Bulletin of the
Museum of
Comparative
Zoology

Pleistocene Mustelidae (Mammalia, Carnivora) from Fairbanks, Alaska

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PLEISTOCENE MUSTELIDAE (MAMMALIA, CARNIVORA) FROM FAIRBANKS, ALASKA

ELAINE ANDERSON[1]

ABSTRACT. Five species of mustelids, *Mustela* cf. *erminea*, *Mustela vison*, *Mustela eversmanni beringiae* ssp. nov., *Gulo gulo*, and *Taxidea taxus*, are reported from late Pleistocene deposits near Fairbanks, Alaska. This is the first record of the steppe ferret in the New World. It is closely related to, if not conspecific with, *Mustela nigripes*, the black-footed ferret. The northernmost occurrence of *Taxidea taxus* is reported. The wolverine, badger and ferret material is characterized by large size, and some of the specimens are the largest known for the species. The Fairbanks area was never glaciated, and the grassy steppes of this refugium supported a large assemblage of Pleistocene mammals.

INTRODUCTION

Remains of Pleistocene mammals are abundant in the frozen sediments of central Alaska, and at least 39 species are known. Many species of carnivores were associated with the large assemblage of herbivores that inhabited the Alaskan refugium in the late Pleistocene. Large carnivores, *Arctodus simus*, *Ursus arctos*, *Panthera leo atrox*, *Homotherium serum*, and *Canis lupus* dominated the scene, but the small carnivores—foxes, dhole, lynx, and the mustelids—were an important part of the fauna. Five species of mustelids, *Mustela* cf. *erminea*, *Mustela vison*, *Mustela eversmanni beringiae* ssp. nov., *Gulo gulo*, and *Taxidea taxus* are now known from the Fairbanks area.

Fossil collecting began in the Fairbanks area with the advent of gold mining in 1928. In 1929, the University of Alaska, under the presidency of C. E. Bunnell, initiated its well known program of collecting the fossils exposed during the mining operations. The university had little money for such ventures, but Childs Frick of the American Museum of Natural History agreed to finance the program, and his support continued until the middle 1950's (except during the war years when little mining was done). Otto W. Geist was in charge of collecting the fossils. Thousands of specimens were collected, but unfortunately, because of the methods of collection, stratigraphic information is almost entirely lacking. Since the University of Alaska had neither the space nor the comparative material, almost all of the specimens were shipped to the Frick Laboratory at the American Museum of Natural History. There, a few groups were studied, but most of the material was put in storage. The Mustelidae was one of the neglected groups, and until 1973, when Anderson reported the presence of ferret, only badger and wolverine were recorded in the faunal lists (Péwé, 1957).

The Fairbanks area, where the fossils were collected, lies between 64°45′ and 65°N latitude, and is situated on the north side of the broad Tanana River valley at the base of the hills that make up part of the Yukon-Tanana River upland (see Fig. 1). Rising 380 to 545 meters above the nearly flat floodplain of the Chena and Tanana rivers, are the low rounded hills of the uplands. Loess, derived from the floodplain and the glacial outwash plains, covers the ridges

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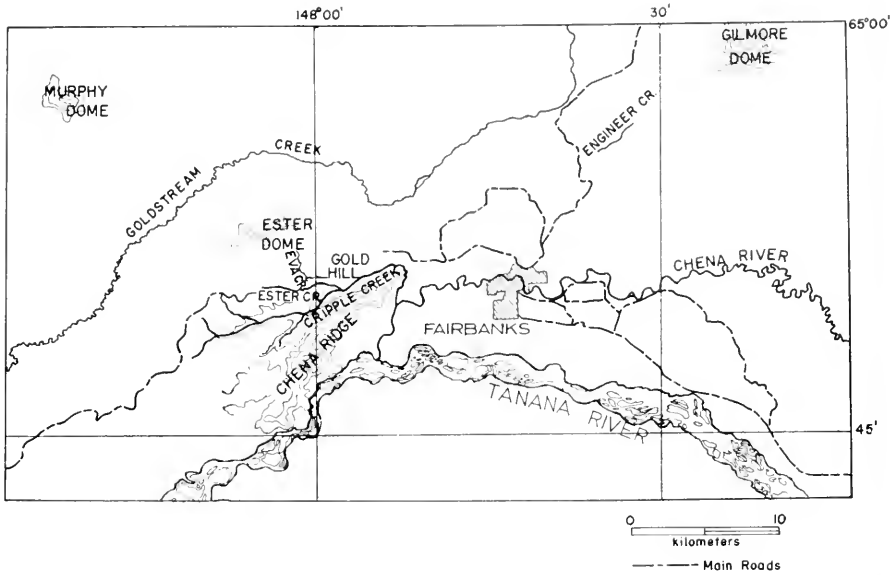

Figure 1. Map of the Fairbanks area.

from a depth of about a meter on the summits to about 30 meters on the middle slopes. The upland valleys are filled with from three to 30 meters of gravel overlaid by three to 90 meters of colluvial silt. The floodplain is underlaid by several hundred feet of interbedded lenses of silt, sand, and gravel (Péwé, 1957). The Fairbanks area was never glaciated, but glaciers from the Alaska Range to the south came within 80 kilometers of the present city of Fairbanks.

The Quaternary in central Alaska is characterized by alternating periods of deposition and erosion of gravel and silt, by warming and cooling of the climate, and by the formation and melting of the permafrost. Gold-bearing gravels were deposited in the creek valleys early in the Quaternary, and were later covered by loess and organic debris which became perennially frozen. Solifluction, the movement of moisture-saturated soil downhill during periods of thawing, was a major factor in the entombment of animal and plant remains. The fossil-laden silt eventually came to rest in the valleys, and was subsequently covered with more loess, and the entire mass became frozen. Today permafrost covers much of the Fairbanks area. Needless to say, mining and collecting fossils in this perennially frozen muck was, and still is, difficult. The fossils were exposed as the miners, using hydraulic methods, removed the frozen overburden from the gold-bearing gravels.

Since most of the bones were transported before burial, mummies and complete skeletons are rare, and most of the specimens are disarticulated. Although a few pre-Wisconsinan deposits are known (Péwé and Hopkins, 1967), the majority of specimens are late Wisconsinan in age.

The mustelid material is generally well preserved, although some of the teeth are broken. The bones vary in color from light to dark brown, and there is no trace of the blue mineral, vivianite, on any of the material I examined. The specimens consist entirely of skulls and mandibles. A femur of *Gulo* was listed in the field notes, but the specimen could not be found.

ACKNOWLEDGEMENTS

I wish to express my deep appreciation to Dr. Richard H. Tedford for letting me study the Alaskan mustelids in the Frick Collection. Beryl Taylor and George Krochak of the Frick Laboratory, American Museum of Natural History, assisted me in locating specimens and field data. Russell D. Guthrie, University of Alaska, showed me some of the collecting areas near Fairbanks, and I would like to thank him and his wife for their generous hospitality during my visit to Fairbanks. For permission to study collections in their care, I am indebted to John A. White, Idaho State University; Peter Robinson, University of Colorado Museum; Charles S. Churcher, University of Toronto; and C. R. Harington, National Museum of Canada. My sincere thanks go to Barbara Lawrence and Charles Mack, Museum of Comparative Zoology; John L. Paradiso and Clyde Jones, Bureau of Sport Fisheries and Wildlife, National Museum of Natural History; Richard G. Van Gelder, American Museum of Natural History; William H. Burt, University of Colorado Museum; and Robert S. Hoffmann, Museum of Natural History, University of Kansas, for making comparative material available to me. Björn Kurtén, University of Helsinki, permitted me to use some of his raw data on *Gulo gulo*. Erica Hansen, Idaho State University, made the illustrations for Figures 1–3; Ms. Dehlin, formerly of the Frick Laboratory, executed Figures 4 and 5 for Childs Frick some years ago. This research was supported by NSF Grant GB 31287 awarded to Professor Bryan Patterson, Harvard University, and is part of a study of Pleistocene mammals of North America.

ABBREVIATIONS

AMNH—American Museum of Natural History
F:AM—Frick Collection, American Museum of Natural History
ISUM—Idaho State University Museum
KU—Museum of Natural History, University of Kansas
MCZ—Museum of Comparative Zoology, Harvard University
NMC—National Museums of Canada
UA—University of Alaska
UCM—University of Colorado Museum
USNM—National Museum of Natural History
I—incisor
C—canine
P—premolar
M—molar
(with superscript (upper) or subscript (lower) tooth)
max.—maxillary
R—right
L—left
N—number in sample
O.R.—observed range
M—mean
S.D.—standard deviation

Mustela sp. cf. *M. erminea* Linnaeus Short-tailed Weasel or Ermine Figure 2 A

Material: Late Pleistocene, F:AM 49340 L ramus w/ $C–M_2$; F:AM 49341 R ramus w/ $C–M_2$; F:AM 49348 R ramus w/ $C–M_1$; F:AM 49349 frag. L ramus w/ P_{3-4}, Fairbanks area, Alaska.

Comparative Material: *Mustela erminea arctica*, Recent, Alaska AMNH 17939, 21917–19, 21921–22, 31369, 31379. KU 2975–76. *Mustela rixosa eskimo* Recent, Alaska AMNH 31383–84, 42811–13, 42815–18. Northwest Territory AMNH 29212.

Four small weasel mandibles were found in the collections from the Fairbanks area. Guthrie (personal communication) believes they were preserved in the nests of ground squirrels, *Spermophilus parryi*. The coronoid process is missing in all of the specimens. The teeth of three of the specimens are slightly worn, but F:AM 49348 shows moderately worn dentition. Comparison with Recent specimens of *Mustela erminea arctica* (Merriam) and *Mustela rixosa eskimo* (Stone), the two subspecies found in central Alaska today, shows that the Pleistocene specimens most closely resemble *Mustela erminea arctica*. Table 1 shows that measurements of tooth row length, length of M_1, length of trigonid of M_1, and width of the talonid of M_1 of the Pleistocene mandibles fall within the observed range of *Mustela erminea arctica* and exceed the observed range of *Mustela rixosa eskimo*.

In his monograph on American weasels, Hall (1951) noted that the basilar length of the skull of *Mustela erminea* measures

TABLE 1. MEASUREMENTS, IN MM, OF *MUSTELA ERMINEA* AND *MUSTELA RIXOSA* FROM ALASKA.

		N	O.R.	M
Depth of ramus below P_{3-4}				
F:AM, Late Pleistocene		4	3.0–3.2	3.05
M. e. arctica (Recent)	♂	7	3.3–4.3	4.02
	♀	3	2.6–3.5	2.96
M. r. eskimo (Recent)	♂	6	2.3–3.4	2.86
	♀	4	2.2–2.5	2.40
Depth of ramus below M_{1-2}				
F:AM, Late Pleistocene		3	2.5–3.3	3.03
M. e. arctica (Recent)	♂	7	3.5–4.8	4.40
	♀	3	2.9–3.7	3.26
M. r. eskimo (Recent)	♂	6	2.7–3.5	3.13
	♀	4	2.5–2.9	2.72
Length C–M_2				
F:AM, Late Pleistocene		3	11.9–12.0	11.93
M. e. arctica (Recent)	♂	7	12.0–15.8	14.52
	♀	3	11.4–12.7	11.90
M. r. eskimo (Recent)	♂	6	9.5–10.8	10.10
	♀	4	9.0–9.7	9.22
Length M_1				
F:AM, Late Pleistocene		3	4.3–4.6	4.46
M. e. arctica (Recent)	♂	7	4.5–5.6	5.01
	♀	3	4.1–4.7	4.33
M. r. eskimo (Recent)	♂	6	3.4–3.8	3.55
	♀	4	3.1–3.5	3.25
Length M_1 trigonid				
F:AM, Late Pleistocene		3	3.0–3.3	3.20
M. e. arctica (Recent)	♂	7	3.1–3.8	3.60
	♀	3	2.9–3.4	3.06
M. r. eskimo (Recent)	♂	6	2.4–2.6	2.50
	♀	4	2.2–2.5	2.30
Width M_1 talonid				
F:AM, Late Pleistocene		3	1.2–1.4	1.33
M. e. arctica (Recent)	♂	7	1.2–1.9	1.57
	♀	3	1.2–1.3	1.23
M. r. eskimo (Recent)	♂	6	1.0–1.2	1.08
	♀	4	0.9–1.0	0.92

more than 32.5 mm in males and more than 31.0 mm in females; in *Mustela rixosa* the basilar length of the skull is less than 32.5 mm in males and 31.0 mm in females. Unfortunately, he did not include any measurements of weasel mandibles. Table 1 shows that there is overlap in measurements between the two species, and this, coupled with pronounced sexual dimorphism and geographic variation, can lead to uncertainty in the identification of cranial material.

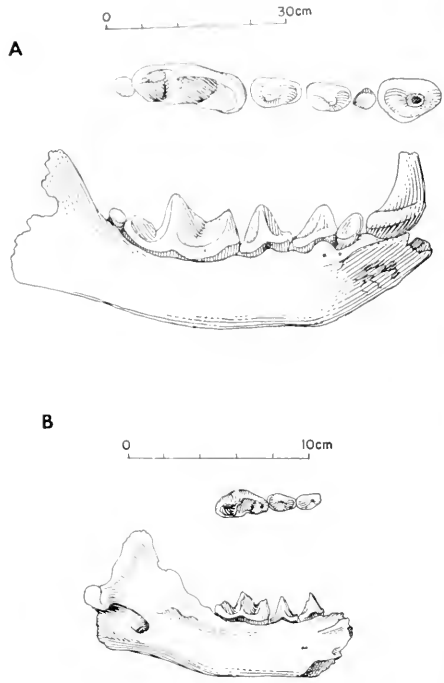

Figure 2. A. *Mustela* cf *erminea* (F:AM 49340); occlusal and lateral views of mandible. B. *Mustela vison* (F:AM 30821); occlusal and lateral views of mandible.

The American ermine is considered to be only subspecifically distinct from the Old World animal. The taxonomic status of the least weasel is uncertain. Some workers (see Jones, 1964) regard *Mustela rixosa* as only subspecifically distinct from the Eurasian *Mustela nivalis*. But, in Sweden, the two species live side by side without interbreeding (Kurtén, personal communication). Until detailed comparative and statistical studies are done on both the Old and New World populations, I am recognizing *Mustela rixosa* as a distinct species.

The ancestry of *Mustela erminea* can be traced back to the late Pliocene in Europe, and the species probably reached North America in late Blancan or early Irvingtonian times. The earliest known North American occurrence is from the Cudahy

TABLE 2. MEASUREMENTS, IN MM, OF *MUSTELA VISON* FROM ALASKA.

	N	O.R.	M	S.D.
Depth of ramus below P_{3-4}				
F:AM 30821	1	7.8	—	—
M. v. ingens (Recent, Alaska)	16	6.1–8.3	7.45 ± .17	.71
Depth of ramus below M_{1-2}				
F:AM 30821	1	8.2	—	—
M. v. ingens (Recent, Alaska)	16	7.0–9.4	8.26 ± .19	.79
Length M_1				
F:AM 30821	1	7.8	—	—
M. v. ingens (Recent, Alaska)	16	7.4–9.0	8.14 ± .12	.49
Length M_1 trigonid				
F:AM 30821	1	5.3	—	—
M. v. ingens (Recent, Alaska)	16	5.1–6.1	5.75 ± .08	.32
Width M_1 talonid				
F:AM 30821	1	3.3	—	—
M. v. ingens (Recent, Alaska)	16	2.7–3.8	3.31 ± .08	.34

fauna, and ermines have been reported from several late Pleistocene and postglacial localities.

Mustela vison (Schreber) Mink
Figure 2 B

Material: Late Pleistocene, F:AM 30821 fragment of left ramus with P_3–M_1, Fairbanks Creek, Alaska.

Comparative Material: *Mustela vison ingens*, Recent, Alaska, MCZ 34165. USNM 6531–32, 7115, 8646, 8696–99, 8702–06, 8708–09, 14463, 20814. Yukon Territory MCZ 34517–18.

A single mandible of *Mustela vison* is known from the Fairbanks area. The jaw is broken off anterior to the second premolar, and the coronoid process is eroded as is the labial side of the condyle. The sharply pointed cusps of the teeth show slight wear. Each tooth is surrounded by a well developed cingulum, and there is an incipient metaconid on M_1. Table 2 shows that measurements of the specimen fall within the observed range of *Mustela vison ingens* (Osgood), the extant subspecies found in the area today. It is the largest subspecies of *Mustela vison*. No morphological differences were observed between the specimen and the comparative material.

The specimen can be distinguished easily from the *Mustela eversmanni* mandibles by the incipient metaconid and wider talonid on M_1, and the longer and narrower P_4. Table 3 shows other differences separating mink from ferret.

Although records of *Mustela vison* extend back to the late Irvingtonian Cudahy fauna, Meade County, Kansas (Getz, 1960), mink are not common in Pleistocene deposits. Since they are found only along streams and lakes, the presence of mink in a fauna is a good indicator of nearby permanent water.

Mustela (*Putorius*) *eversmanni* Lesson
Steppe Ferret

Material: Late Pleistocene, Fairbanks area, Alaska, F:AM 49336 anterior half skull w/R P^{2-4}, L I^3, C, P^{2-3}, P^4 broken, Ester Creek. F:AM 49337 L mandible w/C–M_2, Cripple Creek. F:AM 30827 frag. L ramus w/I_3, C, P_2, P_4–M_1, Cripple Creek. *Mustela eversmanni* Recent, MCZ 23705, 24737, 25333, 40939–40, 54604. USNM 22191, 188449, 259792. AMNH 57338, 60102, 85382. *Mustela eversmanni michnoi* USNM 38365, 172631, 175439, 175441. AMNH 45605–06, 84312.

Mustela putorius Recent, MCZ 3702, 24665, 24738, 25352. USNM 792, 1851, 22394, 115213–214, 121248, 123629, 152668–670, 152673–676, 154158, 319222–223. AMNH 36631–32, 69520, 119621, 163437.

Mustela nigripes, Late Pleistocene, Little Box Elder Cave, Converse County, Wyoming, UCM 21916–18, 21922–24, 21950–52, 21957, 21959, 21962, 21965–70, 21972, 21975, 21977–78, 21980, 21983, 21985, 21989–90, 22010–11, 22022–23, 22151.

Mustela nigripes, Recent, MCZ 4184, 42723, 43727. KU 1487, 1593, 7146, 10177, 11077, 14411. AMNH 1203, 40078, 41994, 42567, 70590, 121610, 140397. UCM 59, 10658, 10660. USNM 14580, 21066, 21965, 21976, 22311, 22427, 22929, 30064–66, 32771, 34977, 35011, 35016–18, 35088, 35376, 65061, 83992–994, 110772, 122620, 155475, 168744, 188450–453, 188455–458, 199737, 201945, 211513, 224450, 228233, 228789, 232400, 234118, 234138,

TABLE 3. COMPARISON BETWEEN *MUSTELA EVERSMANNI-NIGRIPES* AND *MUSTELA VISON*, CRANIAL CHARACTERS.

Variate	*M. eversmanni-nigripes*	*M. vison*
Palate	Wide between canines	Narrow between canines
Basiocciput	Narrow	Wide
Basicranium	Well-defined tube extending from foramen ovale to anterior margin of auditory bullae	Area between foramen ovale and auditory bullae is flat
Auditory bullae	More inflated	Less inflated
Mastoid bullae	Inflated	Not inflated
Auditory meatus	External opening large	External opening small
Infraorbital foramen	Small	Large
Canines, upper and lower	Relatively large	Relatively small
P^3	Short, broad	Long, narrow
P^4	Relatively short protocone	Relatively long protocone
M^1	Inner lobe not expanded	Inner lobe expanded
Mandible	Relatively short and thick	Relatively long, slender
Inferior margin of jaw at angle	Broad, flattened	Pointed, less flattened
Premolars	Relatively short, broad	Relatively long, narrow
M_1	Metaconid absent, talonid narrow	Incipient metaconid, talonid wide
M_2	Relatively small	Relatively large

134970–971, 234973, 241014, 243799, 243818–820, 243909–910, 243990, 245641, 247073, 251453, 285877, 287321, 289498.

