rust resistant oat plants was changed in successive generations in all three lines of descent. The differential between the check on one hand and the rusted and rusted-winnowed lines of descent on the other was attributed to the effects of the fan-mass-selection procedure. A more accurate measure of the effectiveness of the mass-selection procedure is the change that occurred in the frequency of the allele(s) that conditioned resistance to crown rust. A change in gene frequency occurs when a selection pressure, artificial or natural, permits one class of genotypes in one generation to contribute a disproportionate number of offspring to the next.

The frequencies of the dominant resistant (p) and the recessive susceptible (q) alleles were 0.21 and 0.79, respectively, in the F_3 composite (Table 3). After six generations of selfing, the heterozygote frequency would be less than 1%, and in subsequent generations the genotypic frequencies of resistant and susceptible classes estimate the gene frequencies of the resistant and susceptible alleles, respectively. The mean

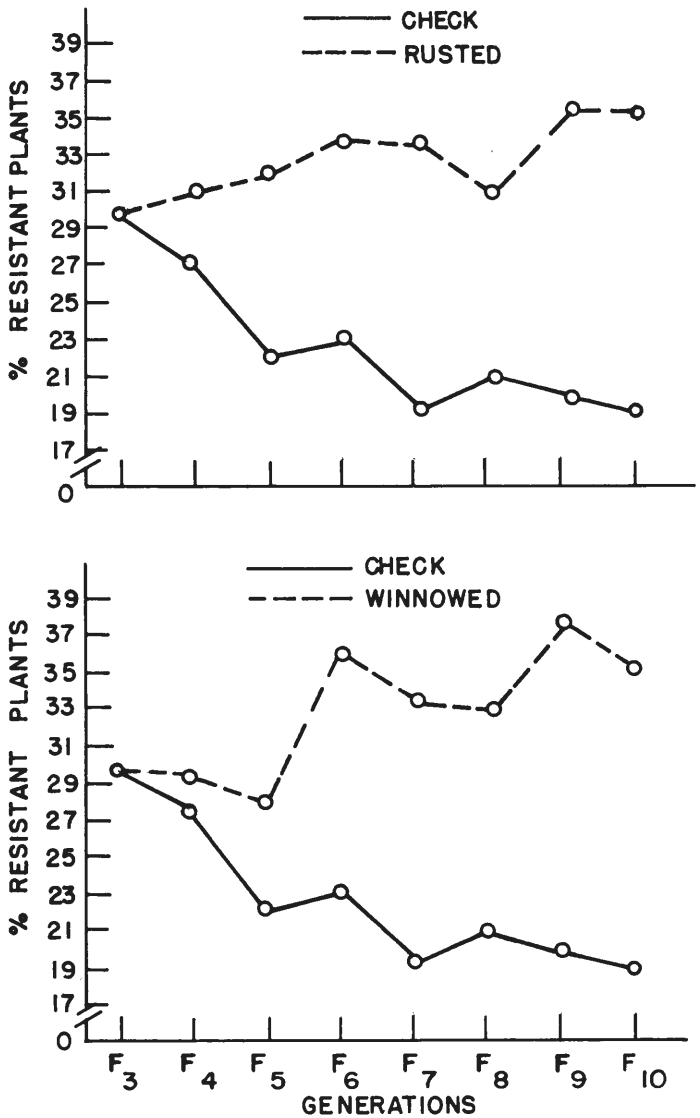

Figure 1. Mean percent of crown rust resistant oat plants in successive generations.

a) check and rusted lines of descent

b) check and rusted-winnowed lines of descent.

Table 3. Gene frequencies of the dominant crown rust resistant allele (p) in the F_3 and F_{10} generations of the check, rusted and rusted-winnowed lines of descent.

Line of descent	Generation	
	F_3	F_{10}
Check	0.21	0.20
Rusted	0.21	0.35
Rusted-winnowed	0.21	0.36

frequency of resistant plants, and thus the gene frequency of the resistant allele for F_8, F_9 and F_{10} of the check, was 0.20, showing that the frequency of the dominant resistance allele(s) in the check did not change from the F_3 to F_{10}. When a constant gene frequency of p = 0.21 was used, the expected percentages of resistant plants in successive generations of the check corresponded closely to the observed values (Figure 2).

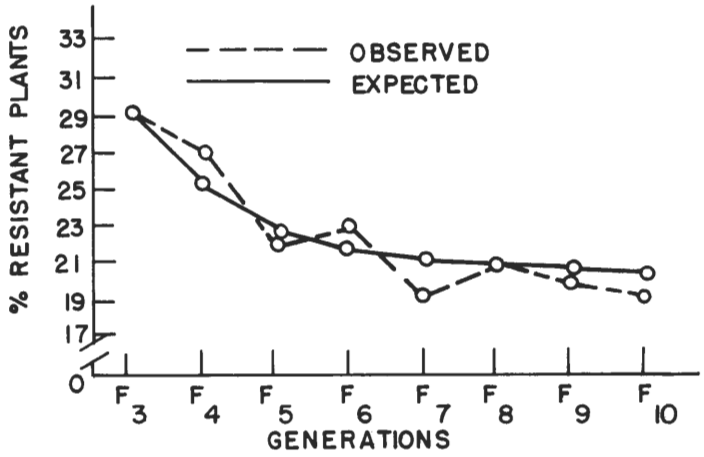

Figure 2. Observed and expected percents of crown rust resistant plants in the check population.

Using the formula given earlier, the selective value (s), the gene frequency of susceptible allele (q) and the change in gene frequency (Δq) were estimated for the successive generations of the rusted and rusted-winnowed lines of descent. Since the only significant source of variation for percentages of resistant seedling in either the rusted or rusted-

winnowed lines of descent was linear, we used the estimated percentages of resistance from a linear model to calculate the s and Δq values between generations. The estimated percentages of resistant seedlings, based on the linear model, are given in column 5 of tables 4 and 5 for the rusted and rusted-winnowed lines of descent, respectively. Selective value, which expresses the strength of selection against the suscepible allele, was 0.27 during the first selection cycle (F_3-F_4) in the rusted line of descent, but it dwindled rapidly to 0.09 in the third cycle and to 0.03 in the seventh (Table 4). The total change in the gene frequency of the susceptible allele from F_3 to F_{10} was 0.14, but over 70% of this change occurred in the first three selection cycles.

Table 4. Estimated selective value (s), gene frequency of susceptible alleles (q) and change in gene frequency (Δq) and percentage crown rust resistance plants in the rusted line of descent.

Generation	s	q	Δq	Estimated percentage resistance*
F_3		.79		30.3
	.27		.049	
F_4		.74		31.0
	.15		.030	
F_5		.71		31.7
	.09		.019	
F_6		.69		32.4
	.07		.015	
F_7		.68		33.1
	.05		.011	
F_8		.67		33.8
	.04		.009	
F_9		.66		34.5
	.03		.007	
F_{10}		.65		35.2

*Based on linear model

In the rusted-winnowed line of descent, the s value decreased from 0.21 in the initial selection cycle to 0.05 in the seventh (Table 5). The q value reduced from 0.79 to 0.64 in 7 selection cycles, but the major portion of this change occurred in the first three cycles. Generally, the s

Table 5. Estimated selective value (s), gene frequency of susceptible alleles (q) and change in gene frequency (Δq) and percentage crown rust resistant plants in the rusted-winnowed line of descent.

Generation	s	q	Δ q	Estimated percentage resistance*
F_3		.79		28.3
	.21		.037	
F_4		.75		29.5
	.16		.031	
F_5		.72		30.7
	.12		.025	
F_6		.70		31.9
	.09		.020	
F_7		.68		33.1
	.07		.016	
F_8		.66		34.3
	.06		.014	
F_9		.65		35.5
	.05		.012	
F_{10}		.64		36.7

* Based on linear model

values and the changes in the gene frequencies in the rusted-winnowed and rusted lines of descent were similar.

Relation of Heading Date and Plant Height to Crown Rust Resistance

The means of heading dates and plant heights of F_{10} oat plants and the percents of crown rust resistance of their F_{11} progenies from the three lines of descent are presented in Table 6. The heading dates of plants from rusted and rusted-winnowed lines of descent were 2.4 and 3.0 days earlier, respectively, than that of the check. Both differences were highly significant, but they did not differ significantly from each other. The means of plant heights for the F_{10} plants from the rusted and rusted-winnowed populations were 4.1 and 7.7 cm shorter, respectively, than that of the check (Table 6). The differences between all three plant height means were significant.

Table 6. Means of heading dates and plant heights of F_{10} oat plants and percents of crown rust resistance of their F_{11} progenies from the check, rusted and rusted-winnowed lines of descent.

Line of descent	Attribute		
	Heading Date (days after May 31)	Plant height (cm)	Resistance (%)
Check	26.7	92.5	26.5
Rusted	24.3**	88.4**	34.5
Rusted-winnowed	23.7**	84.8**	42.0

** Significantly different from the check at the one percent level.

Obviously, the mass selection procedures applied for increasing the gene frequency of the allele(s) which conditioned resistance to crown rust also caused an associated selection for earliness and shortness. The apparent associated selection for increased crown rust resistance and earliness in the rusted and rusted-winnowed lines of descent could result from linkage. If lateness alleles were linked with susceptibility alleles in the original parent varieties, then by reducing the frequency of the susceptibility alleles, as was done in the rusted and rusted-winnowed lines of descent, the heading date means would become earlier. It is possible to test this explanation by examining the heading date means of susceptible versus resistant F_{10} plants within the three lines of descent.

The heading date means for resistant and susceptible F_{10} plants in the check were 26.0 and 27.0 days after May 31, respectively (Table 7).

Table 7. Means of heading dates and plant heights of crown rust resistant and susceptible F_{10} oat plants in the check, rusted and rusted-winnowed lines of descent.

Line of descent	Heading Date (days after May 31)		Plant height (cm)	
	Resistant	Susceptible	Resistant	Susceptible
Check	26.0	27.0	89.2	93.7
Rusted	23.0	25.0**	85.6	90.0*
Rusted-winnowed	22.8	24.0	83.8	86.6

* Significantly different from resistant at 5 percent level.
** Significantly different from resistant at 1 percent level.

This one day differential in heading date suggests that some degree of association (probably linkage) existed between alleles for lateness and susceptibility to crown rust. If the shift to earlier heading date means in the rusted-winnowed and rusted populations were due to changes in the proportions of resistant and susceptible plants, then the heading date means for the two classes of plants should be the same within the rusted-winnowed and rusted populations as in the check. However, the latter assumption was not true. The differential in heading date means between resistant and susceptible plants noted in the check were retained in the rusted and rusted-winnowed populations (Table 7), but the heading date means of both classes of plants were shifted about an equal number of days (2 to 3) earlier. Therefore, it appears that the mass selection procedure used in this study was causing a selection pressure against lateness in two ways: (a) by the association (probably linkage) between alleles for susceptibility to crown rust and lateness, and (b) some selection pressure which acted against lateness independently of the selection pressure against crown rust susceptibility alleles.

There was also an association between alleles for tall plants and susceptibility to crown rust (Table 7). Susceptible F_{10} plants in the check population were 4.5 cm taller than resistant ones. Both classes of plants, i.e., resistant and susceptible, were shorter in the rusted and rusted-winnowed populations than in the check, but the differential between classes was retained.

The second selection pressure against lateness and tallness may be peculiar to the mass-selection procedure we used. We selected against low-density seeds and any plant trait that resulted in low-density seeds would be at a selection disadvantage. In oats there is a positive association between plant maturity and height, and in Iowa, generally, the high temperatures of July are detrimental to the good "grain-filling" of immature oat plants. Therefore, it is likely that the fan mass-selection procedure also selected against lateness and tallness because tall, late plants produced low density seeds.

DISCUSSION

For direct mass selection, i.e., where selection is practices on the attribute for which improvement is sought, to be effective, the heritability of the attribute should be high and the environment must be appropriate to permit different genotypes to develop differential phenotypic expressions. The heritability of an attribute on a single organism basis, e.g., an oat plant or seed, may be high naturally, as Frey and Horner (2) demonstrated for heading date in oats, or it may be manipulated to a higher level as Gardner (3) did with corn grain yield. The importance of using an appropriate environment when practicing mass selection can be well illustrated by disease resistance. When selecting for disease resistance, the effectiveness is very dependent upon the prevalence of the appropriate pathogen and its interactions with the host plant.

The procedure we used to select for crown rust resistance in oats was based on the presence of differential seed density. It was assumed that low density seeds would be produced on rust infected plants, and thus, by separating low from high density seeds by air classification, separation

of resistant from susceptible genotypes would be accomplished. The effectiveness of crown rust disease in reducing the density of oat seeds borne on susceptible plants has been adequately demonstrated by Simons (10).

This mass selection procedure was effective in increasing the frequencies of the crown rust resistant allele(s) from 0.21 to about 0.35 in the rusted and rusted-winnowed lines of descent. In a similar study, Klages (5) subjected a mixture of durum and hard red spring wheat to a severe rust epiphytotic, and he found a sharp increase in the rust resistant durum component. Atkins (unpublished date) found that in a heterogeneous oat population the proportions of genotypes resistant to crown and stem rust and Helminthosporium victoriae M. and M. were increased when the bulk populations were grown under epiphytotics of these diseases.

The total increase in the gene frequency of the crown rust resistance alleles from 7 generations of the mass selection procedure was 0.14 in the rusted and 0.15 in the rusted-winnowed line of descent. Since these values were nearly identical, the winnowing of seeds during the threshing operation appeared to give an adequate density separation, and subsequent winnowing with a seed cleaner was unnecessary. Increases in the frequencies of the resistance allele(s) were most rapid in early generations of selection. This was especially noticeable in the rusted line of descent, in which 70% of the change in gene frequency occurred in the first 3 generations. In the last one or two generations of selection very little change occurred. It appeared that the frequency of the resistance allele(s) was leveling off at about 0.35. This apparent inability of the mass-selection procedure to move the frequency of the resistance allele(s) above 0.35 was somewhat discouraging. This may have been due in part to the addition of crown rust race 290 to the inoculum used in the last 2 selection cycles. The role of this race in selection against plants that were resistant to crown rust races 203 and 216 may have brought about fluctuations in the percentage of resistance in later generations. However, pragmatically, these results suggest that adequate protection from crown rust damage may be attained without having 100% resistant plants, i.e., with multiline cultivars (1). Also suggested is the need for additional experiments to determine the appropriate composition of crown rust resistant and susceptible plants in oat populations to give adequate control of the disease. The materials for these experiments should be composites of homozygous lines so the confounding effects of segregation are not present.

The associations between disease resistance, heading date and plant height found in this study should be investigated further. From experiments where mass selection for plant height was applied to the same oat populations as used herein, Romero and Frey (9) also found positive genetic associations between plant height and heading date. The associations we observed indicate the possible usefulness of indirect mass selection.

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REVIEW OF THE GENUS SLATEROCORIS WAGNER, WITH A KEY AND DESCRIPTIONS OF NEW SPECIES (HEMIPTERA, MIRIDAE)

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ABSTRACT. A key to 46 species of Slaterocoris Wagner, is provided. New species of Slaterocoris are S. arizonensis from Arizona and New Mexico; S. schaffneri from Texas, Nebraska, South Dakota, and North Dakota; S. custeri from South Dakota and New Mexico; S. bifidus, S. knowltoni and S. fuscomarginalis from Utah; S. digitatus, S. basicornis and S. texanus from Texas; S. tibialis and S. sculleni from Oregon; S. dakotae and S. severini from South Dakota; S. fuscicornis from Missouri; S. getzendaneri from Washington; S. ovatus from California; S. burkei from Colorado; S. nicholi from Arizona; S. nevadensis from Nevada; S. woodgatei from New Mexico; S. rarus from New York; S. bispinosus from Mexico; and S. minimus from Wisconsin.

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The genus Slaterocoris Wagner, type Capsus stygicus Say, was revised by Kelton (1968), in which he gave a key to 24 species, of which 9 were new to science. The present writer has now completed his studies of the genus, after starting with a paper (1938) covering species from the eastern United States. I have worked over all the specimens of Slaterocoris accumulated during 55 years of collecting Miridae. Several species are represented only by one or two specimens, but are shown to be distinct by comparing and illustrating the male genital claspers. The present key deals with 46 species, of which 22 are described as new.

KEY TO THE SPECIES OF SLATEROCORIS

1. Legs black, femora may be narrowly pale at apex. 2
   Legs not entirely black, femur or tibia, or both, with some yellow or orange. 9

2. Pubescence on dorsum erect, sparsely set, black; frons smooth. 3
   Pubescence on dorsum closely set, suberect or recumbent, brownish or silvery; frons striate. 4

3. Length of antennal segment II subequal to width of vertex plus dorsal width of an eye; length (♂) 4.2 mm. . . . . robustus Uhl.

Length of antennal segment II not equal to width of vertex plus dorsal width of an eye; length (♂) 3.2 mm. . . . nevadensis n. sp.

4. Pubescence on dorsum brown. 5
Pubescence on dorsum silvery. 7

5. Length of antennal segment II not exceeding width of head. . . . 6
Length of antennal segment II greater than width of head; male clasper (fig. 33) distinctive; length (♂) 5.4 mm. . grandis Kelt.

6. Rostrum not reaching posterior margin of sternum; pubescence deep brown, closely set; male clasper (fig. 37) distinctive; length (♂) 3.7 mm. . . . . schaffneri n. sp.
Rostrum reaching upon middle coxae; pubescence long, more sparsely set; male clasper (fig. 18) distinctive; length (♂) 3.7 mm. . . . . knowltoni n. sp.

7. Length of antennal segment II not equal to width of head. 8
Length of antennal setment II subequal to width of head; male clasper (fig. 32) distinctive. . . . . simplex Kelt.

8. Male right clasper with a sharp spine at middle, apex with four teeth (fig. 31). . . . . argenteus Kelt.
Male right clasper without spine at middle, apex with five digits (fig. 38). . . . . digitatus n. sp.

9. (1) Pubescence on dorsum dark, black or brown. 10
Pubescence on dorsum light, golden or silvery. 28

10. Pubescence on dorsum short and sparsely set, surface almost glabrous. 11
Pubescence on dorsum longer, more dense and easily recognized. 20

11. Legs with the femora more or less black. 12
Legs uniformly yellow or orange yellow. . . . . pallipes Kngt.

12. Femora yellow, blackish on base. 13
Femora black, apices only yellow. 14

13. Tibiae yellow, apex blackish; male clasper distinctive (fig. 21); length (♂) 3.1 mm. . . . . sparsus Kelt.
Tibiae orange yellow, apex not blackish; male right clasper distinctive (fig. 4); length (♂) 3.5 mm. . . . . dakotae n. sp.

14. Hind tibiae yellow, sometimes a bit dusky near base. 18
Hind tibiae fuscous to black. 15

15. Femora reddish on apical half. 16
Femora not reddish. 17

16. Length of antennal segment II exceeding width of vertex plus dorsal width of an eye; length (♂) 4.3 mm. . rubrofemoratus Kngt.
Length of antennal segment II not exceeding width of vertex plus dorsal width of an eye; length (♂) 4.1 mm. . . nicholi n. sp.

17. Hind tibiae black; (♀) length of antennal segment II subequal to width of head; costal margins strongly arcuate; male right clasper distinctive (fig. 12). . . . . atritibialis Kngt.

Hind tibiae fuscous, becoming paler on distal half; (♀) length of antennal segment II greater than width of head; costal margins of hemelytra only moderately arcuate; male right clasper distinctive (fig. 7). . . . . stygicus Say

18. Antennal segments I and II yellow, segment II may be fuscous on apical one-fourth, but never with a fuscous band at base; male right clasper distinctive (fig. 8). . . . pallidicornis Kngt.
Antennal segments I and II fuscous to yellowish, but when yellow, segment II will always have a fuscous band at base. . 19

19. Rostrum only reaching to base of middle coxae, its length scarcely equal to width of head; male right clasper distinctive (fig. 10). . . . . breviatus Kngt.
Rostrum length greater than width of head, reaching to apex of middle coxae; male right clasper distinctive (fig. 43). . . . . solidaginis Kelt.

20. (10) Posterior tibiae black, or black with some yellow. . . . 21
Posterior tibiae yellow or orange. 24

21. Length of antennal segment II subequal to or greater than width of head across eyes. 22
Length of antennal segment II not equal to width of head; length (♂) 4.6 mm, (♀) 4.3 mm. . . . . alpinus Kelt.

22. Rostrum reaching to middle of intermediate coxae. 23
Rostrum only reaching to posterior margin of mesosternum; length (♂) 4.2 mm. . . . . atratus Uhl.

23. Length of antennal segment II exceeding width of head, fuscous to black; length (♂) 4.4 mm, (♀) 4.6 mm. . . fuscicornis n. sp.
Length of antennal segment II subequal to width of head, pale yellowish, sometimes fuscous on base; length (♂) 4.1 mm, (♀) 4.3 mm. . . . . mohri Kngt.

24. (20) Length of antennal segment II exceeding width of head by half the width of vertex; pubescence on dorsum very thick and suberect; length 5.0 mm. . . . . hirtus Kngt.
Length of antennal segment II shorter, length not exceeding width of head plus half the width of vertex. 25

25. Dorsal surface densely clothed with recumbent and suberect brown pubescence. 27
Dorsal surface rather sparsely clothed with recumbent, short pubescence. 26

26. Male right clasper with a single spine on basal half (fig. 30); female segment II black. . . . . arizonensis n. sp.
Male right clasper bispinose on basal half (fig. 25); female antennal segment II yellow. . . . . bispinosus n. sp.

27. Length of antennal segment II subequal (♂) to width of head; male right clasper distinctive (fig. 29). . . . . ambrosiae Kngt.
Length of antennal segment II just slightly less (♂) than width of head; male right clasper distinctive (fig. 28). . severini n. sp.

28. (9) Length of antennal segment II distinctly greater than width of head across eyes. 29
Length of antennal segment II not greater than widh of head. . 30

29. Cuneus elongate, its length (♂) subequal to width of head; tibiae orange yellow; pubescence long, erect, pale yellow; length (♂) 5.6 mm, (♀) 3.9 mm. . . . . longipennis Kngt.
Cuneus shorter, more triangular in shape; pubescence short, sparsely set, more recumbent, golden in color, corium nearly glabrous, male right clasper distinctive (fig. 11); length (♂) 4.1 mm. . . . . getzendaneri n. sp.

30. Length of antennal segment II not equal to width of head. . . . 31
Length of antennal segment II subequal to width of head. . . . 42

31. Femora mostly black, yellow on apex. 32
Femora reddish yellow; length (♂) 3.36 mm, (♀) 3.6 mm. . . . . flavipes Kelt.

32. Small, length not over 3.4 mm. 33
Larger, length 3.5 mm, or more. 35

33. Pubescence short and recumbent. 34
Pubescence on dorsum thick and long, silvery; antennal segment I yellowish brown, segment II colored likewise on basal half; length (♂) 3.4 mm, male claspers distinctive (fig. 15). . . . . pilosus Kelt.

34. Pubescence short and recumbent, silvery to golden; antennae black; length (♀) 3.4 mm. . . . . ovatus n. sp.
Pubescence suberect, sparse, pale to yellowish; antennal segment I pale, base dark, segment II pale at base; length (♂) 3.4 mm, right clasper distinctive (fig. 39). . texanus n. sp.

35. (32) Membrane and veins dark fuscous, the veins do not stand out clearly. 36
Membrane pale, veins infuscated and stand out clearly; tips of femora narrowly yellow; length (♂) 3.7 mm, male claspers distinctive (fig. 40). . . . . bifidus n. sp.

36. Apical half of femora reddish orange; length (♂) 3.5 mm, (♀) 3.6 mm; claspers distinctive (fig. 14). . . . croceipes Uhl.
Apical one-third or less of femora yellowish. 37

37. Tibiae and tips of femora yellow; antennal segment I yellow or pale fuscous. 38
Tibiae and tips of femora pallid, antennal segment I black; length (♂) 4.3 mm, (♀) 4.1 mm; male claspers distinctive (fig. 13). . . . . apache Kelt.

38. Antennal segment I fuscous to black. 39
Antennal segment I yellow, segment II black, pale at base; length (♂) 3.6 mm; male right clasper distinctive (fig. 6). . . . . basicornis n. sp.

39. Length of antennal segment II equal to, or greater than length of fore tibia. 40
Length of antennal segment II not equal to length of fore tibia; antennal segments I and II pale fuscous; length (♂) 3.5 mm; male right clasper distinctive (fig. 3). . . . . custeri n. sp.

40. Length of antennal segment II greater than length of fore tibia. 41
Length of antennal segment II subequal to length of fore tibia; length (♂) 3.8 mm; male right clasper distinctive (fig. 5). . . . . woodgatei n. sp.

41. Dorsum with rather long, suberect pubescence; male right clasper (fig. 26) bifid on apex; length (♂) 4.1 mm. . burkei n. sp.
Dorsum with short, more recumbent pubescence; male right clasper (fig. 2) not bifid on apex; length (♂) 3.6 mm. . . . . sheridani Kngt.

42. (30) Membrane and veins rather uniformly infuscated. . . . 43
Membrane pale, apical margin bordered by a dark fuscous band; veins narrowly bordered by dark fuscous; length (♂) 3.6 mm; male right clasper (fig. 35) distinctive. . . fuscomarginalis n. sp.

43. Dorsal surface densely clothed with suberect, pallid to silvery pubescence. 44
Dorsal surface clothed with recumbent or short, more sparsely set, pale to yellowish pubescence. 45

44. Tibiae fuscous to black; length (♂) 4.8 mm, (♀) 3.7 mm; male right clasper (fig. 22) distinctive. . . . . utahensis Kngt.
Tibiae yellow; length (♂) 4.4 mm; male right clasper (fig. 23) distinctive. . . . . sculleni n. sp.

45. Antennae black; tibiae orange colored; male right clasper (fig. 27) trifid on apex; length (♂) 4.2 mm. . . . . tibialis n. sp.
Antennal segment I pale to yellowish; segment II yellowish, but with annulus at base and apical third blackish; length (♂) 3.7 mm; male claspers distinctive (fig. 44). . . rarus n. sp.

Slaterocoris stygicus (Say)

Capsus stygicus Say, 1832, p. 24
Strongylocoris stygicus: Atkinson, 1890, p. 120
Strongylocoris stygicus: Knight, 1941, p. 79, figs. 113, 114
Slaterocoris stygicus: Wagner, 1956, p. 280
Slaterocoris stygicus: Kelton, 1968, p. 1121

Male. Length 4.2 mm, width 2.0 mm. Head: width .99 mm, vertex .54 mm. Rostrum, length 1.04 mm, reaching to middle of intermediate coxae. Antennae: segment I, length .30 mm; II, 1.12 mm; III, .86 mm; IV, .47 mm, black. Pronotum, length .91 mm, width at base 1.50 mm. Form ovate, black, shining, finely but densely punctate, somewhat rugulose, nearly glabrous, sparsely set with fine, short pubescence; apices of femora, two anterior pairs of tibiae, and bases of trochanters, pale yellowish; hind tibiae fuscous to black, becoming paler on distal half. Male genital claspers distinctive (fig. 7).

Female. Length 4.2 mm, width 2.1 mm. More ovate and robust than the male, but very similar in color, punctation and scanty pubescence. Host plant: Goldenrod (Solidago spp.).

Distribution. Commonly distributed in the eastern United States, and westward to Arizona, Utah, Montana, Colorado, New Mexico, Texas and Wyoming.