Anderson (1973) reported the presence of ferret in central Alaska. Additional studies show that the material is referable to *Mustela eversmanni*, the steppe ferret, an animal closely related to, if not conspecific with, *Mustela nigripes* the black-footed ferret. This is the first record of *Mustela eversmanni* in North America.

Mustela eversmanni beringiae[1] ssp. nov.
Beringian Ferret
Figure 3

Type. F:AM 49336 anterior half of skull with right P^{2-4}, alveoli of I^{1-3}, C; left I^3, C–P^{2-3}, P^4 broken, alveoli of I^{1-2}, M^1, Ester Creek, T 1 S, R 2 W, about 16 km west of Fairbanks, Alaska 64° 50′N, 148°W. Fairbanks D–2, D–3 Quadrangles. Collected in 1938.

Hypodigm. Type plus F:AM 49337 left mandible with C–M_2, alveoli of I_{1-3}, Cripple Creek. F:AM 30827 fragment of left ramus with I_3, C, P_2, P_4–M_1, alveoli of I_{1-2}, P_3, Cripple Creek, T 1 S, R 2 W, west of Fairbanks, Alaska.

Distribution. Known only from late Pleistocene deposits near Fairbanks.

Diagnosis. Large ferret; facial region broader than *Mustela eversmanni michnoi*; massive postorbital processes; pronounced postorbital constriction; broad palate; tooth row crowded; enlarged canines.

A broad facial region characterizes the skull, and measurements of the breadth across the canines, carnassials, interorbital region, and postorbital processes exceed those of all the ferrets I have measured or have seen referred to in the literature. The skull belonged to an adult animal—the teeth are moderately worn, the nasal and palatine sutures are obliterated, and the sagittal crest is well developed. The nasal opening is large, and the opening of the small infraorbital foramen is an elongated oval. Extending from the tips of the broad postorbital processes are distinct ridges that unite in the region of the postorbital constriction to form the sagittal crest. The area between the postorbital processes and the constric-

[1] beringiae—from Beringia, the enormous unglaciated land mass extending from western Alaska to northeastern Siberia during the Pleistocene.

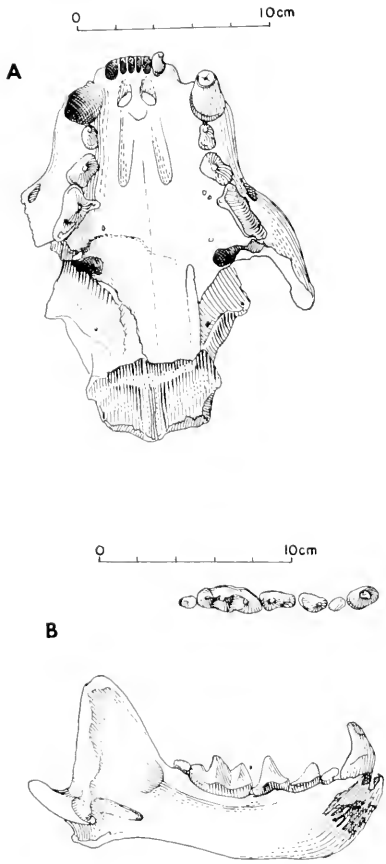

Figure 3. *Mustela eversmanni beringiae* ssp. nov. A. (F:AM 49336 Type) occlusal view of partial skull. B. (F:AM 49337) occlusal and lateral views of mandible.

tion is long and straight. The skull is broken just posterior to the constriction.

The upper teeth are crowded; there is no diastema between the canine and P^2, and P^3 is set obliquely in the jaw with the talon slightly overlapping P^4. The incisor row is curved, and the width from the outer edge of the alveolus of the right I^3 to the outer edge of the alveolus of the left I^3 measures 8.9 mm; this compares with a mean of 6.79 mm (N 7, O.R. 5.8—7.6 mm) for Recent *Mustela eversmanni michnoi* and 6.40 mm (N 67, O.R. 5.4—7.2 mm) for Recent *Mustela nigripes*. The canine is relatively long and slender, and P^3 is relatively short and broad. Measurements of P^4 fall within the observed range of measurements taken on the steppe ferret, and do not show any proportional differences. Only the alveolus of the left M^1 is preserved; it shows that the inner lobe of the tooth was narrow.

The left mandible, F:AM 49337, is perfectly preserved, only the incisors are missing (Fig 3B). The teeth are moderately worn and are close together. P_2 is set obliquely in the jaw and P_4 slightly overlaps M_1. As with the other species of ferrets, the lower premolars are relatively short and broad. M_1 shows no trace of a metaconid, the talonid of M_1 is ridged and relatively narrow, and M_2 is small. F:AM 30827, a partial left ramus broken off behind M_1, has more heavily worn teeth than F:AM 49337. The jaw is relatively massive in both specimens, the length of the tooth row exceeds those of *Mustela eversmanni michnoi* in my sample, but measurements of the teeth fall within the observed range of the other ferrets measured. (See Table 4.)

Comparison of the Alaskan material with both Pleistocene and Recent *Mustela* (*Putorius*) *nigripes* Audubon and Bachman, Recent *Mustela* (*Putorius*) *eversmanni* Lesson and Recent *Mustela* (*Putorius*) *putorius* Linnaeus showed that the specimens most closely resemble *Mustela* (*Putorius*) *eversmanni michnoi* Kashchenko, 1910, the South Transbaikalian Siberian Polecat. This is the largest subspecies and it inhabits the steppes south and west of Lake Baikal and neighboring areas of Mongolia (Stroganov, 1962). The skull of this subspecies shows a broad facial region, pronounced postorbital constriction, and a crowded tooth row.

Stroganov (1962) reports that *Mustela eversmanni* shows more geographic variation than other ferrets, and about 20 subspecies are recognized. For this reason, I used only specimens labeled *Mustela eversmanni michnoi* and *Mustela eversmanni larvatus*, a synonym of the former (see Ellerman and Morrison-Scott, 1966:265) in my statistical analysis.

TABLE 4. MEASUREMENTS, IN MM, OF *MUSTELA EVERSMANNI* AND *MUSTELA NIGRIPES*.

	N	O.R.	M	S.D.
Breadth across rostrum (C–C)				
F:AM 49336	1	21.8	—	—
M. eversmanni michnoi Recent	7	15.8–19.8	17.81 ± .53	1.40
M. nigripes Recent	75	15.1–19.6	16.80 ± .11	.91
Little Box Elder Cave Pleist.	1	16.8	—	—
Breadth across carnassials (P^3–P^4)				
F:AM 49336	1	28.4	—	—
M. eversmanni michnoi Recent	7	21.0–26.2	24.57 ± .60	1.61
M. nigripes Recent	75	21.2–25.8	23.63 ± .12	1.02
Little Box Elder Cave Pleist.	—	—	—	—
Interorbital breadth				
F:AM 49336	1	21.8	—	—
M. eversmanni michnoi Recent	7	16.4–19.3	17.64 ± .39	1.02
M. nigripes Recent	78	14.9–19.5	17.08 ± .11	1.05
Little Box Elder Cave Pleist.	2	18.0–21.4	19.70	—
Breadth across postorbital processes				
F:AM 49336	1	26.3	—	—
M. eversmanni michnoi Recent	7	20.0–23.6	21.84 ± .50	1.33
M. nigripes Recent	78	18.4–23.9	20.96 ± .16	1.42
Little Box Elder Cave Pleist.	2	21.8–25.4	23.60	—
Breadth across postorbital constriction				
F:AM 49336	1	14.9	—	—
M. eversmanni michnoi Recent	7	10.2–15.9	12.42 ± .67	1.78
M. nigripes Recent	77	9.8–16.0	12.41 ± .12	1.09
Little Box Elder Cave Pleist.	3	12.5–16.3	13.96	—
Length C–M^1				
F:AM 49336	1	22.1	—	—
M. eversmanni michnoi Recent	7	18.7–22.1	21.00 ± .43	1.15
M. nigripes Recent	77	17.5–21.9	19.74 ± .29	2.62
Little Box Elder Cave Pleist.	1	ca21.4	—	—
Length P^3				
F:AM 49336	1	4.4	—	—
M. eversmanni michnoi Recent	7	3.8–4.6	4.28 ± .09	.26
M. nigripes Recent	70	3.5–4.2	3.86 ± .02	.17
Little Box Elder Cave Pleist.	2	3.8–4.4	4.1	—
Width P^3				
F:AM 49336	1	2.6	—	—
M. eversmanni michnoi Recent	7	2.0–2.7	2.31 ± .09	.25
M. nigripes Recent	70	1.9–2.5	2.18 ± .02	.16
Little Box Elder Cave Pleist.	2	2.2–2.3	2.25	—
Length P^4				
F:AM 49336	1	8.5	—	—
M. eversmanni michnoi Recent	7	7.0–8.5	8.10 ± .19	.52
M. nigripes Recent	79	6.7–8.0	7.41 ± .03	.28
Little Box Elder Cave Pleist.	7	7.3–8.1	7.71 ± .11	.30
Width P^4 protocone				
F:AM 49336	1	4.4	—	—
M. eversmanni michnoi Recent	7	3.4–4.3	3.80 ± .12	.31
M. nigripes Recent	79	3.2–4.0	3.67 ± .02	.18
Little Box Elder Cave Pleist.	7	3.5–4.1	3.77 ± .08	.21

TABLE 4. (CONTINUED)

	N	O.R.	M	S.D.
Length of mandible				
F:AM 49337	1	45.0	—	—
M. eversmanni michnoi Recent	7	38.5–46.6	43.25 ± 1.51	4.00
M. nigripes Recent	73	36.4–45.6	42.14 ± 0.24	2.09
Little Box Elder Cave Pleist.	6	35.8–42.2	38.91 ± 1.48	3.64
Height of mandible				
F:AM 49337	1	22.0	—	—
M. eversmanni michnoi Recent	7	20.0–23.1	21.41 ± .39	1.03
M. nigripes Recent	73	17.1–22.5	20.55 ± .13	1.17
Little Box Elder Cave Pleist.	6	18.4–21.8	19.75 ± .45	1.10
Depth of jaw below P_{3-4}				
F:AM 49337, 30827	2	9.2	—	—
M. eversmanni michnoi Recent	7	8.3–10.7	9.31 ± .21	.56
M. nigripes Recent	78	7.3–9.5	8.49 ± .07	.63
Little Box Elder Cave Pleist.	18	7.1–10.0	8.66 ± .21	.90
Depth of jaw below M_{1-2}				
F:AM 49337	1	9.8	—	—
M. eversmanni michnoi Recent	7	7.3–10.5	9.14 ± .23	.63
M. nigripes Recent	78	7.1–9.6	8.67 ± .07	.63
Little Box Elder Cave Pleist.	20	7.7–9.9	8.55 ± .16	.70
Length C–M_2				
F:AM 49337	1	26.4	—	—
M. eversmanni michnoi Recent	2	23.9–25.1	24.50	—
M. nigripes Recent	76	21.5–26.1	24.09 ± .11	1.03
Little Box Elder Cave Pleist.	10	21.5–25.3	23.37 ± .43	1.36
Length of M_1				
F:AM 49337, 30827	2	8.5–8.8	8.65	—
M. eversmanni michnoi Recent	7	7.6–9.6	8.94 ± .25	.65
M. nigripes Recent	77	7.3–9.1	8.27 ± .04	.40
Little Box Elder Cave Pleist.	24	7.3–9.0	8.24 ± .09	.45
Length of M_1 trigonid				
F:AM 49337, 30827	2	6.1–6.4	6.25	—
M. eversmanni michnoi Recent	7	5.5–6.8	6.35 ± .18	.48
M. nigripes Recent	77	5.2–6.4	5.85 ± .02	.25
Little Box Elder Cave Pleist.	23	5.3–6.4	5.92 ± .19	.91
Width M_1 talonid				
F:AM 49337, 30827	2	2.4–2.5	2.45	—
M. eversmanni michnoi Recent	7	2.1–2.6	2.45 ± .08	.23
M. nigripes Recent	79	2.1–2.6	2.34 ± .01	.13
Little Box Elder Cave Pleist.	23	2.0–2.5	2.26 ± .02	.12

Extant steppe or Siberian ferrets are found in steppe and forest-steppe zones of Eurasia, from Hungary and Yugoslavia to the Amur region of Siberia, south to the plains of central Asia, Mongolia and northeast China (Stroganov, 1962).

There is still disagreement as to the generic and specific status of Old World ferrets. Pocock (1936) and Ellerman and Morrison-Scott (1966) recognize a single species, *Mustela* (*Putorius*) *putorius*. However, Russian scientists (Ognev, 1931 and Stroganov, 1962), with larger samples to work with, recognize *Putorius putorius* and *Putorius eversmanni* as distinct species. Stroganov lists the following cranial charac-

ters as distinctive of *Mustela eversmanni*: a larger, bulkier skull, appreciable constriction of the postorbital region, and a longer facial region. In addition, the canines and carnassials are relatively larger than those of *Mustela putorius*. There are also pronounced differences in body size, coloration, and habitat of the two species. *Mustela putorius* inhabits forest biotopes and farmlands; *Mustela eversmanni* lives on the steppes and seldom enters forests. In areas where the ranges of the two species overlap, the two forms remain distinct.

Although postorbital constriction is correlated with increasing age in most mustelids, skulls of *Mustela putorius* do not show the pronounced constriction seen in the other species. The mean of the measurements of postorbital constriction of *Mustela putorius* in my sample is 16.31 mm (N 24, O.R. 12.6–18.2 mm); this compares with a mean of 12.41 mm for *Mustela eversmanni* and *Mustela nigripes* (see Table 4).

Pocock (1936:715) noted "the close similarity in all dimensions" of a male skull of *Mustela eversmanni* from the Altai, and a male skull of *Mustela nigripes* from Montana. I took 26 measurements on 19 skulls of *Mustela eversmanni* and on 79 skulls of *Mustela nigripes*; there were no significant differences in size between the two species (see Table 4). The only difference that appeared on scatter diagrams was a narrower basioccipital region in *Mustela nigripes*. Both species inhabit steppe regions, have a long sinuous body, and similar coloration. *Mustela nigripes* has never been abundant on the Great Plains, and today it is considered to be an endangered species. Unlike the steppe ferret, which feeds on a wide variety of small animals, the black-footed ferret feeds primarily on *Cynomys*. The geographic range of *Cynomys* and *Mustela nigripes* are nearly identical and the two species are associated in most Pleistocene localities except Old Crow River; *Cynomys* has not been reported from Fairbanks.

The Pleistocene history of *Mustela eversmanni* is poorly known, especially in Siberia. It is reported from late Pleistocene deposits in Europe; whether late middle Pleistocene ferrets are *Mustela putorius* or *Mustela eversmanni* is uncertain. Both species may be derived from the smaller early middle Pleistocene species, *Mustela* (*Putorius*) *stromeri* Kormos (Kurtén, 1968).

The earliest record of *Mustela nigripes* is from an upper Illinoian deposit in Clay County, Nebraska, and it is known from Sangamon deposits in Nebraska and at Medicine Hat, Alberta. Wisconsinan records include Old Crow River, Yukon Territory; Orr Cave, Montana; Jaguar Cave, Idaho; Little Box Elder Cave, Wyoming; Chimney Rock, Colorado; Isleta Cave, New Mexico; and Moore Pit, Texas. The specimen from Burnet Cave, New Mexico (see Schultz and Howard, 1935) is a juvenile with deciduous dentition; whether it is a mink or a ferret cannot be determined. The partial right ramus, NMC 16323, from Old Crow River, Locality 65, may be referable to *Mustela eversmanni beringiae*.

Ferrets entered the New World from Siberia, spread across Beringia, and then advanced southeastward to the Great Plains through ice-free corridors. Kalela (1940, in Kurtén, 1957) reported that during the period from 1880 to 1940, *Mustela putorius* extended its range in Finland from the Karelian Isthmus north to central Ostrobothnia and west to the Gulf of Bothnia. The rate of migration was 7.5 km annually or 750 km in a century. When climatic conditions permitted, this rate was probably applicable for ferrets spreading across Siberia and into the New World.

The question of conspecificity between *Mustela eversmanni* and *Mustela nigripes* is yet to be resolved. That the two species are closely related cannot be doubted, but until detailed comparative and statistical studies are made on the large collections of *Mustela eversmanni* in Soviet institutions; these data are compared with the information already compiled on *Mustela nigripes*; and behavioral and chromosomal studies

are undertaken on both species, I regard them as distinct.

Gulo gulo (Linnaeus) Wolverine
Figure 4

Material: Late Pleistocene, Fairbanks area, Alaska, F:AM 30795 skull with complete dentition, Goldstream. F:AM 30796 anterior ½ skull w/R I^{2-3}, P^1–M^1, L I^3, P^{1-4}, Ester Creek. F:AM 30797 L ramus w/C, P_2–M_1, top of gravel at 21 Goldstream, 40 feet below original surface. F:AM 30798 skull and associated jaw symphysis w/R C, P^2–M^1, L I^1, I^3–C, P^{2-4}; jaw symphysis w/R and L C, P_2–M_1, Old Eva Creek. F:AM 30799 partial anterior ½ skull w/R C, P^2–M^1, Cripple Creek. F:AM 30800 R max. w/ P^4, Ester Creek. F:AM 30805 frag. R ramus w/ P_3–M_1, Fairbanks Creek. F:AM 30806 L ramus w/P_2–M_1, No. 2 Goldstream stripping area. F:AM 30807 frag. R ramus w/P_3–M_2, No. 2 Goldstream stripping area. F:AM 30808 R ramus w/P_4–M_1, Cripple Creek. F:AM 30809 L ramus w/C, P_3–M_1, Cripple Creek. F:AM 30810 L ramus w/P_2–M_2, Engineer Creek. F:AM 30811 frag. R ramus w/P_4–M_1, Cripple Creek. F:AM 68003 R max w/C broken, P^{3-4}, M^1 and assoc. frag. R. ramus w/ M_{1-2}, Gold Hill. F:AM 68005 frag. R ramus w/P_{3-4}, Gold Hill.

Comparative material: Postglacial, Moonshiner Cave, Bingham County, Idaho, ISUM 19585–19599, 19643, 19667, 17 skulls and skull fragments; ISUM 19601–19639, 39 mandibles.
Recent, Alaska, MCZ 47398–99, 48566–68, 50528. AMNH 137270. Yukon Territory MCZ 34516. Northwest Territory AMNH 3448–49, 3450, 34506–09, 37432–33. Measurements of 24 male and 13 female skulls from Alaska (data from Björn Kurtén).

The outstanding feature of the wolverine material from the Pleistocene of Alaska is the large size of the specimens. Comparisons with samples from postglacial Moonshiner Cave, Idaho, and the Recent of Alaska and northern Canada show that the Alaskan Pleistocene specimens exceed the others in all measurements except the inner lobe of M^1, the depth of the jaw below P_{3-4}, and the length of the lower tooth row (C–M_2) (see Table 5). No attempt was made to sex the fossil material. If I had, the size differences would have been even more pronounced.

The well preserved skull, F:AM 30795 (see Fig. 4A–B) from Goldstream, is the largest wolverine skull known to me. The condylobasal length measures 172 mm. The largest specimen in my sample has a condylobasal length of 151 mm, and the largest specimen in Ognev's sample from the U.S.S.R. measured 157.8 mm (1935:587). Hall and Kelson (1959) give an observed range of 127–140 mm for basal length for the extant animal in North America. Other cranial measurements of F:AM 30795 are equally large, especially the mastoid breadth, breadth across the carnassials, and the approximate zygomatic breadth. The well developed sagittal crest projects above the dorsal surface of the skull, but unfortunately, the overhanging projection is broken off at the occiput. The powerful mastoid processes point obliquely forward and downward. A partial skull, F:AM 30796, and a right maxilla. F:AM 30800, represent skulls nearly as large as F:AM 30795.

The dentition of F:AM 30795 is complete and shows moderate wear. The length of the upper tooth row (C–M^1) measures 62.8 mm compared with 53.0 mm for the largest specimen from Moonshiner Cave, and 55.6 mm for the maximum length in my Recent sample. Stroganov (1962:245) gives an observed range of 49–60 mm for the length of the upper tooth row for Siberian *Gulo gulo*. The incisors of F:AM 30795 are all worn down to the same level. The tips of both canines were broken off during the life of the animal, and the remaining portions of the fangs are worn smooth. The massive cheek teeth are crowded, but do not overlap, and the tooth row is dominated by the enormous carnassial with its small talon.

F:AM 30797 (Fig. 4C), a complete left mandible lacking only the incisors, first premolar and last molar, is the largest lower jaw from the Fairbanks region. Its total length, measured from the symphysis at the alveolus of I_1 to the most distant edge of the condyle, is 112.8 mm, a measurement larger than any in the postglacial or Recent sample. The teeth are only slightly worn, and are close together with P_2 sitting slightly obliquely in the jaw. The posterior

TABLE 5. MEASUREMENTS, IN MM, OF *GULO GULO*.

		N	O.R.	M	S.D.
Condylobasal length					
F:AM Collection		2	139.4–172.0	155.70	—
Moonshiner Cave, Id.		3	134.0–145.0	140.66	—
G. gulo, Recent	♂	29	140.0–151.0	146.05 ± .58	3.26
	♀	18	132.6–141.0	135.00 ± .65	2.61
Zygomatic breadth					
F:AM Collection		2	100.0–119.2	109.6	—
Moonshiner Cave, Id.		—	—	—	—
G. gulo, Recent	♂	29	98.3–113.2	105.0 ± .57	3.04
	♀	17	92.5–100.0	95.97 ± .42	1.69
Breadth across rostrum (C–C)					
F:AM Collection		4	41.4–48.6	44.92	—
Moonshiner Cave, Id.		7	36.1–42.3	38.92 ± .94	2.50
G. gulo, Recent	♂	9	40.0–43.9	42.51 ± .40	1.20
	♀	8	37.0–39.9	37.94 ± .35	.99
Breadth across carnassials (P^4–P^4)					
F:AM Collection		3	67.1–76.7	72.40	—
Moonshiner Cave, Id.		8	51.4–63.0	59.82 ± .73	2.07
G. gulo, Recent	♂	9	63.6–69.3	66.97 ± .59	1.77
	♀	8	59.7–63.8	61.47 ± .49	1.40
Interorbital breadth					
F:AM Collection		3	41.0–46.7	44.70	—
Moonshiner Cave, Id.		4	36.7–44.6	40.60	—
G. gulo, Recent	♂	9	39.1–45.4	41.38 ± .28	1.56
	♀	8	36.0–40.9	37.75 ± .15	.69
Breadth across postorbital processes					
F:AM Collection		2	48.2–56.8	52.50	—
Moonshiner Cave, Id.		4	44.0–53.5	48.37	—
G. gulo, Recent	♂	9	45.7–54.3	48.61 ± .94	2.83
	♀	7	42.4–49.5	45.50 ± 1.05	2.79
Mastoid breadth					
F:AM Collection		2	85.0–108.0	96.50	—
Moonshiner Cave, Id.		5	76.2–87.3	81.18	—
G. gulo, Recent	♂	9	83.1–94.6	90.05 ± 1.14	3.43
	♀	8	78.4–85.6	82.50 ± .82	2.19
Length C–M^1					
F:AM Collection		5	51.3–62.8	57.72	—
Moonshiner Cave, Id.		11	46.4–53.0	50.47 ± .69	2.29
G. gulo, Recent	♂	9	51.0–55.6	53.28 ± .42	1.28
	♀	8	43.4–51.3	48.63 ± 1.43	4.05
Length P^4					
F:AM Collection		6	21.6–23.4	22.70 ± .51	1.27
Moonshiner Cave, Id.		15	18.0–22.3	20.36 ± .28	1.06
G. gulo, Recent	♂	28	20.2–23.2	21.30 ± .13	.70
	♀	21	18.6–20.1	19.37 ± .09	.40
Width P^4 protocone					
F:AM Collection		6	12.6–13.5	12.96 ± .44	1.10
Moonshiner Cave, Id.		15	10.4–13.4	11.58 ± .22	.86
G. gulo, Recent	♂	28	11.4–13.1	12.31 ± .08	.47
	♀	18	10.6–12.1	11.15 ± .10	.43

TABLE 5. (CONTINUED)

		N	O.R.	M	S.D.
Width M^1					
F:AM Collection		5	13.5–15.8	14.80	—
Moonshiner Cave, Id.		18	12.0–14.2	13.39 ± .16	.72
G. gulo, Recent	♂	29	13.7–15.7	14.45 ± .09	.51
	♀	18	12.5–13.9	13.05 ± .09	.40
Length M^1 constriction					
F:AM Collection		5	6.3–6.6	6.46	—
Moonshiner Cave, Id.		18	5.1–6.2	5.72 ± .06	.29
G. gulo, Recent	♂	29	5.6–6.5	5.99 ± .04	.26
	♀	18	4.9–5.9	5.53 ± .06	.29
Length M^1 inner lobe					
F:AM Collection		5	7.1–9.0	8.06	—
Moonshiner Cave, Id.		18	6.6–8.5	7.56 ± .12	.51
G. gulo, Recent	♂	29	7.3–9.7	8.20 ± .06	.34
	♀	18	6.8–8.1	7.22 ± .08	.35
Length mandible					
F:AM Collection		5	96.0–112.8	105.82	—
Moonshiner Cave, Id.		16	89.2–107.0	95.41 ± .82	3.28
G. gulo, Recent	♂	9	99.5–107.2	103.76 ± 1.28	3.85
	♀	8	94.2–99.4	95.86 ± .66	1.89
Depth of jaw below P_{3-4}					
F:AM Collection		9	18.4–22.2	20.62 ± .44	1.33
Moonshiner Cave, Id.		26	16.0–21.4	18.64 ± .32	1.67
G. gulo, Recent	♂	9	19.3–22.6	20.82 ± .94	2.83
	♀	8	17.9–19.0	18.42 ± .42	1.19
Depth of jaw below M_{1-2}					
F:AM Collection		9	22.0–29.6	25.70 ± .55	1.66
Moonshiner Cave, Id.		26	20.0–26.1	22.21 ± .32	1.67
G. gulo, Recent	♂	9	23.2–25.7	24.52 ± .58	1.76
	♀	8	19.6–22.3	21.35 ± .55	1.56
Length C–M_2					
F:AM Collection		7	59.7–70.1	63.14 ± .74	1.97
Moonshiner Cave, Id.		26	54.7–64.6	58.82 ± .20	1.02
G. gulo, Recent	♂	9	61.3–66.4	64.70 ± .54	1.64
	♀	8	57.5–62.1	59.86 ± .55	1.56
Length M_1					
F:AM Collection		10	22.0–24.6	23.15 ± .57	1.81
Moonshiner Cave, Id.		38	18.5–23.1	20.80 ± .09	1.29
G. gulo, Recent	♂	29	21.6–25.2	22.80 ± .32	1.74
	♀	18	19.5–22.0	20.85 ± .48	2.05
Length M_1 trigonid					
F:AM Collection		9	16.9–19.3	18.15 ± .27	.83
Moonshiner Cave, Id.		38	14.2–17.6	15.87 ± .15	.97
G. gulo, Recent	♂	9	16.2–19.0	17.93 ± .28	.80
	♀	8	15.6–17.1	16.43 ± .17	.49
Width M_1 talonid					
F:AM Collection		9	7.0–8.1	7.62 ± .13	.41
Moonshiner Cave, Id.		38	5.8–8.4	6.83 ± .29	.55
G. gulo, Recent	♂	9	7.1–7.9	7.40 ± .09	.27
	♀	8	6.0–7.3	6.70 ± .18	.52

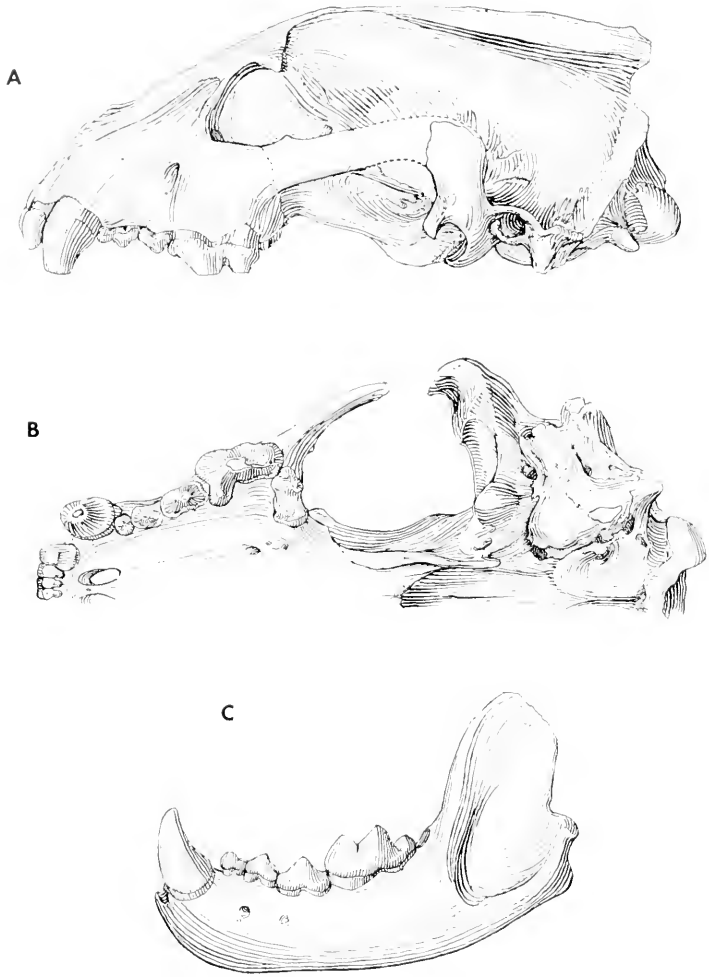

Figure 4. *Gulo gulo* (F:AM 30795) A. lateral and B. ventral views of skull; C. (F:AM 30797) lateral view of mandible. Scale 1:1.

part of P_4 is expanded. M_1 is a massive tooth with a powerful trigonid and reduced talonid; there is no trace of a metaconid. F:AM 30797 was also found at Goldstream, but it did not belong to the same individual as F:AM 30795. Except for larger size, the mandibles from the Pleistocene of Alaska do not differ from the extant *Gulo* living in the area today.

Kurtén and Rausch (1959) in their study of Alaskan and Fennoscandian wolverines noted that a significant difference was found between the two populations in the length of M^1 measured at the constriction. They found that the Recent specimens from Alaska had a more strongly constricted M^1 than those from Scandinavia. This is not the case with the late Pleistocene Alaskan specimens—the M^1 shows less constriction than those from Scandinavia. One of their fossil specimens from Europe also showed this reduced constriction of M^1. On a scattergram the specimens from Moonshiner Cave show nearly the same proportions as

the sample from Fennoscandia. Comparisons with other late Pleistocene samples of *Gulo* are now being made.

Circumboreal in distribution, wolverines inhabit tundra and taiga regions, and today in America are found primarily in Alaska and northern Canada. Wolverines are rare in Pleistocene deposits. The earliest American records are late Irvingtonian from Port Kennedy Cave, Pennsylvania and Cumberland Cave, Maryland. Wisconsinan deposits containing *Gulo* include Old Crow River, Yukon Territory; Little Box Elder Cave, Wyoming; Chimney Rock Animal Trap, Colorado; Jaguar Cave, Idaho; and Fairbanks. Wolverines show a gradual increase in size during Rancholabrean times; postglacial and extant animals are smaller.

Gulo is descended from *Plesiogulo*, a large Pliocene form with a less specialized dentition that inhabited Eurasia and North America. *Gulo* makes its first appearance in early middle Pleistocene deposits in Europe as a slightly smaller form called *Gulo schlosseri* Kormos. It gave rise to *Gulo gulo* which appears during the Mindel glaciation in Europe and China. *Gulo* probably reached America in the Kansan. American wolverines were formerly considered to be a distinct species, *Gulo luscus* (Linnaeus); Kurtén and Rausch (1959) showed that the American population is only subspecifically distinct from the Eurasian.

Taxidea taxus (Schreber) Badger
Figure 5

Material: Late Pleistocene, Fairbanks area, Alaska. F:AM 30786 skull and associated mandible w/R I^{1-2}, C–M^1, L complete upper dentition, R I_{1-3}, C, P_3–M_2, L I_{1-3}, ½ P_2, P_3–M_2, Goldstream. F:AM 30787 skull w/ L C, P^4–M^1, Goldstream. F:AM 30788 R ramus w/ C, P_4–M_1, head of Goldstream. F:AM 30789 L ramus w/M_1 broken, Cleary. F:AM 30790 frag. L jaw, toothless, Goldstream. F:AM 30826 L ramus w/M_{1-2}, Cripple Creek. F:AM 30827 R ramus w/P_3–M_1, Ester Creek. F:AM 30828 R ramus w/P_2, M_2, frag. M_1, Cripple Creek. F:AM 30829 L ramus, toothless, Ester Creek. F:AM 30830 frag. R ramus w/ P_{2-4}, M_1 broken, Cripple Creek. F:AM 30831 L ramus w/C, Cripple Creek. F:AM 30832 L ramus w/ C, P_2–M_1, all broken, Cripple Creek. F:AM 30833 L max. w/P^3–M^1, Cripple Creek. F:AM 30834 L max. w/P^{3-4}, Cripple Creek. F:AM 30835 anterior half skull w/R C, P^3, L ½P^3, Lower Goldstream. F:AM 30836 anterior half skull w/R C, P^3–M^1, L ½P^3, Cripple Creek. F:AM 30837 skull w/R I^{1-2}, C–M^1, L I^{2-3}, C, ½P^2, P^3, Ester Creek. F:AM 30837A frag. R ramus w/P_2–M_2, Ester Creek. F:AM 30838 partial skull w/R and L P^4–M^1, Ester Creek. F:AM 30839 L ramus w/ C, P_3–M_1, Fairbanks Creek. F:AM 30840 frag. R ramus w/M_1, Cripple Creek. Field numbers: F:AM 4493 L max. w/P^3–M^1, Gold Hill. F:AM 4717 R max. w/C, P^2 broken, P^{3-4}, Gold Hill. F:AM 4737 L ramus w/ P_{2-3}, P_4–M_1 broken, Gold Hill. F:AM 6135 L ramus w/M_{1-2}, C–P_4 broken off at roots, Engineer Creek. F:AM 6411 jaw symphysis w/ R C–M_2, L P_{3-4}, all broken, Cripple Creek. F:AM 68004 frag. R ramus w/P_4, Gold Hill. U.A. acc. no. 552 (on loan to Frick Laboratory) skull w/R and L P^3–M^1, Cripple Creek.

Late Pleistocene, Little Box Elder Cave, Converse County, Wyoming, UCM 21928. Postglacial, Moonshiner Cave, Bingham County, Idaho, ISUM 19650, 19671–79, 19682–85, 19687, 19701–04, 19705, (36 specimens), 19706 (31 specimens), 19731–32, 19735–49, 19752, 19761–64, 19766, 19769, 19771, 19773–75, 19777, 19780–81, 19795, 19799–19806, 19814–834.

Recent. *Taxidea taxus jeffersonii* MCZ 8517, 9223, 12402, 41389–90. UCM 5150, 5237, 5284, 5882, 6678, 10682–84, 10687. E.R. Warren collection, not cataloged 2635, 9135. *Taxidea taxus berlandieri* UCM 11548–550. UCM 3698, no data.

Badgers are not found in Alaska today. Their closest occurrence is along the Peace River, lat. 58°N, in northern Alberta (Preble, 1908), about 1800 km southeast of the Fairbanks area. During the late Pleistocene, badgers inhabited the unglaciated, grassy steppes of central Alaska and northern Yukon (Gold Run Creek, Harington, 1970, and Dominion Creek, Harington, personal communication). Remains of *Taxidea* outnumber the other Alaskan mustelids in the Frick collection.

The Alaskan badgers are characterized by large size. The condylobasal length of U.A. acc. no. 552 is 144.6 mm, a measurement that exceeds all other Pleistocene, postglacial, and Recent records. The condylobasal length of the large skull from Little Box Elder Cave, UCM 21928, (see Anderson,

TABLE 6. MEASUREMENTS, IN MM, OF *TAXIDEA TAXUS*

	N	O.R.	M	S.D.
Condylobasal length				
F:AM Collection	3	137.7–144.6	140.60	—
Moonshiner Cave, Id.	11	118.0–129.2	124.55 ± .61	2.04
Taxidea taxus, Recent	16	114.0–132.0	122.47 ± 1.22	4.89
Zygomatic breadth				
F:AM Collection	2	90.6–100.1	95.35	—
Moonshiner Cave, Id.	9	72.4–80.1	76.96 ± 1.31	3.95
Taxidea taxus, Recent	16	72.4–87.7	77.91 ± 1.18	4.74
Breadth across rostrum (C–C)				
F:AM Collection	6	38.4–46.2	41.96 ± 1.20	2.94
Moonshiner Cave, Id.	18	32.1–37.8	35.00 ± .36	1.53
Taxidea taxus, Recent	20	30.5–37.9	34.15 ± .46	2.06
Breadth across carnassials (P^4–P^4)				
F:AM Collection	3	45.2–49.6	47.40	—
Moonshiner Cave, Id.	18	38.5–44.6	40.94 ± .41	1.74
Taxidea taxus, Recent	20	37.7–44.4	40.85 ± .38	1.68
Interorbital breadth				
F:AM Collection	6	32.9–39.7	36.91 ± 1.07	2.61
Moonshiner Cave, Id.	21	25.6–35.0	29.90 ± .53	2.47
Taxidea taxus, Recent	19	24.6–31.4	27.50 ± .37	1.64
Breadth across postorbital processes				
F:AM Collection	6	39.9–44.6	42.28 ± .65	1.60
Moonshiner Cave, Id.	22	31.8–37.0	35.03 ± .28	1.32
Taxidea taxus, Recent	20	30.8–40.3	35.25 ± .53	2.40
Mastoid breadth				
F:AM Collection	3	90.0–91.4	90.80	—
Moonshiner Cave, Id.	12	66.0–83.3	73.89 ± .64	2.22
Taxidea taxus, Recent	19	70.2–86.8	76.39 ± 1.09	4.64
Length C–M^1				
F:AM Collection	9	40.7–47.3	44.74 ± .68	2.04
Moonshiner Cave, Id.	34	36.1–44.3	40.32 ± .33	1.93
Taxidea taxus, Recent	20	35.3–43.0	39.87 ± .38	1.73
Length P^3				
F:AM Collection	9	7.3–8.6	7.87 ± .13	.39
Moonshiner Cave, Id.	4	6.5–7.3	6.90	—
Taxidea taxus, Recent	14	6.2–7.5	6.64 ± .10	.40
Length P^4				
F:AM Collection	10	11.5–13.9	12.88 ± .24	.75
Moonshiner Cave, Id.	40	10.8–13.5	11.86 ± .08	.53
Taxidea taxus, Recent	19	10.3–13.5	11.73 ± .18	.80
Width P^4 protocone				
F:AM Collection	10	10.2–12.1	11.15 ± .20	.63
Moonshiner Cave, Id.	40	9.0–11.9	9.91 ± .09	.57
Taxidea taxus, Recent	19	9.0–11.3	10.05 ± .14	.61
Width M^1				
F:AM Collection	8	10.1–12.0	10.93 ± .19	.56
Moonshiner Cave, Id.	44	9.1–11.8	10.07 ± .09	.63
Taxidea taxus, Recent	19	9.3–11.6	10.28 ± .15	.67