Slaterocoris robustus (Uhler)

Stiphrosoma robusta Uhler, 1895, p. 45
Strongylocoris robustus: Tucker, 1907, p. 60
Strongylocoris uniformis: Van Duzee, 1925, p. 396
Slaterocoris robustus: Knight, 1968, p. 90, fig. 112
Slaterocoris robustus: Kelton, 1968, p. 1132, fig. 19

Male. Length 3.9 mm, width 1.8 mm. Head: width 1.19 mm, vertex .68 mm. Rostrum, length .88 mm, reaching to base of middle coxae. Antennae: segment I, length .30 mm; II, .91 mm, with fine short pubescence intermixed with erect long pale bristles; III, .61 mm; IV, .38 mm; black. Dorsal surface clothed with sparsely set, erect, long brownish black bristles; black, shining, rugulose and finely punctate. Legs uniformly black. Male genital segment and claspers (fig. 1) distinctive of the species.

Female. Length 3.9 mm, width 2.1 mm; costal margins arcuate. Head: width 1.36 mm, vertex .85 mm, frons broad and smooth. Antennal segment II, length .78 mm, less than width of vertex. Pronotum, length .92 mm, width at base 1.66 mm. More robust than the male, but very similar in color and pubescence. Breeds on Artemisia tridentata.

Distribution. California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Texas, Utah and Wyoming.

Slaterocoris grandis Kelton

Slaterocoris grandis Kelton, 1968, p. 1131, fig. 17

Male. Length 5.6 mm, width 2.2 mm. Head: width 1.05 mm; frons striate; pubescence black, dense. Rostrum, length 1.26 mm, reaching upon middle coxae. Antennae: segment I, length .35 mm; II, 1.33 mm; III, .98 mm; IV, .49 mm; black. Pronotum, width 1.75 mm; calli punctate. Pubescence on dorsum black, long and dense. Legs black. Male right clasper distinctive (fig. 33).

Female. Length 4.9 mm, width 2.45 mm. Head: width 1.15 mm, vertex .57 mm. Antennae: segment I, length .35 mm, black; II, 1.25 mm, black; III, .87 mm, black, often pale yellow at base; IV, .45 mm, black. Pronotum, width 1.89 mm at base. More robust than the male but very similar in color and pubescence.

This species is distinguished by the large size, by the black antennae and legs, by the striate frons, by the long black pubescence on the dorsum, and by the male genitalia. Male right clasper distinctive (fig. 33). Collected on Helianthus sp.

Distribution: Near El Salto, Durango, Mexico.

Slaterocoris solidaginis Kelton

Slaterocoris solidaginis Kelton, 1968, p. 1131, fig. 18

Male. Length 4.2 mm, width 2.0 mm. Head: width 1.12 mm; frons striate; pubescence brownish, short. Rostrum, length 1.05 mm, reaching to base of middle coxae. Antennae: segment I, length .31 mm, black at base, yellowish towards apex; II, 1.12 mm, black; III, .84 mm; IV, .42 mm; black. Pronotum, width 1.64 mm; calli finely rugulose punctate. Dorsal surface pubescence brownish, short, appressed. Femur black, apex yellowish; tibia pale yellow. Male right clasper distinctive (fig. 43).

Female. Length 4.13 mm, width 2.1 mm. Head: width 1.19 mm, vertex .64 mm. Antennae: segment I, length .31 mm, apical half yellowish brown; II, 1.01 mm, yellow, base and apex black; III, .73 mm, black; IV, .42 mm, black. Pronotum, 1.64 mm wide at base. Similar to the male in aspect, but broader, and antennal segment II mostly yellow. Collected on Solidago sp. and Artemisia douglasiana Bessey.

Distribution. Widely distributed in California and known from Nevada.

Slaterocoris alpinus Kelton

Slaterocoris alpinus Kelton, 1968, p. 1128, fig. 4

Data is drawn from the original description.

Male. Length 4.6 mm, width 1.8 mm. Head: width 1.06 mm; vertex rugulose punctate; frons punctate, pubescence brownish. Rostrum, length .80 mm, reaching to base of middle coxae. Antennae: segment I, length .28 mm; II, .80 mm; III, .66 mm; IV, .35 mm. Pronotum, width 1.43 mm, calli finely punctate. Pubescence on dorsum brownish, rather long and dense. Femur black, apex sometimes lighter; tibiae black. Right clasper of the male distinctive of the species (fig. 41).

Female. Length 4.34 mm, width 2.10 mm. Head: width 1.19 mm. Antennae: segment I, length .27 mm; II, .82 mm; III, .70 mm; IV, .35 mm; black. More robust than the male but very similar in color and pubescence.

Described from Boulder, Colorado, and not reported elsewhere. This species is distinguished by the black antennae and legs, by the brownish and rather long pubescence on the dorsum, and by the male genitalia. The right clasper has equal teeth at apex, with three stubby teeth at the base of the outer tooth, and a bifurcate subapical tooth (fig. 41).

Slaterocoris nevadensis new species

Allied to robustus (Uhl.) but size smaller; second antennal segment shorter, its length not equal to width of vertex plus dorsal width of an eye; male right clasper distinctive (fig. 20).

Male. Length 3.2 mm, width 1.6 mm. Head: width 1.05 mm, vertex .68 mm; black. Rostrum, length .81 mm, black, reaching to apex of middle coxae. Antennae: segment I, length .24 mm, black; II, .74 mm, black, clothed with short, pale pubescent hairs; III, .44 mm, black; IV, .27 mm, black. Pronotum, length .74 mm, width at base 1.36 mm; calli moderately convex, smooth; disk finely and closely pubctate, shining.

Dorsal surface black, shining, finely punctate; clothed with moderately long, suberect, brownish black hairs. Membrane and veins uniformly

dark fuscous brown. Ventral surface black, shining, moderately clothed with erect dark brown pubescent hairs. Legs black, shining, tibiae set with rather long brownish black spines. Genital segment and claspers distinctive; right clasper (fig. 20) long and slender, bifid on apex.

Holotype: ♂ May 25, 1963, Moapa, Nevada (R. C. Bechtel); N. S. N. M. collection. Paratype: 1♂, taken with the type.

Slaterocoris schaffneri new species (fig. 37)

In the key this species runs in the couplet with knowltoni but differs in the shorter, but thicker, suberect brown pubescence; also differs by the shorter rostrum which does not reach posterior margin of mesosternum; distinguished by form of the male right clasper (fig. 37).

Male. Length 3.9 mm, width 1.7 mm. Head: width 1.10 mm, vertex .61 mm; black, with erect brown hairs on frons and vertex. Rostrum, length .78 mm, not reaching to posterior margin of mesosternum. Antennae: segment I, length .27 mm, black; II, .78 mm, black, thickly clothed with short brown pubescence; III, .61 mm; IV, .34 mm; black. Pronotum, length .88 mm, width at base 1.50 mm; disk moderately convex, transversely rugulose, shining, thickly clothed with suberect brown pubescence. Scutellum transversely rugulose, thickly clothed with suberect brown pubescence. Dorsal surface black, thickly clothed with prominent, suberect brown pubescence. Cuneus moderately deflexed; membrane and veins uniformly dark brownish black. Ventral surface black, venter clothed with suberect brown pubescence. Legs uniformly brownish black. Genital segment distinctive, right clasper (fig. 37) very unusual, terminating with three curved digits, plus two or three stubs which suggest that other digits were broken out at some point of development. Several males were examined and the two figures presented show only a very limited amount of variation (fig. 37).

Female. Length 4.1 mm, width 1.9 mm. Head: width 1.19 mm, vertex .68 mm. Rostrum, length .78 mm, not reaching to posterior margin of mesosternum. Antennae: segment I, length .28 mm; II, .78 mm; III, .61 mm; IV, .34 mm. Pronotum, length .88 mm, width at base 1.60 mm. Color and pubescence similar to the male.

Holotype: ♂ May 12, 1969, Iredell (2 mi. west) Bosque Co., Texas (J. C. Schaffner); U. S. N. M. collection. Allotype: ♀, taken with the type. Paratypes: 4♂, taken with the types. 3♂, 5♀, May 24, 1968, taken at the type locality (J. C. Schaffner). 5♂, 4♀, May 29, 1969, Iredell, type locality (J. C. Schaffner). 16♂, 10♀, May 6, 1970, type locality (J. C. Schaffner). NEBRASKA: 1♂, War Bonnet Canyon (through C. V. Riley). NORTH DAKOTA: 1♂ July 14, 1920, Kidder County (A. A. Nichol). SOUTH DAKOTA: 1♂, 4♀ August 19, 1927, Custer (H. H. Knight).

Slaterocoris knowltoni new species (fig. 18)

Runs in the couplet with schaffneri, but easily distinguished by the longer pubescence, and the rostrum reaching upon the middle coxae; the male right clasper distinctive (fig. 18).

Male. Length 3.7 mm, width 1.7 mm. Head: width 1.0 mm, vertex .54 mm; black, vertex strongly impressed, having a sharp, elevated basal carina; frons with transverse striate lines; eyes reddish brown. Rostrum, length .85 mm, reaching upon apex of middle coxae. Antennae:

segment I, length .30 mm, black, narrow apex pallid; II, .91 mm, black, set with numerous suberect bristles; III, .71 mm, black, with short pubescence but intermixed with several erect long bristles; IV, .37 mm, brownish black. Pronotum, length .78 mm, width at base 1.39 mm; disk moderately convex, transversely rugulose, finely punctate; calli convex, basal edges indicated by an impressed line; disk clothed with rather sparsely set, erect, long brownish pubescent hairs. Scutellum transversely striate and rugulose.

Dorsal surface black, clothed with rather long erect, and suberect, moderately sparse brown hairs. Cuneus depressed, hairs shorter. Membrane and veins dark brownish to black. Ventral surface black, venter with rather long, erect, brownish hairs. Legs black, hind pair rather long, set with erect hairs and bristles. Genital segment with distinctive right clasper (fig. 18).

Holotype: ♂ June 20, 1963, Cedar Creek, Utah (G.F. Knowlton); U.S.N.M. collection. Named for the collector, Dr. George Knowlton, who has done extensive collecting of Hemiptera and Homoptera in the state of Utah. Paratypes: 2♂ May 27, 1969, Kelton Pass, Box Elder Co., Utah (G.F. Knowlton).

Slaterocoris argenteus Kelton

Slaterocoris argenteus Kelton, 1968, p. 1134, fig. 21

Male. Length 4.2 mm, width 1.68 mm. Head: width .98 mm, vertex .48 mm; frons striate, pubescence silvery. Rostrum, length .82 mm, reaching upon the middle coxae. Antennae: segment I, length .27 mm; II, 1.12 mm; III, .87 mm; IV, .36 mm; black. Pronotum, width 1.33 mm at base; calli finely rugulose punctate. Pubescence on dorsum silvery, fine and dense, appears matted. Legs black. Male right clasper (fig. 31) distinctive of the species.

Female. Length 3.5 mm, width 1.82 mm. Head: width .99 mm, vertex .61 mm. Antennae: segment I, length .24 mm; II, .87 mm; III, .70 mm; IV, .35 mm; black.

This species resembles simplex in the silvery pubescence and black legs, but is distinguished from it by the larger size, by fine pubescence on the dorsum, by the longer antennal segment II, and by the male genitalia.

Distribution. Described from Durango, Mexico.

Slaterocoris simplex Kelton

Male. Length 3.9 mm, width 1.75 mm. Head: width .98 mm; frons striate; rostrum, length .87 mm, reaching to base of middle coxae. Antennae: segment I, length .28 mm; II, .94 mm; III, .66 mm; IV, .40 mm; black. Pronotum, width 1.47 mm; calli finely rugulose punctate. Pubescence on the dorsum silvery, long and dense, matted. Legs black. Male right clasper distinctive (fig. 32).

Female. Length 4.0 mm, width 2.0 mm. Head: width .98 mm, vertex .54 mm. Antennae: segment I, length .28 mm; II, .91 mm; III, .70 mm; IV, .42 mm. Pronotum, width 1.47 mm. Shorter and broader than the male, but very similar in pubescence and general aspect. Collected on Helianthus spp.

Distribution. Collected near El Salto, Durango, Mexico.

Slaterocoris digitatus new species (fig. 38)

In the key this species runs in the couplet with argenteus Kelton, but is distinguished by the male right clasper, which is without a spine at middle but the apex terminating with five spines or digits (fig. 38).

Male. Length 3.7 mm, width 1.76 mm. Head: width .99 mm, vertex .58 mm; black. Rostrum, length .75 mm, reaching to base of middle coxae. Antennae: segment I, length .30 mm, black, apical edge pale; II, 1.05 mm, brownish black, thickness subequal to first segment; III, .78 mm; IV, .34 mm, fuscous. Pronotum, length .88 mm, width at base 1.49 mm; edges of calli impressed.

Dorsal surface black, densely clothed with recumbent and appressed, silvery sericeous pubescence, and intermixed with more erect silvery hairs. Membrane fuscous to black, veins black. Hemelytra with costal margin only slightly arcuate; cuneus turned down moderately. Ventral surface black, rather thickly clothed with recumbent, silvery pubescence. Legs black, tibiae set with rather long black spines. Genital segment and claspers distinctive; right clasper terminating with five spines or digits (fig. 38).

Female. Length 3.4 mm, width 1.9 mm. Head: width 1.05 mm, vertex .68 mm. Rostrum, length 1.02 mm, reaching to apex of middle coxae. Antennae: segment I, length .25 mm; II, .92 mm; III, .57 mm; IV, broken; all segments black. Pronotum, length .85 mm, width at base 1.50 mm. Dorsal surface black, shining, densely clothed with appressed and recumbent, silvery sericeous pubescence, and intermixed with more erect silvery hairs. Membrane and veins fuscous to black as in the male.

Holotype: ♂ August 16, 1968, South Rim Trail, Chisos Mts., altitude 6700♀7200 ft., Big Bend National Park (J.E. Hafernik); U.S.N.M. collection. Allotype: ♀ August 15, 1969, South Rim Trail, Big Bend National Park, Brewster County, Texas (Board and Hafernik). Paratype: 1♂, taken with the holotype.

Slaterocoris pallipes (Knight)

Strongylocoris pallipes Knight, 1926, p. 254
Strongylocoris pallipes Knight, 1941, p. 79, fig. 114
Slaterocoris pallipes: Wagner, 1956, p. 280
Slaterocoris pallipes: Kelton, 1968, p. 1122, fig. 2

Male. Length 4.5 mm, width 2.0 mm. Head: width 1.16 mm, vertex .60 mm; frons punctate and weakly striate. Rostrum, length 1.12 mm, reaching base of middle coxae. Antennae: segment I, length .37 mm; II, 1.28 mm, black, basel half yellowish brown; III, .98 mm; IV, .47 mm. Pronotum, length .93 mm, width at base 1.57 mm. Black, shining, with punctation and pubescence very similar to stygicus Say, but legs entirely pale yellowish. Male genital claspers distinctive (fig. 9).

Female. Length 5.0 mm, width 2.5 mm. Head: width 1.27 mm, vertex .73 mm. Pronotum, length 1.07 mm, width at base 1.81 mm. More robust than the male but very similar in coloration, punctation and pubescence.

Distribution. Maryland, North Carolina and Virginia. Found breeding on Baccharis halimifolia L.

Slaterocoris dakotae new species (fig. 4)

Runs in the couplet with sparsus Kelton in the key, but size larger; male claspers very different, form of right clasper more nearly like that of robustus (Uhl.); legs orange colored, bases of femora brownish black.

Male. Length 3.5 mm, width 1.5 mm. Head: width 1.04 mm, vertex .56 mm, black. Rostrum reaching to base of middle coxae. Antennae: segment I, length .20 mm, dusky yellow; II, .78 mm, yellowish to pale fuscous; III, .51 mm, fuscous; IV, missing. Pronotum, length .71 mm, width at base 1.3 mm; disk finely, closely punctate, moderately shining; calli smooth, moderately convex.

Dorsal surface black, shining, clothed with short, recumbent, rather sparsely set, brownish simple pubescence, apical half of some hairs appear golden in some angles of light. Hemelytra with costal margin only slightly arcuate; cuneus turned down only moderately; membrane and veins uniformly dark fuscous. Ventral surface black, moderately shining. Legs orange yellow, bases of femora brownish black, coxae black; tibiae orange yellow, apices not darker, spines black, tarsi fuscous. Genital segment and claspers distinctive of the species (fig. 4).

Holotype: ♂ June 28, 1924, Interior, South Dakota (H. C. Severin); Knight collection.

Slaterocoris rubrofemoratus Knight

Slaterocoris rubrofemoratus Knight, 1968, p. 90, fig. 111

Slaterocoris rubrofemoratus: Kelton, 1968, p. 1127, fig. 11

In the key this species runs in the couplet with nicholi, both species with apical half of femora red, but rubrofemoratus with the second antennal segment longer.

Male. Length 4.1 mm, width 1.7 mm. Head: width 1.08 mm, vertex .61 mm. Rostrum, length .88 mm, reaching upon middle coxae. Antennae: segment I, length .30 mm, black; II, 1.02 mm, black, cylindrical, slightly thicker on apical half; III, .71 mm; IV, .30 mm, black. Dorsal surface black, shining; clothed with suberect, yellowish brown simple pubescence, hairs rather sparsely set on hemelytra. Hemelytra with costal margin only slightly arcuate, cuneus turned downward. Membrane uniformly dark fuscous, veins black. Legs black, apical half of femora ruby red; tibiae black but showing reddish on knees. Male claspers distinctive of the species (fig. 17).

Female. Length 3.6 mm, width 1.9 mm, costal margin more strongly arcuate. Head: width 1.19 mm, vertex .71 mm. Antennae: segment I, length .28 mm; II, .88 mm; III, .68 mm, IV, .31 mm. More robust than the male but very similar in color and pubescence.

Host plant, Artemisia tridentata.

Distribution. Nevada and Utah.

Slaterocoris nicholi new species

In the key this species runs in the couplet with rubrofemoratus Kngt. from which it may be separated by the shorter second antennal segment; also may be distinguished by structure of the male right clasper (fig. 16).

Male. Length 4.1 mm, width 1.8 mm. Head: width 1.05 mm, vertex .61 mm; vertex with foveate impression each side just before the sharp

carina, frons smooth. Rostrum, length .82 mm, reaching to middle of the intermediate coxae, fuscous tinted with red. Antennae: segment I, length .24 mm, fuscous brown; II, .88 mm, fuscous brown, more black on apical half, clothed with short pale to brown pubescence; III, .68 mm; IV, .30 mm. Pronotum, length .78 mm, width at base 1.36 mm; rugulose punctate, shining; calli smooth, separated by impressed, transverse rugulose lines; disk sparsely set with rather short, suberect, brownish pubescent hairs. Scutellum finely rugulose.

Dorsal surface black, shining, sparsely clothed with short, recumbent to suberect, brownish to golden pubescent hairs. Cuneus moderately deflexed; membrane and veins uniformly fuscous brown. Ventral surface shining black; venter clothed with brownish pubescence. Legs blackish to reddish, femora strongly red on apical half; tibiae reddish yellow, tips fuscous; hind tibiae fuscous to black, reddish on base, tarsi blackish. Male right clasper (fig. 16) distinctive of the species.

Holotype: ♂ June 22, 1925, Grand Canyon, alt. 7000 ft., Arizona (A.A. Nichol); Knight collection. Paratype: ♂ June 24, 1925, alt. 7000 ft., Williams, Arizona (A.A. Nichol). Named for the collector, Andrew A. Nichol, who as a member of the 5th Marines, fought at Bellou Woods, and was gassed in the battle of the Marne. After months spent in army hospitals, he sought employment in Arizona for health reasons. While employed by the Agricultural Experiment Station in Tucson, he did extensive collecting of Miridae in Arizona. Study of this material over the years has revealed numerous new species, and now after a period of 45 years we name another new one for Andrew Nichol.

Slaterocoris atritibialis (Knight)

Strongylocoris atritibialis Knight, 1938, p. 2, fig. 6
Strongylocoris atritibialis Knight, 1941, p. 80, fig. 114
Slaterocoris atritibialis: Wagner, 1956, p. 280
Slaterocoris atritibialis: Kelton, 1968, p. 1122

Male. Length 4.6 mm, width 2.4 mm. Head: width 1.21 mm, vertex .65 mm. Rostrum, length 1.12 mm, reaching upon middle coxae. Antennae: segment I, length .34 mm; II, 1.26 mm; III, 1.0 mm; IV, .43 mm; black. Pronotum, length 1.12 mm, width at base 1.77 mm. Hemelytra with costal margin strongly arcuate. Dorsal surface nearly glabrous, rugulose, finely punctate; clothed with fine, short pubescence. General coloration, deep black; membrane very dark brown; legs black, tibiae and tarsi dark brown, the hind tibiae always black. Genital claspers distinctive for the species (fig. 12).

Female. Length 4.5 mm, width 2.5 mm; costal margins more strongly arcuate than in the male, but very similar in coloration.

Collected on Solidago spp. and Aster spp.

Distribution. Widely distributed in the eastern United States, and ranging westward into Colorado and Wyoming. CANADA: Alberta, Manitoba, British Columbia, Ontario and Quebec.

Slaterocoris pallidicornis (Knight)

Strongylocoris pallidicornis Knight, 1938, p. 4, fig. 5
Slaterocoris pallidicornis: Kelton, 1968, p. 1123, fig.

Allied to atritibialis Kngt., but differs in the longer second antennal segment; first and second antennal segments and all three pairs of tibiae pale.

Male. Length 4.55 mm, width 1.9 mm. Rostrum, length 1.12 mm, reaching to middle of intermediate coxae. Antennae: segment I, length .34 mm, yellowish, fuscous on base; II, 1.25 mm, pale to yellowish, frequently fuscous on apical one-fifth; III, .91 mm, blackish; IV, .47 mm, fuscous. Pronotum, length .91 mm, width at base 1.55 mm. Hemelytra with costal margin only slightly arcuate. Dorsum sparsely clothed with moderately short, brownish pubescent hairs; black, shining, thickly rugulose punctate; membrane brownish black. Legs black, apices of femora and coxae, tibiae, and tarsi except apical segment, pale to yellowish. Genital claspers distinctive (fig. 8).

Female. Length 4.2 mm, width 2.2 mm. Head: width 1.12 mm, vertex .62 mm. Antennae: segment I, length .35 mm, pale yellowish; II, 1.12 mm, pale yellowish; III, .82 mm, fuscous, narrowly pale at base; IV, .39 mm, fuscous.

Collected mostly on Solidago and Symphoricarpos.

Distribution. United States: Colorado, Minnesota, South Dakota, North Dakota and Wyoming. Canada: Alberta, Manitoba, Nova Scotia, Saskatchewan.

Slaterocoris breviatus (Knight)

Strongylocoris breviatus Knight, 1938, p. 1, fig. 3
Strongylocoris breviatus: Knight, 1941, p. 79, fig. 114
Slaterocoris breviatus: Wagner, 1956, p. 280
Slaterocoris breviatus: Kelton, 1968, p. 1132, fig. 20

Male. Length 4.3 mm, width 2.0 mm. Rostrum, length 1.05 mm, just reaching to base of middle coxae. Antennae: segment I, length .35 mm, yellowish brown, blackish on base; II, 1.3 mm, brownish to black; III, .95 mm, blackish; IV, .47 mm. Pronotum, length .91 mm, width at base 1.51 mm. Hemelytra with costal margin moderately arcuate. Dorsal surface finely and closely rugulose punctate; sparsely clothed with short pale pubescence. General coloration deep black, shining; femora black, apices yellowish; tibiae yellowish, apices and more or less on basal half of hind pair, fuscous. Male genital claspers distinctive (fig. 10).

Female. Length 4.1 mm, width 2.2 mm; costal margins more sharply arcuate than in the male. Head: width 1.2 mm, vertex .64 mm. Antennae: segment I, length .31 mm, yellow, base black; II, 1.17 mm, yellow, apical one-fourth and narrow ring at base, blackish.

Distribution. District of Columbia, Illinois, Maryland, Maine, Massachusetts, Minnesota, Montana, New Hempshire, New York, Pennsylvania and Wyoming. CANADA: Alberta and Nova Scotia.

Breeds on goldenrod (Solidago altissima).

Slaterocoris atratus (Uhler)

Stiphrosoma atrata Uhler, 1894, p. 268
Strongylocoris atratus: Van Duzee, 1917, p. 377 (Cat.)
Strongylocoris atratus: Knight, 1938, p. 6, fig. 9
Slaterocoris atratus: Wagner, 1956, p. 280
Slaterocoris atratus: Kelton, 1968, p. 1135, fig. 23

Male. Length 4.2 mm, width 2.2 mm. Head: width 1.12 mm, vertex rugulose punctate. Rostrum, length .91 mm, extending to base of middle coxae. Antennae: segment I, length .28 mm, black; II, 1.17 mm, black; III, missing. Dorsum clothed with brownish black, suberect, rather long and dense pubescence. Legs black, femur paler on apex. (Descriptions from Kelton.) The male claspers of this species are distinctive (fig. 42).

In a study of types at the California Academy of Sciences in 1931, the writer made the illustration (Fig. 42) from two type specimens conserved there. This illustration was published earlier by Knight (1938). The record of atratus for New Jersey by J. B. Smith (1910) was a misidentification, as no specimens from the eastern United States are recognized today. Also, I may add that when I studied the Van Duzee collection and Academy types in 1931, I did not see any California specimens we could identify as atratus Uhler.

Slaterocoris fuscicornis new species

In the key this species runs in the couplet with mohri Kngt. from which it may be separated by the longer second antennal segment, which in length exceeds width of head; also distinguished by structure of the male right clasper (fig. 36).

Female. Length 4.6 mm, width 2.4 mm. Head: width 1.15 mm, vertex .71 mm, black, a small red spot beneath base of antenna; clothed with erect brownish pubescence. Rostrum, length 1.25 mm, reaching to middle of intermediate coxae, brownish to black. Antennae: segment I, length .34 mm, black; II, 1.25 mm, more slender than segment I, clothed with erect pubescent hairs, the length of which slightly exceeds thickness of segment, black; III, 1.02 mm, black; IV, .52 mm, black. Pronotum, length 1.0 mm, width at base 1.76 mm; calli smooth, only slightly elevated, posterior margin with impressed line; disk only moderately elevated, finely rugulose punctate, clothed with erect, rather long pubescent hairs. Scutellum moderately elevated, transversely rugulose.

Dorsal surface black, clothed with erect, moderately dense fine brownish hairs. Cuneus rather strongly deflexed. Membrane and veins uniformly brownish black. Ventral surface black, strongly pubescent. Legs black, trochanters and tips of femora pallid, tinged with brown; tibia brownish black, front and middle pair pale brownish on apical half; tarsi brownish, apical segment black.

Male. Length 4.3 mm, width 2.2 mm. Head: width 1.05 mm, vertex .61 mm, brownish black. Rostrum, length 1.05 mm, reaching to middle of intermediate coxae. Antennae: segment I, length .30 mm, fuscous brown; II, 1.19 mm, thickness about equal to segment I on apical half, fuscous brown, paler on base; pubescence pale, length not equal to thickness of segment; III, broken. Pronotal length .95 mm, width at base 1.6 mm.

Dorsal surface brownish black, pubescence similar to the male. Membrane and veins dark fuscous brown. Ventral surface brownish black. Legs dark brown, coxae and tips of femora pale, tinged with brown; tibiae pale, tinged with brown. Genital segment distinctive, male right clasper (fig. 36) shows distinctions from mohri Kngt.

Holotype: ♀ May 29, 1950, Camdenton, Missouri (J. C. Schaffner); Knight collection. Allotype: ♂ "Mo." in the C. V. Riley collection. Paratype: ♀ "Mo." in the C. V. Riley collection.

Slaterocoris ovatus new species

In the key this species runs in the couplet with texanus, and may be distinguished by the small size and ovate form; pubescence on dorsum rather short, recumbent and golden brown in color.