TABLE 6. (CONTINUED)

	N	O.R.	M	S.D.
Length M^1 inner				
F:AM Collection	8	9.5–12.6	10.95 ± .39	1.09
Moonshiner Cave, Id.	44	9.7–12.5	10.90 ± .11	.70
Taxidea taxus, Recent	19	9.6–12.9	11.16 ± .21	.93
Length mandible				
F:AM Collection	8	95.2–109.0	99.01 ± 1.70	4.81
Moonshiner Cave, Id.	48	73.7–98.3	85.63 ± .65	4.56
Taxidea taxus, Recent	20	78.8–93.5	86.18 ± .99	4.32
Depth of jaw below P_{3-4}				
F:AM Collection	18	15.1–21.3	17.85 ± .41	1.73
Moonshiner Cave, Id.	74	12.0–18.1	14.42 ± .13	1.08
Taxidea taxus, Recent	20	12.0–16.3	14.35 ± .27	1.23
Depth of jaw below M_{1-2}				
F:AM Collection	17	19.5–26.0	22.58 ± .37	1.56
Moonshiner Cave, Id.	74	16.2–21.5	18.54 ± .14	1.18
Taxidea taxus, Recent	20	15.6–22.0	18.28 ± .35	1.58
Thickness of jaw below M_1				
F:AM Collection	17	8.1–12.0	10.23 ± .27	1.14
Moonshiner Cave, Id.	28	7.0–9.4	8.18 ± .13	.71
Taxidea taxus, Recent	20	6.5–8.6	7.65 ± .18	.71
Length C–M_2				
F:AM Collection	9	51.2–59.3	54.64 ± .71	2.15
Moonshiner Cave, Id.	48	43.4–53.6	49.14 ± .33	2.33
Taxidea taxus, Recent	19	44.6–52.0	48.79 ± .48	2.09
Length P_4				
F:AM Collection	9	8.2–9.8	9.14 ± .19	.57
Moonshiner Cave, Id.	7	7.2–8.6	7.88 ± .20	.53
Taxidea taxus, Recent	15	7.3–8.7	8.15 ± .12	.48
Length M_1				
F:AM Collection	12	13.1–15.2	14.38 ± .21	.73
Moonshiner Cave, Id.	20	11.6–14.9	13.20 ± .20	.89
Taxidea taxus, Recent	16	12.3–14.6	13.55 ± .17	.66
Length M_1 trigonid				
F:AM Collection	7	7.7–10.5	9.48 ± .37	.99
Moonshiner Cave, Id.	20	7.7–9.9	8.70 ± .15	.66
Taxidea taxus, Recent	16	8.3–9.9	8.87 ± .11	.45
Width M_1 talonid				
F:AM Collection	11	5.6–7.2	6.34 ± .14	.47
Moonshiner Cave, Id.	22	4.9–6.5	5.80 ± .09	.43
Taxidea taxus, Recent	18	5.3–7.0	6.03 ± .12	.51

1968) measures 142.2 mm. Table 6 shows that the largest specimen from Moonshiner Cave has a condylobasal length of 129.2 mm, and the largest Recent skull in my sample measures 132.0 mm. Long (1972) gives an observed range of 121.5–139.9 mm for the greatest length of the skull of *Taxidea taxus jeffersonii*, the largest extant subspecies. Other big late Pleistocene badgers are known from Dominion Creek, Yukon Territory, Rancho La Brea, McKittrick, and Maricopa, California, Burnet Cave and Sandia Cave, New Mexico (personal observations). I am presently reviewing all of the

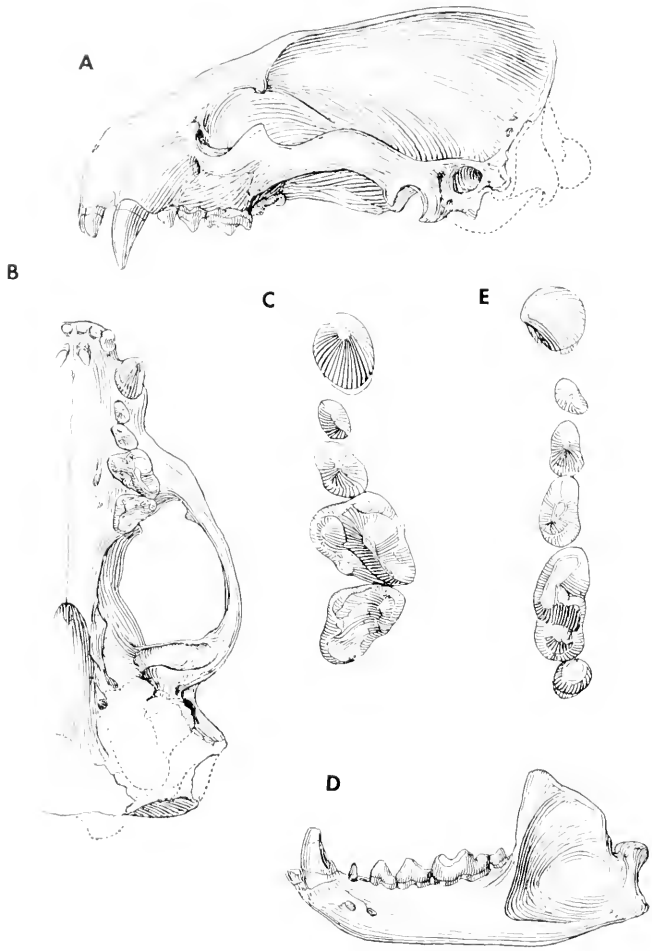

Figure 5. *Taxidea taxus* (F:AM 30786) A. lateral and B. ventral views of skull; C. occlusal view of upper dentition; D. lateral view of mandible; E. occlusal view of lower dentition. Scale 1/1.

Pleistocene *Taxidea* material. Preliminary studies indicate that all of the material is referable to *Taxidea taxus*, but subspecific designation of the Blancan and late Rancholabrean material seems warranted. A trend in the evolution of *Taxidea* during the Pleistocene is a gradual increase in size culminating in the huge Rancholabrean forms; there was a slight decrease in size during postglacial times, and this was followed by a slight increase in size in Recent times. The largest extant badgers are found in the northern parts of their range.

All of the measurements taken on the Alaskan material, except the length of M^1, which is quite variable, exceed those in my postglacial and Recent sample. Pronounced size differences are noticed in zygomatic breadth, mastoid breadth, and length of mandible (see Table 6).

The well preserved skull, U.A. acc. no. 552, belonged to an adult animal. The low broad skull is characterized by strong zygomatic arches, well developed sagittal and lambdoidal crests, a wide occiput with highly inflated tympanic bullae, and sepa-

rate paraoccipital processes. The incisors, canines, and P^2's are missing; P^3–M^1 are moderately worn and close together. Three other complete skulls, three partial skulls, and four maxillary fragments are known from the Fairbanks area. Large size is characteristic of all of them. F:AM 30837 and 30787 have condylobasal lengths of 139.5 mm and 137.7 mm respectively; F:AM 30836 has a rostrum breadth of 46.2 mm compared to 43.6 mm for U.A. acc. no. 552.

Eighteen badger mandibles were found in the Fairbanks area. Of these, F:AM 30832 is the largest, the total length of this massive jaw measures 109 mm; this compares with a measurement of 98.3 mm for the largest specimen from Moonshiner Cave and 93.5 mm in my Recent sample. The teeth of F:AM 30832 are heavily worn, and this plus the great size indicate advanced age. The teeth of several of the specimens are broken. Morphologically, the specimens do not differ from the Recent sample. As Hall (1944) noted, the number of accessory cusps on the talonid of M_1 is extremely variable in Recent badgers; this is also true in the Alaskan population.

Geographic variability, sexual dimorphism, and individual variation are pronounced in badgers. Most fossorial of the Mustelidae, badgers inhabit plains and open forests where friable soil is available for digging. Their diet consists of insects and small vertebrates, especially rodents. Although badgers are inactive during cold spells, they are not true hibernators. The presence of badgers in Alaska during the late Pleistocene indicates a milder climate then, for today their northern distribution is limited by subarctic conditions. Hall (1944) cites the vicissitudes of the boreal climate as the major factor preventing intercontinental exchange of Old and New World badgers, and he postulated that if this exchange had occurred, the genus *Meles* would be found in North America as well as Eurasia, and *Taxidea* would be restricted to the southern latitudes of the New World. At the time Hall wrote this (1944), the Alaskan badgers were unknown. Why they did not spread farther West across Beringia is unknown.

Badgers are common in Pleistocene deposits in western United States, and a few have been recovered from sites in the East including Cumberland Cave, Maryland; Welsh Cave, Kentucky; Baker Bluff, Tennessee; and Peccary Cave, Arkansas. The probable ancestor of *Taxidea* is *Pliotaxidea nevadensis* (Butterfield) known from Hemphillian faunas in Nevada and Oregon. It was smaller and had larger tympanic bullae than *Taxidea*. Today *Taxidea taxus* is found from southern Canada to southern Mexico and from the Pacific Coast east to Michigan and Ohio.

CONCLUSIONS

During the late Pleistocene at least five species of mustelids inhabited an ice-free refugium in interior Alaska. Although stratigraphic information is lacking, all of the mustelid material is believed to be Wisconsinan in age. Péwé and Hopkins (1967) do not list any species of mustelids from pre-Wisconsinan age deposits in the Fairbanks region, and carbon-14 dates obtained on bison, musk ox, and mammoth material from the same area fall between 12,460 and >40,000 years B.P. (B. Taylor, personal communication).

The mammalian fauna of Alaska and northeastern Siberia was similar during the Wisconsinan, since biogeographically, it was one vast area. At the height of the glaciation, many species of animals ranged across the Beringian refugium unable to move onward because of the ice. Some of them, for example, *Saiga*, *Bos* (yak), *Taxidea*, and *Megalonyx*, did not extend their range, but many others, mainly the Eurasian immigrants, moved southward when the ice-free corridors were open. Hopkins (1967) postulated that an ice-free corridor probably existed in the Yukon Territory, northern British Columbia, and northern Alberta during the mid-Wisconsinan, a period of mild climatic conditions between

35,000 and 25,000 years ago; the corridor was closed from about 22,000 years to at least 14,000 years ago; and then it reopened again after the Bering land bridge had been drowned by rising sea levels. Thus, movements of animals to and from the Beringian refugium took place in mid-Wisconsinan and very late Wisconsinan postglacial times.

As Hopkins (1967) and Guthrie (1968) postulated, grasslands must have been more extensive in the refugium during the late Pleistocene in order to have supported the enormous numbers of herbivores that lived there. The remains of three obligatory grazers, *Bison*, *Equus*, and *Mammuthus*, make up more than 85 per cent of the fossils collected in the Fairbanks area, and the presence of many plains dwellers including *Taxidea taxus* and *Mustela eversmanni* further supports this hypothesis.

Large size was characteristic of many species during the Pleistocene, and remains of *Gulo gulo* and *Taxidea taxus* from the Fairbanks deposits are the largest recorded. This may be an example of Bergmann's principle—that the same species of warm-blooded animal tends to be larger in the colder parts of its range—but an abundant food supply and few enemies may also have been factors.

The extinction or extirpation of many members of the Beringian fauna about 10,000 years ago was probably due to multiple factors including abrupt changes in the climate which resulted in changes in the vegetation (for example, an increase in the tundra-taiga and bogs at the expense of grasslands). This affected the large mammals more than it did the small ones. Of the mustelids, *Taxidea taxus* and *Mustela eversmanni* disappeared from Alaska, but survived in areas much farther south; *Gulo gulo*, *Mustela vison* and *Mustela erminea* still inhabit the area today. Man was undoubtedly a factor in the extinction of some species, but it is doubtful that he had anything to do with the disappearance of two of the Alaskan mustelids.

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Bulletin of the
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Studies on the Deep Sea Protobranchia (Bivalvia): The Family Tindariidae and the Genus Pseudotindaria

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STUDIES ON THE DEEP SEA PROTOBRANCHIA (BIVALVIA);[1] THE FAMILY TINDARIIDAE AND THE GENUS *PSEUDOTINDARIA*

H. L. SANDERS[2] AND J. A. ALLEN[3]

ABSTRACT. In the present paper we have erected a new family of Protobranchia, the Tindariidae, to include those nuculanoid bivalves that lack a siphon but bear papillae on their posterior margin edge, have a single loop of the hind gut that penetrates the right side of the mantle, and possess a palp with few ridges. A new genus, *Pseudotindaria*, is created for those nuculanoid protobranch bivalves that have shell morphologies essentially similar to the Tindariidae but with soft parts that are markedly different. Siphons are present, the hind gut is a complex configuration of loops and coils on either side of the body and it does not penetrate the mantle, and palp ridges are numerous. The morphologies of the hard and soft part anatomies, the horizontal and vertical distributions, size-frequency histograms, and reproductive patterns of the tindariid and pseudotindariid species in our Atlantic samples are discussed. Two new species are described. On the basis of shell morphology, *Tindaria* and *Pseudotindaria* can be interpreted as recent descendants of the Paleozoic ctenodont Protobranchia.

INTRODUCTION

The objects and aims of our researches on the fauna of the deep sea, and on the Protobranchia in particular, have been given in the prologue to these studies, (Sanders & Allen, 1973). This is the third paper in a series, all of which illustrate the initial problems that had to be resolved in our analysis and reappraisal of the deep-sea protobranch bivalves of the Atlantic.

As noted in the first paper (Sanders & Allen, 1973), the tindariid protobranchs represent an anomalous group within the Order Nuculanoidea, having features that divide them sharply from the remainder of the order. Verrill & Bush (1897), Theile (1935), Vokes (1967) and Knudsen (1970) all place the genus *Tindaria* (= *Tyndaria*) in the family Malletiidae, even though Verrill & Bush (1898) stated that "the genus *Tindaria* differs so widely from *Malletia* and other genera that it seemed necessary to establish a new subfamily (Tindarinae) for it."

Dall (1895) included the following subgenera: *Tindaria*, *Tindariopsis*, *Neilonella* and *Pseudoglomus* in the Malletiidae and Knudsen (1970) retained the genus *Neilonella* there as well. Theile (1935) divided the genus *Tindaria* into two sections each with a single subgenus, *Tindaria* and *Pseudoglomus*.

Because *Tindaria* differs so markedly in its morphology from both *Pseudoglomus* and *Neilonella* as well as other members of the family Malletiidae, we propose that a new family be erected, the Tindariidae.

[1] This research was supported by grants GB 563, GA 31105 and GB 36554 from the National Science Foundation, GR 3/812 from the Natural Environment Research Council, and from the Royal Society of London. Contribution no. 2983 from the Woods Hole Oceanographic Institution.

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The genera *Pseudoglomus*, *Neilonella* and *Malletia* will be the subjects of future papers.

The present study shows that some species, although having typical tindariid shells, have greatly different anatomies from the true tindariids. On the basis of these profound anatomical differences we find it impossible to include these species within the same family. We propose that those forms having papillae around the incurrent aperture, lacking well defined siphons, and having a hind gut configuration consisting of a single deep loop on the right side of the body, be included in the family Tindariidae. Excluded from the family are those forms with a well-developed siphon and complex hind gut configuration that extends on both sides of the body. These we include within a new genus *Pseudotindaria*, described here. The precise affinities of this genus will be deferred to a future paper. This interpretation in no way conflicts with earlier definitions of the genus *Tindaria*, all of which mention posterior papillae (e.g. Theile, 1935).

TINDARIIDAE New Family

The family is characterized as follows: valves rounded, ovate, robust, swollen, somewhat unequilateral, concentrically lined; umbo medially and somewhat anteriorly directed; hinge line strong, supporting a series of well-developed teeth that are continuous beneath the umbo; ligament external and opisthodetic; posterior sensory tentacle present or absent; true siphons lacking; incurrent region of mantle edge fringed with elongate papillae; palps small; sorting ridges of the palp broad, few in number; palp proboscides large, elongate; gill axis somewhat oblique to the antero-posterior axis of the body; gill filaments few; hind gut, with lumen of large diameter and a single typhlosole, making a single loop to the right side of the body and penetrating into the mantle to a greater or lesser extent; 'byssal' gland small.

Although they show several features that sharply differentiate them from other protobranchs, the tindariids clearly fall within our definition of the Order Nuculanoidea (Sanders & Allen, 1973). For example, all species of the family have a posterior incurrent current and an anterior mantle sense organ.

Tindaria Bellardi 1875

Type species *T. arata* Bellardi, by monotypy

Tindaria is the sole genus of the family, the generic characters of the genus are those that define the family. Many species are listed in the literature (see Smith, 1885; Clarke, 1962; Knudsen, 1970) but, for reasons that will become obvious, unless the soft parts have been described many of these species cannot be placed in the genus with confidence. Of the features that distinguish both the genus and family, the most distinctive are 1) the lack of siphons and the long fringing papillae of the incurrent region, 2) the small size of the palps relative to the size of the animal, 3) the very few ridges on the inner surface of the palps, 4) the oblique placement of the gill in relation to the anterior-posterior axis, 5) the relatively small number of gill filaments, 6) the small size of the 'byssal' gland, 7) the single loop of the hind gut on the right side of the body.

Tindaria callistiformis Verrill & Bush, 1897
Figures 1–11 & 27

Tindaria callistiformis, Verrill & Bush, 1897. Amer. J. Sci., p. 59, figs. 10, 20, 21 (Type locality: U.S. Fish Comm. Sta. 2566; Lat. 37°23'N, Long. 63° 8'W, type specimen: U.S. Nat. Mus.); Verrill & Bush, 1898. Proc. U.S. Nat. Mus., No. 1139, p. 881, pl. 78, fig. 1; 80, figs. 6, 7.

Previous records. Depth range = 3342 to 4795 m. North America Basin—2 stations. Refs. Verrill & Bush, 1897, 1898.

Present records. Depth range = 3305 to 5042 m.

Cruise		Station No.	Depth (m)	No. of specimens	Latitude	Longitude	Gear	Date
				North America Basin				
Chain 50		77	3806	622	38°0.7′N	69°16.0′W	ES	30.6.65
Chain 50		78	3828	181	38°0.8′N	69°18.7′W	ES	30.6.65
Chain 50		85	3832	882	37°59.2′N	69°26.2′W	ES	5.7.65
Atlantis II	40	175	4667	1	36°36.0′N–36°36.0′N	68°29.0′W–68°31.0′W	ES	29.11.67
Chain 50		84	4749	1	36°24.4′N	67°56.0′W	ES	4.7.65
Atlantis II	24	121	4800	2	35°50.0′N	65°11.0′W	ES	21.8.65
Atlantis II	24	122	4833	3	35°50.0′N–35°52.0′N	64°57.5′W–64°58.0′W	ES	21.8.65
Atlantis II	24	123	4853	1	37°29.0′N	64°14.0′W	ES	22.8.65
Atlantis II	24	124	4862	2	37°26.0′N–37°25.0′N	63°59.5′W–63°58.0′W	ES	22.8.65
Chain 50		81	5042	1	34°41.0′N	66°28.0′W	ES	2.7.65
				Angola Basin				
Atlantis II	42	197	4592–4597	2	10°29.0′S	9°04.0′E	ES	21.5.68
Atlantis II	42	196	4612–4630	1	10°29.0′S	9°04.0′E	ES	21.5.68
				Argentine Basin				
Atlantis II	60	259A	3305–3317	5	37°13.3′S	54°45.0′W	ES	26.3.71
Atlantis II	60	256	3906–3917	37	37°40.9′S	52°19.5′W	ES	24.3.71
				Guiana Basin				
Knorr 25		307	3835–3862	1	12°35.4′N–12°40.8′N	58°59.3′W–59°09.2′W	ES	3.3.72
Knorr 25		288	4417–4429	13	11°02.2′N–11°03.8′N	55°05.5′W–55°04.8′W	ES	25.2.72
Knorr 25		287	4934–4980	10	13°16.0′N–13°15.8′N	54°52.2′W–54°53.1′W	ES	24.2.72

Specific description. We can make but few additions to the excellent description of shell morphology given by Verrill & Bush (1898). The small medial teeth immediately below the umbo insert in a dorsal arc, away from the ventral edge of the hinge plate (Figs. 1 & 27a). The external ligament extends posteriorly in the mid-line of the escutcheon to about the posterior limit of the umbo at the insertion of the ninth tooth of the posterior plate series. The anterior ligament is short, not extending beyond the beak of the umbo.