Female. Length 3.4 mm, width 1.8 mm. Head: width .98 mm, vertex .54 mm, black. Rostrum, length .92 mm, reaching to apex of middle coxae, brownish black. Antennae: segment I, length .20 mm, black; II, .82 mm, brownish black; III, .51 mm; IV, broken. Pronotum, length .68 mm, width at base 1.32 mm; disk black, closely punctate, calli smooth, basal margin delimited by an impressed line.

Dorsal surface black, costal margins distinctly arcuate, rather thickly clothed with short, recumbent, golden brown pubescence. Costal margin distinctly arcuate; cuneus only moderately deflexed. Membrane fuscous brown, subtranslucent, veins brown. Ventral surface brownish black, shining. Legs dark brown, tibiae and tips of femora pale yellow; tarsi yellow, apical segment fuscous.

Holotype: ♀ May 21, 1938, Barstow, California (John Standish); Knight collection. Paratype: ♀ December 6, San Diego, Texas (E.A. Schwarz).

Slaterocoris mohri (Knight)

Strongylocoris mohri Knight, 1941, p.81, fig. 115
Slaterocoris mohri: Kelton, 1968, p.1130, fig. 16

Female. Length 4.30 mm, width 2.5 mm. Head: width, 1.12 mm, vertex .64 mm. Rostrum, length 1.0 mm, reaching to middle of intermediate coxae. Antennae: segment I, length .30 mm, black, slightly pale on apex; II, .99 mm, cylindrical, tapering to become more slender on basal than on apical half, pale, apex black, pubescence pale; III, .65 mm, black, pale on base; IV, .43 mm, black. Pronotum, length .95 mm, width at base 1.73 mm. Hemelytra strongly arcuate, costal edge sharp, slightly reflexed, cuneus approximately triangular. General coloration black, moderately shining, clothed with long, rather fine, erect pale to brownish pubescence. Legs mostly black, with tips of femora slightly paler; tibiae pale to brownish, darker on basal half, hind pair nearly black; tarsi pale, apical segment black.

Male. Length 4.20 mm, width 2.10 mm. Head: width 1.05 mm, vertex .58 mm. Rostrum, length .95 mm, pale to brownish, reaching upon apex of middle coxae. Antennae: segment I, length .30 mm, pale brownish; II, 1.05 mm, pallid; III, broken, pallid. Color and pubescence very similar to the female. Male right clasper distinctive (fig. 34).

This has been a rare species, seldom collected. The species was described from two females, both taken in Illinois. Dr. Kelton obtained

a male specimen in Illinois which he described and figured (1968). I have found a male specimen that was in U. S. N. M. labeled "Mo." C. V. Riley collection; and present a figure of the male right clasper (fig. 34).

Slaterocoris hirtus (Knight)

Strongylocoris hirtus Knight, 1938, p. 4, fig. 4
Slaterocoris hirtus: Wagner, 1956, p. 280
Slaterocoris hirtus: Kelton, 1968, p. 1130, fig. 15

Distinguished from allied species with erect pubescence by the longer second antennal segment, which exceeds width of head; male claspers distinctive (fig. 45).

Male. Length 4. 6 mm, width 2. 2 mm. Head: width 1. 12 mm, vertex . 56 mm. Rostrum, length 1. 12 mm, just reaching to base of middle coxae. Antennae: segment I, length . 38 mm; II, 1. 43 mm, black, basal one-fifth pale; III, . 86 mm, black; IV, . 47 mm, black. Hemelytra with costal margin moderately arcuate on distal half. Clothed with thickly set, erect, golden brown to blackish pubescence. Legs black, tibiae, tarsi except apical segment, and apices of femora, pale, tibial spines fuscous.

Female. Length 4. 3 mm, width 2. 4 mm. Head: width 1. 12 mm, vertex . 60 mm. Antennae: segment I, length . 35 mm; II, 1. 21 mm, pale, apical one-fourth blackish; III, . 74 mm; IV, . 43 mm. More robust than the male but very similar in color and pubescence. Host plant is Silphium perfoliatum L.

Distribution. Known from Iowa, Illinois and Kansas.

Slaterocoris arizonensis new species

Allied to ambrosiae Kngt., but differs in that length of antennal segment II is slightly greater than width of head; also distinguished by form of the male right clasper (fig. 30).

Male. Length 3. 9 mm, width 1. 6 mm. Head: width . 88 mm, vertex . 47 mm; black, shining. Rostrum, length 1. 02 mm, reaching to apex of middle coxae, fuscous and brown. Antennae: segment I, length . 24 mm, black; II, . 98 mm, black, clothed with fine pubescence, length of bristles about equals thickness of segment; III, . 64 mm, black; IV, . 37 mm, black. Pronotum, length . 71 mm, width at base 1. 29 mm; disk finely punctate and rugulose, clothed with suberect brown pubescence. Scutellum moderately convex, black, transversely striate and rugulose.

Hemelytra black, clothed with recumbent and in part suberect, golden brown pubescence. Membrane and veins evenly shaded with fuscous brown, a small clear spot bordering apex of cuneus. Ventral surface black, venter with suberect pubescence. Legs black, tips of femora and the tibiae pale yellowish, tarsi fuscous. Male right clasper distinctive in form (fig. 30).

Female. Length 4. 1 mm, width 1. 8 mm. Head: width 1. 02 mm, vertex . 58 mm. Rostrum, length 1. 09 mm, reaching upon apex of middle coxae, black. Antennae: segment I, length . 28 mm, black; II, . 98 mm, slender; III, . 68 mm, black; IV, . 37 mm, black. Pronotum, length . 74 mm, width at base 1. 42 mm. Dorsal surface and brown pubescence very similar to the male. Legs black, tibiae and tips of femora yellow.

Holotype: ♂ April 16, 1928, Superior, Arizona (A.A. Nichol); Knight collection. Allotype: ♀ July 26, 1959, 14 mi. north of Luis Moya, alt. 6440 ft. (R.B. Selander and J.C. Schaffner). Paratype: ♂ Aug. 1-10, 1916, James Springs, New Mexico (John Woodgate).

Slaterocoris bispinosus new species

Closely allied to arizonensis, but male claspers are different; right clasper bispinose on basal half (fig. 25); antennal segment II relatively longer; female antennal segment II yellow on basal half.

Male. Length 3.9 mm, width 1.6 mm. Head: width .92 mm, vertex .47 mm. Rostrum, length .95 mm, reaching upon apex of middle coxae. Antennae: segment I, length .27 mm; II, 1.12 mm, black; III, .51 mm; IV, .37 mm. Pronotum, length .72 mm, width at base 1.29 mm; finely punctate, black.

Dorsal surface black, finely punctate, clothed with moderately dense, recumbent and suberect, brownish pubescence; costal margins only moderately arcuate; cuneus moderately deflexed; membrane and veins uniformly black. Ventral surface black, shining; venter with rather long pubescence. Legs black, femora narrowly pale on apex, tibiae pallid, tarsi black. Male right clasper distinctive (fig. 25), bispinose near middle, or where basal half is expanded.

Female. Length 3.6 mm, width 1.7 mm. Head: width .98 mm, vertex .54 mm. Rostrum, length 1.42 mm, reaching upon apex of middle coxae, brownish to black. Antennae: segment I, length .28 mm, black, narrow apex yellowish; II, .98 mm, black, basal half yellow; III, .72 mm, black; IV, .37 mm, black. Pronotum, length .72 mm, width at base 1.26 mm. Dorsal surface black, shining, finely punctate; pubescence similar to the male.

Holotype: ♂ July 28, 1970, 10 mi. south of Rio Verde, S.L.P., Mexico (Hart, Murray, Phelps, Schaffner); U.S.N.M. collection. Allotype: same data as the type. Paratypes: 3♀, taken with the types.

Slaterocoris ambrosiae (Knight)

Strongylocoris ambrosiae Knight, 1938, p. 5, fig. 2
Slaterocoris ambrosiae: Wagner, 1956, p. 280
Slaterocoris ambrosiae: Kelton, 1968, p. 1134, fig. 22

Allied to hirtus Kngt., but readily distinguished by the smaller size, black antennae with shorter second segment; distinguished by the male right clasper (fig. 29).

Male. Length 3.7 mm, width 1.5 mm; costal margin of hemelytra only slightly arcuate. Head: width .92 mm, vertex .48 mm. Rostrum, length .87 mm, reaching upon base of middle coxae. Antennae: segment I, length .23 mm; II, .82 mm, not equal to width of head; III, .60 mm; IV, .30 mm. Dorsal surface thickly clothed with erect, brownish black pubescent hairs. General coloration black, moderately shining; tibiae and tips of femora pale to yellowish, tarsi fuscous to black. Genital claspers distinctive of the species (fig. 29).

Female. Length 3.5 mm, width 1.8 mm. Head: width .99 mm, vertex .56 mm. Antennae: segment I, length .22 mm; II, .92 mm; III, .65 mm; IV, .30 mm. Hemelytra with costal margin more arcuate but very similar to the male in color and pubescence.

Host plant is Ambrosia psilostachya.

Distribution. Arizona, Iowa, Kansas, Missouri, New Mexico, South Dakota. MEXICO: Durango.

Slaterocoris severini new species

Allied to ambrosiae Kngt., but differs in the shorter second antennal segment which in length is less than width of head; male right clasper (Fig. 28) distinctive in form.

Male. Length 3.5 mm, width 1.5 mm. Head: width .93 mm, vertex .51 mm; black, frons and vertex clothed with long, erect brown hairs. Rostrum, length .90 mm, reaching upon intermediate coxae. Antennae: segment I, length .27 mm, black; II, .85 mm, thickness subequal to segment I, brownish black, clothed with fine, short, pale to golden pubescence; III, .68 mm, brown; IV, .34 mm. Pronotum, length .74 mm, width at base 1.26 mm; disk moderately convex, calli poorly defined, disk rugulose punctate. Dorsal surface brownish black, rather thickly clothed with erect, golden brown hair. Cuneus deflexed; membrane fuscous brown, veins and cells shaded darker. Ventral surface brownish black. Legs brownish black, tibiae and tips of femora pale yellow. Male right clasper distinctive (fig. 28).

Holotype: ♂ June 24, 1935, Newton Hills, Canton, South Dakota (H. C. Severin); Knight collection.

Slaterocoris longipennis Knight

Slaterocoris longipennis Knight, 1968, p. 90, fig. 114

Slaterocoris longipennis: Kelton, 1968, p. 1123, fig. 6

Distinguished from related species by the erect golden yellow pubescence, short rostrum, and the very long hemelytra of the male; male claspers distinctive (fig. 24).

Male. Length 5.6 mm, width 2.0 mm. Head: width 1.08 mm, vertex .58 mm, black. Rostrum, length .92 mm, reaching to base of middle coxae. Antennae: segment I, length .30 mm; II, 1.19 mm, cylindrical, thickness almost equal to that of segment I, thickly clothed with long pubescence; III, .88 mm; IV, .34 mm. Pronotum, length .85 mm, width at base 1.53 mm; disk finely rugulose punctate, shining. Dorsal surface black, densely clothed with suberect and erect, long, pale to golden yellow pubescent hairs. Hemelytra very long, base of cuneus located beyond apex of genital segment; membrane dark fuscous, veins nearly black. Legs black, apical one-fifth of femora yellow; tibiae yellowish, shaded with black, more yellow at base, hind pair yellow. Genital segment and claspers distinctive of the species (fig. 24).

Female. Length 3.9 mm, width 1.8 mm; costal margin arcuate. Antennae: segment I, length .30 mm; II, .68 mm, slender, not equal to thickness of segment I; III, .58 mm; IV, .34 mm. Legs with all tibiae yellow, apices fuscous. More robust and the hemelytra shorter than in the male, but color and pubescence very similar.

Host plant is Tetradymia glabrata.

Distribution. California, Nevada, Utah, Wyoming.

Slaterocoris getzendaneri new species

In the key this species runs in the couplet with longipennis Kngt. from which it may be separated by the more triangular shaped cuneus, and by the short and sparsely set pubescence on dorsal surface; right clasper of the male distinctive (fig. 11).

Male. Length 4.1 mm, width 1.9 mm; costal margin distinctly arcuate. Head: width 1.05 mm, vertex .56 mm; black, eyes brown. Rostrum, length 1.0 mm, reaching to middle of intermediate coxae. Antennae: segment I, length .28 mm, fuscous; II, 1.12 mm, fuscous to black, finely pubescent; III, .52 mm; IV, .40 mm. Pronotum, length .78 mm, width at base 1.49 mm; disk moderately convex, surface finely punctate. Dorsal surface black, sparsely clothed with short golden pubescence; cuneus deflexed; membrane and veins black. Ventral surface black, venter clothed with rather long, fine brownish hairs. Legs black, tips of coxae and tips of femora pale to yellowish, tibiae orange yellow. Male right clasper distinctive (fig. 11).

Holotype: ♂ July 8, 1929, Orting, Washington (C.W. Getzendaner); Knight collection.

Slaterocoris flavipes Kelton (fig. 19)

Slaterocoris flavipes Kelton, 1968, p. 1126, fig. 9

Data drawn from the original description.

Male. Length 3.36 mm, width 1.54 mm. Head: width 1.05 mm; vertex very faintly punctate and rugulose; frons smooth; pubescence silvery, long and dense. Rostrum, length .84 mm, reaching to base of middle coxae. Antennae: segment I, length .27 mm, brownish orange, base black; II, .80 mm, middle paler; III, .59 mm, brown; IV, .31 mm, brown. Pronotum, width 1.48 mm, calli very finely punctate. Femur reddish yellow, base often black, tibiae orange.

Female. Length 3.6 mm, width 1.82 mm. Head: width 1.19 mm. Antennae: segment I, length .28 mm, light brown, base black; II, .73 mm, brown; III, .45 mm, black; IV, .31 mm, black. Very similar to the male in color and pubescence. This species may be recognized by the reddish yellow legs, and by the long silvery pubescence.

Described from Indio, California, and San Diego County (E. P. Van Duzee).

Slaterocoris sparsus Kelton

Slaterocoris sparsus Kelton, 1968, p. 1125, fig. 7

Male. Length 3.1 mm, width 1.54 mm. Head: width 1.12 mm; vertex and frons smooth; pubescence brown, short and sparse. Rostrum, length .94 mm, reaching upon the middle coxae. Antennae: segment I, length .24 mm; II, .84 mm, black, paler at base; III, .66 mm, black; IV, .31 mm, black. Pronotum, width 1.33 mm; calli finely punctate and sparsely pubescent. Pubescence on dorsum brown to black, short and sparse. Legs yellow, base of femur and apex of tibia blackish. Legs yellow, base of femur and apex of tibia blackish. Genital segment distinctive, see right clasper (fig. 21).

Female. Length 3.8 mm, width 1.96 mm. Head: width 1.29 mm. Antennae: segment I, length .24 mm, yellow, base black; II, .85 mm,

brown, paler towards base; III, .70 mm, black; IV, .40 mm, black. Pronotum, width 1.61 mm. More robust than the male but very similar in pubescence and coloration.

Distribution. Described from Hot Springs, California, and Ventura County, California.

Slaterocoris pilosus Kelton

Slaterocoris pilosus Kelton, 1968, p. 1127, fig. 12

Male. Length 3.36 mm, width 1.54 mm. Head: width 1.12 mm; frons smooth, pubescence pale, dense. Rostrum, length .87 mm, reaching to middle coxae. Pronotum, width at base 1.29 mm; calli smooth. Antennae: segment I, length .24 mm, yellowish brown; II, .80 mm, black, often yellowish brown on basal half; III, .63 mm, black; IV, .28 mm, black.

Female. Length 3.43 mm, width 1.68 mm. Head: width 1.19 mm. Antennae: segment I, length .24 mm, yellow, darker at base; II, .70 mm, yellow, apex darker; III, .52 mm, black; IV, .28 mm, black. Pronotum, width at base 1.36 mm. More robust than the male, but very similar in color and pubescence; second antennal segment more yellowish.

Distinguished by the small size, silvery pubescence on the dorsum, by the smooth frons, and by the male claspers (fig. 15).

Collected on Artemisia tridentata.

Distribution. CANADA: British Columbia. UNITED STATES: Idaho, Washington.

Slaterocoris texanus new species

In the key this species runs in the couplet with ovatus, but the body form is more elongate; antennal segment II is yellowish with base dark; male right clasper distinctive (fig. 39).

Male. Length 3.4 mm, width 1.8 mm. Head: width 1.05 mm, vertex .58 mm. Rostrum, length .85 mm, reaching upon middle coxae, brownish black. Antennae: segment I, length .28 mm, yellowish, fuscous at base; II, .82 mm, fuscous brown, with fine short pubescence; III, .52 mm, fuscous; IV, missing. Pronotum, length .74 mm, width at base 1.42 mm; finely rugulose punctate.

Dorsal surface black, shining, finely rugulose punctate. Pubescence short, sparse, recumbent, pale to golden. Costal margins only slightly arcuate; cuneus rather strongly deflexed. Membrane uniformly dark fuscous, veins more black. Ventral surface black, shining. Legs black, tibiae and apical half of femora orange yellow, tips of trochanters pale; tarsi black. Male right clasper distinctive of the species (fig. 39).

Holotype: ♂ Aug. 15, 1969, Big Bend National Park, South Rim Trail, Texas (Board and Hafernik); U.S.N.M. collection.

Slaterocoris bifidus new species

This species runs in the key to near croceipes Uhl. but differs in having the membrane pale, the veins dark so they stand out clearly; the male right clasper with a bifid process near middle (fig. 40).

Male. Length 3.7 mm, width 1.7 mm. Head: width 1.07 mm, vertex .58 mm. Rostrum, length .82 mm, reaching upon front coxae. Antennae: segment I, length .28 mm, black; II, .82 mm, cylindrical, slender, not

attaining thickness of segment I, pale pubescent; III, .40 mm, black; IV, .35 mm, fuscous. Pronotum, length .72 mm, width at base 1.39 mm; disk finely punctate, shining.

Dorsal surface shining black, clothed with sparsely set, recumbent to suberect, pale to golden pubescent hairs. Membrane pale, almost clear on basal half including areoles, making the veins stand out more clearly than in other species; apical half of membrane infuscated. Ventral surface black, shining, the venter pale pubescent. Legs black, tips of femora and the tibiae pallid. Male right clasper distinctive (fig. 40).

Holotype: ♂ May 19, 1940, White Valley, Millard County, Utah (R. W. Fautin); Knight collection.

Slaterocoris croceipes (Uhler)

Stiphrosoma croceipes Uhler, 1893, p. 373
Strongylocoris croceipes: Tucker, 1907, p. 60
Slaterocoris croceipes: Knight, 1968, p. 90, fig. 110
Slaterocoris croceipes: Kelton, 1968, p. 1128, fig. 13

Male. Length 3.6 mm, width 1.6 mm. Head: width 1.15 mm, vertex .61 mm; black, smooth and shining. Rostrum, length .95 mm, reaching near apex of middle coxae. Antennae: segment I, length .27 mm, black, brownish yellow above on apical half; II, 1.10 mm; III, .74 mm; IV, .30 mm; black. Pronotum, length .81 mm, width at base 1.42 mm; disk rugulose punctate, calli smooth. Dorsal surface black, shining, clothed with sparsely set, suberect to recumbent, golden brown pubescence. Ventral surface shining black. Femora orange yellow, black on basal half, tibiae pale yellow, tarsi black. Genital claspers distinctive of the species (fig. 14).

Female. Length 3.7 mm, width 1.9 mm. Head: width 1.3 mm, vertex .78 mm. Rostrum, length 1.09 mm, reaching upon apex of middle coxae. Antennae: segment I, length .30 mm, black; II, 1.02 mm, slender, black, more brownish on middle; III, .64 mm; IV, .30 mm, black. Very similar to the male in color, pubescence and punctate dorsum.

I collected this species on Chrysothamnus sp. around American Fork, Utah, and on Chrysothamnus nauseosus at Mercury, Nevada (Knight 1968).

Distribution. Arizona, California, Colorado, Nevada, Oregon and Utah.

Slaterocoris apache Kelton

Slaterocoris apache Kelton, 1968, p. 1126, fig. 10

This description is drawn from a paratype specimen.

Male. Length 4.2 mm, width 1.75 mm. Head: width 1.22 mm, vertex .62 mm; smooth, frons weakly striate. Rostrum, length .95 mm, reaching to base of middle coxae. Antennae: segment I, length .34 mm, black; II, 1.19 mm, black, pale pubescent; III, .88 mm; IV, .30 mm; black. Pronotum, length .92 mm, width at base 1.46 mm. Pubescence on dorsum silvery, rather long, sparsely set, not crowded; surface shining black, finely rugulose punctate. Membrane and veins dark fuscous. Legs black, tips of coxae, apical one-third of femur, orange yellow, tibiae pallid to yellow, tarsi fuscous. Genital segment distinctive, right clasper furnishes a good character (fig. 13).

Female. Length 4.0 mm, width 1.87 mm; costal margins moderately arcuate. Antennae: segment I, length .34 mm, brownish black, apex and dorsal surface more yellowish brown. Slightly more robust than the male, but color and pubescence quite similar.

Collected mostly on Chrysothamnus nauseosus.

Distribution. Colorado, Utah.

Slaterocoris basicornis new species

Runs in the key near croceipes Uhl., but differs from other species by the yellow first antennal segment; the male right clasper differs from others with a pair of bidentate spines set near middle (fig. 6).

Male. Length 3.6 mm, width 1.5 mm. Head: width 1.09 mm, vertex .61 mm. Rostrum, length .85 mm, reaching upon apex of middle coxae. Antennae: segment I, length .28 mm, yellow, narrowly fuscous on base; II, .88 mm, black, basal one-fourth yellow; III, .64 mm, black; IV, .30 mm, black. Pronotum, length .78 mm, width at base 1.46 mm; disk finely punctate, calli rather narrow, poorly defined, finely and sparsely pubescent.

Dorsal surface black, shining, pubescence sparse, short, inconspicuous, mostly pallid hairs, surface nearly glabrous. Cuneus moderately deflexed. Membrane and veins fuscous black, central area somewhat clear. Ventral surface black, shining. Legs black, apical one-fourth of femora and the tibiae orange yellow, tarsi black. Male right clasper distinctive (fig. 6).

Holotype: ♂ August 14, 1969, Green Gulch, Big Bend National Park, Brewster County, Texas (Board and Hafernik); U.S.N.M. collection.

Slaterocoris custeri new species

Allied to sheridani Kngt. but differs in the shorter antennal segments; length of segment II not equal to length of fore tibia; male right clasper distinctive (fig. 3).

Male. Length 3.4 mm, width 1.6 mm. Head: width 1.08 mm, vertex .57 mm; black, eyes brown. Rostrum, length .78 mm, reaching upon middle of intermediate coxae, brownish to black. Antennae: segment I, length .25 mm, fuscous to yellowish; II, .78 mm, yellow shaded with fuscous; III, .40 mm, fuscous; IV, .34 mm, fuscous. Pronotum, length .72 mm, width at base 1.97 mm, black, shining, finely punctate; pubescence short, sparsely set.

Dorsal surface black, shining, sparsely clothed with short, recumbent, pale yellowish to golden pubescence. Costal margins nearly parallel, cuneus moderately deflexed; membrane clear to pale fuscous in part, veins fuscous. Ventral surface black, shining. Legs black, apical one-third of femora pale to yellowish, tibiae pale yellowish, tarsi fuscous to black; fore tibia length .85 mm. Genital segment distinctive, right clasper (fig. 3) distinctive of the species.

Holotype: ♂ August 19, 1927, Custer, South Dakota (H.H. Knight); Knight collection. Paratypes: 1♂, taken with the type. 1♀ July 30, 1927, Sundance, Wyoming (H.H. Knight).

Slaterocoris woodgatei new species

Allied to custeri, but with longer antennal segments; segment II subequal in length to the fore tibia; male right clasper (fig. 5) distinctive, with two spines arising from a common base near middle.

Male. Length 3.8 mm, width 1.7 mm; costal margins slightly arcuate. Head: width 1.09 mm, vertex .58 mm. Rostrum, length .85 mm, reaching to apex of middle coxae. Antennae: segment I, length .27 mm, fuscous brown; II, .85 mm, brownish black; III, .44 mm, fuscous; IV, .34 mm, brown. Pronotum, length .85 mm, width at base 1.5 mm; black, shining, rugulose punctate, calli smooth.

Dorsal surface black, shining, finely punctate, sparsely clothed with a few short pale to golden pubescent hairs, appearing nearly glabrous. Membrane and veins uniformly dark fuscous. Ventral surface brownish black, venter with golden yellow suberect pubescence. Legs brownish black, apices of femora and the tibiae, yellow; tarsi fuscous to black. Male right clasper (fig. 5) distinctive of the species.

Holotype: ♂ June 7-17, 1916, alt. 6400 ft., Jemez Springs, New Mexico (John Woodgate); Knight collection. Paratypes: 2♂, taken with the holotype.

Slaterocoris burkei new species

In the key this species runs in the couplet with sheridani Kngt., but the male right clasper (fig. 26) is very different with the apex bifid.

Male. Length 4.1 mm, width 1.6 mm. Head: width 1.12 mm, vertex .61 mm. Rostrum, length .95 mm, reaching upon base of middle coxae. Antennae: segment I, length .30 mm; II, 1.05 mm, cylindrical, black, pale pubescent; III, .85 mm, black; IV, .34 mm, black. Pronotum, length .78 mm, shining black, rugulose punctate; calli smooth, separated by impressed line and punctures; disk and margins bearing rather long, erect, pale yellowish hairs. Scutellum rather strongly transversely rugulose. Hemelytra with costal margins nearly parallel; surface shining black, rugulose punctate; bearing rather sparsely set suberect and erect, pale golden hairs. Membrane and veins rather evenly shaded by dark fuscous, veins somewhat darker. Ventral surface black, shining, bearing rather long suberect to erect golden pubescence. Legs black, apical one-fifth of femora and the tibia pallid, tarsi black. Male right clasper distinctive (fig. 26) with apex bifid.

Holotype: ♂ July 22, 1967, 2 mi. west of Ridgeway, Colorado (H.H. Burke); U.S.N.M. collection.

Slaterocoris sheridani Knight

Slaterocoris sheridani Knight, 1968, p.92, fig.113

Slaterocoris sheridani: Kelton, 1968, p.1125, fig.8

Allied to robustus (Uhler) in form of claspers (fig. 2), but distinguished by the narrower head, shorter pubescence, and by yellow color of the tibiae and apices of femora.

Male. Length 3.5 mm, width 1.56 mm. Head: width 1.05 mm, vertex .54 mm. Rostrum, length .85 mm, reaching upon base of middle coxae. Antennae: segment I, length .30 mm, black; II, .85 mm, thickness at apex equal to segment I, clothed with short, fine yellowish pubescence; III, .61 mm, black; IV, .32 mm. Pronotum, length .75 mm, width at base 1.32 mm; disk finely rugulose punctate, shining. Dorsal surface black, shining, clothed with rather short, recumbent, and in part suberect, golden yellow pubescent hairs. Hemelytra average in length;

membrane dark fuscous to black, veins black. Legs black, apical one-third of femora and the tibiae, golden yellow. Genital segment and claspers distinctive of the species (fig. 2).

Female. Length 3.7 mm, width 1.82 mm. Head: width 1.19 mm, vertex .72 mm. Antennae: segment I, length .24 mm, brownish; II, .85 mm, yellowish brown; III, .58 mm, black; IV, .30 mm, black. Pronotum, length .71 mm, width at base 1.53 mm. More robust than the male, but color and pubescence very similar.

Distribution. Arizona, Colorado, New Mexico, and Wyoming.

Slaterocoris fuscomarginalis new species

Separated from related species by the unusual infuscation of the membrane; clear in the middle but apical margin bordered by band of dark fuscous, areoles clear but the veins dark fuscous including edge of adjoining membrane; male right clasper distinctive (fig. 35).

Male. Length 3.7 mm, width 1.6 mm. Head: width 1.05 mm, vertex .58 mm. Rostrum, length .85 mm, reaching to middle of intermediate coxae. Antennae: segment I, length .24 mm; II, 1.05 mm, black, pale pubescent; III, broken. Pronotum, length .74 mm, width at base 1.36 mm; disk black, shining, rugulose punctate, calli rather obscure. Hemelytra black, shining, closely rugulose punctate.

Dorsal surface rather sparsely set with suberect, pale to golden hairs. Cuneus moderately deflexed. Membrane pale, apical margin bordered with a wide band of dark fuscous, veins including a narrow margin of membrane, dark fuscous. Ventral surface shining black, pale pubescent. Legs black, tips of femora, and the tibiae pallid to yellowish. Right genital clasper (fig. 35) distinctive of the species.

Holotype: ♂ May 19, 1940, White Valley, Millard County, Utah (R. W. Fautin) Knight collection. Mr. Fautin, doing research on the food of trout, was sweeping the banks of a stream when this species was collected. Paratypes: ♂ June 9, 1969, Snowville, Box Elder Co., Utah (G. F. Knowlton). ♂ June 18, 1969, So. Curlew Valley, Box Elder Co., Utah (G. F. Knowlton). ♂ June 13, 1969, 6 mi. NW of Holbrook, Idaho (G. F. Knowlton).

Slaterocoris utahensis Knight

Slaterocoris utahensis Knight, 1968, p. 92, fig. 115

Slaterocoris utahensis: Kelton, 1968, p. 1123, fig. 5

Allied to longipennis but size somewhat smaller, and pubescence pallid; distinguished by the male claspers (fig. 22).

Male. Length 4.8 mm, width 1.9 mm; costal margin nearly straight. Head: width 1.0 mm, vertex .51 mm. Rostrum, length .74 mm, reaching upon the middle coxae. Antennae: segment I, length .30 mm; II, 1.02 mm, cylindrical, thickness less than segment I; III, .72 mm; IV, .30 mm. Dorsal surface black, rather densely clothed with suberect, long pallid pubescence, not golden yellow as in longipennis. Hemelytra rather long, base of cuneus just above tip of genital segment; membrane dark fuscous, veins black. Legs black, tips of femora pale yellowish; tibiae black, hind pair more nearly fuscous. Genital claspers distinctive (fig. 22).

Female. Length 3.7 mm, width 1.8 mm. Head: width 1.10 mm, vertex .66 mm. Antennae: segment I, length .32 mm; II, .78 mm; III, .62

mm; IV, .34 mm. Legs black, tips of femora and the tibiae yellow. More robust than the male, color except tibiae and the pubescence very similar to the male.

Distribution. Colorado, Utah, and Idaho.

Slaterocoris sculleni new species

In the key this species runs in the couplet with utahensis Kngt., but differs in having yellow tibiae; male right clasper distinctive (fig. 23).

Male. Length 4.2 mm, width 1.5 mm; costal margins nearly straight. Head: width 1.02 mm, vertex .43 mm. Rostrum, length .85 mm, reaching upon base of middle coxae. Antennae: segment I, length .30 mm; II, 1.02 mm, brownish black, more slender on basal half, with pale to yellowish pubescence; III, .71 mm; IV, broken. Pronotum, length .78 mm, width at base 1.36 mm; disk rugulose punctate, calli smooth. Dorsal surface thickly clothed with rather long, suberect and recumbent, pallid pubescence. Membrane and veins rather uniformly fuscous brown. Legs black, tips of femora pallid, tibiae pale yellowish, tarsi fuscous. Male right clasper distinctive (fig. 23).

Holotype: ♂ August 19, 1930, Crater Lake Park, South Rim, alt. 7100 ft., Oregon (H.A. Scullen); Knight collection. Named for the collector, Dr. H.A. Scullen, specialist with the Sphecidae, Hymenoptera, who took his Ph. D. degree at Iowa State College, in the early years.

Slaterocoris tibialis new species

In the key this species runs beyond croceipes Uhl.; the right clasper is trifid on apex, but structure of basal half and spine near middle separate the species (fig. 27).

Male. Length 4.2 mm, width 1.6 mm; costal margins nearly parallel. Head: width 1.15 mm, vertex .61 mm. Rostrum, length .88 mm, reaching upon the middle coxae. Antennae: segment I, length .28 mm, black, narrow apex pallid; II, 1.05 mm, black, pale pubescent; III, broken. Pronotum, length .74 mm, width at base 1.45 mm; disk rugulose punctate, calli smooth. Dorsal surface black, shining, finely rugulose punctate; clothed with sparsely set, suberect, medium long, pale to golden, pubescent hairs. Cuneus moderately deflexed. Membrane and veins uniformly dark fuscous. Ventral surface shining black. Legs black, tips of femora and the tibiae orange yellow, tarsi fuscous. Male right clasper distinctive (fig. 27), trifid on apex and with a sharp spine at middle of clasper.

Holotype: ♂ June 17, 1934, 17 mi. east of Klamath Falls, Oregon (Joe Schuh); Knight collection. Paratypes: 1♂, taken with the type. 2♂ July 19, 1953, Lower Klamath Lake, Oregon (Joe Schuh).

Slaterocoris rarus new species

In the key to species this one runs to the end of the key. It is unusual in many respects with the male claspers (fig. 44) distinguishing it from all other species.

Male. Length 3.7 mm, width 1.8 mm; costal margins rather strongly arcuate. Head: width .98 mm, vertex .52 mm. Rostrum, length .95 mm, reaching to near apex of middle coxae. Antennae: segment I, length .30 mm, yellow, base fuscous; II, .98 mm, dusky yellow, apical one-third and annulus at base, blackish, clothed with pale yellowish short

pubescence; III, .80 mm, fuscous; IV, .40 mm, fuscous. Pronotum, length .85 mm, width at base 1.32 mm; disk finely rugulose punctate; calli smooth, slightly convex, with a strong puncture at the inner angle of each callus. Dorsal surface black, shining, minutely punctate; pubescence inconspicuous, nearly glabrous, sparsely set with short, recumbent, pale to golden pubescent hairs. Cuneus moderately deflexed. Membrane and veins dark fuscous brown. Ventral surface brownish black, venter more strongly pubescent. Genital segment distinctive, right clasper (fig. 44) bifid on apex.

Holotype: ♂ July 30, 1915, Batavia, New York (H.H. Knight); Knight collection. This specimen was taken in my first year of specialized collecting of Miridae. I eventually collected all known eastern species of Slaterocoris, but of rarus I never collected another specimen, nor have I seen a second specimen of this species.

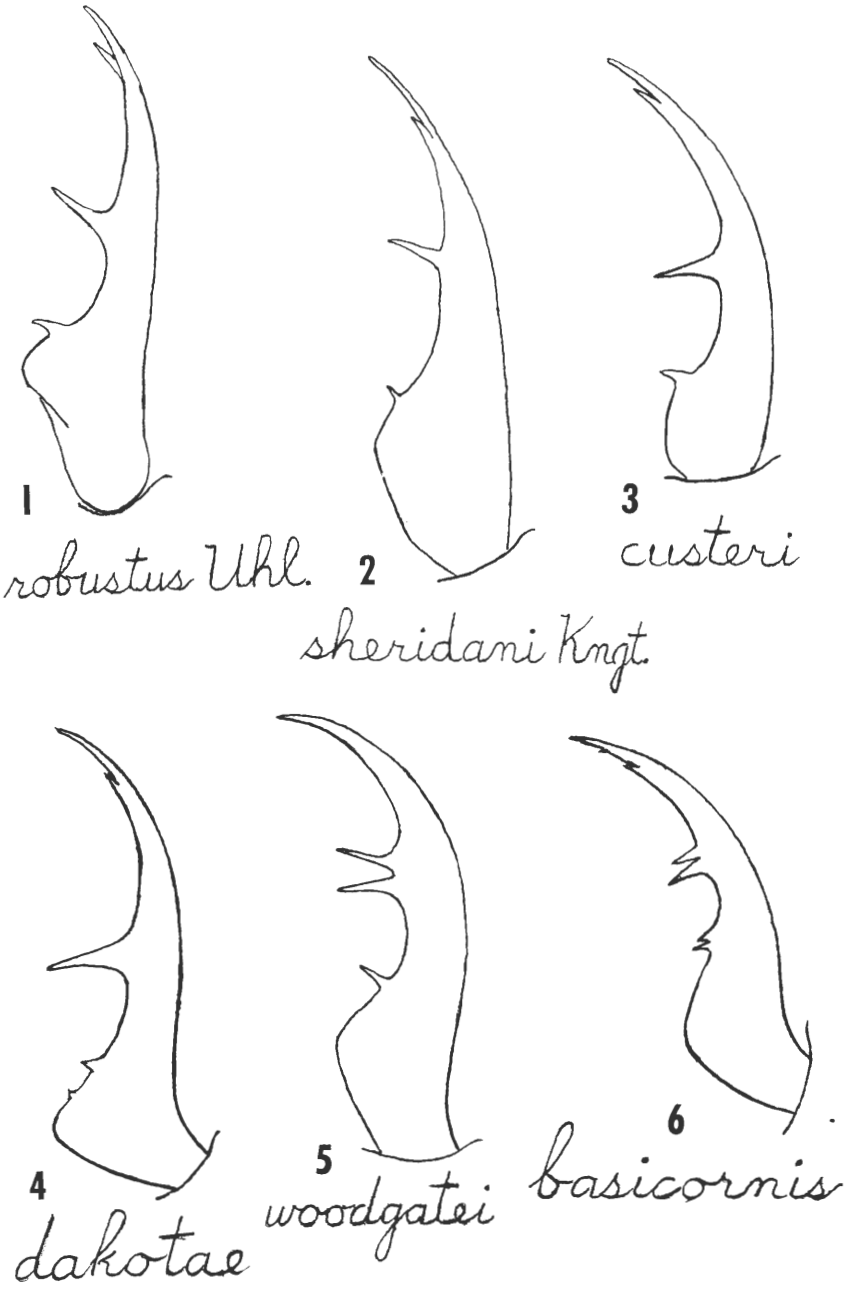
Slaterocoris minimus new species

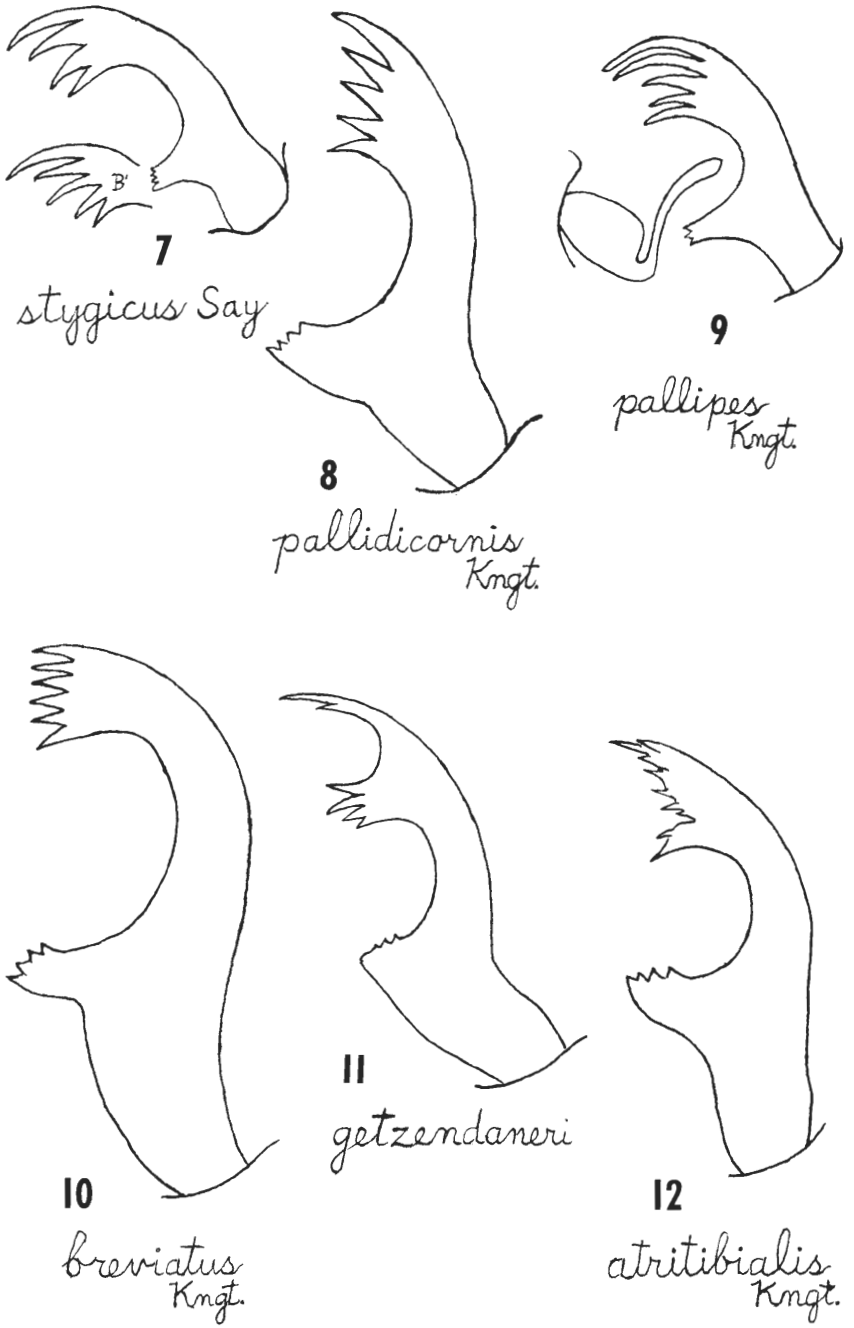
Distinguished by the small size, dorsal surface nearly glabrous, and length of second antennal segment distinctly greater than width of head. Antennal segment I pale yellow, base black; antennal segment II yellowish on basal one-third, but with a black annulus at base. Male genital claspers distinctive of the species (fig. 46). In the key this species runs to the couplet with getzandaneri, but differs in the small size and yellow first antennal segment.

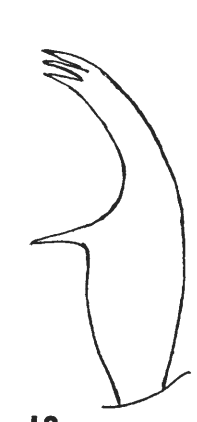
Male. Length 3.2 mm, width 1.9 mm. Head: width 1.0 mm, vertex .57 mm, black, eyes brown. Rostrum, length .95 mm, reaching to posterior margin of mesosternum. Antennae: segment I, length .33 mm, pale yellow, base blackish; II, 1.09 mm, basal one-fourth pale yellow, base with a black annulus; III, .74 mm, fuscous to black; IV, .47 mm, black. Pronotum, length .81 mm, width at base 1.39 mm; disk finely punctate, calli smooth, moderately convex.

Dorsal surface black, shining, nearly glabrous, sparsely set with short pale hairs; costal margins moderately arcuate; membrane and veins uniformly dark fuscous or black. Ventral surface black, moderately shining. Femora black, apical one-fourth yellow; tibiae yellowish, somewhat infuscated apically. Genital segment distinctive, apex of right clasper fan-shaped, the edge serrate with six short teeth (fig. 46).

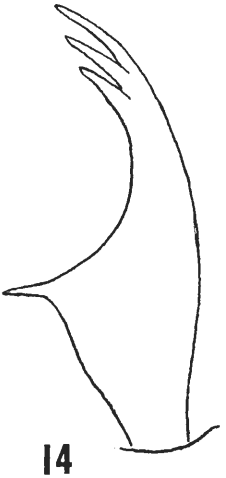
Holotype: ♂ June 29, 1970, Peshtigo River, Forest County, Wisconsin (A. E. Akin); Knight collection.


1
robustus Uhl.
2
sheridani Kngt.
3
custeri
4
dakotae
5
woodgatei
6
basicornis

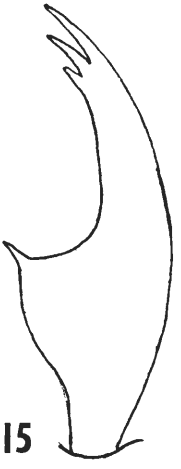

B'
7
stygicus Say
8
pallidicornis
Kngt.
9
pallipes
Kngt.
10
breviatus
Kngt.
11
getzendaneri
12
atritibialis
Kngt.



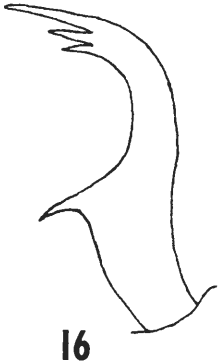
13
apache Kelt.



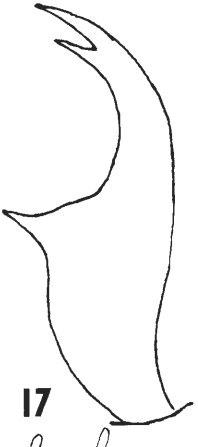
14
croceipes Uhl.



15
pilosus Kelt.

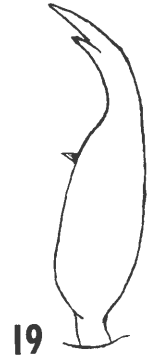


16
nicholi



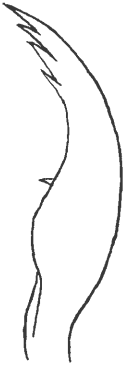
17
rubrofemoratus
Kngt.

18
knowltoni

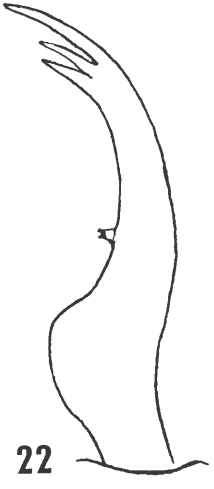


19
flavipes Kelt.

20
nevadensis



21
sparsus Kelt.



22
utahensis
Kngt.

23
sculleni

24
longipennis
Kngt.

25
bispinosus

26
burkei

27
tibialis

28
severini

29
ambrosiae Kngt.

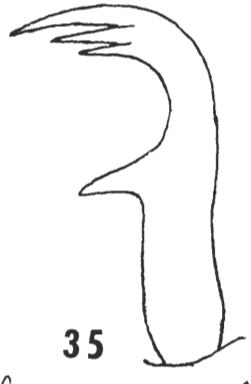
30
arizonensis

31
argenteus Kelt.

32
simplex Kelt.

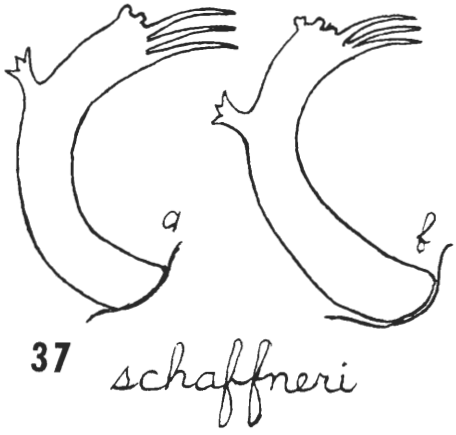
33
grandis Kelt.

34
mohri Kngt.



35
fuscomarginalis

36
fuscicornis



37 schaffneri

38 digitatus

39 texanus

40 bifidus

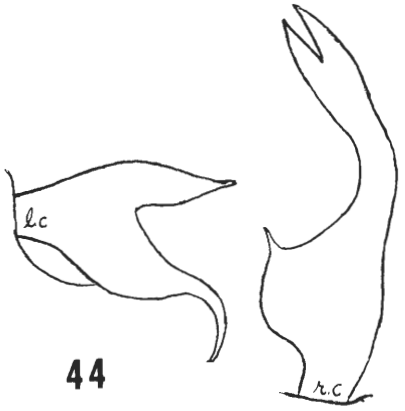
41 alpinus Kelt.

42

atratus Uhl.

43

solidaginis Kelt.



44

rarus

45

hirtus Kngt.

46

minimus

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THE LUMBOSACRAL PLEXUS (Plexus lumbosacralis) OF THE GOAT (Capra hircus)

N. G. Ghoshal[1] and R. Getty[2]

ABSTRACT. The lumbosacral plexus of the goat has been grossly studied on fifteen embalmed specimens. Breed, age, sex and body weight of the animals were not considered in this investigation.

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INTRODUCTION

Morphological description of the lumbosacral plexus of the goat is not available in the literature. Linzell (1959) described the variable origins of different nerves while studying the innervation of the mammary glands in the sheep and goat with observations on the lumbosacral autonomic nerves.

For a better understanding of the species differences, if any, this investigation was undertaken. An attempt has been made to be as consistent as possible with the Nomina Anatomica Veterinaria (1968).

MATERIAL AND METHODS

Fifteen goats have been dissected for this investigation. Breed, age, sex, and body weight of the animals were not considered in this study.

The animals were anesthetized with pentobarbitol sodium and exsanguinated via a cannula placed in the right common carotid artery. The specimens were embalmed with the following solution: isopropyl alcohol, 60%; formalin, 4%; phenol, 6%; corn syrup, 2.5%; and water, 27.5%. The specimens thus prepared were kept in a cooler for 2 to 3 days and were then dissected.

The composite findings are illustrated in Figs. 1 and 2 drawn from the ventral and lateral aspects, respectively.

RESULTS

Lumbar plexus

1. The ventral branch of the L_1 nerve is called the iliohypogastric nerve. It emerged through the intervertebral foramen between the first and second lumbar vertebrae in a caudoventral manner. At first it coursed between the Mm. quadratus lumborum and psoas major and gave off a delicate twig to join the ilioinguinal nerve immediately after the

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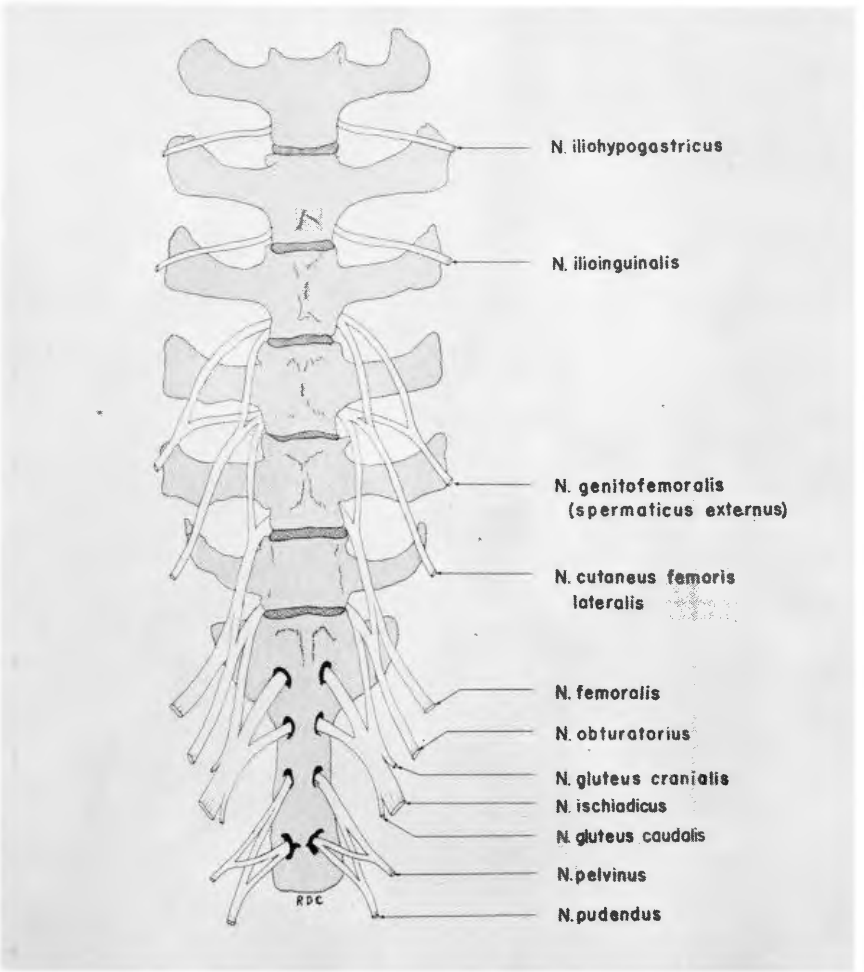

Figure 1. Lumbosacral plexus of the goat (ventral view).

latter's emergence (one specimen). Then it passed along the deep face of the aponeurotic origin of the M. transversus abdominis for a short distance and, after piercing the latter, split into a medial and lateral branch.

The relatively stronger medial branch coursed between the Mm. transversus abdominis and obliquus internus abdominis. On its course it furnished twigs to both muscles and finally penetrated the M. rectus abdominis. Some of its fibers terminated in the skin of the ventral abdominal wall as the ventral cutaneous branch (Ramus cutaneus ventralis).

The lateral branch was slender and pierced the M. obliquus internus abdominis at approximately the dorsal third of the abdominal wall. It extended farther ventrally between the latter muscle and the M. obliquus

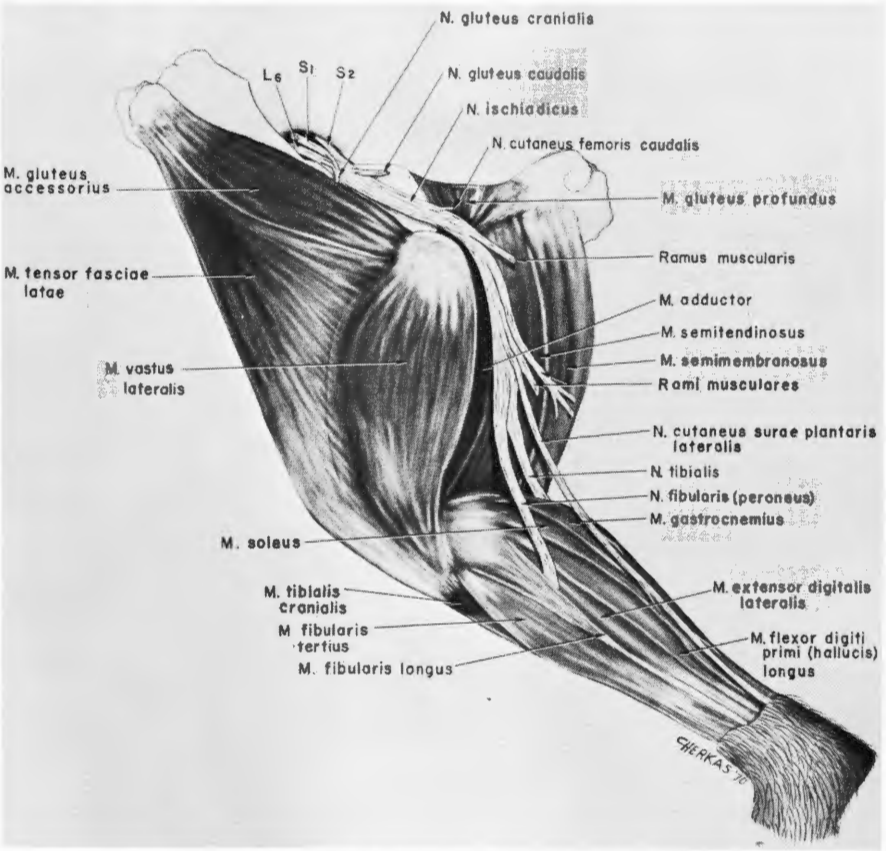

Figure 2. Deep dissection of gluteal and thigh regions (lateral view).

externus abdominis and penetrated the M. obliquus externus abdominis near the middle of the abdominal wall. In this position it lay between the Mm. obliquus externus abdominis and cutaneus trunci. After supplying them it ramified in the skin and fascia of the ventral third of the lateral abdominal wall as the lateral cutaneous branch (Ramus cutaneus lateralis).