The incurrent region has four or five papillae on each side and lacks mantle fusion between the posterior apertures. The gills are small, with 10 to 14 gill plates on each demibranch, and 7 to 10 palp ridges. The hind gut passes close to the anterior adductor muscle, but is not contiguous with it. The anterior adductor muscle is slightly larger than the obliquely orientated posterior adductor muscle (Fig. 2).

Morphology of the soft parts. No detailed account of the soft part anatomy has been given hitherto. Lack of mantle fusion and siphons (note, siphons may be formed in the Nuculanoidea without fusion of the mantle tissues, Yonge, 1959) is reminiscent of the condition in the Nuculoidea (Sanders and Allen, 1973). However, unlike the members of that order, the posterior mantle edge is highly specialized and divided into excurrent, incurrent and feeding regions in addition to the ventral pedal gape (Fig. 3).

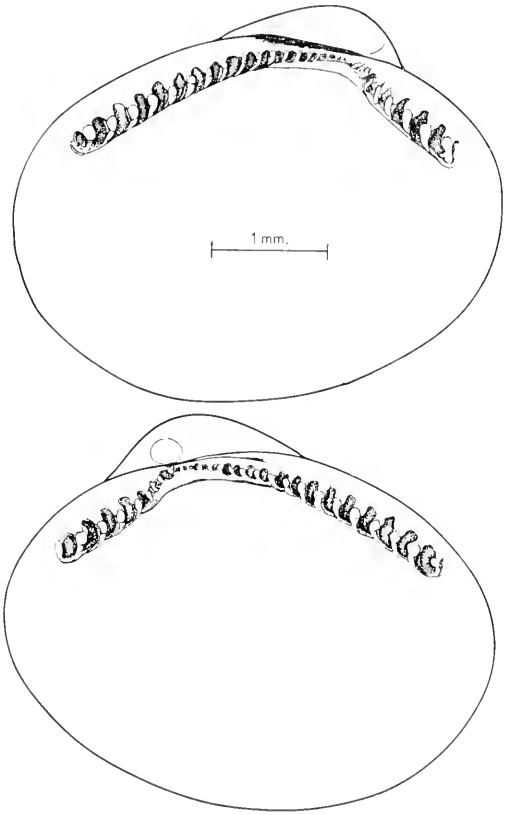


Figure 1. *Tindaria callistiformis* Verrill & Bush. Internal views of the left and right valves.

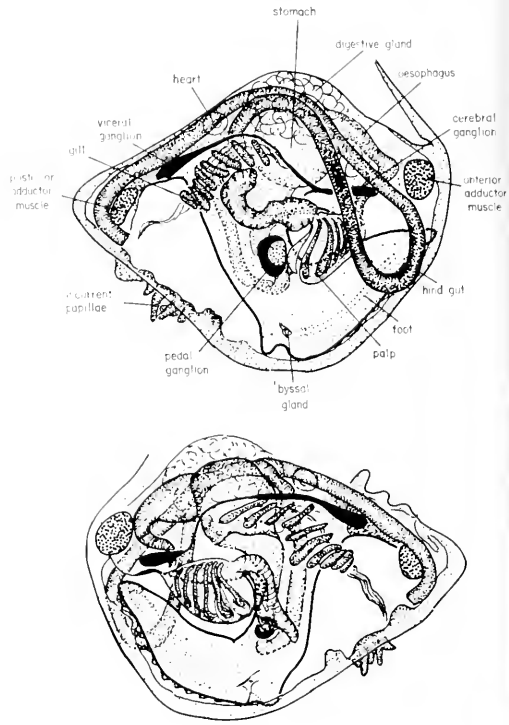


Figure 2. *Tindaria callistiformis* Verrill & Bush. Semidiagrammatic drawing of the body and mantle organs as seen from right and left sides.

The excurrent region occupies a very small portion of the posterior mantle margin. A narrow channel is defined by the ventral edge of the posterior adductor muscle and by a pair of low ridges, formed by the inner muscular mantle folds, to which the attenuate distal end of the gill axes are attached. The anus is positioned opposite this narrow channel. There is no development of the inner muscular fold of the mantle edge to form an incomplete siphon as Knudsen (1970) described for some other parts. The incurrent region is wider than the excurrent and defined by four to six pairs of short conical papillae, the number depending on the size of the specimen. On the right side immediately adjacent to the lower papilla there is a single sensory tentacle. The papillae are developed from the middle sensory lobe. In cross section, the papillae are radially divided into 12 to 15 haemocoelic cavities running the length of the papillae with longitudinal muscle fibres at the center.

Ventral to the incurrent region there is a feeding aperture which is formed by the extended overlapping and folded portions of the inner and middle mantle folds, and it is through this aperture that the palp proboscides are extended (Fig. 3). The inner muscular fold in the region of the posterior apertures is much broader than elsewhere. Gland cells are present in the outer mantle epithelium in the region immediately posterior to the feeding aperture. These extend anteriorly, although less densely, to the inside of the muscular fold in the region of the pedal aperture (Fig. 4).

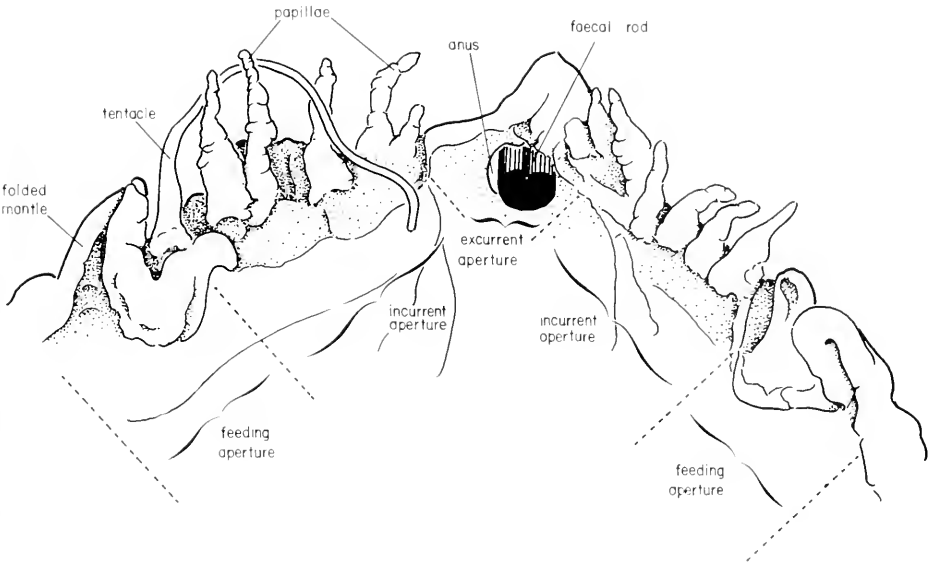


Figure 3. *Tindaria callistiformis* Verrill & Bush. Detail of the posterior mantle edge spread open and viewed from the ventral side; the limits of the various apertures indicated with dashed lines.

An anterior sense organ, derived from the middle sensory fold, is well-developed. The left sense organ is somewhat larger than the right, the latter positioned immediately below the ventral limit of the hind gut loop. For a comparatively robust shell, the adductor muscles are small and characteristically situated close to the pallial line and very near the shell margin. The 'quick' and 'catch' parts of the adductor muscles are clearly defined. The anterior muscle is circular in outline, while the posterior adductor is oval with the long axis oblique to the antero-posterior shell axis.

The gill axis lies parallel to the posterior dorsal margin of the shell and thus somewhat obliquely to the anterior-posterior axis of the body and shell. The number of gill plates is small, varying with the size of the animal. They are widely separate and alternate on either side of the axis (Fig. 2). The gill extends across the posterior third of the body to the ventral side of the excurrent region. Posteriorly, the gill plates do not extend much beyond the posterior limit of the body, thus the gill axes are extended posteriorly. The anterior limit of the gill axis is far removed from the insertion of the palp. The gill axis is highly muscular, with fibres extending its length and also reaching vertically to each gill plate (Fig. 5). The gill plates are finger-shaped and sub equal. There is no fusion between mantle and gill, and connections between the inner filaments of the two gills are apparently lacking.

The palps are remarkable for their small size and the small number of ridges (seven to nine), the exact number being dependent on the size of the animal (Fig. 6). The palp ridges are broad, high and deeply grooved on the mid-anterior face. The most posterior ridge is well anterior to the posterior thickened edge of the palp.

The foot is typically nuculanoid with a well-defined neck at its junction with the body. Within the neck are large pedal ganglia and associated statocysts. Small papillae fringe the entire edge of the divided sole. The heel is small and triangular and internally there is a small 'byssal' gland with paired apertures opening at the junction be-

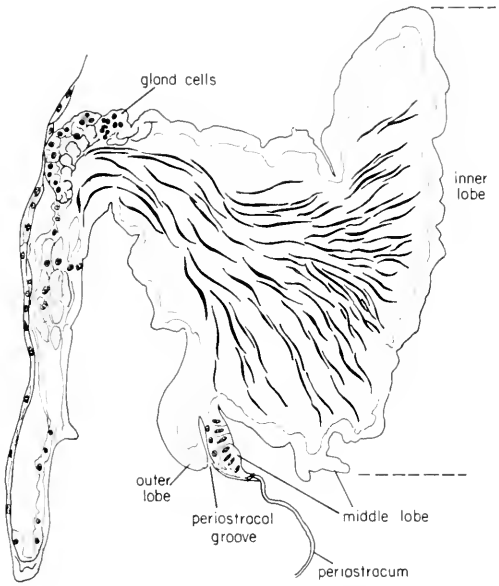


Figure 4. *Tindaria callistiformis* Verrill & Bush. Transverse section through the mantle edge.

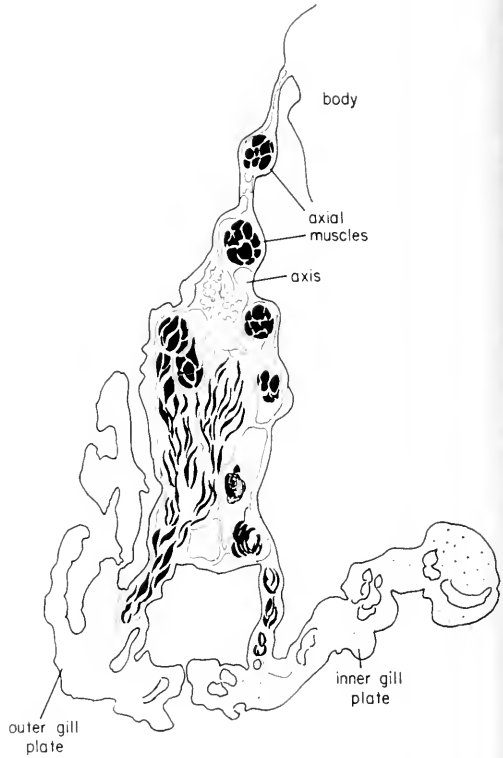


Figure 5. *Tindaria callistiformis* Verrill & Bush. Transverse section through the left gill showing axial muscles and outline of gill plates.

tween heel and foot. Numerous subepithelial mucous glands open on to the sole of the foot on either side and in the mid line (Fig. 7).

The gut also is basically nuculanoid with a single loop of the hind gut on the right side of the body. The mouth is posterior to and some distance from the anterior adductor muscle. This may be due in part to its displacement by the loop of the hind gut, which passes close to the adductor muscle. It may also have functional significance in relation to the posterior ingress of food material into the mantle cavity. The oesophagus is long, first taking an anterior course to the posterior dorsal edge of the anterior adductor muscle where it is displaced slightly to the left of the sagittal plane. At this point it turns dorsally and posteriorly to open on the left anterior side of a huge stomach. The oesophagus is inflated close to its junction with the stomach and the stomach occupies much of the body space (Figs. 2 & 8). Although the stomach is large, there are only six very low crested sorting ridges on its right side. Much of the remainder of the stomach is lined with a gastric shield which has a well-defined tooth on the anterior dorsal side close to the apertures of the three ducts of the digestive diverticula. The combined mid gut and style sac penetrate the neck of the foot, pass to the posterior and left side of the pedal

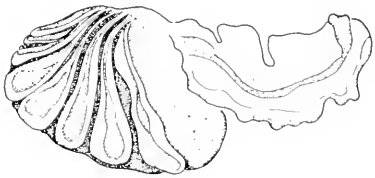


Figure 6. *Tindaria callistiformis* Verrill & Bush. Lateral view of inner surface of a proximal palp to show detail of ridging.

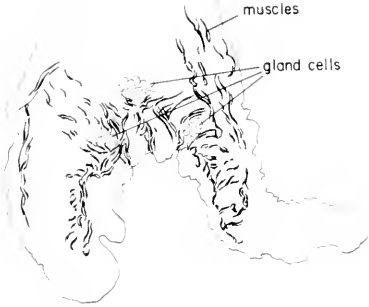


Figure 7. *Tindaria callistiformis* Verrill & Bush. Transverse section of the foot to show position of the muscles and pedal glands.

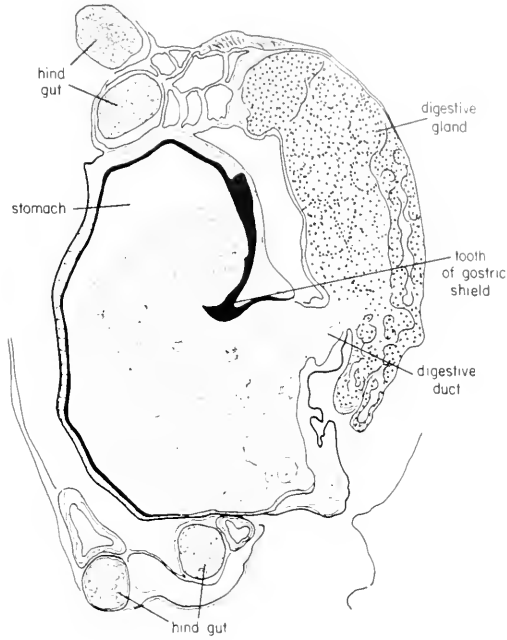


Figure 8. *Tindaria callistiformis* Verrill & Bush. Transverse section through the body to show detail of stomach, hind gut and digestive gland.

ganglion and join with the hind gut just ventral to the latter. The hind gut turns and follows a dorsal course parallel with the style sac, with a shallow, ill-defined U-bend posterior to the stomach. The hind gut then forms a single loop to the right and the loop together with some body tissue penetrates the right mantle to a position close to the pallial line. A typhlosole is present throughout the length of the hind gut.

The ganglia and their connectives are large, as the visceral and cerebral ganglia are elongated. A pair of statocysts dorsal and postero-lateral to the pedal ganglia are filled with small crystals (which are not calcium carbonate) lacking ducts to the outside. Transverse muscle fibres in the foot are found dorsal and ventral to the ganglia and the statocysts.

The kidney is small and multilobed. Sexes are separate.

Size, Reproduction and Age. All three stations from which large numbers of *T. callistiformis* were collected showed similar population histograms. Each was strongly skewed to the left (Fig. 9). Yet, we might not adequately be sampling the smallest juvenile stages which could pass through the 0.42 mm openings in our screens. The eggs on hatching are at least 0.15 mm long and the size of the metamorphosed post-larvae settling onto the bottom (assuming a lecithotrophic mode of reproduction) must be somewhat larger. We feel our histograms do not significantly distort the length-frequency composition of *T. callistiformis* at the sampling sites. Analysis of 60 specimens from Station 77, representative of the size range, indicates that gonadal development does not occur until this species reaches a size of between 4.0 and 4.5 mm total length. This was confirmed by examination of the specimens from Stas. 78 and 85 which show that all specimens larger than 4.5 mm had some gonadal development and the larger the specimen the more mature was the gonad. Only in an exceptionally small percentage (2.6 to 3.0 per cent depending on the sample) of the total population was any sign of gametogenesis evident. Great disparity exists in the sex ratio with only one female to every five males. The most mature female (6.5 mm

total length) was dissected and the eggs counted; these numbered 230 having a maximum length of 145 μ. From our past observations on a wide range of abyssal protobranchs, we would estimate this specimen to be 3/4 mature. The eggs were maturing simultaneously. There is no evidence of brooding.

Growth rate measurements using ^{228}Ra chronology (Turekian et al., 1975) show that *Tindaria callistiformis* having a length of 4 mm are about 50 to 60 years old, while the largest specimen, having a length of 8.4 mm, has an age of 100 years or longer.

The moderate degree of variation in shell shape appears to have no intimate relation to the size of the specimen. Thus, the height/total length ratio varies from 0.62 to 0.83 over much of the size range (Figs. 10 and 11). However, if the five largest specimens are ignored, there is a tendency for the height/total length ratio to decrease with increasing size. Similarly, there appears to be no increase in length posterior to the umbo with increasing length. Although anterior in position, there is considerable variation in the position of the umbo, the extreme limits being between 55 per cent and 76 per cent of the total length. The maximum total length recorded is 8.4 mm.

Tindaria hessleri, new species
Figures 12–16 & 27

Holotype: MCZ 279902, from *Atlantis II*, Cruise 31, Station 141, in 2031 m.
Depth range = 1739 to between 2051 and 2357 m.

Cruise No.	Station No.	Depth (m)	No. of Specimens	Latitude	Longitude	Gear	Date
			W. Europe Basin				
Sarsia	S–44	1739	19	43°40.8′N	3°35.2′W	ES	16.7.67
			Cape Verde Basin				
Atlantis II 31	138	1944–1976	2	10°36.0′N	17°52.0′W	ES	4.2.67
Atlantis II 31	141	2131	3	10°30.0′N	17°51.5′W	ES	5.2.67
Atlantis II 31	139	2099–2187	1	10°33.0′N	17°53.0′W	ES	4.2.67
Atlantis II 31	145	2105–2192	1	10°36.0′N	17°49.0′W	ES	6.2.67
Atlantis II 31	144	2051–2357	7	10°36.0′N	17°49.0′W	ES	5.2.67

Specific description. Shell stout, robust, with strong, uniform, concentric ridges, somewhat oval in outline and extended posteriorly; umbos anterior in position, moderately swollen beaks prominent and strongly curved medio-anteriorly; escutcheon present and forms moderate concavity (Fig. 27B); elongate, narrow, external ligament extends posteriorly along the escutcheon to about the insertion of the eleventh tooth on the posterior hinge plate and anteriorly to about the insertion of the sixth or seventh tooth of the anterior hinge plate; dorsal shell margin strongly convex; antero-dorsal margin short, sloping rapidly to form a continuous curve with the anterior margin; postero-dorsal margin long, sloping more gradually to form a smooth curve with posterior margin; posterior end narrow, evenly rounded; anterior end broad, rounded, but with dorso-anterior shorter than ventro-anterior margin; ventral margin long and only slightly convex. Hinge plate broad and strong with a continuous row of teeth; posterior hinge plate long with about 21 to 22 teeth, 14 through 21 or 22 large and robust, more medial teeth progressively smaller and very reduced in size at confluence of the anterior and posterior hinge plates; anterior hinge plate short and thick bearing about 10 teeth, distal five large and strong, more proximal teeth as on posterior hinge plate become gradually smaller with minute proximal teeth inserting dorsally (Fig. 12).

Tindaria hessleri differs from *T. callisti-*

Figure 9. *Tindaria callistiformis* Verrill & Bush. Size frequency histograms of samples from two stations. The dashed lines indicate the sizes at which gametogenesis is evident.

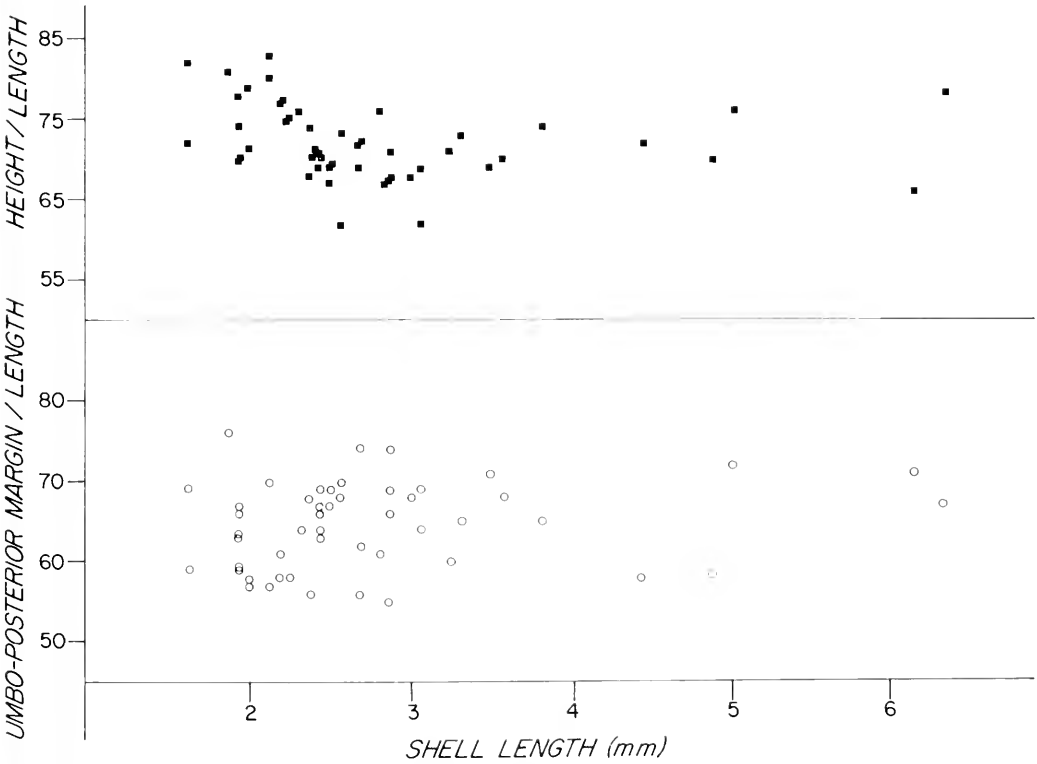


Figure 10. *Tindaria callistiformis* Verrill & Bush. Graph showing height/total length (■) and umbo to posterior margin/total length (○) plotted against total length.

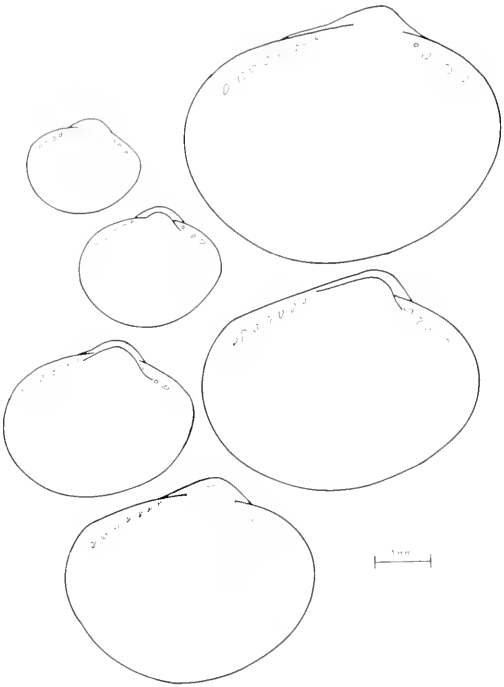


Figure 11. *Tindaria callistiformis* Verrill & Bush. Growth series in lateral view.

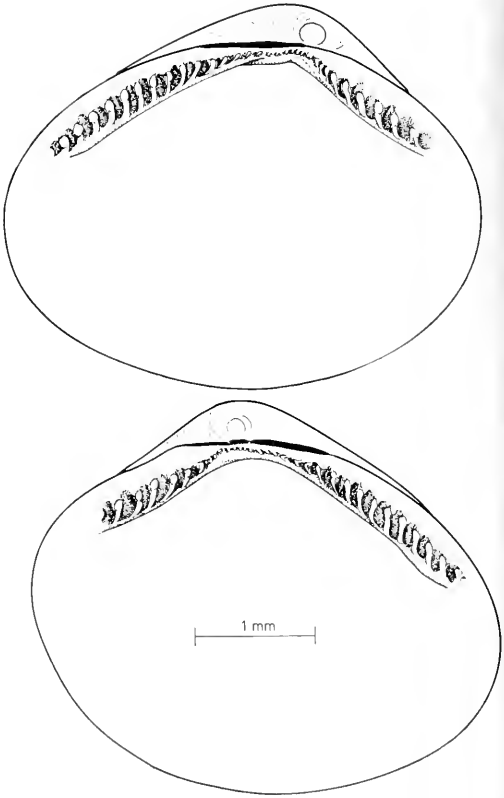


Figure 12. *Tindaria hessleri* Sanders & Allen. Internal views of the left and right valves.

formis in the following ways: *T. hessleri* is less smoothly convex and more triangular in outline; the ventral margin of the valve is deepest directly beneath the umbo rather than more posteriorly; the dorsal margin is more strongly convex; the anterior margin is not as broadly rounded; and the hinge plates are less massive.

Incurrent region, three papillae on each side; adductor muscles oval and equal in size; gill small with 7 to 14 plates on each side of the axis; palp with 8 to 10 ridges; hind gut extends into the mantle of the right side to a position short of the pallial line, part of hind gut lies adjacent to the posterior face of the anterior adductor muscle; visceral ganglion placed anterior to the posterior adductor muscle.

Morphology of the soft parts. The morphology of *T. hessleri* is very similar to that of *T. callistiformis* (Fig. 13). However, unlike the latter species, there is a permanent excurrent aperture formed by the fusion of the muscular lobe and the inner part of the sensory fold of the mantle, between the incurrent and excurrent regions (Fig. 13). There are only three pairs of papillae on each side of the incurrent region and sectioned material suggests that mantle fusion dorsal to this region involves the homologue of a pair of papillae that have fused together. There is *no* single sensory tentacle but mantle extensions at the dorsal side of the feeding aperture may possibly serve the same function. The latter aperture is well-developed with the muscular and sensory folds of the mantle showing considerable hypertrophy. These are folded in preserved specimens but in life they must be capable of considerable extension.

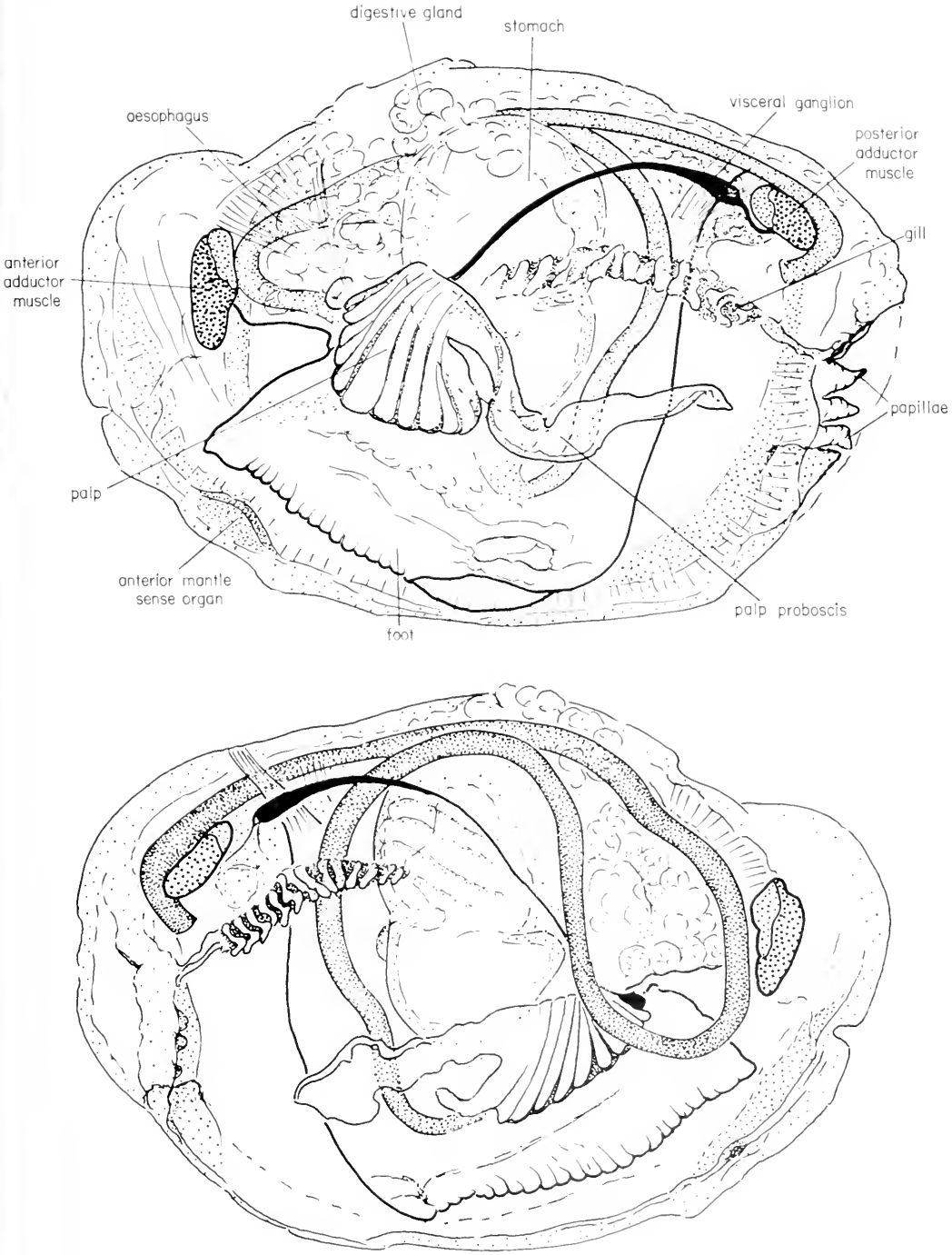


Figure 13. *Tindaria hessleri* Sanders & Allen. Semidiagrammatic drawings of the body and mantle organs as seen from the left and right sides.

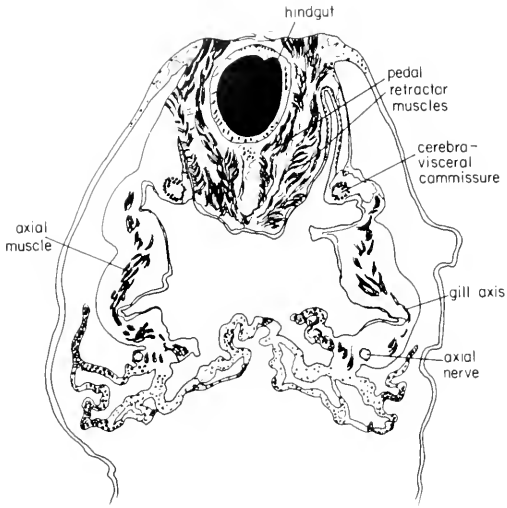


Figure 14. *Tindaria hessleri* Sanders & Allen. Transverse section through the posterior part of the body and gills to show axial and pedal retractor muscles.

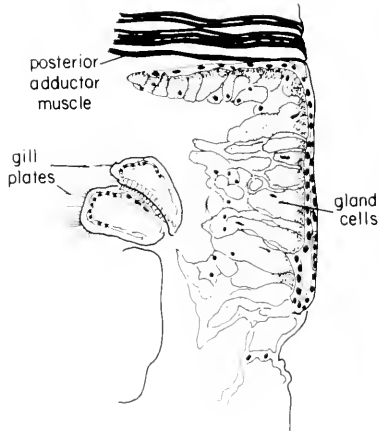


Figure 15. *Tindaria hessleri* Sanders & Allen. Transverse section through the right margin of the hypobranchial cavity showing the distribution of basiphilic gland cells.

There is no mantle fusion either dorsal or ventral to the feeding aperture, but aposition or overlapping of the mantle edges at these points makes an efficient functional separation. Adjacent to this region is a well-defined area of acidophilic mucus secreting cells at the surface of the inner mantle epithelium. The adductor muscles are oval in cross section with the longitudinal axis vertical in the anterior muscle and oblique in the posterior muscle. To the inside of the inner muscular lobe and at 90 degrees to it are a series of fine pallial retractor muscles extending inwards for a short distance; these are present along the entire perimeter of the mantle (Fig. 13).

In specimens of a similar size there are more gill filaments than in *T. callistiformis* and, as in the latter species, they are arranged alternately along the axis. Behind the body, the tips of the filaments of the inner demibranch are extended and fuse with the filaments of the inner demibranch of the opposite gill and with adjacent filaments of the same demibranch, thus forming a membranous junction. The filaments of the outer demibranches are also extended and make a strong ciliary junction with the mantle (Fig. 14). The gill axis is very muscular and it must be concluded that in life the gills form a pumping system in many ways analogous to that of the Septibranchia. The hypobranchial cavity is thus entirely separate from the rest of the mantle, the lateral mantle walls of the cavity being lined with basiphilic gland cells (Fig. 15). No fecal material passes into the mantle cavity. When the gill is contracted the volume of the hypobranchial cavity is very small.

The palps are very similar to those of *T. callistiformis* except that, depending on the size of the animal, the number of ridges is somewhat greater, and these lie relatively closer together than in the latter species. The palps (and mouth) lie far posterior to the anterior adductor muscle. The course of the gut is essentially the same as in the previous species but the lumen is relatively smaller and does not extend as far into the mantle, never reaching the inner muscular lobe of the mantle—even in the smallest specimens. The foot is similar to that of *T. callistiformis*, however, the 'byssal' gland is somewhat larger. Nervous

system and kidney are as in the previous species; sexes are separate.

Size and Reproduction. The small number of specimens and the opaqueness of the shell makes an analysis of reproductive potential similar to that given for *T. callistiformis* impossible. However, sections show that a specimen of 2.5 mm total length contains approximately 350 ova with a maximum length of 110 μ. The ova are maturing simultaneously.

Relatively few shells (eight) were available for studies on dimensional variation (Fig. 16). It appears to be of the same order as *Tindaria callistiformis* and *Pseudotindaria galatheae* with the height length ratio varying from 0.69–0.81 and with the total length/umbo to posterior margin length varying from 58 per cent to 67 per cent, the umbo being anterior in position.

It gives us great pleasure to name this species after Dr. R. R. Hessler, of the Scripps Institution of Oceanography—colleague, collaborator and friend—who has contributed so significantly to our knowledge of the abyssal fauna.

Tindaria cytherea (Dall, 1881) Figures 17–22

Nucula cytherea Dall, 1881, Bull. M.C.Z., *9*, No. 2: 123 (*Blake* Station without number Yucatan Strait, 640 fms. (= 1171 m)). Holotype. U. S. Nat. Mus. 63137.

Malletia veneriformis Smith, 1885, Chall. Rep. *13*: 246, pl. 20, figs. 9, 9a. (*Challenger* Station 33, off Bermuda, 435 fms (= 796 m).)

Malletia cytherea (Dall), 1886, Bull. M.C.Z., *12*, No. 6: 254, pl. 8, figs. 1, 1a. [in part, figure only.]

Malletia amabilis Dall, 1889, Bull. M.C.Z., *18*: 438, pl. 40, fig. 8. [New name for *Malletia cytherea* Dall 1886 in part, description only, not figure.]

Tindaria cytherea (Dall) Verrill & Bush, 1898, Proc. U.S.N.M. No. 1139.

Previous records. Depth range = 711 to 1325 m.
North America Basin—1 station. Ref. Smith, 1885.
Gulf of Mexico Basin—1 station. Ref. Dall, 1886.
Caribbean Basin—4 stations. Refs. Dall, 1881, 1886; Smith, 1885.
Present record. Depth 1000 m.

Cruise	Station No.	Depth (m)	No. of Specimens	Latitude	Longitude	Gear	Date
			North America Basin				
Pamlirus	Bermuda #1	1000	1	32°16.5′N	66°42.5′W	AD	13.4.60

We have collected a single large specimen of a tindariid species off Bermuda in 1000 meters that is similar to or identical with a number of forms described from the same general region and depth. These are *T. cytherea*, (Dall) *T. amabilis* (Dall) and *T. veneriformis* (Smith) (Fig. 17). Dall (1886) synonymized *T. cytherea* and *T. veneriformis* and later Verrill and Bush (1898) synonymized *T. cytherea* and *T. amabilis*, although Dall (1889) believed that they were separate. Dall (1881, 1886, 1889) described two specimens, one in 1881 as *Nucula cytherea*, and the second in 1886 as *Malletia cytherea*. In 1889 he stated that the second specimen described in 1886 was sufficiently different from the specimen described in 1881 to warrant the erection of a second species which he named *M. amabilis*. The position is confused by the fact that the specimen described as *N. cytherea* (Dall, 1881) is figured in his second paper (Dall, 1886) while the specimen described in 1886 is figured in his third paper (Dall, 1889). We agree with Verrill and Bush (1898) that these all refer to the same species as indicated in the synonymy.

We have but a single specimen, measuring 9.2 mm total length, height 7.6 mm. Its description is as follows:

Description of Shell. Shell stout, robust, straw-colored, with strong, uniform, concentric ridges; oblong oval in outline with anterior end slightly truncate, inequilateral; umbo anterior in position, prominent, with beaks strongly curved antero-medially; escutcheon present; external ligament elongate, moderately large, extending posteriorly

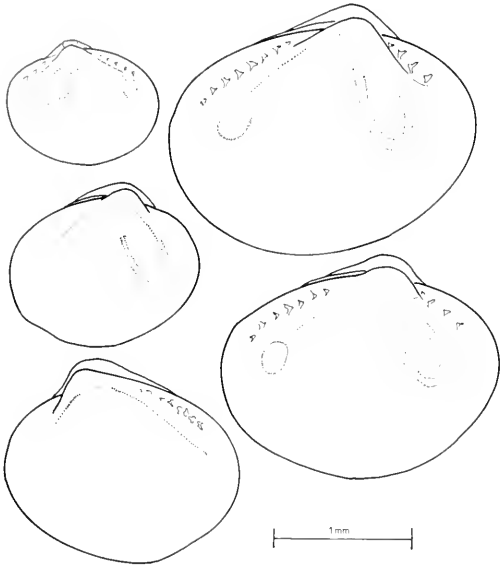


Figure 16. *Tindaria hessleri* Sanders & Allen. Growth series in lateral view.

to about the insertion of the fourteenth tooth of the posterior hinge plate series and anteriorly to about the sixth tooth of the anterior series; inner layer forms a small crescent-shaped section immediately below the beaks; dorsal shell margin strongly convex with both antero- and postero-dorsal shell margins steeply sloping away from the umbos; long postero-dorsal margin forms a smooth curve with the rather broadly rounded posterior end; antero-dorsal margin forms a smooth curve with the slightly truncated anterior end; ventral margin smooth, long, and only shallowly convex; hinge plate strong, moderately broad with teeth continuous beneath the umbo; long posterior hinge plate bearing about 24 teeth which are directed primarily medially, proximal teeth smallest, distal teeth increasingly larger to tooth 16 to 18, the latter being large, long, and robust, thereafter teeth diminish in length but remain robust; anterior hinge plate with about 14 medially directed teeth, teeth 6 to 13 strong and long, more proximal teeth progressively smaller.