2. The ventral branch of the L_2 nerve is called the ilioinguinal nerve. It emerged through the intervertebral foramen caudal to the corresponding vertebra and immediately received a delicate twig from the iliohypogastric nerve (in one specimen), as mentioned before. It inclined more caudoventrad while coursing between the Mm. quadratus lumborum and psoas major and innervated them by muscular twigs. At the lateral edge of the former muscle it gave off a very large nerve which passed caudoventrally between the transverse fascia and M. transversus abdominis, accompanying the muscular twigs of the cranial branch of the A. circumflexa ilium profunda for a short distance and finally entered

the M. rectus abdominis. In one specimen (out of 15), this large branch joined the contribution from the ventral root of L_3 to constitute the genitofemoral nerve. On its way it innervated the abdominal musculature at several places. The ilioinguinal nerve at first extended along the deep face and then pierced the aponeurotic origin of the M. transversus abdominis and split into medial and lateral branches of almost equal size which pursued similar course as described for the iliohypogastric nerve.

3. The genitofemoral nerve is known as the external spermatic nerve in veterinary textbooks. In the literature, it is also referred to as the inguinal or genital nerve due to its disposition and supply, respectively. It emerged at a more oblique angle through the intervertebral foramen caudal to the third lumbar vertebra between the Mm. psoas major and psoas minor which received small twigs. In one specimen (out of 15) the genitofemoral nerve also received a contribution from the ventral root of the L_2. Linzell (1959) observed it as arising from L_3 in 9 cases, and in 12 cases from the L_3 and L_4; the latter was also observed by us. From its cranial aspect, shortly after its emergence, it detached a slender branch which at first coursed between the transverse fascia and the M. transversus abdominis and at approximately the middle of the abdominal wall came to lie caudal to the caudal branch of the A. circumflexa ilium profunda. At this level it pierced the M. transversus abdominis and supplied the lateral abdominal musculature. The genitofemoral nerve during its course gave off a very slender communicating branch to the N. cutaneus femoris lateralis and received a branch from L_4 nerve. Later, it continued in a very oblique manner over the ventral border of the M. psoas major. In its further course it split into several branches entwining the A. circumflexa ilium profunda, immediately before its bifurcation into cranial and caudal branches. A few twigs entered the M. transversus abdominis. Later, these branches coursed along the A. iliaca externa and finally descended in the medial part of the inguinal canal, accompanying the external pudic vessels. A Ramus femoralis of this nerve could not be ascertained in the goat as in man.

4. The N. cutaneus femoris lateralis - The lateral cutaneous femoral nerve emerged through the intervertebral foramen caudal to the fourth lumbar vertebra between the Mm. psoas major and psoas minor. Linzell (1959) described a variable origin of this nerve. He observed it as arising from L_3 and L_4 in two cases, similar to our findings, while in 12 cases he found it arising from L_4. At this position it released a few muscular twigs to the neighboring muscles. Close to the ventral border of the M. psoas major it received a slender communicating branch given off the ventral branch of the third lumbar nerve. Following the union the lateral cutaneous femoral nerve continued caudoventrad, at first being lateral to the A. circumflexa ilium profunda. Subsequently, it pierced the lateral abdominal musculature together with the caudal branch of the preceding vessel, and descended on the medial surface of the M. tensor fasciae latae. Near the subiliac lymph nodes it divided into two branches; the cranial branch distributed itself to the fascia and skin of the ventrolateral aspect of the lateral abdominal wall, while the caudal branch innervated the fascia and skin of the thigh and the lateral surface of the stifle joint.

5. The N. femoralis - The femoral nerve mainly derived its fibers from the ventral branch of the L_5 nerve and a communicating branch from the ventral root of the preceding nerve. According to Linzell (1959) the femoral nerve most frequently arose from the L_5 and next most common origin as L_4 and L_5; the latter was also observed by us. It passed between the Mm. psoas major and psoas minor in an oblique caudoventral direction and released a muscular twig to innervate the M. psoas major. Later, it coursed between the Mm. psoas major and iliacus, where it gave off at least two muscular branches to supply them.

The saphenous nerve (N. saphenus) was given off at the lateral border of the M. iliopsoas by the femoral nerve. It accompanied the parent nerve, being medial to and parallel with same, until the femoral nerve entered the M. quadriceps femoris. Thereafter, the saphenous nerve continued ventrally along the deep face of the M. sartorius. Before entering the femoral canal it innervated the Mm. iliopsoas, pectineus, adductor, and sartorius by means of muscular twigs. Finally, it ramified in the fascia and skin on the medial aspect of the thigh, craniomedial aspect of the middle two-thirds of the leg, and plantaromedial aspect to the tarsus and the area immediately distal to it (Ghoshal 1966; Ghoshal and Getty 1967, 1968).

6. The N. obturatorius - The obturator nerve essentially derived its fibers from the ventral branches of the L_5 and L_6 nerves, with an inconstant very small contribution from the communicating branch (of the ventral root of the L_4) to the femoral nerve. Linzell (1959) found the obturator nerve as arising from the L_5 and L_6 only. It passed obliquely caudomedial to the M. psoas minor along the shaft of the ilium towards the obturator foramen. It crossed the craniomedial aspect of same, continued distad and innervated the muscle on the medial aspect of the thigh.

Plexus sacralis

1. The N. gluteus cranialis - The cranial gluteal nerve was chiefly derived from the ventral branches of the L_6 and S_1 nerves. It passed through the dorsal part of the greater ischiatic foramen, accompanying the cranial gluteal vessels, to appear on the gluteal surface of the ilium. Here it split variably into several muscular branches to innervate the Mm. gluteus medius and gluteus profundus. It continued farther between the accessory head of the M. gluteus medius and M. gluteus profundus to finally distribute itself inside the M. tensor fasciae latae.

2. The N. gluteus caudalis - The caudal gluteal nerve was a relatively slender branch given off the dorsal aspect of the ischiatic nerve at the caudal limit of the greater ischiatic foramen, being deep to the M. gluteus medius. It derived its fibers mainly from the L_6, S_1 and S_2 nerves, and, in fact, was indistinguishable from the ischiatic nerve at its origin. It ran caudad along the lateral aspect of the sacrospinotuberal ligament and was distributed mainly to the M. gluteobiceps.

3. The N. cutaneus femoris caudalis - The caudal cutaneous femoral nerve arose as a slender branch from the caudal aspect of the ischiatic nerve, following the origin of the preceding nerve, on the lateral surface of the sacrospinotuberal ligament. Unlike the ox, the single nerve entered the pelvic cavity through the angle of divergence of the caudal

gluteal and internal pudic arteries at the lesser ischiatic foramen, and usually joined the pudic nerve, immediately before the branching off of the deep perineal nerve. Sometimes, the caudal cutaneous femoral nerve arose by two delicate rootlets, lying close to each other, from the ischiatic nerve. However, shortly they joined together to form a single nerve before proceeding towards the pelvic cavity. In the absence of its cutaneous branches the fascia and skin on the caudal aspect of the thigh were supplied by the pudic and sensory branches of the ischiatic nerves (Nn. clunium caudales).

4. The Rami musculares - Several muscular branches of variable size detached along the dorsal and caudal aspects of the ischiatic nerve to supply the Mm. gluteus medius, gluteobiceps, gluteus profundus, gemelli, obturatorius externus, quadratus femoris, semitendinosus, semimembranosus, and adductor. Some of these muscular branches coursed caudodistally through the septum between the Mm. gluteobiceps and semitendinosus, and ramified in the fascia and skin on the caudal half of the lateral surface and adjoining caudal surface of the thigh (Nn. clunium caudales).

5. The N. ischiadicus - The ischiatic nerve derived its origin primarily from the ventral branches of the L_6 and S_1 nerves, with a small contribution from the ventral branch of the S_2 nerve. It emerged through the greater ischiatic foramen as a wide, flat band, coursing caudad along the lower part of the Lig. sacrospinotuberale and the origin of the M. gluteus profundus. Near the trochanter major of the femur, it gradually passed distad, being placed on the Mm. gemelli, obturatorius externus and quadratus femoris. The ischiatic nerve apparently divided into fibular and tibial nerves, usually half an inch below the origin of the lateral plantar cutaneous sural nerve (NAV: N. cutaneus aurae caudalis), near the middle of the thigh. The course of the latter nerves and their sympathetic connections have been described by Ghoshal (1966) and Ghoshal and Getty (1967, 1968 and 1969).

In the majority of cases the lateral plantar cutaneous sural nerve arose directly from the ischiatic nerve, but sometimes it was also given off either from the fibular or tibial nerve (Ghoshal 1966; Ghoshal and Getty 1967, 1968). This nerve ramified in the fascia and skin on the lateral aspect of the tarsus.

ACKNOWLEDGMENTS

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ARTERIAL SUPPLY OF THE DIGESTIVE TRACT OF THE SHEEP (OVIS ARIES)[1]

Kusmat Tanudimadja and Robert Getty

ABSTRACT. Ten ewes and five rams of a Southdown crossbreed were studied. They varied from 4-8 years of age, and weighed from 80-120 lbs. in the female, and from 130-180 lbs. in the male. Observations were made by means of dissections of embalmed specimens injected with latex, and documented by means of 4 illustrations. Vessel diameter and length were also measured and documented in table form.

The a. celiaca supplied, with its branches, the diaphragm, stomach, greater omentum, liver, spleen, pancreas and cranial part of the duodenum. In the sheep the occurrence of a common trunk, truncus celiacomesentericus, which gave rise to the aa. celiaca and mesentericus cranialis, was more frequent than in the ox and goat. The ramification of the a. celiacus was classified into three types. The a. ruminalis dextra did not terminate as in the ox by anastomosing with the a. ruminalis sinistra in the left longitudinal groove. The A. ruminalis dextra and the a. lienalis always presented a common trunk. In 60% of the cases the a. ruminalis sinistra and the a. reticularis arose from a common trunk. Occasionally the a. ruminalis sinistra arose from the truncus lienoruminalis. The a. mesentericus cranialis arose immediately behind the a. celiaca from the ventral surface of the abdominal aorta; variations of the origin of this artery were observed. The collateral branch, a branch of the truncus intestinalis in the ox, was absent in the sheep. The aa. jejunales formed first and second degree arcades before they entered into the intestinal wall in the proximal two-thirds of the jejunum. These arcades disappeared at the terminal part of the distal third of the jejunum and were replaced by straight arteries. The aa. jejunales supplied vascularization to the last part of the centrifugal colon. An anastomotic branch existed between the truncus intestinalis and the a. ileocecalis. The a. rectalis caudalis of the ewe arose from the a. urogenitalis, while in the ram it arose from the a. pudenda interna. The a. rectalis media was absent in the sheep.

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[1]Original results from a 1963 M.S. thesis by Dr. Tanudimadja under the direction of Dr. Getty, Department of Veterinary Anatomy, Iowa State University of Science and Technology, Ames, Iowa 50010.

INTRODUCTION

In the textbooks of the anatomy of the domestic animals (Chauveau 1889; Martin and Schauder 1935; Ellenberger and Baum 1943; Nickel et al. 1961; Sisson and Grossman 1953) little has been described about the anatomy of the sheep with the exception of May (1955). The reader is usually referred to the anatomy of the ox. The arterial differences in the sheep in comparison to that of the ox, and the relatively few references available in the literature, prompted this macroscopic anatomical study of the arterial blood supply of the digestive tract of the sheep.

MATERIALS AND METHODS

In this study 15 Southdown cross sheep were used—10 ewes and 5 rams. Five ewes were dissected, in part, by the students in the classes of gross anatomy in 1962 (Specimens no. 11 through 15) and the remainder (Specimens no. 1 through 10) were done by the senior author in 1961-62. The ages varied from 4 to 8 years and the weights ranged from 80 to 120 pounds in the female, and 130 to 180 pounds in the male.

The specimens were prepared according to the following procedure. For 3 to 4 days feed was withheld from the animals. The animals were given a general anesthetic of either chloral hydrate magnesium sulfate solution or Equithesin. An anticoagulant, Chlorazol Fast Pink B solution[2] (2 grams in 4000 cc of 0.85 per cent sodium chloride solution), was injected to prevent the blood from clotting during exsanguination. The left carotid artery was dissected and the animals were bled by means of their own heart action. To prolong this heart action in order to exsanguinate as much blood as possible, an 0.85 per cent saline solution was introduced through the external jugular vein.

Pre-injection perfusions with acetic acid, 1 per cent sodium citrate, 4 per cent sodium nitrite and sodium chloride solutions were used. Baker (1946) found that 5 per cent acetic acid solution prevents tissue contraction and does not fix protein, thus leaving the tissue pliable. This characteristic better enables the injection material to fill the smallest vessels. Christensen (1953) used as perfusion fluid, 1 per cent sodium citrate, followed by 4 per cent sodium nitrite, in order to relax the smooth muscles of the arterioles and dilate the lumen. Since cementex,[3] a latex compound, was used, it was necessary to flush the vessels with a saline solution to prevent clotting of the latex which would occur if it contacted the acetic acid.

Perfusion and injection of the arteries was accomplished by air pressure with special apparatus, consisting of two 5-gallon bottles (one for the injection material and the other for the perfusion solutions and the embalming fluid), an open mercury manometer, plastic tubes, glass tubes, and rubber stoppers for the bottles. A valve was attached to the manometer to control the air pressure. Air was obtained from a compressor. The manometer was connected with the bottles via a Y-tube on one side and with the air inlet on the other.

[2]Allied Chemical and Dye Corporation, 40 Rector Street, New York, N.Y.

[3]Cementex Company, New York, N.Y.

Before injection took place into the left carotid artery, in some of the specimens an attempt was made to bypass the heart and lung. After opening the left thoracic wall between the third and fourth ribs, the origin of the aorta at its base (before the bifurcation into the common brachiocephalic trunk and thoracic aorta) was clamped by a hemostatic forcep. This procedure allowed more material to fill the vessels revealing more anastomotic branches.

Injection material used for the arteries was red cementex, a latex compound. Hill (1937) found that 2 per cent ammonia water will increase the sliding ability of latex. Besides this ability, ammonia water has the ability to prevent clotting of the latex for a certain period of time. Based on this characteristic, the cementex was diluted with 2 per cent ammonia water in a ratio of 4:1.

After flushing the arteries with saline solution, cementex was injected at a pressure of 120 mm Hg. More cementex was used in specimens in which the heart and lung were not bypassed. To preserve the specimens, regular embalming fluid of the Department of Anatomy and Histology, College of Veterinary Medicine, Iowa State University, was injected into the external jugular vein. The formula of the embalming fluid is as follows: 60% isopropyl alcohol; 4% formaldehyde (40%); 6% phenol (melted); 5% corn syrup (diluted 50-50 in water); and 25% water.

RESULTS

The Stomach, including the Liver, Spleen and Pancreas

All the measurements given represent averages as listed in Table 1. The outside diameter and the length of the individual arteries were measured. The diameter was taken at the origin, and the length was measured from the origin of the vessel until the first branch or a bifurcation occurred.

The numbers in parentheses after the individual arteries refer to Figure 1, except where otherwise indicated.

The a. celiaca (1) arose from the ventral wall of the abdominal aorta on the level with the space between the last thoracic and first lumbar vertebrae, between the crura of the diaphragm. It was 4.0 cm long with an outside diameter of 9.6 mm in the ewe, and, in the ram, 4.6 cm long and an outside diameter of 11.0 mm. It passed in a cranioventral direction, between the cranial part of the rumen and the cranial part of the pancreas, and to the right of the crus of the diaphragm and the caudal vena cava.

It was observed that in five cases the celiac artery arose from a common trunk (termed the tr. celiacomesentericus concordant with Sieber, 1903) with the cranial mesenteric artery (Fig. 2/2). In the ewe the common trunk was a 1.9-cm long vessel with a diameter of 10.9 mm in specimen no. 1. In the ram the measurements were 3.5 cm and 11.2 mm, respectively. The celiac artery with its branches supplied the diaphragm, stomach, greater omentum, liver, spleen, pancreas and cranial part of the duodenum.

The modes of ramification of the a. celiaca are various and could be classified into the following types (Fig. 2):

1. Type I, 60% of the cases, showed that the a. hepatica and a. gastrica sinistra arose separately. The a. lienalis and the a. ruminalis

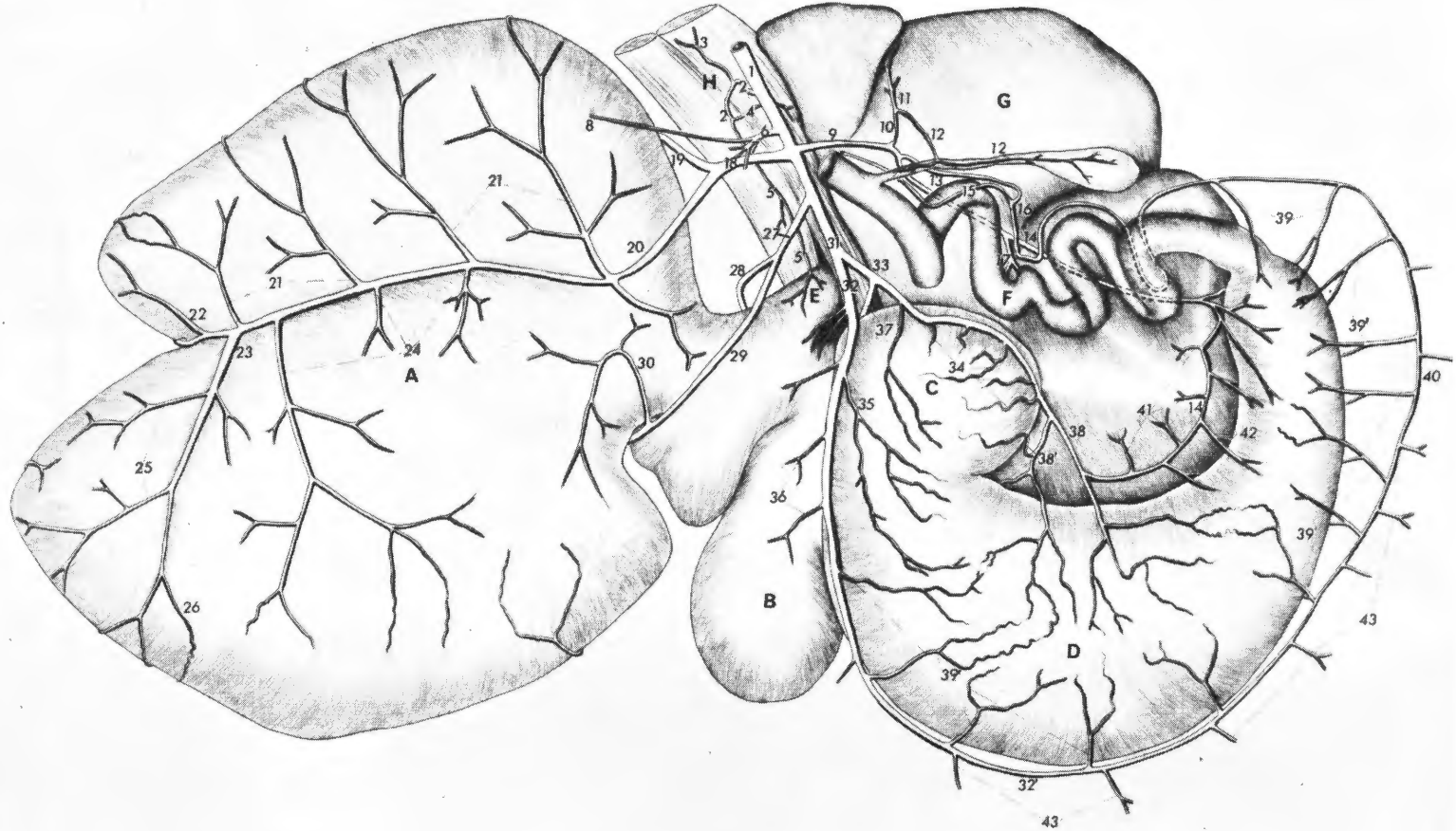
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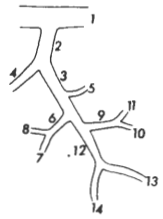
Figure 1. Arteries to the stomach (schematic). Right view.

A. Rumen
B. Reticulum
C. Omasum
D. Abomasum

E. Esophagus
F. Duodenum
G. Liver
H. Crura diaphragmatica

1 A. celiaca
2 A. phrenica dorsalis caudalis
3 Ramus proximalis of 2
4 Ramus distalis of 2
5 Ramus distalis of 2
5' Twig to esophagus
6 Common trunk of 7 and 8
7 Rami pancreatici
8 A. epiploica
9 A. hepatica
10 A. cystica
11 Ramus caudatis et partis dextra hepatis
12 Branch to gallbladder and duct
13 A. gastroduodenalis
14 A. gastrica dextra
15 A. pancreaticoduodenalis cranialis
16 A. gastroepiploica dextra
17 Ramus partis sinistra hepatis
18 Truncus lienoruminalis
19 A. lienalis
20 A. ruminalis dextra
21 Rami dorsales of 20
22 A. coronaria dextra dorsalis
23 A. coronaria dextra ventralis
24 Rami ventrales of 20
25 Rami caudales of 23
26 Ramus cranialis of 23
27 Truncus reticuloruminalis
28 A. reticularis
29 A. ruminalis sinistra
30 Ramus ruminalis of 29
31 A. gastrica sinistra
32 Ramus ventralis of 31
32' A. gastroepiploica sinistra
33 Ramus dorsalis of 31
34 Rami omasici of 33
35 Rami omasici of 32
36 Rami reticulares of 32
37 A. reticularis accessoria
38 Ramus anastomoticus with 14
38' Rami abomasici of 38
39 Rami pylorici of 16
39' Rami abomasici of 32 and 40
40 A. gastroepiploica dextra
41 Branches of 14 to lesser omentum
42 Rami abomasici of 14
43 Rami epiploici of 32' and 40



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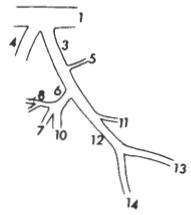

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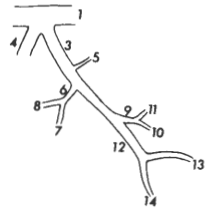

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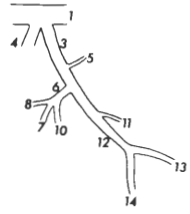

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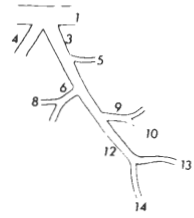

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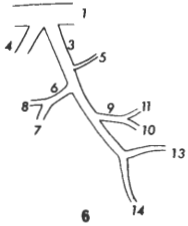

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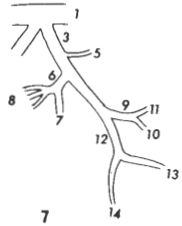

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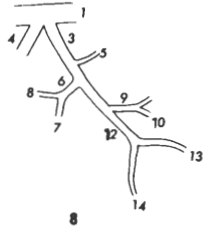

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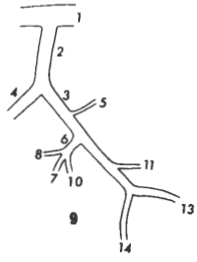

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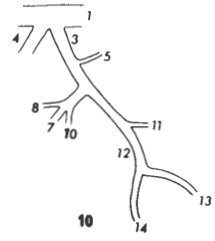

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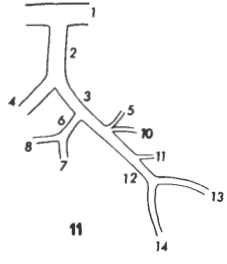

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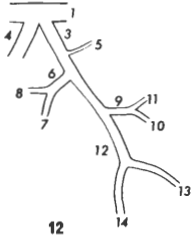

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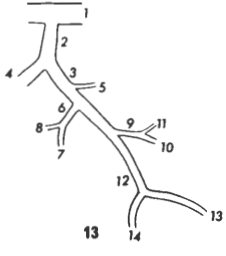

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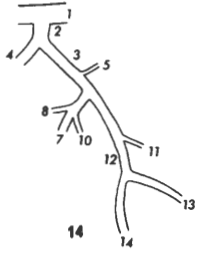

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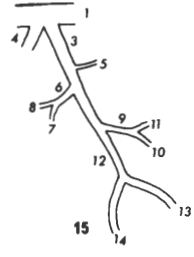

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Figure 2. Types of ramification of the A. celiaca.

1. Aorta abdominalis
2. Truncus celiacomesentericus
3. A. celiaca
4. A. mesenterica cranialis
5. A. hepatica
6. A. truncus lienoruminalis
7. A. ruminalis dextra
8. A. lienalis
9. Truncus reticuloruminalis
10. A. ruminalis sinistra
11. A. reticularis
12. A. gastrica sinistra
13. Ramus dorsalis of 12
14. Ramus ventralis of 12

Type I 60% Specimen No: 1, 3, 5, 6, 7, 8, 12, 13, 15.
The A. hepatica and the A. gastrica sinistra arise separately.
The A. lienalis and the A. ruminalis dextra arise from the Truncus lienoruminalis.
The A. ruminalis sinistra and the A. reticularis have a common trunk, the Truncus reticuloruminalis.

Type II 33% Specimen No: 2, 4, 9, 10, 14.
The Truncus lienoruminalis gives rise to the A. ruminalis sinistra.

Type III 7% Specimen No: 11.
The A. hepatica, A. gastrica sinistra and the A. ruminalis sinistra have a common trunk.

dextra had a common trunk, the truncus lienoruminalis. The a. ruminalis sinistra and the a. reticularis arose by a common trunk, the truncus reticuloruminalis.

2. Type II, 33% of the cases, revealed that the truncus lienoruminalis gave rise to the a. ruminalis sinistra.

3. Type III, 7% of the cases, established that the aa. hepatica, gastrica sinistra and ruminalis sinistra had a common trunk.

The a. celiaca gave off the following branches:

The a. phrenica caudalis dorsalis (2) arose 2.0 to 2.5 cm from the origin of the celiac artery and passed in a cranial direction. After 1 to 2 cm it gave off proximal branches (right and left) (3) for the right and left dorsal portion of the diaphragm, respectively. The continuing vessel coursed in a ventral direction and divided into two branches, the right and left distal branches (4, 5) for the right and left distal part of the diaphragm, respectively. The distal branches gave off twigs (5') to the esophagus.

The rami pancreatici (7), 2 to 4 in number, arose from a common vessel (6) with the a. epiploica, from the caudal wall of the celiac artery. It entered the left lobe of the pancreas where it ramified extensively. The rami pancreatici may arise separately.

The a. epiploica (8), which came off either separately or with the rami pancreatici supplied the greater omentum. It passed between the two layers of the greater omentum in a caudal direction and gave off ventral twigs which anastomosed with the rami epiploici (43).