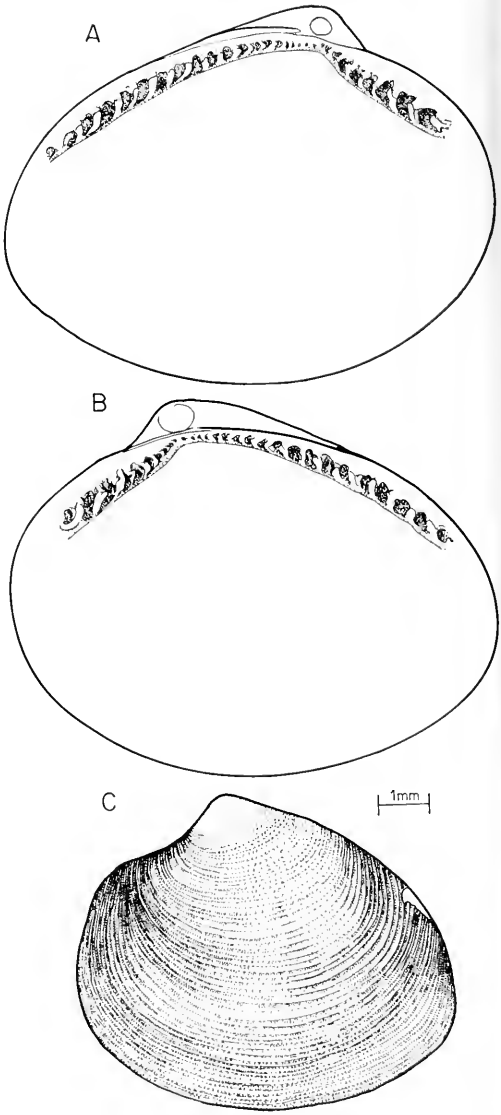


Figure 17. *Tindaria cytherea* (Dall). A & B, internal views of the valve (Type specimen USNM No. 63137, Blake Collection, Yucatan Strait 640 fm); C, external lateral view of specimen collected by authors.

Remarks. This specimen differs from the descriptions given by Dall (1881, 1886) and Smith (1885) primarily by the somewhat more obvious external ligament and the straight ventro-medial edge of the anterior margin. In this respect it resembles the

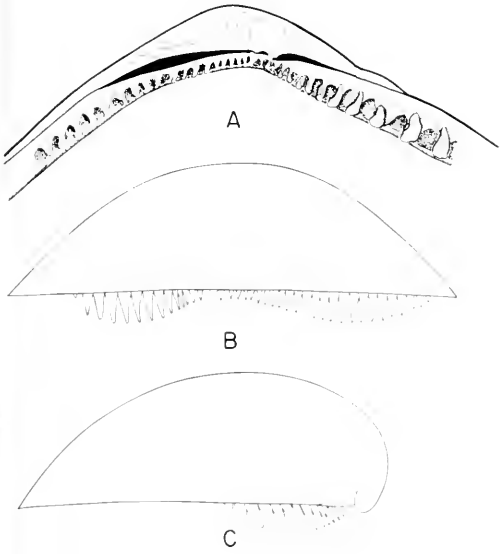


Figure 18. *Tindaria cytherea* (Dall). Detail of the hinge and teeth of the specimen collected by the authors. A, left valve, umbonal region; semidiagrammatic presentation of right valve in dorsal (B) and posterior view (C).

type specimen of *M. amabilis* (Dall) rather than the type specimen of *M. cytherea* (Dall) (Fig. 17) in which the ventro-medial edge is curved. Shell proportion, shape and thickness alter with growth in many deep-sea protobranch species. These changes are most evident in the very largest specimens. Our single individual is larger than any of the other specimens that we refer to this species and we attribute the differences in our specimen to its larger size.

Description of the soft parts. Incurrent region with 7 papillae on either side, no single tentacle; adductor muscles very small, oval and dorsal in position, anterior adductor muscle somewhat larger than the posterior; gills moderately large, 24 gill plates on each side of the axis; hind gut penetrates slightly into the mantle, ventral limit of hind gut loop scarcely ventral to the ventral edge of the anterior adductor muscle; vis-

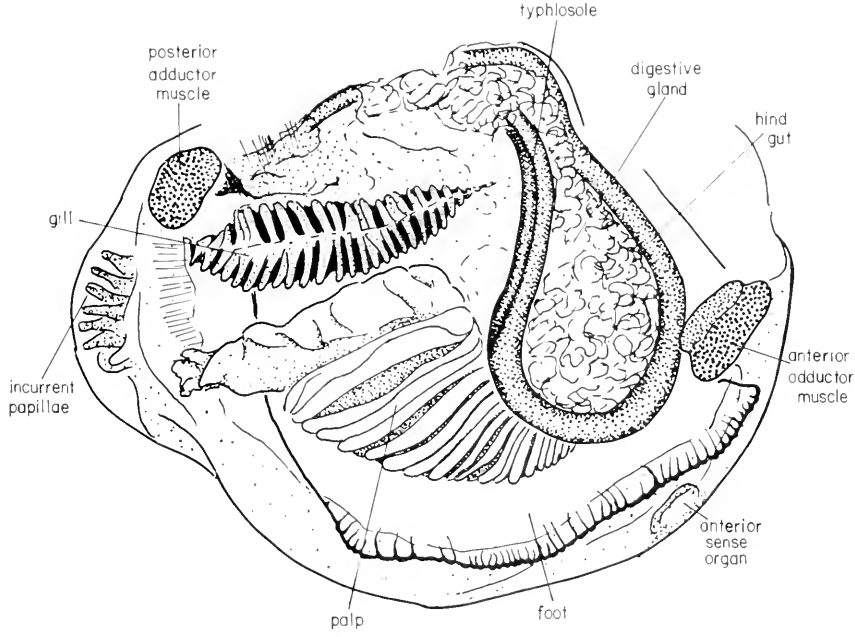


Figure 19. *Tindaria cytherea* (Dall). Semidiagrammatic drawing of the body and mantle organs as seen from the right side.

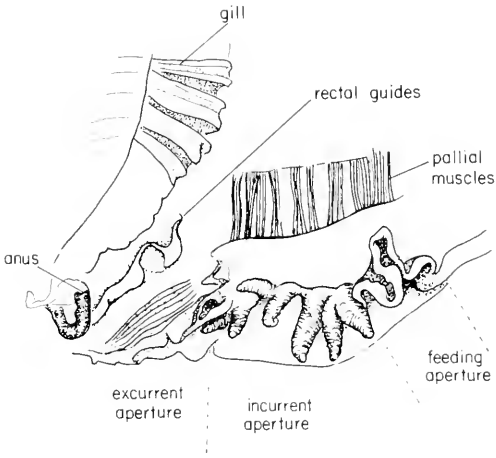


Figure 20. *Tindaria cytherea* (Dall). Detail of the posterior part of the left mantle margin.

Figure 21. *Tindaria cytherea* (Dall). Latero-ventral view of gill.

ceral ganglion close to the posterior adductor muscle.

Remarks. Fortuitously, the soft parts of our single specimen had become detached from the shell on preservation. There are no great differences in the morphology of the soft parts from those of other species, many being the consequence of the large size of the specimen (Fig. 19). Hence, the development and the extension of the inner mantle fold to form a feeding aperture below the incurrent region is particularly well marked (Fig. 20). Similarly, the anterior sense organ is well-developed. The gills are large (Fig. 21) but not fused to form an obvious pumping organ, although in life, with the aid of peripheral interlocking cilia, they could possibly function as such. The gill axes which connect with the ventral side of the excurrent region probably act as guides during the expulsion of faeces from the anus. The palps, probably because of the large size of this specimen, have a greater number of ridges (18) than in other species of *Tindaria*, but they are small in comparison with other protobranch genera of the same size. The palp proboscides are extremely large and elongate. The mouth, unlike the other species here described, is close to the anterior adductor muscle. The course of the gut is similar to that of *T. callistiformis* and *T. hessleri*. The stomach is extremely large, with an extensive gastric shield on the left dorsal side, and bears a tooth close to the three apertures of the digestive diverticula. There are 10 sorting ridges on the right side (Fig. 22). The ganglia are extremely large.

Tindaria miniscula, new species
Figures 23–28

Holotype: M.C.Z. 279901, from *Atlantis II* cruise 42, Station 197, in 4565 to 4595 m.
Depth range: 4559–4566 to 4612–4630 m.

Cruise	Station No.	Depth (m)	No. of Specimens	Latitude	Longitude	Gear	Date
			Angola Basin				
Atlantis II	198	4559–4566	7	10°24.0′S–10°29.0′S	9°04.0′E–9°09.0′E	ES	21.5.68
Atlantis II	197	4565–4595	27	10°29.0′S	9°09.0′E	ES	21.5.68
Atlantis II	196	4612–4630	2	10°29.0′S–10°29.0′S	9°03.0′E–9°04.0′E	ES	21.5.68

Specific Description. Shell minute, strong, elongate, oval in outline, with uniform concentric ridges; umbo large and swollen; beaks prominent and strongly curved medially; escutcheon forms a conspicuous concavity in dorsal margin (Fig.

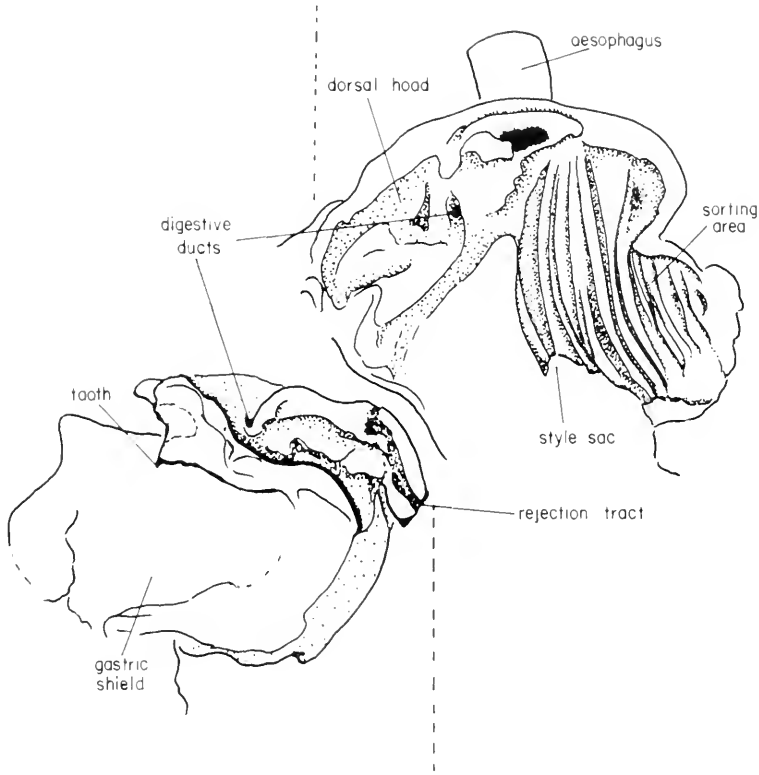


Figure 22. *Tindaria cytherea* (Dall). Internal detail of the left and right sides of the stomach.

27c); external ligament elongate, narrow, extending posteriorly to near the insertion of the second tooth of posterior hinge plate series and extending anteriorly to the insertion of the first tooth of anterior series; dorsal shell margin weakly convex; anterodorsal margin short, rather straight and, distally, sloping ventrally to form a smooth curve with the anterior margin; posterodorsal margin longer, slightly convex to form continuous curve with the posterior margin; anterior and posterior margins evenly rounded; ventral margin elongate and moderately convex.

Hinge plate thin, rather weak with a relatively broad edentulous space separating the anterior and posterior rows of teeth; posterior hinge series with six chevron-shaped teeth; anterior hinge series shorter, with three similar teeth (Fig. 23).

Tindaria miniscula differs from *T. callistiformis*, *T. hessleri* and *T. cytherea* in its small size, oval shape, few teeth on thin hinge plate, the extensive endentulous space on hinge plate beneath umbo and the more medial position of the umbo.

Morphology of the soft parts. Incurrent region with three papillae to the left side and two to the right; adductor muscles small, unequal in size; gill very small with six to seven plates to each demibranch; palp with five to six ridges; hind gut penetrates mantle of right side almost to the pallial line; part of hind gut lies adjacent to the posterior face of the anterior adductor

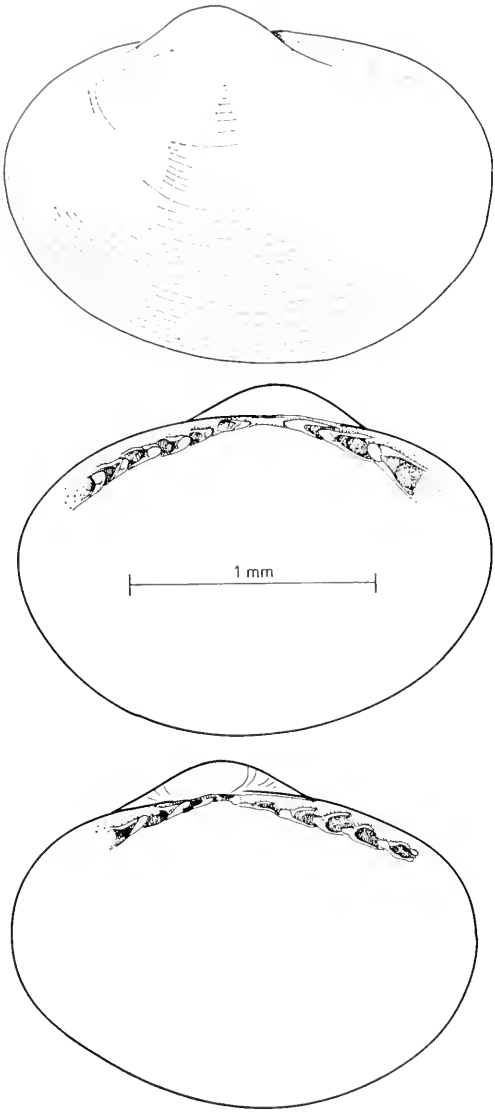


Figure 23. *Tindaria miniscula* Sanders and Allen. External view of the left valve and internal view of the left and right valves.

muscle; visceral ganglion contiguous with the posterior adductor muscle.

The two papillae to the left of the incurrent region alternate with the three to the right so that the dorsalmost papilla is on the right, i.e., the two most ventral are on the left. The third left ventral papilla may possibly be homologous to the single nuculanid tentacle but in form and histology it cannot be separated from the others. A pair of well marked faecal guides or ridges mark the ventral limit of the excurrent aperture. Below the incurrent region the extended inner mantle folds overlap to form a feeding aperture. Separation of the aperture is not permanent. Inward of the feeding aperture and the incurrent aperture is a band of very large epithelial gland cells. Adductor muscles are small and the posterior is larger. The gills are very small, approximately seven pairs of alternating gill plates set tangentally across and behind the posterior part of the body. The gill axes are attached to the mantle edge at the level of the faecal guides. There are a few muscle fibers in the axes and two well-developed muscles in the plate. The palp is relatively large, extending approximately half the total length of the animal; the palp proboscides are stout (Fig. 24). The mouth is set posterior to the anterior adductor muscle, the oesophagus extends forwards, turning short of the anterior adductor muscle, posterodorsally to the stomach. The lumen of the oesophagus is exceptionally large, as is the stomach. The latter occupies the bulk of the body space. The stomach is almost entirely lined with the gastric shield, and is surrounded by a fine network of muscle fibers. Diatom frustules are the main organic content of the stomach. It is possible that the digestive gland is composed of two regions, the umbo non-pigmented and the remainder a pale brown color, but sections indicate no obvious histological differences. The hind gut forms a single loop to the right-hand side of the body, penetrating the lumen of the mantle and skirting the anterior adductor muscle, but not reaching the inner mantle lobe. At its maximum point of penetration it lies some distance dorsal to the anterior mantle sense organ. The hind gut also extends deep into the foot ventral to the pedal ganglia. A typhlosole is present along the entire length of

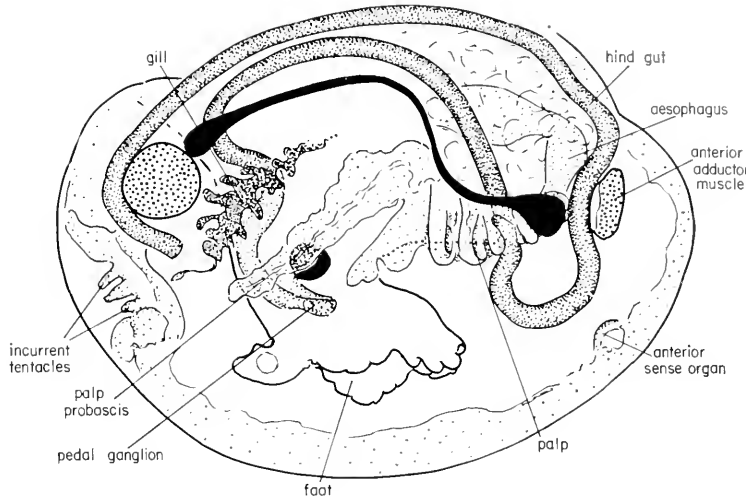


Figure 24. *Tindaria miniscula* Sanders & Allen. Semidiagrammatic drawing of the body and mantle organs as seen from the right side.

the gut. The foot is relatively small, and placed far back on the visceral mass. It bears a relatively large, triangular, posteriorly directed heel and a small 'byssal' gland. The sole of the foot is small, divided and peripherally papillate with glands to the inside of the papillae. The ganglia are large, particularly the pedal, the visceral and cerebral ganglia are attenuate pear-shape. There is a pair of small but typical protobranch statocysts dorsal to the pedal ganglia. The kidney is very small; sexes are separate, whole mounts showing initial stages in ovarian development with approximately 12 ova lateral to the stomach.

Although the total number of specimens in our samples is small, and the size range is so much smaller than in other species (0.8 to 2.5 mm), the population histogram remains clearly skewed to the left as it is in *Tindaria callistiformis* (Fig. 25). Similarly, the height/length ratio shows a wide range of values varying from 0.66 to 0.78 over the length range (Fig. 26). However, we may not have sampled the smaller juvenile stages which might have passed through the

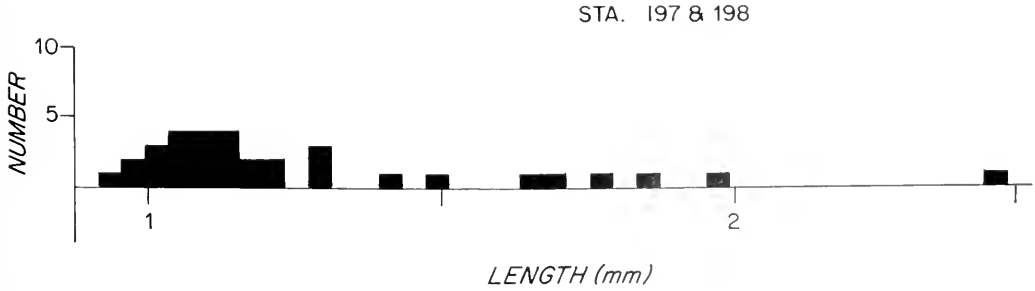


Figure 25. *Tindaria miniscula* Sanders & Allen. Size frequency histogram of specimens collected at Stations 197 and 198.