The a. hepatica (9) passing to the right toward the visceral surface of liver, was bordered on the right side by the caudal vena cava. In the ewe this vessel was 7.8 cm long and 3.8 mm in diameter, while in the ram the sizes were 8.0 and 3.3 mm, respectively. The a. hepatica gave off the following branches:

The a. cystica (10), with its branches, supplied the gallbladder, caudate process and right lobe of the liver. Close to its origin, twigs were given off to the porta hepatis and the portal lymph nodes. After 1 to 1.5 cm the a. cystica divided into two branches. The first branch, ramus caudatis et partis dextra hepatis (11), passed to the caudate process and the right lobe of the liver, supplying both lobes, respectively. The second branch (12) coursed toward the bile duct, which it followed sending twigs to it, and terminated in the gallbladder.

The a. gastroduodenalis (13) left the hepatic artery a few centimeters after the a. cystica. It passed in the lesser omentum toward the duodenum and, after arriving at the latter, divided into two vessels: the a. pancreaticoduodenalis cranialis (15) and the a. gastroepiploica dextra (16, 40). The former passed in a caudal direction along the dorsal side of the descending duodenum. Branches were given off to this part of the doudenum, and, close to its origin, to the pancreas. At the caudal flexure of the duodenum it anastomosed with the a. pancreaticoduodenalis caudalis of the a. mesenterica cranialis. The a. gastroepiploica dextra ran in a caudoventral direction, parallel to the duodenum for a distance of 2 cm of the abomasum and followed the greater curvature of the abomasum. This distance became larger at the first half of the abomasum (4 to 5 cm) and after that the artery ran very close to the greater curvature. This vessel gave off 4 to 5 small branches to the pylorus (39) and

abomasum (39'), and sent fine branches to the greater omentum (43). Finally, it anastomosed with the ventral branch (32) of the a. gastrica sinistra.

The a. gastrica dextra (14) left the hepatic artery 3 cm after the a. gastroduodenalis. It passed parallel to the duodenum, in the hepatoduodenal ligament toward the pylorus of the abomasum. A small branch was given off to the descending duodenum and formed an anastomosis with the duodenal branch of the a. gastroduodenalis. After giving off this branch, the a. gastrica dextra closely followed the lesser curvature of the abomasum and anastomosed with the dorsal branch of the a. gastrica sinistra. Along its course, the a. gastrica dextra gave off branches, rami abomasici (42), to the pylorus and abomasum. The rami abomasici formed anastomoses with branches from the a. gastroepiploica dextra (39, 39'). It was also observed that the a. gastrica dextra gave off twigs to the lesser omentum (41).

The continuing vessel (17) of the a. hepatica passed as the ramus sinistra along the incisura interlobularis and there divided into several branches. One branch entered into the pars intermedia infraportalis, while another supplied the left part of the liver.

The truncus lienoruminalis (18) was 2.0 cm long and 4.4 mm in diameter in the ewe and 2.1 cm long and 4.5 mm in diameter in the ram. It massed in a right-caudal direction and divided into:

The a. lienalis (19) was 4.0 cm long with a diameter of 3.7 mm in the ewe and 5.8 cm long and 3.2 mm in diameter in the ram. This artery passed dorsal to the left along the dorsal surface of the rumen where it divided into a cranial and caudal branch. The former, which was the larger and supplied the cranial third of the spleen, gave off an intermediate branch which ramified in the middle third of the spleen. In specimen no. 2 the A. lienalis was double, while in specimen no. 7 this artery divided into three vessels. In five cases (Fig. 2) the truncus lienoruminalis gave off the a. ruminalis sinistra.

The a. ruminalis dextra (20) was 43.4 cm long and 3.9 mm in diameter in the ewe and 49.7 cm long and 3.7 mm in diameter in the ram. It left the parent vessel in a caudoventral direction toward the right longitudinal groove. It then ran in the groove, reaching the caudal transverse groove to run parallel to the left longitudinal groove on the left surface of the rumen. In its course the a. ruminalis dextra gave off:

The rami dorsales (21), 4 to 5 in number, passed in a caudodorsal direction, and 5 to 8 rami ventrales, passed in a candoventral direction (24). These branches ramified in the dorsal and ventral walls of the rumen, respectively.

The a. coronaria dextra ventralis (23) left the a. ruminalis dextra in a ventral direction in the right ventral coronary groove. In its course it gave off the rami craniales (26) and the rami caudales (25) in a cranial and caudal direction, respectively. These branches ramified in the right ventral wall of the rumen.

The a. coronaria dextra dorsalis (22) was quite small and ramified in the right dorsal blind sac of the rumen.

The a. coronaria sinistra ventralis (Fig. 3/8) was given off by the a. ruminalis dextra after the latter passed the caudal transverse groove. It passed in a cranioventral direction and gave off the rami craniales (10) and rami caudales (11) which ramified in the caudoventral region of the rumen.

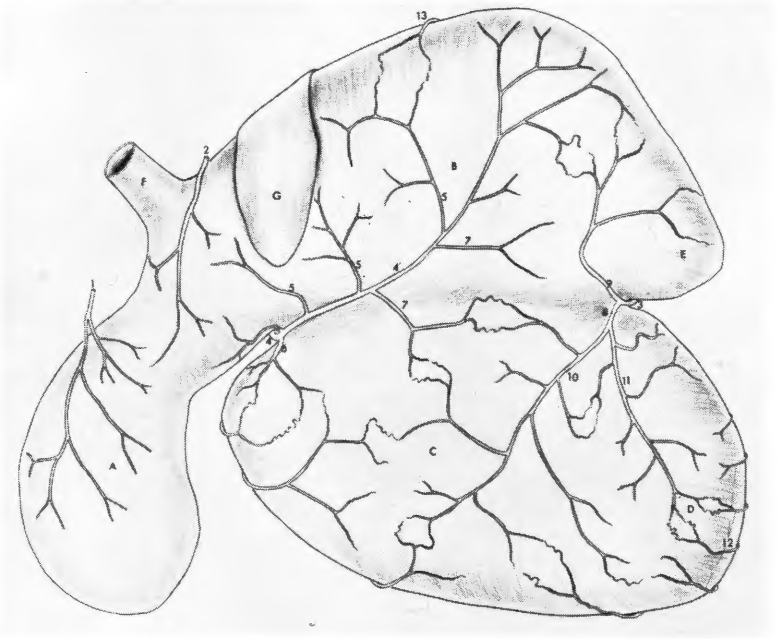

Figure 3. Arteries to the stomach (schematic). Left view.

A. reticulum
B. Dorsal sac of rumen
C. Ventral sac of rumen
D. Ventral blind sac of rumen
E. Dorsal blind sac of rumen
F. Esophagus
G. Spleen

1. A. reticularis
2. A. esophagica caudalis
3. A. ruminalis dextra
4. A. ruminalis sinistra
4'. Ramus ascendens of 4
5. Ramus dorsalis of 4
6. Ramus descendens of 4
7. Ramus ventralis of 4
8. A. coronaria sinistra ventralis
9. A. coronaria sinistra dorsalis
10. Rami cranialis of 8
11. Rami caudalis of 8
12. Branches from A. coronaria dextra ventralis
13. Branch from Ramus dorsalis of 3

The a. coronaria sinistra dorsalis (Fig. 3/9) coursed in a craniodorsal direction and ramified in the left part of the dorsal blind sac.

The truncus reticuloruminalis (27) passed ventrally toward the cranial transverse groove of the rumen. In the ewe it was 4.0 cm long and 4.3 mm in diameter, while in the ram it was 2.2 cm long and 4.3 mm in diameter. In five cases (Fig. 2) the a. ruminalis sinistra came off from the truncus lienoruminalis and in these cases the a. reticularis then came off from the a. gastrica sinistra. The truncus reticuloruminalis was the common trunk of:

(a) The a. ruminalis sinistra (29, Fig. 3/4) left the parent vessel in a ventral direction, bounded on the left by the pancreas and the portal vein and coursed toward the cranial sulcus. In the ewe it was 33.8 cm long and 3.8 mm in diameter, and in the ram it was 34.8 cm long and 3.7 mm in diameter. On the right surface of the rumen it gave off branches (30) which ramified in the cranial ruminal sac. It then turned to the left side of the rumen and divided into two branches, the ramus ascendens (Fig. 3/4') and the ramus descendens (Fig. 3/6). The ramus ascendens first passed in a caudodorsal direction to ascend dorsally in the left longitudinal groove. Three to five strong branches, rami craniales (5), were given off to supply the left dorsal region of the rumen. Two to three branches, rami caudales (7), passed to the left wall of the rumen. Anastomoses with branches of the aa. coronaria sinistra were observed. The ramus descendens ramified in the cranial part of the left ventral sac of the rumen.

(b) The a. reticularis (Fig. 3/1) was 4.7 cm long and 2.5 mm in diameter in the ewe and in the ram 4.5 cm long and 2.4 mm in diameter. It passed craniodorsal and to the left of the rumen, caudal to the cardia in the reticuloruminal fold, where it descended cranioventrally. Two centimeters from its origin it gave off the a. esophagica caudalis (Fig. 3/2), which ramified in the cardia and the esophagus. Anastomoses with the a. esophagica cranialis of the truncus bronchoesophageus were not found. Furthermore, it gave off branches to the rumen, rami ruminales, which vascularized the craniodorsal and caudodorsal wall of the rumen, respectively. Finally the a. reticularis ramified in the cranial wall of the reticulum. An a. phrenica caudalis ventralis was not observed.

The a. gastrica sinistra (31), measured to the bifurcation in the ewe was 4.4 cm long and 4.6 cm in the ram. The diameter in the ewe was 5.6 mm and in the ram 5.9 mm. It passed in a ventral direction, slightly cranial and divided at the transition of the reticulo-omasum into two branches, the ramus dorsalis and the ramus ventralis.

The ramus dorsalis (33) passed along the greater curvature of the omasum towards the transition of the omasoabomasum, where it extensively ramified in this area. The main vessel (38) followed the lesser curvature of the abomasum and joined the a. gastroepiploica dextra. Shortly after its origin it gave off a branch, the a. reticularis accessoria (37), which passed in a cranioventral direction to the omasum and the reticulum. After 4 to 5 cm this branch gave off a branch which passed toward the rumen and ramified in the right wall of the rumen, to form anastomoses with the other ruminal branches of the ramus dorsalis and ramus gastrici of the a. gastroepiploica sinistra. A few centimeters thereafter a branch came off, passing in a left and ventral direction, to

supply the right cranial wall of the reticulum and anastomosed with branches of the a. reticularis and rami reticularis of the a. gastrica sinistra.

The ramus dorsalis gave off branches, rami omasici (34), to the omasum. In its course along the convex border of the omasum 10 to 15 small branches arose to supply the reticular lymph nodes. At the transition, omasabomasum, 4 to 5 branches (38') were given off, which ramified in this area. One branch followed the lesser curvature of the abomasum and joined the a. gastroepiploica dextra.

The ramus ventralis (32) passed in a ventral direction toward the transition of the omasoabomasum. It followed the reticulo-omasal groove, to give off branches, rami reticulares (36), to the reticulum, and rami omasici (35) to the omasum. Smaller branches went off to the reticuloabomasal lymph node which lies dorsal and ventral in the reticulo-ruminal groove. The continuing vessel of the ramus ventralis, the a. gastroepiploica sinistra (32'), ran in the greater omentum, first to the left and later on at a distance of 1 cm from the greater curvature of the abomasum. In its course it gave off branches (39') to the abomasum, and formed anastomoses with the branches from the ramus dorsalis of the a. gastrica sinistra. Besides this, numerous branches, rami epiploica (43), which joined with the branches of the a. epiploica and the a. pancreaticoepiploica, were given off to the greater omentum.

The Intestinal Tract

The arteries which supply the intestine are the a. mesenterica cranialis, a. mesenterica caudalis and intestinal branches of the a. iliaca interna.

The same procedure of measuring the arteries to the stomach was used for the intestinal arteries.

The numbers in parentheses after the individual arteries refer to Figure 4, except where otherwise indicated.

The a. mesenterica cranialis (1) arose from the abdominal aorta just behind the a. celiaca. In the ewe it was 8.5 cm long with a diameter of 9.5 mm. In the ram it was 8.9 cm long and 10.6 mm in diameter. As has been previously described, the a. mesenterica cranialis may arise by a common trunk with the a. celiaca (Fig. 2). The former passed in a ventral direction between the pancreas and caudal vena cava, caudal to the transverse colon and crossed the last part of the spiral colon. It then divided into two trunks: the truncus jejunalis (18) and the truncus ileocecocolicus (7). The following branches of the a. mesenterica cranialis were dissected and are described as follows:

The rami pancreatici arose in a variable number from the a. mesenterica cranialis. They ramified extensively in the pancreas. One or two branches passed to the greater omentum.

The a. pancreatica magna (2) arose from the caudal wall of the a. mesenterica cranialis and passed in a caudal direction. After 1 to 2 cm it divided into several branches, most of which ramified in the pancreas. Two to tbree branches went to the greater omentum as rami epiploici.

The a. pancreaticoepiploica (3) arose from the parent vessel 1 cm dorsal to the a. pancreatica magna. Crossing the portal vein it turned caudally and to the right towards the right lobe of the pancreas. Here it ramified in the pancreas with 2 to 3 branches going to the greater omentum.

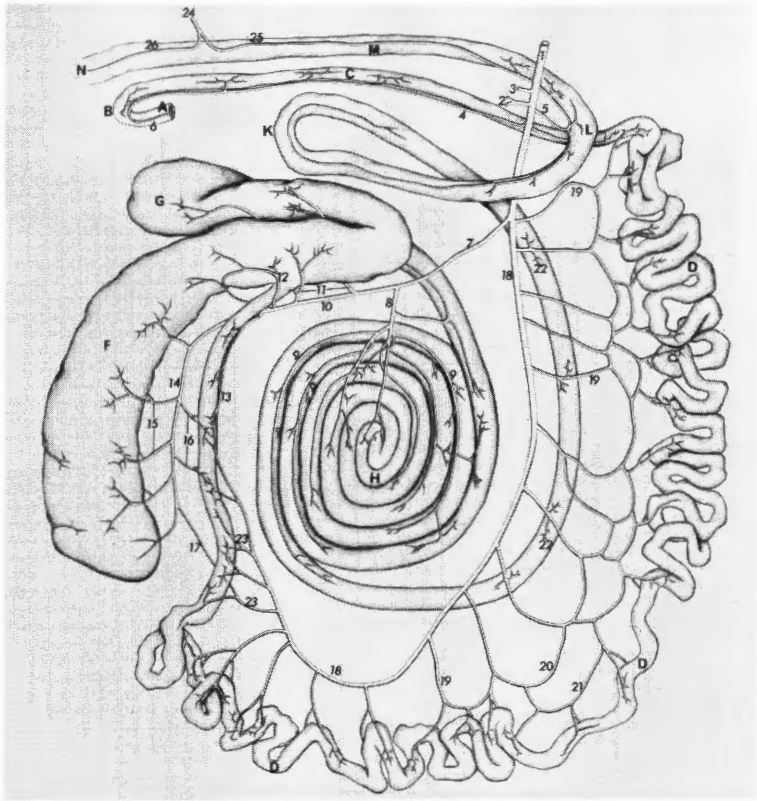

Figure 4. Arteries to the intestine (schematic).

A. Duodenum descendens
B. Pelvic flexure of duodenum
C. Duodenum ascendens
D. Jejunum
E. Ileum
F. Cecum
G. Ansa proximalis of Colon descendens
H. Colon labyrinth
K. Ansa distalis of Colon descendens
L. Colon transversum
M. Colon descendens
N. Rectum

1. A. mesenterica cranialis
2. A. pancreatica magna
3. A. pancreaticoepiploica
4. A. pancreaticoduodenalis caudalis
5. A. colica media
6. A. pancreaticoduodenalis cranialis
7. Truncus ileocecocolicus
8. Truncus colicus
9. Rami colici
10. A. ileocecolica
11. Rami Ansae proximalis of Colon descendens
12. Rami Ansae proximalis of Colon descendens
13. Ramus ileus
14. A. ileocecalis
15. Rami cecales
16. Rami ilei
17. Ramus anastomoticus of 10 and 18
18. Truncus intestinalis
19. Aa. jejunales
20. Primary arcades
21. Secondary arcades
22. Rami colici
23. Rami ilei of 18
24. A. mesenterica caudalis
25. A. colica sinistra
26. A. rectalis cranialis

The a. pancreaticoduodenalis caudalis (4) left the a. mesenterica cranialis in a left and caudal direction 6 cm from its origin from the abdominal aorta. In two specimens it arose from the first a. jejunalis. It then passed to the left, turned caudally and ran parallel to the duodenum descendens to which branches were given off. Along its course pancreatic branches were given off. At the caudal flexure of the duodenum the a. pancreaticoduodenalis caudalis joined the a. pancreaticoduodenalis cranialis.

The a. colica media (5) arose 6 to 8 cm distal to the origin of the a. mesenterica cranialis and passed in a cranial direction. In the ewe the diameter was 1.4 mm and in the ram, 1.3 mm. It divided into 3 to 5 branches. Two to three branches passed in a right and ventral direction to supply the ansa distalis of the ascending colon. One to two vessels supplied the beginning and middle parts of the transverse colon. A fifth vessel passed in a left and caudal direction to follow the descending colon, to supply it and form anastomoses with the a. colica sinistra, a branch of the a. mesenterica caudalis. In two specimens the a. colica media arose from the truncus ileocecocolicus. In 5 specimens the a. colica media gave off pancreatic branches.

The truncus ileocecocolicus (7), one of the terminal branches of the a. mesenterica cranialis, in the ewe 3.6 mm in diameter and 1.9 cm long and in the ram 3.8 mm in diameter and 2.5 cm long, passed in a caudal direction and divided into the a. ileocecocolica, the truncus ileocecalis and the truncus colicus. In two specimens the a. colica media arose from the truncus ileocecalis. In addition, branches were given off to the ansa distalis of the descending colon. Pancreatic branches were also observed.

The truncus colicus (8), 3.3 mm in diameter in both sexes, arose from the ventral wall of the truncus ileocecocolicus and passed toward the ansa centralis of the spiral colon. In three sheep it had a double origin, in two others four came off, and the remainder showed a single vessel (Fig. 4). This trunk, with its branches, the rami colici (9), supplied the centrifugal and centripetal coils of the colon, except the last part, which received its blood supply from the aa. jejunales. Connections among the rami colici were observed, and in two cases anastomoses with the truncus jejunalis on the one hand, and with the a. ileocecocolica on the other were observed. Twigs arose from the rami colici to the colic lymph nodes.

The a. ileocecocolica (10) arose from the truncus ileocecocolicus after the truncus colicus. It passed in a ventral direction and supplied the ansa proximalis of the ascending colon, the cecum and the ileum. The following branches were dissected:

The rami ansae proximalis (11, 12), 3 to 4 in number, arose from the dorsal surface of the parent vessel. They passed in a dorsal direction and terminated in the ansa proximalis of the ascending colon. Anastomoses with the terminal branches of the truncus colicus, especially of the first branch, were observed.

The rr. ilei (13) were given off at the end of the ileum. They followed the ileum and gave off branches to it. The rr. ilei terminated at the middle of the ileum.

The a. ileocecalis (14) formed the continuation of the a. ileocecocolica.

In the ewe it was 2.5 mm in diameter and 18.8 cm long, while in the ram the sizes were 2.6 mm and 20.9 cm, respectively. It passed caudoventrally in the ileocecal ligament toward the apex of the cecum, at the same distance from the ileum and the cecum. At the free edge of the ligament it continued in the caudal part of the mesentery of the jejunum and formed an anastomosis with the terminal branches of the truncus jejunalis. The a. ileocecalis sent 10 to 15 branches, rami cecales (15), to the cecum at regular distances of 1 cm. These branches divided into two, a right and left one, before they terminated in the cecum. The right and left vessels joined each other at the dorsal region of the cecum. Twigs were given off from the ileocecal artery to the cecal lymph nodes.

Rami ilei (16) left at variable distances of 1 to 5 cm from the a. ileocecalis and ramified in the ileum. The terminal branch of the rr. ilei joined the rami ilei of the a. ileocecocolica and was called the ramus anastomoticus (17). They passed in a caudoventral direction, left of the ileum, to join the terminal branch of the truncus intestinalis.

The truncus intestinalis (18) is the continuing vessel of the a. mesenterica cranialis. In the ewe it was 44.3 cm long and in the ram 53.0 cm. It passed in the cranial mesentery in a curved course. The following branches of the truncus intestinalis were dissected:

The aa. jejunales (19) varied in number from 18 to 24 in the individual animals. The distance between one vessel and the other varied from 0.5 to 4 cm. The proximal branches arose closer to each other. The aa. jejunales passed in a direction parallel to the jejunum. They were 4 to 5 cm long and divided into two branches before they entered the jejunum. These branches joined each other, forming an arcade (20). At several places a second arcade (21) was formed. From the first or second arcade the rami jejunales entered the jejunum. These rami formed anastomoses with each other. Twigs to the jejunal lymph nodes came off from the aa. jejunales. Besides this the aa. jejunales gave off branches to the last centrifugal colon, the rami colici (22). Anastomoses of these rami with branches of the a. colica media were observed.

The rami ilei (23) passed toward the ileum which they supplied. Branches went to the lymph nodes of the ileum. A branch continued to pass in a dorsal direction and anastomosed with the rami ilei of the a. ileocecalis.

The a. mesenterica caudalis (24) arose at the level of the fifth lumbar vertebra from the ventral wall of the abdominal aorta. In the ewe it was 8 cm long and the diameter was 3.1 mm, while in the ram the measurements were 9.1 cm and 3.8 mm, respectively. Passing in a ventral direction in the caudal mesentery toward the descending colon, it soon divided into two branches, the a. colica sinistra and the a. rectalis cranialis.

The a. colica sinistra (25) passed cranially in the mesentery of the descending colon. It gave off three to four branches to both sides of this part of the colon. Connections between the right and left branches were observed. The most cranial branch formed an anastomosis with a branch of the a. colica media.

The a. rectalis cranialis (26) passed in a caudal direction in the mesorectum toward the anus. Along its course it gave off branches to both sides of the rectum, where they ramified into caudal and cranial

TABLE 1. MEASUREMENTS OF VESSELS TO THE DIGESTIVE TRACT IN THE EWE AND RAM.

Name of Artery	Outside Diameter in mm		Length in cm	
	ewe (N=5)	ram (N=5)	ewe (N=10)	ram (N=5)
A. celiaca	9.6 (9.0-10.5)	11.0 (10.5-11.8)	4.0 (3.0- 4.5)	4.6 (4.0- 5.0)
Tr. celiacomesentericus	10.9[a]	11.2[a]	1.9[b] (1.0- 3.0)	3.5[a]
A. hepatica	3.8 (3.5- 3.9)	3.3 (3.0- 3.8)	7.8 (7.0- 8.5)	8.0 (7.0 - 8.5)
Tr. lienoruminalis	4.4 (4.1- 4.7)	4.5 (4.2- 4.8)	2.0 (1.5- 2.5)	2.1 (2.0- 2.5)
A. lienalis	3.7 (3.5- 3.9)	3.2 (2.4- 3.9)	4.0 (3.5- 5.0)	5.8 (4.0 - 5.5)
A. ruminalis dextra	3.9 (3.6- 4.1)	3.7 (3.1- 4.2)	43.4 (38.5-45.5)	49.7 (45.0-52.5)
Tr. reticuloruminalis	4.3[c] (4.3- 4.4)	4.3[c]	4.0[d] (3.5- 4.5)	4.3[c] (4.0- 4.5)
A. ruminalis sinistra	3.8 (3.5- 4.1)	3.7 (3.0- 4.1)	33.8 (28.0-40.0)	34.8 (30.9-38.0)
A. reticularis	2.5 (2.3- 2.7)	2.4 (2.3- 2.5)	4.7 (3.5- 6.0)	4.5 (4.0- 5.0)
A. gastrica sinistra	5.6 (4.7- 6.3)	5.9 (4.8 - 6.5)	4.4 (3.5- 5.5)	4.6 (4.0- 5.0)
A. mesenterica cranialis	9.5 (9.0-10.0)	10.6 (10.0-11.0)	8.5 (7.0-10.5)	8.9 (8.5- 9.5)
A. pancreaticoduodenalis caudalis	1.1 (1.0- 1.2)	1.1 (1.0- 1.3)		
A. colica media	1.4 (1.3- 1.5)	1.3 (1.2- 1.4)		
Tr. intestinalis			44.3 (39.0-48.0)	53.0 (50.0-58.0)
Tr. ileocecocolicus	3.6 (3.4- 3.9)	3.8 (3.5- 4.1)	1.9 (1.5- 2.5)	2.5 (2.0- 3.0)
Tr. colicus	3.3 (3.1- 3.7)	3.3 (3.1- 3.5)		
A. ileocecalis	2.5 (2.3- 2.7)	2.6 (2.4- 2.7)	18.8 (17.0-20.0)	20.9 (19.0-23.0)
A. mesenterica caudalis	3.1 (2.7- 3.9)	3.8 (2.1- 3.2)	8.0 (6.5- 9.5)	9.1 (8.0- 9.5)
A. colica sinistra	1.1 (1.0- 1.3)	1.1 (1.0- 1.2)		
A. rectalis cranialis	1.1 (1.0- 1.2)	1.2 (1.1- 1.3)		
A. rectalis caudalis	1.0 (1.0- 1.1)	1.1 (1.1 - 1.2)		

a - N=1; b - N=4; c - N=3; d - N=6.

branches. These cranially and caudally directed arteries formed anastomoses with each other. The cranial branch of the a. rectalis cranialis joined the most caudal branch of the a. colica sinistra. At the end of the rectum the a. rectalis cranialis divided into two to three branches, which passed ventral to the ampulla and formed an anastomosis with branches of the a. rectalis caudalis.

Intestinal branches from the a. iliaca interna

A branch from the a. iliaca interna, namely the a. urogenitalis, supplied the rectum. In the ram the a. urogenitalis gave off the a. vesicalis caudalis and a. ramus muscularis, while in the ewe it gave off the a. uterica caudalis and the a. rectalis caudalis, which gave off the a. vesicalis caudalis and the a. perinei. The vessel concerned is the a. rectalis caudalis and the discussion of the other vessels is described in more detail by Tanudimadja, Getty and Ghoshal (1968).

In the ewe the a. rectalis caudalis passed in a caudal direction and supplied the caudal third and ventral part of the ampulla of the rectum. Along its course it gave off the a. vesicalis caudalis and the a. perinei. It then passed dorsally to ramify in the dorsal sphincter muscle of the anus. Anastomotic branches existed between these branches and the branches of the a. rectalis cranialis.

In the ram the a. rectalis caudalis arose from the dorsal face of the a. pudenda interna. It passed caudally and ramified in the ampulla of the rectum and the anus.

DISCUSSION

The stomach of the ruminant shows distinct differences in structure compared to other domestic animals. It consists of three fore-stomachs, the poventriculi: rumen, reticulum and omasum; and a fourth part, the abomasum. These four parts are arranged in such a way that the rumen lies largely to the left side of the median plane, the recitulum cranial to it and the omasum to the right of the median line. The abomasum is located on the ventral wall of the abdomen covered in part by the omasum and the rumen. Thus, because of the considerable extent of development of the stomach, additional blood supply is brought to it.

The principal arterial supply of the stomach in man and animals is derived from the unpaired a. celiaca (Ellenberger 1943; Sisson and Grossman 1953), the first visceral branch of the abdominal aorta. Generally speaking, the a. celiaca divides into three chief branches, the a. lienalis, a. gastrica sinistra and the a. hepatica, which extend to the spleen, stomach and liver-duodenum respectively. In the ruminants, due to the enormous development of the stomach into four parts (rumen, reticulum, omasum and abomasum), additional branches are established to accommodate the arterial blood supply to these parts. The artery to the spleen arises with the a. ruminalis dextra and the a. ruminalis sinistra gives rise to the a. reticularis.

It was observed that the a. celiaca arose from the ventral face of the abdominal aorta at a level between the last thoracic vertebra and the first lumbar vertebra. Happich (1961), however, found a slightly different location, namely at the level of the last thoracic vertebra. Scupin

(1960) and Otto (1961) in their study of the goat, also found a different result and Horowitz and Venzke (1966) reported that it arose at the thirteenth thoracic or first lumbar vertebral level.

In 30% of the specimens in this study the a. celiaca arose from the common trunk, truncus celiacomesentericus. Kattauer (1926) reported that in the sheep he examined 20% showed this variation, while in the ox, Kadar (1926) found a percentage of 4.42. None of the seven goats and three oxen dissected by the students in the classes of gross anatomy at Iowa State University revealed this variation. Scupin (1960) and Otto (1961) did not indicate the presence of this common trunk in the goat. Sieber (1903), however, observed this variation in the sheep and goat. Franzke (1958) described a case in the sheep, but Happich (1961) did not find this in the specimens that he dissected. Anderson and Weber (1969) reported this common trunk as a constant finding in sheep they dissected.

The parietal branch of the a. celiaca, the a. phrenica caudalis dorsalis, corresponded with that of the goat and ox (Scupin 1960; Horowitz and Venzke 1966; and Sieber 1903). The a. phrenica caudalis ventralis, as reported by Sieber (1903) in the ox and by Scupin (1960) in the goat, could not be established, in accord with Happich (1961).

The distribution of the a. hepatica corresponded with the investigation of Rustamov and Polyakov (1958) and Happich (1961). Scupin (1960) and Anderson and Weber (1969) considered the vessel which comes from the a. celiaca as a common trunk. Therefore, Scupin called it the truncus hepatogastricus.

In our 1963 studies, the a. ruminalis dextra and the a. lienalis always presented a common trunk. Anderson and Weber (1969) confirm this finding, while the a. ruminalis sinistra occasionally arose from this common trunk (Fig. 2). The a. lienalis of the ox (Sieber 1903) ramified at the surface of the organ, while in the sheep it first entered the hilus before it ramified. It was observed that the a. lienalis could be double, even triple, although the incidence was very low. If the a. lienalis was double, the two vessels corresponded with the ramus cranialis and ramus caudalis. In the case of three vessels, the middle one is the ramus intermedius.

The course of the a. ruminalis dextra of the sheep resembled that of the goat (Scupin 1960). It was observed that the a. coronaria dextra ventralis developed extensively due to the great development of the ventral blind sac of the rumen. The a. coronaria dorsalis dextra did not terminate as the ramus longitudinalis of the ox, in accord with Rustamov and Polyakov (1958) and Happich (1961).

In 60% of the cases the a. ruminalis sinistra and the a. reticularis arose from a common trunk, the truncus reticuloruminalis. Sieber (1903) stated that the a. ruminalis sinistra in the ox is smaller than its right fellow. In the sheep they are the same size. Occasionally, the a. ruminalis sinistra arose from the truncus lienoruminalis (Fig. 2). Consequently, the a. reticularis came off from the a. gastrica sinistra. According to Sieber (1903), Scupin (1960) and Happich (1961) the a. reticularis gave rise to the a. esophagica caudalis ventralis which was also established in this study. However, the anastomosis with the a. esophagica cranialis, a branch of the truncus bronchoesophageus, was not found.

The a. gastrica sinistra is considered to be the continuation of the

a. celiaca, as later also reported by Anderson and Weber (1969). Opposite the omasum it divided into the dorsal and ventral branches. The former gave rise to the a. reticularis accessoria, which was also found in the goat (Scupin 1960), but not in accord with Yoshikawa et al. (1956). In the ox, this vessel was not present (Chauveau 1889; Sieber 1903; Montane et Bourdelle 1917; Ellenberger und Baum 1943; Sisson and Grossman 1953; McLeod 1958). In the sheep the presence of the a. reticularis accessoria was confirmed by May (1964), Rustomov and Polyakov (1958) and Happich (1961).

The intestinal tract of the sheep is formed by the small intestine, the cecum and the large intestine. Generally speaking the intestinal tract of man and animals receives its arterial blood supply from three sources:

1. The a. mesenterica cranialis supplies the largest part of the tract, that is the small intestine, the cecum and the largest part of the large intestine. It also supplies the pancreas.

2. The a. mesenterica caudalis supplies the last part of the large intestine and the rectum.

3. The a. rectalis caudalis, in the ewe is a branch of the a. urogenitalis and in the ram a branch of the a. pudenda interna. The a. rectalis caudalis ramifies in the ampulla of the rectum and in the anal region.

Due to the fact that the a. mesenterica cranialis supplies the largest part of the intestinal tract, one is likely to assume that the vessel should not be the best developed (Table 1). The measurements of the a. mesenterica cranialis were the same as the a. celiaca. It was observed that this artery arose immediately behind the a. celiaca in accord with Sieber (1903), Montane et Bourdelle (1917), and May (1964), although according to Happich (1961) it came off 1 cm behind the latter.

In the sheep the a. mesenterica cranialis did not give rise to the a. duodenalis caudalis, which was present in the goat (Scupin 1960). Instead, the a. pancreaticoduodenalis (Fig. 4) was given off by the a. mesenterica cranialis.

The a. mesenterica cranialis gave off the rami pancreatici, a. pancreatica magna, a. pancreaticoepiploica and a. colica media. In contrast to the goat, the latter vascularized the ansa distalis of the descending colon. After releasing these branches the a. mesenterica cranialis then bifurcated into the truncus ileocecocolicus and the truncus jejunalis. The former divided into the truncus colica and the a. ileocecocolica. Scupin (1960) reported that in the goat the a. ileocecocolica gave rise to the ramus ilecus antimesenterialis. In the sheep, this branch was absent, in accord with May (1964) and Happich (1961). The truncus intestinalis did not give off the ramus collateralis as in the ox (Sieber 1903; Montane et Bourdelle 1917; Martin and Schauder 1935; McLeod 1958). The truncus intestinalis gave rise to the aa. jejunales, which supplied the jejunum and a part of the ileum. At the proximal two-thirds of the length of the jejunum the aa. jejunales formed arcades, however, not more than secondary ones. From these arcades, rami jejunales entered the wall of the jejunum. Starting from the point the rami entered the wall, the term "mural" branches (Noer 1943) could be introduced because of the ramification of these branches in the wall of the intestine. The arcades disappeared at the distal part of the jejunum, in accord with Scupin (1960) in the goat, and in contrast to the ox which showed seven

part arcades (Sieber 1903). The aa. jejunales, in the distal one-third of the jejunum, passed in a relatively straight course, although they bifurcated before they entered the intestinal wall to supply the right and left walls of the intestine. A. ramus anastomoticus between the aa. jejunales and the a. ileocecocolica was established at this distal part, similar to that in the goat (Scupin 1960). In the ox this anastomosis did not exist (Sieber 1903).

The aa. jejunales gave off branches to the last centrifugal coil of the colon. This could be expected if these arteries take care of the vascularization of the colon concerned, since the location of this part of the colon is between the truncus intestinalis and the jejunum. No other vessels were observed to supply either chiefly or partly this part of the colon.

The a. mesenterica caudalis of the sheep revealed a similar picture in comparison with the goat (Scupin 1960) and the ox (Sieber 1903; Martin und Schauder 1935; McLeod 1958).

Regarding the intestinal branch of the a. iliaca interna, that is the a. rectalis caudalis, it should be noted that in the ewe and goat (Scupin 1960), this vessel was given off by the a. urogenitalis, while in the ram the a. pudenda interna gave rise to the a. rectalis caudalis. An a. rectalis media was not observed in accord with May (1964) and Happich (1961).

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BLOOD VESSELS OF THE GENITALIA AND ACCESSORY GENITAL ORGANS OF SWINE (SUS SCROFA DOMESTICUS). II. VEINS[1]

Quiterio Nunez[2] and R. Getty[3]

ABSTRACT. Ten animals, five males and five females, were used for the investigation of the venous drainage of the genital tract and accessory genital organs of swine (Sus scrofa domesticus). Additional material consisting of ten uteri from nonpregnant female pigs was employed for the preparation of corrosion specimens. The general pattern of the venous disposition with variations is discussed and supplemented by three original illustrations.

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INTRODUCTION

This is Part II of a two part series of papers on the blood supply of the genitalia and accessory genital organs of swine. The first part was on the arteries (Nunez and Getty 1969). Anatomical descriptions regarding the veins of the genital tract of the swine are limited in the literature (Montane and Bourdelle 1920; Ellenberger and Baum 1943; Bevandic 1943; Schwarz and Badawi 1962; Lange 1959; Lebedewa 1960; Barone et al. 1962; Bickhardt 1961). Most of them are mentioned in a comparative manner to the equine and the bovine. Because of increasing interest and research in reproductive problems in swine, it was felt in 1962 that a detailed study of the blood supply to, and the venous drainage of the male and female genitalia should contribute to a better understanding of those problems related to reproductive anatomy and physiology.

MATERIALS AND METHODS

After preparation for arterial studies (Nunez and Getty 1969), the ten pigs (five males and five females) of the Yorkshire and Hampshire breeds were prepared for venous study by the following method. The animals were removed from the cooler after three days and placed at room temperature for about 12 hours for the injection of the venous system. This effort diminished the resistance of the valves of the veins due to post mortem degeneration (autolysis) of the valves. The abdominal cavity

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[1] Original results taken in toto from a 1964 M.S. thesis by Dr. Nunez under the direction of Dr. Getty, Department of Veterinary Anatomy, Iowa State University.

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was then opened on the right side and the viscera of the digestive system were removed, after securing the vessels. The caudal vena cava was cannulated just caudal to the origin of the renal veins. Blue latex, diluted in the ratio of 5:5 in 2% ammonia water, was injected slowly at a pressure of 70 mm Hg. The amount of latex solution injected for both arteries and veins varied according to the size of the animal. It is of interest to note that the quantity of the diluted latex used for venous injection was relatively greater than that for the corresponding arteries.

For the procedure for making corrosion specimens see Part I of this series (Nunez and Getty 1969). The only difference in that procedure was that 300 cc of blue latex instead of red was used for the venous injections.

RESULTS

The draining of the venous blood from the mammary gland of the female and the prepuce of the male was accomplished by the tributaries of the Vv. thoracica interna and pudenda externa.

The two tributaries, the V. epigastrica cranialis, from the abdominal wall, and the V. musculophrenica, from the medial side of the costal arch, joined at the level of the last costosternal articulation to form the V. thoracica interna. It coursed as a satellite of the A. thoracica interna under the M. transversus thoracis toward the thoracic inlet, and emptied into the V. cava cranialis, medial to the first rib. In its course, the vein received the veins corresponding to branches of the artery to the mammary gland. By means of these vessels the medial and lateral surfaces of the 1st pair of mammary glands were drained.

The musculophrenic vein corresponded to the artery of the same name. It drained the lateroventral area of the diaphragm and the medial aspect of the costal arch.

The V. epigastrica cranialis (Fig. 1/87) was much larger than the preceding vein. The V. thoracica interna appeared to be the direct continuation of the V. epigastrica cranialis. The V. epigastrica cranialis consisted of two veins, the medial and lateral veins, connected by means of anastomotic bridges. Both ran forward on either side of the corresponding artery and anastomosed while approaching the thoracic cavity. Near the entrance of the thoracic cavity, the medial vein received the V. subcutanea abdominis as a tributary vein. The V. epigastrica cranialis received the drainage from the parts of the mammary glands and prepuce (medial roots) which were supplied by the A. epigastrica cranialis. By means of these satellite vessels it was also connected with the V. subcutanea abdominis (Fig. 1/89). The roots of the V. epigastrica cranialis anastomosed with the roots of the V. epigastrica caudalis.

The V. subcutanea abdominis was a large tributary of the V. epigastrica cranialis and, in general, did not accompany any artery (Fig. 1/97). It coursed cranially in the fatty tissue of the ventral wall of the abdomen. The two Vv. subcutanei abdomines were connected by anastomotic bridges (Fig. 1/97''). Laterally, each received radicles from the caudal root of the Vv. pudenda externa, circumflexa femoris medialis, saphena parva and saphena magna. In its caudocranial course, the V. subcutanea abdominis connected the roots of the cranial tributaries of the V. pudenda

externa. In the female, the vessel anastomosed on its ventromedial side with its counterpart by communicating bridges which formed a network in the fatty tissue. They drained the medial and lateral aspects of the mammary gland, the fatty tissue and the skin of the region. In the male, it received a large tributary which drained a large venous plexus. This plexus surrounded, superficially, the ventral aspect of the preputial cavity (Fig. 2/19). In this plexus the radicles, which drained the ventral and lateral aspects of the preputial orifice, converged.

The V. subcutanea abdominis gradually increased in diameter, receiving a lateral vein from the cranial aspect of the thigh at the level of the beginning of the "knee" fold. It then continued laterally to the abdominal and thoracic mammary glands. It collected several tributaries from the lateral aspect of the mammary glands and from the lateral wall of the abdomen (Fig. 1/97^{iv}). Near the angle of the arch of the ribs it received a tributary (Fig. 1/97^{v}) which, after coursing deeper along the median line, became superficial and drained the medial aspect of the 2nd, 3rd and 4th mammary glands. In the male, it drained the fatty tissue, Mm. preputiales craniales, and the umbilicus. This tributary vein was single in some specimens, and joined either the left or right V. subcutanea abdominis. At the level of the angle of the arch of the ribs the latter vessel pierced the muscular wall and joined the medial vein of the Vv. epigastrici craniales.

The V. pudenda externa consisted of two veins which were connected at places by anastomotic bridges (Fig. 2/15, 3/15). The veins coursed parallel to the corresponding artery in the inguinal canal. It was observed, in one of ten specimens, that the right vessels were tributaries of the Truncus pudendoepigastricus, while those of the left side joined the Vv. iliaca externa and femoralis. In four specimens the vessels of both sides were affluents of the Vv. femoralis and profunda femoris. In two specimens the right vessels showed the same disposition as the preceding vessels, while their counterparts joined the V. femoralis, whereas the left vessels discharged into the Vv. femoralis and profunda femoris. In one specimen, the right vessels joined the V. femoralis while their counterparts terminated in the Vv. femoralis and profunda femoris. In the last specimen, the right vessel emptied into the Vv. femoralis and profunda femoris whereas the left vessels were tributaries of the Truncus pudendoepigastricus.

In the female the cranial and caudal vessels joined the V. pudenda externa, medial to the Lnn. inguinales superficiales (Figs. 3/16 and 21). The cranial root was composed of two vessels placed on each side of the lateral cranial branch of the A. pudenda externa. The venous radicles generally followed the course and ramifications of the satellite artery and anastomosed with the V. subcutanea abdominis and Vv. epigastrici craniales.

The cranial root coursed deeper in the fatty tissue, lateral to the rows of the mammary glands. It received two tributaries which coursed craniodorsolaterally to the median line. They drained the lateral and medial aspects of the three mammary glands and connected the V. pudenda externa to the V. subcutanea abdominis (Fig. 1/20). They may be considered as mammary veins, in agreement with Bickhardt (1961).

Near the Lnn. inguinales superficiales, the cranial root also received

tributaries which followed the ramifications of the middle cranial and medial cranial branches of the A. pudenda externa.

The right and left caudal roots of the V. pudenda externa were formed by a common trunk. The latter anastomosed with the V. pudenda interna in the perineal region and received a single vessel which drained the fatty tissue and the perivulvar tissues. Each caudal root coursed forward in the interfemoral space. It received, laterally, affluents which drained the subcutaneous tissue of the dorsomedial side of the thigh. By means of the affluents the vessel anastomosed with the Vv. subcutanea abdominis, profunda femoris, circumflexa femoris medialis and saphena parva. On its medial side it connected with its counterpart by anastomotic bridges. The caudal root in its further course accompanied the caudal branch of the A. pudenda externa to the inguinal region where it became a paired vessel. It received a tributary which came from the fatty tissue and from the Lnn. inguinales superficiales.

In the male three tributaries—the lateral cranial, medial cranial, and caudal roots—usually joined the V. pudenda externa medial to the Lnn. inguinales superficiales (Fig. 2/16, 18 and 21).

The lateral cranial root was poorly developed. Its course and distribution were similar to those of the cranial root of the V. pudenda externa in the female.

The left and right medial cranial roots were satellites of the corresponding branches of the A. pudenda externa. The distribution of these roots accompanied the ramifications of the corresponding artery. In the specimens in which the medial cranial branch of the A. pudenda externa was better developed, the vein extended from the superficial ventral aspect of the preputial cavity. It coursed parallel to the satellite artery in the septum of the preputial diverticulum. Further, it continued laterally to the preputial sheath of the penis and to the inguinal region. Variable numbers of radicles from the venous plexus of the preputial cavity (Fig. 2/19) joined the medial cranial branch of the V. pudenda externa.

This venous plexus may be regarded as the ventral venous plexus of the sheath of the bovine penis (Ashdown 1958). The plexus was around the preputial orifice and extended caudally between the two recurrent arteries of the sheath. At the level of the fornix, slender radicles connected the plexus with the ventral branch of the V. dorsalis penis. The medial cranial root drained the fatty tissue, skin, preputial tissues of the preputial cavity, the sheath of the penis and the middle and cranial parts of the suspensory ligament of the penis, and was connected with the V. subcutanea abdominis.

The caudal root (Fig. 2/21) coursed parallel to the satellite artery enclosed in the fatty tissue of the interfemoral space. It extended from the septum scroti to the inguinal region, crossing the medial aspect of the spermatic cord. Two veins, the lateral and medial roots, joined the caudal root of the V. pudenda externa in the septum scroti. The distribution of these roots followed the course and ramifications of the accompanying caudal branch of the A. pudenda externa. A large radicle, which drained the tissues around the insertion of the M. cremaster externus, joined the caudal root at the level of the cranial aspect of the septum scroti. Near the caudal border of the spermatic cord it received the scrotal root of the V. pudenda interna (Fig. 2/25). The caudal root in its

further course was connected with its counterpart and collected a superficial tributary which drained in the scrotal fold and anastomosed with the roots of the Vv. subcutanea abdominis, circumflexa femoris medialis and profunda femoris. Before reaching the inguinal region the vessel became paired and the corresponding vessels were placed on either side of the satellite artery. They received radicles which came from the Lnn. inguinales superficiales.

The V. spermatica externa (Fig. 2/12) drained the M. cremaster externus in both the male and female. It coursed craniodorsally along the M. cremaster externus. In the male the radicles were connected with the radicles of the caudal root of the V. pudenda externa. In its cranial third the V. spermatica externa usually became a paired vessel. It joined the V. pudenda externa. In one out of ten specimens the vessel of the right side joined the V. circumflexa ilium profunda.

The venous drainage of the testicle, epididymis and ductus deferens was performed by the V. spermatica interna and the V. deferentialis.

The V. spermatica interna (Fig. 2/5), one of the components of the spermatic cord, consisted of various vessels which extended craniodorsally to the cortex of the pampiniform plexus through the inguinal canal. The vessel coursed craniolaterally to the seminal gland. In this course it was embedded in the plica vasculosa and connected the V. deferentialis by a communicating branch. The V. spermatica interna then passed medial to the ureter receiving the V. vesicalis cranialis. The V. spermatica interna may join the V. iliaca communis and the V. cava caudalis or the V. circumflexa ilium profunda. In three out of five specimens the V. spermatica interna on both sides joined the V. cava caudalis; in one specimen the right vessel joined the V. iliaca communis while the left went to the V. cava caudalis; and in the last specimen the left vein joined the V. circumflexa ilium profunda and the right one terminated in the V. cava caudalis. The pampiniform plexus (Fig. 2/7) was formed by numerous radicles which were derived from the testicle and the epididymis. The radicles of the testicle (Vv. testiculares) (Fig. 2/8) ran parallel into the albuginea at the lateral and medial faces of the testicle toward its cranial border. At this point they became flexuous and joined the radicles coming from the medial face of the epididymis to form a complicated venous network arrangement, which enlaced the tortuous course of the A. spermatica interna.

The V. deferentialis drained the ductus deferens (Fig. 2/36). It coursed along with the satellite artery in the inguinal canal in a craniodorsal direction to the abdominal cavity. In its course it was connected with the satellite vein of the deferential branch of the A. urogenitalis. The V. deferentialis, after leaving the inguinal canal, gave off an anastomotic vein to the V. spermatica interna. In the abdominal cavity it was seen accompanied by the corresponding artery on the lateral face of the ligament of the urinary bladder. At the level of the dorsal border of the ureter it turned cranially and joined the V. vesicalis cranialis (Fig. 2/35). Before reaching the dorsal border of the ureter the V. deferentialis received a slender tributary which drained the tissues surrounding the A. deferentialis.

The V. utero-ovarica in the female corresponds to the V. spermatica interna in the male (Fig. 3/5). It drained a pampiniform plexus found

near the ovary. The V. utero-ovarica coursed in the cranial border of the broad ligament embedded with its satellite artery. It followed the deep face of the ureter to join either the V. cava caudalis of the V. iliaca communis, or in one out of five specimens, it was noticed that the right V. utero-ovarica emptied directly into the V. iliaca communis. In one out of four specimens examined, the left vein joined the V. uterina media and the latter than drained into the V. iliaca communis. The pampiniform plexus is a triangular, vascular body embedded in the broad ligament (Fig. 3/7). It faced the ovary and the vertex is continued dorsally in the V. utero-ovarica. Small radicles from the roots of the V. uterina media and satellite radicles of the branches of the A. utero-ovarica constituted the pampiniform plexus of the ovary. The course and disposition of these radicles resembled those of the satellite arteries.

The V. uterina media coursed parallel to the homologous artery embedded in the mesometrium. It accompanied the deep face of the ureter close to the V. utero-ovarica to empty into the V. iliaca communis. In one out of five specimens examined the left veins joined the V. utero-ovarica.

The roots of the V. uterina media had a conspicuous arrangement in the distal third of the mesometrium. They became plexiform and enlaced the branches of the satellite arteries. In the virgin uterus it was possible to recognize that usually two roots, the caudal and the cranial, joined the V. uterina media (Fig. 3/36' and 36''). The former coursed from the ventrocaudal third of the body of the uterus parallel to the A. uterina caudalis. Its radicles anastomosed with those which corresponded to the V. uterina caudalis and with the fellow of the opposite side along the ventral wall of the body of the uterus. It thus drained the caudal and middle thirds of the uterus. In its cranial course in the mesometrium, the caudal root received a large tributary which extended from the cranial third of the ventral face of the body of the uterus. The radicles of this branch formed arcades on the mesometrial border of the uterine horn. Numerous rootlets (Ramuli uterini) from the wall of the uterine horn drained into these arcades.

The cranial root ran ventrally, contained within the mesometrium. Several radicles which extended from the cranial, middle and caudal aspects of the uterine horn converged to the cranial root. These radicles, like those of the caudal root, formed arcades which drained the wall of the uterine horn (Distal arcades of Barone et al. 1962). The most cranial radicles anastomosed with those of the V. utero-ovarica along the uterine tube and on the tip of the uterine horn. Between the cranial and caudal roots and the radicles of the Rami cervico-uterini (V. uterina media), anastomotic bridges could be seen.

The V. urogenitalis (Fig. 2/40, 3/40), a large tributary of the V. iliaca interna, coursed within the retroperitoneal fatty tissue located lateral to the rectum. The vein joined the ventral wall of the V. iliaca interna at the point where the latter approached the pelvic cavity. Two roots, the cranial and caudal, joined the V. urogenitalis (Fig. 2/41 and 51). The distribution of the cranial and caudal roots of the V. urogenitalis followed, in general, the ramifications of the satellite arteries.

In the male the cranial root (Fig. 2/41) arose from the lateral and ventral aspects of the seminal gland (Fig. 2/49), the ductus deferens

(Fig. 2/50), the prostate gland (Fig. 2/42), and the cranial third of the urethra (Fig. 2/47). Several interlobular radicles of the seminal gland joined it at the ventrolateral aspect (Fig. 2/49). They drained the lateral and medial aspects of the glandular structure. Numerous small rootlets joined these radicles. The rootlets arose from the venous plexus which was formed on the dorsolateral aspect of the urethra and prostate gland (Fig. 2/46). The caudal root (Fig. 2/51) was larger than the cranial and was assumed to be the main root of origin. The disposition of its radicles was intricate, but the distribution of the caudal roots followed the same pattern as that of the corresponding satellite arteries. A large prostatic radicle (Fig. 2/52), which coursed craniocaudally, drained the prostate gland to join the caudal root. This vein received several radicles from the dorsolateral aspect of the seminal gland. Its rootlets were connected to those of the cranial root and also to the urethral plexus.

Two larger radicles, which coursed along the lateral and medial faces of the bulbourethral gland, joined the caudal root. The lateral radicle coursed on the lateroventral aspect of the V. uterina media, forming the V. uterina caudalis (Fig. 3/50').

In the female the vesicular radicles (Fig. 3/47) (V. vesicalis caudalis) drained the cranial third of the urethra and anastomosed with those of the V. vesicalis cranialis and with the radicles of the V. uretherica. Communicating veins were seen to anastomose with the V. obturatorius, V. pudenda interna and with those of the Ramus obturatorius from the V. profunda femoris (Fig. 3).

The course and distribution of the caudal root resembled those of the satellite artery. It drained the vagina and the cranial portion of the vestibule of the vulva. The Vv. perinei, satellites of the corresponding arteries, joined the V. rectalis caudalis and were anastomosed with the rootlets of the vein which superficially drained the perivulvar tissues (Vv. caudales laterales) (Fig. 3/82).

The V. pudenda interna was one of the largest tributaries of the V. iliaca interna. In the male (Fig. 2/60), it was formed at the level of the dorsomedial aspect of the first bend of the sigmoid flexure of the V. dorsalis penis. From its origin the V. pudenda interna continued dorsally along the medial aspect of the M. ischiocavernosus. In this course, it received a tributary from the caudal branch of the V. pudenda externa which drained the scrotum (Fig. 2/67). Then the right and the left vessels anastomosed forming a venous plexus which extended to the ischial arch. On its caudal aspect the plexus received a common trunk which drained the V. profunda penis (Fig. 2/62), the Vv. bulbourethrae (Fig. 2/61), and the radicles from the Mm. ischiocavernosus and bulbocavernosus (Fig. 2/63). The V. pudenda interna continued its course towards the pelvic cavity. After approaching it, the vein usually became a paired vessel and ran parallel to the satellite artery, lateral to the bulbourethral gland and rectum. In this course it received on its cranial aspect a tributary which drained the ventrolateral aspect of the bulbourethral gland and caudal third of the urethra (Fig. 2/66). The rootlets of this vein were connected with those of the V. urogenitalis and it received, caudally, the Rami perinei (Fig. 2/64) and the radicles from the M. bulbocavernosus. The V. pudenda interna gave off a communicating tributary to the Ramus obturatorius of the V. profunda femoris (Fig. 2/60').

This vessel drained the M. obturator internus and the fatty tissue of the ventral wall of the pelvic cavity and was connected with its fellow of the opposite side, under the cranial third of the pelvic part of the urethra.

The V. dorsalis penis (Fig. 2/68) drained the body of the penis. It coursed on the dorsal aspect of it medial to the satellite artery. Two tributaries, the dorsal and ventral roots from the distal end of the penis, joined the V. dorsalis penis at the middle third of the penis. The dorsal root ran superficially along the dorsal aspect of the penis and drained the albuginea of the corpus cavernosum of the penis. Some radicles pierced the albuginea in the erectile tissue. The ventral root coursed along the ventral aspect of the corpus cavernosum urethrae. At the level of the fornix of the prepuce it was connected with branches of the V. pudenda externa.

In the female, the course and distribution of the V. pudenda interna were similar to those of the corresponding artery (Fig. 3/60). In general, it arose and anastomosed with the deep radicles of the caudal root of the V. pudenda externa. The V. pudenda interna ran dorsally towards the pelvic inlet. In this course, it received a tributary which drained the perivulvar veins (Fig. 3/82'). Near the ischial arch it received the V. dorsalis clitoridis. Then the V. pudenda interna divided into right and left vessels. Each usually became paired and extended to the lesser ischiatic notch. They passed laterally to the vagina and rectum within the retroperitoneal fatty tissue. In this course they received the tributaries which corresponded to the satellite arteries. By means of them the V. pudenda interna drained the vulva, the cavernous bodies of the clitoris and the caudal third of the urethra, and anastomosed with the V. urogenitalis. A large vessel from the V. pudenda interna joined the Ramus obturatorius of the V. femoris profunda (Fig. 3/60'). This vessel passed through the fatty tissue along the ventrolateral wall of the pelvic inlet. It received several radicles as tributaries which drained the fatty tissue of the region of the M. obturator internus.

The V. rectalis caudalis (Fig. 2/75, 3/75) coursed parallel to the satellite artery in the ischiorectal fossa. It drained either into the V. pudenda interna or into the V. glutea caudalis. This variation depended on the pattern of the satellite artery. In the male, it supported the draining of the Mm. bulbocavernosus, the sphincter ani externus, the perineum, and the dorsolateral aspect of the bulbourethral gland. In the female, it drained the vestibule of the vulva, the perineum, the Mm. sphincter ani externus and the constrictor vestibuli. The rootlets of this vein joined the rootlets of the vein which drained the perivulvar tissues externally (V. caudalis lateralis).

DISCUSSION

The venous drainage from the ventral wall of the abdominal cavity (including the mammary glands, prepuce and scrotum), generally speaking, fall into three categories according to their topography; the cutaneous system, the subcutaneous system and the deep system. The superficial or cutaneous system is exclusively for the skin. However, these three systems anastomosed with each other. The relationship between the artery and the corresponding vein also was variable. In some areas the

veins were not satellites of the arteries (e.g., V. subcutanea abdominis), whereas at places two veins accompanied each artery (e.g., V. pudenda interna, V. epigastrica cranialis), or only one vein was a satellite to each artery (e.g., V. thoracica interna). Having observed variations in the venous system in other areas it should be assumed that the above description cannot be considered the only pattern.

In all cases investigated the V. thoracica interna consisted of a single vessel formed by the union of the V. epigastrica cranialis and the V. musculophrenica at the level of the last costosternal articulation. The V. epigastrica cranialis was a double vessel placed on either side of the homologous artery. The medial vessel drained the V. subcutanea abdominis, contrary to the findings of Montane and Bourdelle (1920) and Bickhardt (1961). The V. epigastrica cranialis received radicles which drained the mammary glands (2nd, 3rd and 4th pairs) being connected in this manner with the V. subcutanea abdominis. It was observed that the valves in this vein were directed to the V. thoracica interna.

The V. subcutanea abdominis extended from the interfemoral space toward the angle of the costal arch. Although the tributaries which drained the ventral wall of the prepuce (venous plexus) and those which ran deeper in the median line have not been distinguished by Bickhardt (1961), the distribution of the vessel followed, in general, his descriptions. It should be noted, however, that the valves of this vein were directed towards the thoracic cavity.

The V. pudenda externa consisted of two veins which coursed parallel to the satellite artery inside the inguinal canal. The terminations of these veins were variable. In most cases, one of them joined the V. femoralis while the other joined the V. profunda femoris. In only two cases, both formed the pudendoepigastric trunk, concurring with the findings of Bickhardt (1961) and Lebedewa (1960).

The V. pudenda externa was formed by two roots, the cranial and the caudal roots, in the female. In the male, the confluence of three roots (lateral cranial, medial cranial and caudal) formed the origin of the parent vessel, contrary to the findings of Bickhardt (1961).

The disposition of the cranial root of the V. pudenda externa in the female agrees with the descriptions of Bickhardt (1961) and Lebedewa (1960). However, it was seen that the valves of the cranial root, in agreement with Lebedewa (1960), were directed to the V. pudenda externa. No valves were observed in the communicating veins which were connected with the V. subcutanea abdominis and V. pudenda externa. The caudal root of the V. pudenda externa was formed by the veins which were satellites to the arteries. The deep rootlets were joined to the V. pudenda interna in the perineum in the female, and up to the scrotal septum in the male. The valves in this root were directed to the V. pudenda externa, in agreement with Lebedewa (1960). In the male the medial cranial root extended in the preputial diverticulum only as a satellite to the arterial branch which was better developed and connected with the V. subcutanea abdominis.

The V. spermatica externa followed the disposition of its satellite artery, however, it was seen that its roots anastomosed with those of the caudal roots of the V. pudenda externa.

The V. spermatica interna and the V. deferentialis drained the

pampiniform plexus and the epididymis, respectively. Several anastomoses were found between the V. deferentialis and the pampiniform plexus. The Vv. testiculares in the testicle did not follow the arterial pattern. It was not possible to observe the abrupt bend of the testicular veins like the arteries in the mediastinum testis. They appeared as semi-coiled vessels which followed the septa. The larger vessels (Vv. testiculares) were embedded in the albuginea and ran in the opposite direction to the corresponding arteries. In fact, they were directed to the cranial border of the testicle, while the arteries appeared to emerge from the caudal border. The pampiniform plexus extended to the cranial third of the inguinal canal. Histological sections were not studied in the course of this investigation. Macerated specimens showed that the disposition of the veins which formed the pampiniform plexus resembled those which constitute the cavernous tissue of the bulbus vestibuli of the vulva. The V. deferentialis joined the V. vesicalis cranialis. The latter joined the V. spermatica interna. The termination of the V. spermatica interna was variable. In one out of five specimens, the right vessel joined the V. iliaca communis, confirmed by Schwarz and Badawi (1962) in both vessels in three females and one male. In the present investigation it was also noted that the left vessel joined the V. circumflexa ilium profunda in one of five specimens.

The V. utero-ovarica was the direct continuation of the pampiniform plexus of the ovary which drained the ovary, ovarian bursa, uterine tube and connected with the roots of the V. uterina media to support mainly the drainage of the uterus. Except for the variations in its termination and disposition, this vessel followed the description of Lange (1959) and Barone et al. (1962). In one of five specimens it was noted that the right vessel drained into the V. iliaca communis (Schwarz and Badawi 1962). In other instances, the left vessel assumed this disposition.

The V. uterina media was relatively less developed in relation to the accompanying artery. It was possible to recognize two roots forming the V. uterina media in the virgin uterus. They anastomosed between them and became plexiform within the layers of the mesometrium along the mesometrial curvature of the uterine horn, contrary to the findings of Barone et al. (1962). In all cases only the venous arches close to the mesometrial border of the uterine horn were observed. These arches were formed by the radicles which drain the uterine walls. It was interesting to note that the roots forming the V. uterine media were larger than the parent vessel itself, which probably was due to the cranial root anastomosing with the root of the V. utero-ovarica. Therefore, the drainage of the uterus was mainly accomplished by means of the V. utero-ovarica. Besides there were also transverse anastomoses between the caudal root of the V. uterina media and the ventrolateral wall of the body of the uterus, as well as communications between the V. uterina media and V. urogenitalis, confirmed by Lange (1959) and Barone et al. (1962). However, the termination of the V. uterina media was variable. In one out of five specimens the left vessel joined the V. utero-ovarica.

The V. urogenitalis in the male followed the same disposition as its satellite artery. It drained into the V. iliaca internus. A venous plexus was found at the beginning of the pelvic part of the urethra. This plexus was drained by the roots of the V. vesicalis cranialis, the roots of the

V. urogenitalis and the radicles of the cranial root of the Ramus obturatorius. Anastomoses between the V. urogenitalis and the V. pudenda interna were observed. In the main roots the valves were directed to the V. urogenitalis. In the female, the disposition of the V. urogenitalis followed the same pattern as that of its artery. However, it was noted that the cranial root anastomosed with the V. uterina media and with the V. vesicalis cranialis through the ureteral radicles. It was also observed that some radicles of the cranial roots anastomosed with the radicles of the Ramus obturatorius. The caudal root only drained the vagina and communicated with the V. pudenda interna. The Vv. perinei partly drained the vestibule of the vulva and the perineal region into the V. rectalis caudalis, in agreement with Lange (1959), but it was found that the Vv. perinei anastomosed with the roots which drained the musculature of the vulva superficially through the dorsolateral cutaneous vein of the tail.

The V. pudenda interna was found to be variable in disposition. In some cases it was a paired vessel. In the female it arose by a common trunk in the perineal region. This trunk anastomosed with the V. pudenda externa. The V. pudenda interna was connected with the caudal root of the Ramus obturatorius, in agreement with Lebedewa (1962). Also in agreement with her, the valves of the V. pudenda externa were directed to the V. iliaca interna, while those which correspond to the communicating vessel were directed to the Ramus obturatorius. This means that the venous blood of the vulva and its related structures (clitoris) drained either into the V. iliaca interna or into the V. profunda femoris.

In the male, the V. pudenda interna was the continuation of the V. dorsalis penis to the first bend of the sigmoid flexure. Three veins drained the penis. One of them coursed along the dorsal part of the body, being embedded in the albuginea ("cavernosum vein" of Montane and Bourdelle 1920). In this present investigation this term was omitted because it was not in accord with the anatomical disposition. The other two veins, in agreement with Montane and Bourdelle (1920), ran ventrally at each side of the cavernous bodies of the urethra. As pointed out, these vessels drained into either the ventral plexus of the prepuce (V. pudenda externa) or the V. dorsalis penis or continued in the cavernous bodies of the urethra, contrary to Montane and Bourdelle (1920). The V. pudenda interna anastomosed with the V. pudenda externa upon the scrotal septum. At the level of the ischial arch the two Vv. pudendae externae anastomosed between them forming a venous plexus which drained the veins of the upper part of the penis and urethra (crus of the penis and erectile tissue of the urethra). As in the female, the V. pudenda interna in the male also anastomosed with the Ramus obturatorius.

The V. rectalis caudalis principally drained the perineum, in agreement with Lange (1959).

SUMMARY AND CONCLUSIONS

The details of the venous drainage of the mammary glands as well as of the male and female reproductive tract are described. Gross dissections were supplemented by the study of corrosion specimens.

Injection methods were followed by gross dissections which were supplemented by the study of corrosion specimens. Storing the specimen

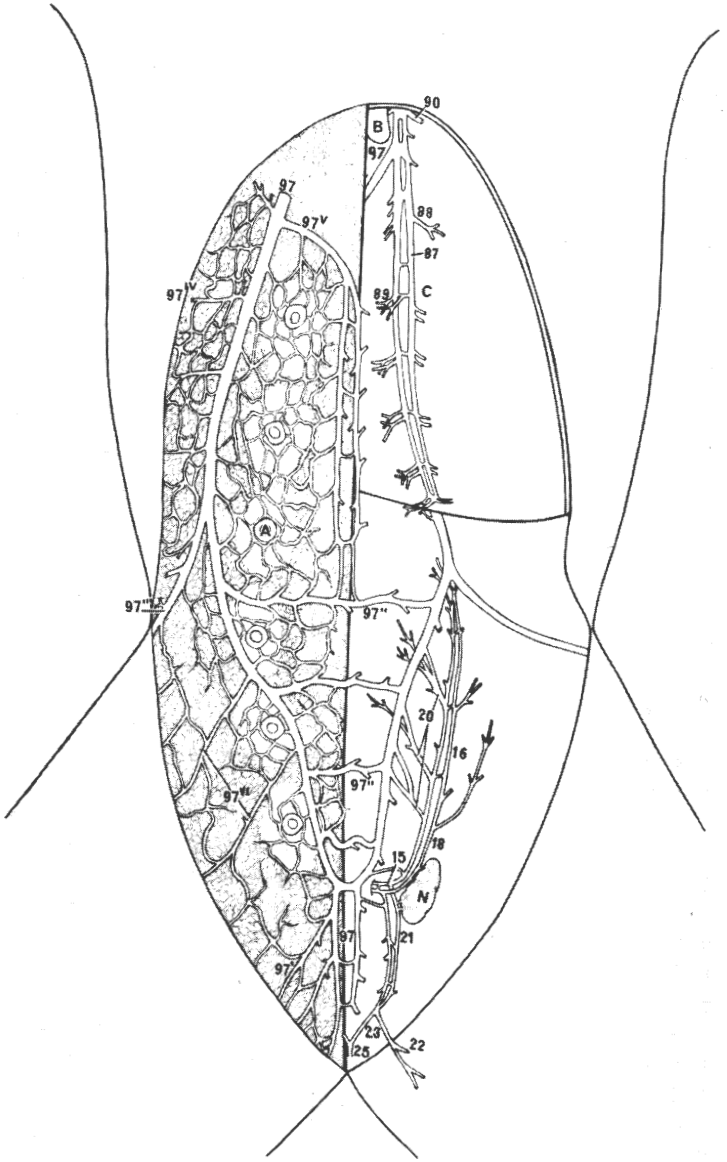
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Figure 1. Veins from the ventral aspect of the trunk in the female pig (schematic).

The right side has been dissected superficially. The cranial portion of the left side was exposed after removing the M. rectus abdominis while the caudal portion was deeply dissected and the mammary glands were removed.

A. Mammary gland
B. Xiphoid process (sternum)
C. M. rectus abdominis (cut)
N. Lnn. inguinales superficiales (reflected

15. V. pudenda externa
16. Cranial root of 15
20. Communicant radicles from 97
21. Caudal root from 15
22. Superficial radicle of 21
23. Deep radicle of 21
25. Anastomosis from 15 to the V. pudenda interna
87. V. epigastrica cranialis
88. Lateral roots of 87
89. Medial roots of 87
90. V. musculophrenica
97. V. subcutanea abdominis
97'. Anastomotic radicles from 97 to the V. circumflexa femoris medialis and V. saphena parva
97''. Communicant bridges between 97 of both sides
97'''. Root from the knee fold
97^{iv}. Roots from the lateral wall of the trunk
97^{v}. Root from the median plane of the ventral aspect of the trunk
97^{vi}. Anastomotic radicles to the V. saphena magna

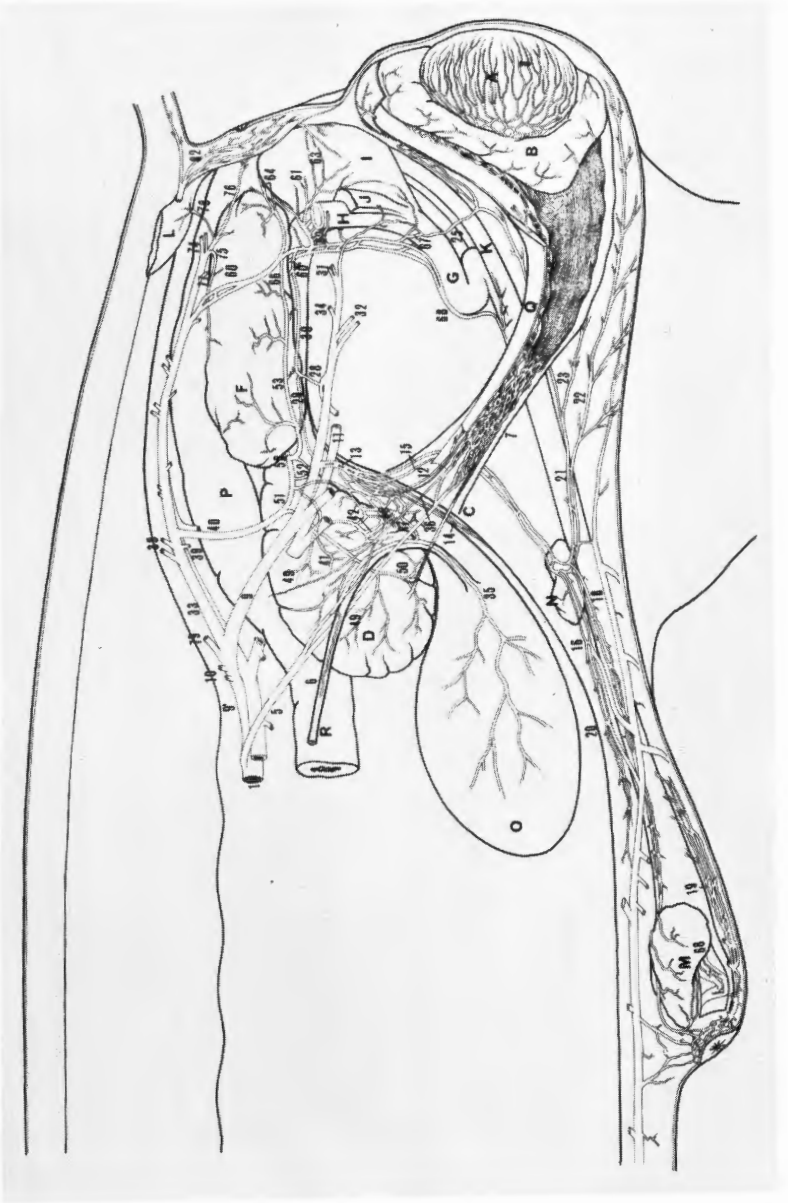
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Figure 2. Veins from the genital tract of the male swine (schematic)

A. Testicle
B. Epididymis
C. Ductus deferens
D. Seminal gland
F. Bulbourethral gland
G. Penis
H. Crus of the penis cut away from ischial arch
I. M. bulbocavernosus
J. M. ischiocavernosus
K. M. retractor penis
L. M. ischiococcygeus
M. Preputial diverticulum
N. Lnn. inguinales superficiales (lifted)
O. Urinary bladder
P. Rectum
Q. M. cremaster externus
R. Ureter

1. V. cava caudalis
5. V. spermatica interna
6. V. ureterica
7. Pampiniform plexus
8. Vv. testiculares
9. V. iliaca externa
9'. V. iliaca communis (left)
10. V. circumflexa ilium profunda
11. V. femoris profunda
12. V. spermatica externa
13. Truncus pudendoepigastricus
14. V. epigastrica caudalis
15. V. pudenda externa
16. Lateral cranial root of 15
18. Medial cranial root of 15
19. Venous plexus of the prepuce
20. Communicant radicles between 15 and V. subcutanea abdominis
21. Caudal root of 15
22. Superficial root of 21
23. Deep root of 21
25. Anastomotic root of 21 to 60
28. Ramus obturatorius
29. Cranial root of 28
30. Caudal root of 28
31. Caudoproximal root of 11
32. V. circumflexa femoris medialis
33. V. iliaca interna
34. Anastomotic root between 11 and 60
35. V. vesicalis cranialis
36. V. deferentialis
38. V. glutea cranialis
39. V. obturatoria
40. V. urogenitalis
41. Cranial root of 40
42. Prostatic radicles
46. Venous plexus of the urethra
47. Urethral radicles
49. Glandular radicles from the seminal gland
50. Deferential radicles
51. Caudal root of 40
52. Prostatic radicle
53. Lateral radicle of 51
58. Medial radicle of 51
60. V. pudenda interna
60'. Communicant radicle to 28
61. Vv. bulbourethrae
62. Vv. profundae penis
63. Muscular radicles
64. Rami perinei
66. Radicle from the ventrolateral part of the bulbourethral gland
67. Communicant radicle to 15
68. V. dorsalis penis
68'. Dorsal root of 68
74. V. glutea caudalis
75. V. rectalis caudalis
76. V. perinealis
77. Root from the bulbourethral gland
78. Root from the M. ischiococcygeus
79. V. sacralis media
82. Cutaneus radicles of the Vv. caudales laterales

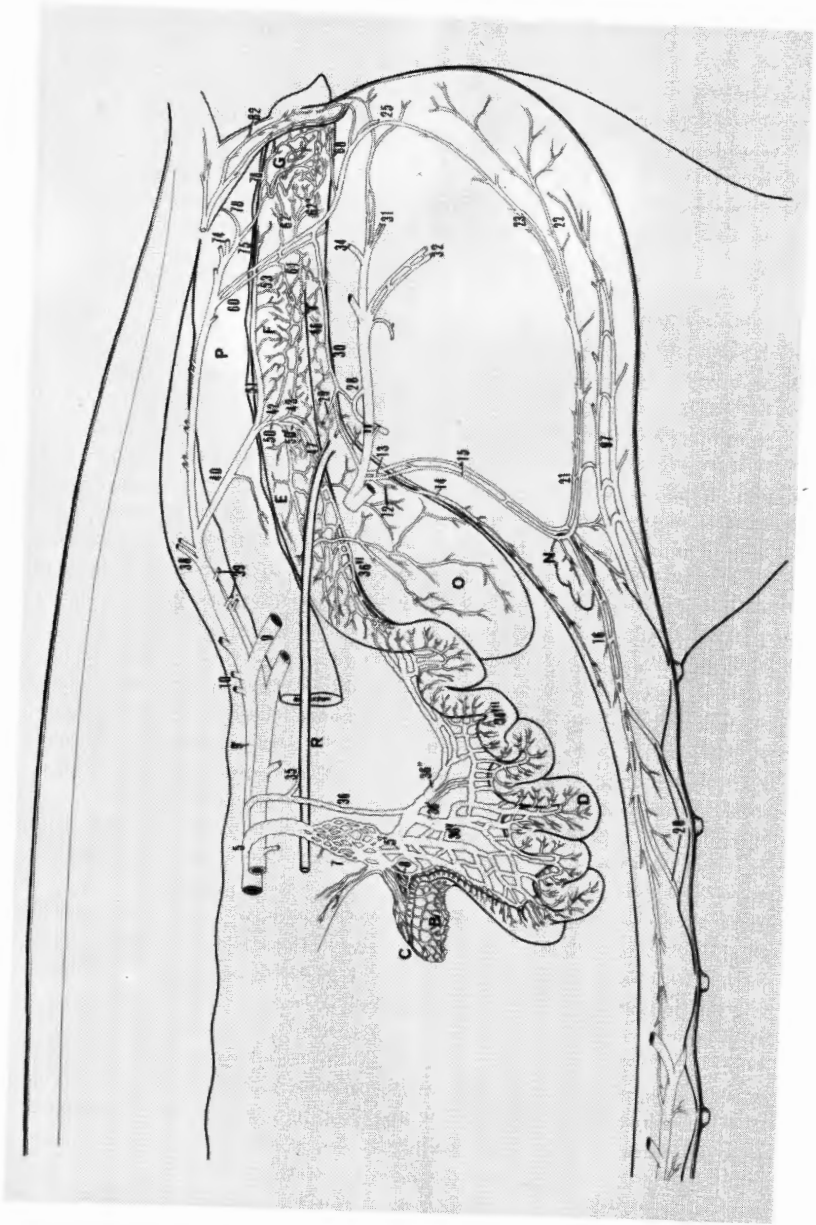
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Figure 3. Veins from the genital tract of the female pig (schematic)

A. Ovary
B. Ovarian bursa
C. Uterine tube
D. Uterine horn
E. Body of uterus
F. Vagina
G. Vulva
H. Crus of the clitoris cut away from the ischial arch
L. M. ischiococcygeus
N. Lnn. inguinales superficiales (lifted)
O. Urinary bladder
P. Rectum
R. Ureter
S. M. spincter ani externus
T. Urethra
U. M. constrictor vestibuli
V. M. constrictor vulvae
X. Broad ligament (cut away from its origin)

1. V. cava caudalis
5. V. utero-ovarica
5'. Rami tubouterini
5''. Venous plexus of 5'
6. Ramus uretericus
7. Pampiniform plexus
8. Vv. ovarici
9. V. iliaca externa
9'. V. iliaca communis
10. V. circumflexa ilium profunda
11. V. profunda femoris
12. V. spermatica externa
13. Truncus pudendoepigastricus
14. V. epigastrica cranialis
15. V. pudenda externa
16. Cranial root of 15
20. Communicant radicles between 15 and V. subcutanea abdominis
21. Caudal root of 15
22. Superficial radicle of 21
23. Deep radicle of 21
25. Anastomosis between 15 and 60
28. Ramus obturatorius
29. Cranial root of 28
30. Caudal root of 28
31. Caudoproximal branch of 11
32. V. circumflexa femoris medialis
34. Communicant vein between 11 and 60
35. V. vesicalis cranialis
36. V. uterini media
36'. Cranial root of 36
36''. Caudal root of 36
36^{v}. Anastomotic radicles to 5
36^{vi}. Anastomotic radicles to 40
36^{vii} Ramuli uterini
38. V. glutea cranialis
39. V. obturatoria
40. V. urogenitalis
41. Cranial root of 40
42. Rami vaginalis
43. Rami urethralis
46. Urethral (venous) plexus
47. V. vesicalis caudalis
50. Rami uterini
50'. Rami cervicouterini
51. Caudal root of 40
53. Vaginal radicles of 51
60. V. pudenda interna
60'. Communicant radicle to 28
61. V. urethralis
62'. Rami vestibularis
62''. V. profunda clitoridis
68. V. dorsalis clitoridis
74. V. glutea caudalis
75. V. rectalis caudalis
76. V. perinealis
78. Root from the M. ischiococcygeus
82. Cutaneous radicles of the Vv. caudales laterales
97. V. subcutanea abdominis

for a considerable time at room temperature permitted one to overcome the valvular resistance of the veins.

The general pattern of the venous disposition in some areas followed the course of the corresponding arteries. The venous drainage of the mammary glands was accomplished through the V. thoracica interna and its tributaries and the V. pudenda externa. They followed the course of their respective satellite arteries.

The V. subcutanea abdominis was not accompanied by an artery. It drained the subcutaneous and cutaneous systems related to the mammary glands. It was connected with the V. epigastrica cranialis. The V. pudenda externa principally drained the last two pairs of mammary glands (inguinal glands). Accordingly, the venous blood can flow either along the course of the A. pudenda externa, V. epigastrica cranialis or the V. subcutanea abdominis.

The area between the last pair of mammary glands and the perineum was drained by means of the caudal root of the V. pudenda externa and the V. subcutanea abdominis.

Variations of the termination of the V. spermatica interna (V. uteroovarica in the female) and the V. uterina media were reported. They terminated either in the V. iliaca communis or in the V. cava caudalis. Anastomosis between these two vessels was also noticed. The V. uteroovarica mainly drained the ovary, the uterine tube and the tip of the uterine horn. It received the roots of the V. uterine media. The V. urogenitalis drained the urethral venous plexus. In the male, it further drained the accessory genital glands, whereas in the female, it drained the cervix of the uterus and the vagina.

Anastomoses were observed between the V. vesicalis caudalis and cranialis and also between the V. urogenitalis and the roots of the Ramus obturatorius.

The V. pudenda interna drained the vagina, the clitoris and the cranial portion of the vulva in the female. It communicated with the Ramus obturatorius of the V. profunda femoris, the V. pudenda externa, and the V. urogenitalis. In the male, the V. dorsalis penis formed the V. pudenda interna. The latter formed a venous plexus at the level of the ischial arch and anastomosed with the Ramus obturatorius, as in the female.

The V. perinealis was not a satellite of the artery in the female. It joined the V. rectalis caudalis. The V. perinealis drained the caudal portion of the vulva and was connected with the radicles of the V. caudalis lateralis. The penis was drained by means of three veins, one of which coursed dorsally along the penis while the other two coursed ventrally along the cavernosus tissue of the urethra. They converged to form the V. dorsalis penis. The ventral veins communicated at the level of the fornix of the prepuce with the venous plexus which was placed on the ventral wall of the prepuce.

The ventral venous plexus of the prepuce was drained by the V. subcutanea abdominis and V. pudenda externa.

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