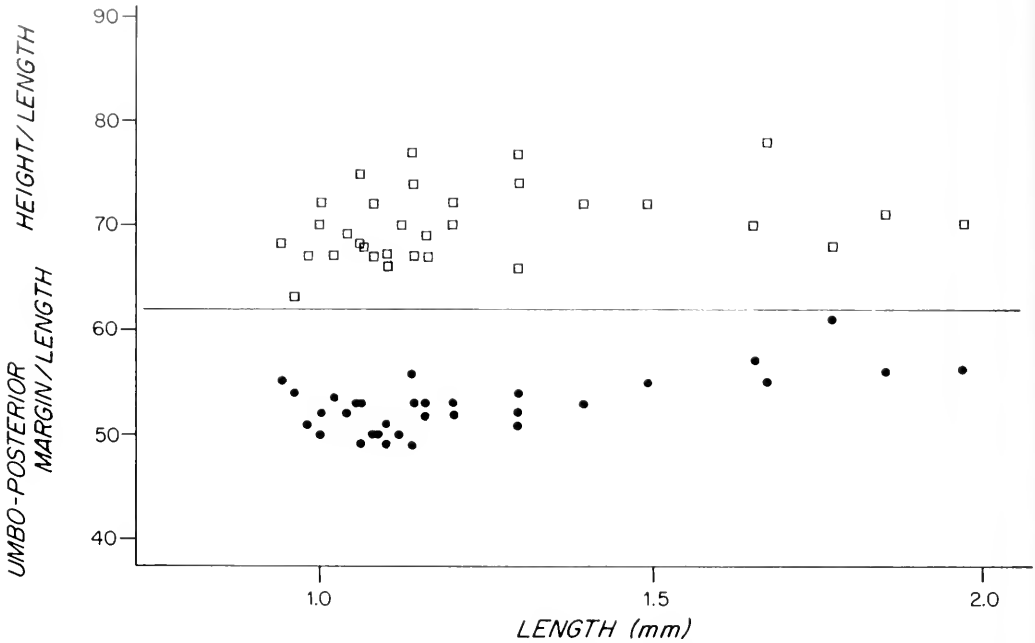


Figure 26. *Tindaria miniscula* Sanders & Allen. Graph showing height/total length (□) and umbo to posterior margin/total length (●) plotted against total length.

0.42 mm apertures of our screen. The umbo, unlike other species of *Tindaria*, is almost central in position in the smallest specimens and becomes progressively more anterior as the size of the shell increases (52 per cent to 57 per cent), i.e., there is an increase in length of the posterior part of the body with increasing age (Fig. 28).

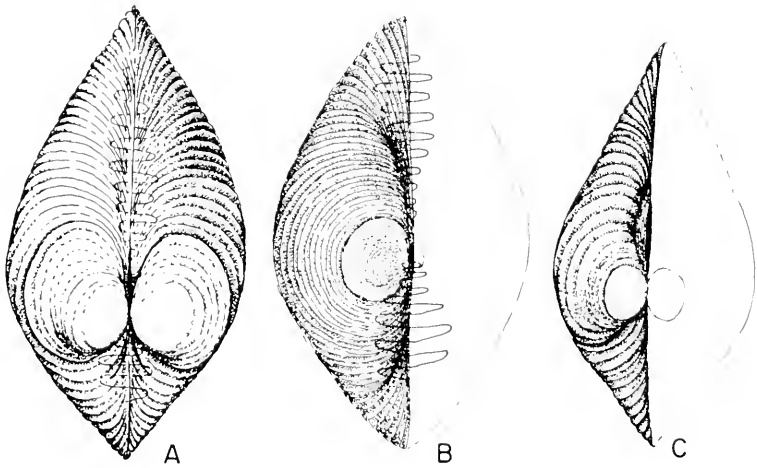


Figure 27. Dorsal views of A, *Tindaria callistiformis*; B, *Tindaria hessleri*; C, *Tindaria miniscula*.

Family INCERTAE SEDIS[1]
Pseudotindaria new genus

Type species: *P. erebus* (Clarke, 1959)

Shell stout, oval in outline, inequilateral and with strong, uniform, concentric ridges; external ligament extends anterior and posterior to the umbo; hinge plate strong and continuous below umbo, with at most a minute endentulous area between the anterior and posterior hinge teeth series; siphons present and fused ventrally; siphonal embayment shallow; gills horizontal to the anteroposterior axis, or nearly so; palps moderately large with many narrow ridges on the inner faces; mouth opens close to the anterior adductor muscle; hind gut coils on both sides of the body and does not penetrate the mantle.

[1] Considering the present systematic state of the protobranchiate bivalves and the need to erect a number of additional families to include the diversity of morphologies, we feel that it is premature at this time to assign the genus *Pseudotindaria* to a presently defined family.

Tindaria	*Pseudotindaria*
1) Rounded, robust shell concentrically lined	1) Same
2) Hinge line strong, supporting a series of well-developed teeth, continuous below the umbo	2) Same
3) Ligament external	3) Same
4) Tentacle present or absent	4) Tentacle present
5) No siphons, fringing papillae around inhalent region	5) Siphonate, without papillae
6) Palp with few ridges	6) Palp with many ridges
7) Relatively few gill plates	7) Relatively many gill plates
8) Hind gut with typhlosole, single loop to the right of body penetrating the mantle	8) Hind gut without typhlosole, loops and/or coils to right and left of body crossing before and behind the stomach, does not penetrate mantle
9) 'Byssal' gland small and ovoid	9) 'Byssal' gland very large and cylindrical
10) Ganglia very large, pedal ganglia in a median position within foot	10) Ganglia small, pedal ganglia in upper half of foot

Pseudotindaria erebus (Clarke, 1959)
Figures 29–40

Tindaria erebus Clarke, 1959. Proc. Malacol. Soc. London, 33: 236. Text. fig. 1(1). (Type locality: m v *Theta*, Station 9, Lat. 31°42′N, Long. 68° 08′W; type specimen, Mus. Comp. Zool., No. 218182.)

Neilonella galathea Knudsen, 1970. Galathea Rep., XI, p. 58. Text fig. 38, B–D; Plate 5, fig. 2, Plate 6, fig. 6. (Type locality: Galathea Station 66, Lat. 4°00′S, Long. 8°25′E; type specimen, Zool. Mus. Univ. Copenhagen.)

Previous records: Single station west of Bermuda at 31°42′N, 68°08′W in 5203 m (Clarke, 1959). Single station off W. Africa 4°00′S, 8°25′E at 4018 m depth (Knudsen, 1970).

Present record: Depth range = 2644–2754 to 5007 m.

Cruise No.	Station No.	Depth (m)	No. of Specimens	Latitude	Longitude	Gear	Date
			North America Basin				
Chain 50	85	3834	1	37°59.2′N	69°26.2′W	ES	5.7.65
Atlantis II 24	123	4853	1	37°59.2′N	64°14.0′W	ES	22.8.66
Atlantis II 17	93	5007	2	34°39.0′N	66°56.0′W	ES	14.12.65
			Canaries Basin				
Discovery	6714	3301	1	27°13′N	15°41′W	ES	20.3.68

Cruise No.	Station No.	Depth (m)	No. of Specimens	Latitude	Longitude	Gear	Date
			Cape Verde Basin				
Atlantis II 31	148	3814–3828	2	10°37.0′N	18°14.0′W	ES	7.2.67
Atlantis II 31	149	3861	12	10°30.0′N	18°18.0′W	ES	7.2.67
			Brazil Basin				
Atlantis II 31	156	3459	3	00°46.0′S–00°46.5′S	29°28.0′W–29°24.0′W	ES	14.2.67
Atlantis II 31	155	3730–3783	2	00°03.0′S	27°48.0′W	ES	13.2.67
			Guiana Basin				
Knorr 25	307	3835–3862	22	12°35.4′N–12°40.8′N	58°59.3′W–59°09.2′W	ES	3.3.72
Knorr 25	288	4417–4429	9	11°02.2′N–11°03.8′N	55°05.5′W–55°04.8′W	ES	25.2.72
Knorr 25	287	4934–4980	87	13°16.0′N–13°15.8′N	54°52.2′W–54°53.1′W	ES	24.2.72
			Angola Basin				
Atlantis II 42	200	2466–2754	36	9°41.0′S–9°43.5′S	10°55.0′E–10°57.0′E	ES	22.5.68
Atlantis II 42	195	3797	145	14°40.0′S	9°54.0′E	ES	19.5.68

Description of Shell. The specimens in our collection depart from Knudsen's (1970) description only by having a very narrow and not a 'rather wide' edentulous space separating the anterior and posterior hinge teeth series. They differ from the specimen described by Clarke (1959) by having one more tooth in both the anterior and posterior hinge series.

With the additional material from our collections we can add further observations to the precise descriptions given by Clarke (1959) and Knudsen (1970) (Figs. 29, 30 & 31). Shell stout, with strong, uniform concentric ridges, oval in outline and slightly extended posteriorly; umbones low, anterior in position; beaks not prominant, curved medially and slightly anteriorly; escutcheon forms a shallow concavity; external ligament elongate, narrow, extending posteriorly in escutcheon to about insertion of sixth or seventh tooth on the posterior hinge plate and anterior to the third tooth of the anterior hinge plate; hinge plate strong and moderately thick with a minute edentulous gap immediately below the umbonal beak; posterior hinge plate with about 14 teeth, medial teeth small, and on the dorsal side of the hinge plate, distally the teeth enlarge the bases nearly spanning the width of the hinge plate; anterior hinge plate with about 11 teeth, medial three or four teeth minute, rod-shaped and restricted to the upper half of the hinge plate; distally the teeth enlarge becoming chevron-shaped and rather stout; postero-dorsal shell margin slightly convex forming a smooth curve with the posterior margin; antero-dorsal margin short but longer than in *T. callistiformis* or *T. hessleri*, margin straight medially or even slightly concave, anteriorly convex forming a continuous curve with anterior end; ventral margin long and relatively convex.

Morphology of the soft parts. Siphons are developed posteriorly from the inner muscular fold (Figs 32 & 33). They are fused dorsally but not ventrally so that the lumen of the excurrent siphon is not separated by tissue from the incurrent, nor is the latter separated by tissue fusion from the mantle gape below. Central and ventral ridges are present and when these are apposed they effectively separate the lumen of the excurrent and incurrent siphons as well as the feeding aperture below. A single tentacle is inserted below the incur-

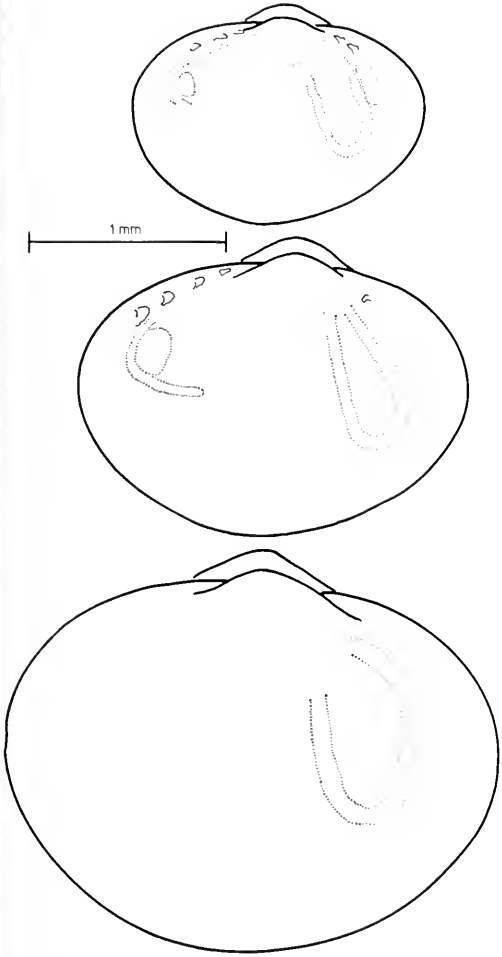


Figure 28. *Tindaria miniscula* Sanders & Allen. Growth series in lateral view.

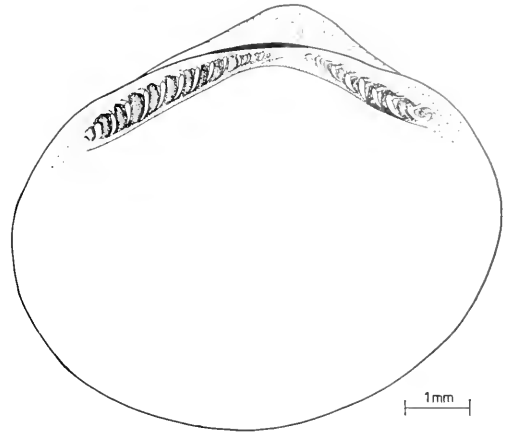


Figure 29. *Pseudotindaria erebus* (Clarke). Internal view of left valve of type specimen No. 218182 Museum of Comparative Zoology, Harvard.

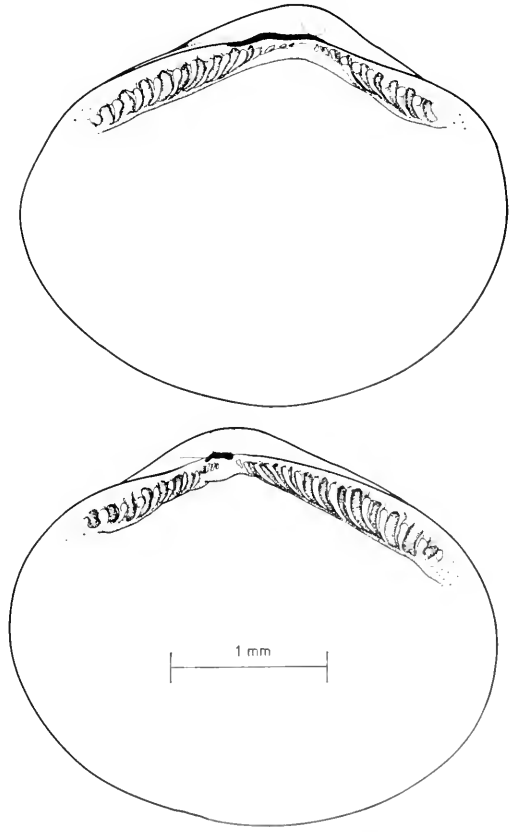


Figure 30. *Pseudotindaria erebus* (Clarke). Internal view of left and right valves of specimen from Station 195.

rent aperture on the right side and, histologically, it is similar to that of *Tindaria*. A food aperture is also developed from the hypertrophied inner muscular fold giving rise to a third, but smaller, channel. The anterior sense organ is well-developed. Adductor muscles are oval, although not greatly elongate, and situated at a relatively greater distance in from the shell margin than is the case in *Tindaria*. Although there is no marked development of the siphonal embayment, the siphons can be retracted within the valves; the retractor muscles are

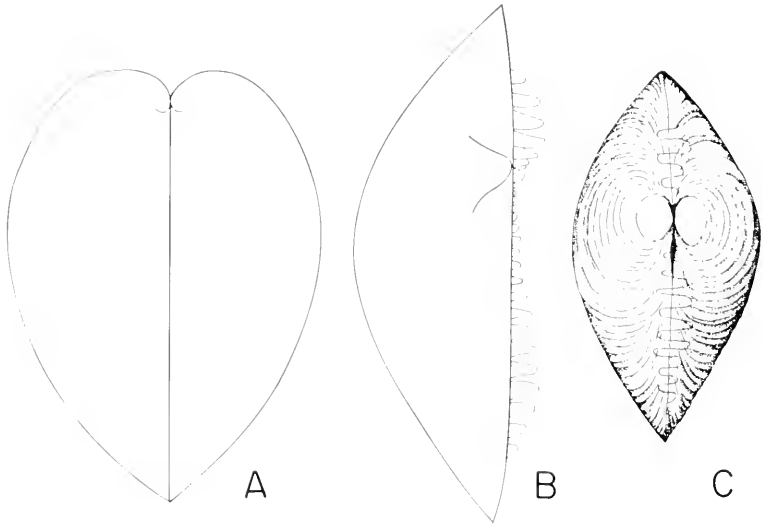


Figure 31. *Pseudotindaria erebus* (Clarke). A, anterior view of shell in outline; B, dorsal view of valve in outline; C, dorsal view of entire shell.

not particularly well-developed. There is no great concentration of gland cells internal to the feeding aperture; although there are small mucous cells lining the main mantle rejectory tract leading to this area.

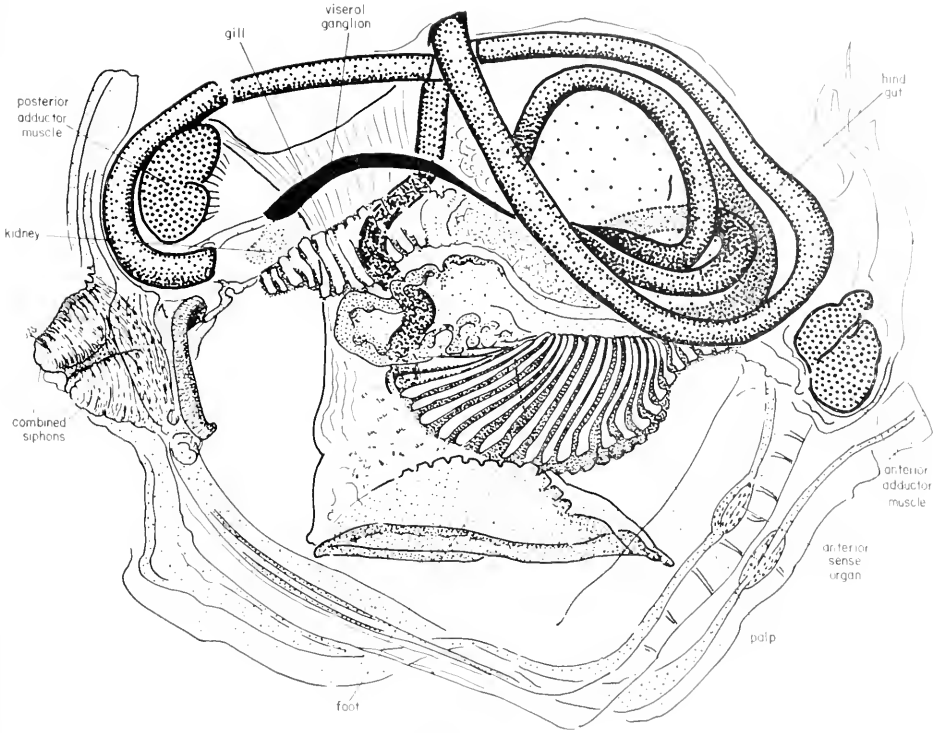
The gills are more or less horizontal with 14 to 16 plates on each side of the axis, the plates on either side alternating. The gill plates are approximately equal in size, those of the inner demibranch slightly larger than those of the outer, particularly posterior to the body; each has a fan of three muscles in the transverse plane which penetrate the axis as a retractor muscle, and on either side of the retractor muscle are longitudinal muscles running the length of the axis (Fig. 34). There is no tissue fusion to the mantle and/or the body opposite to form a diaphragm because the separation of the hypobranchial cavity from the remainder of the mantle cavity is accomplished by ciliary junctions. Note that the cerebro-visceral connectives lie close to the junction of the gill axis with the body.

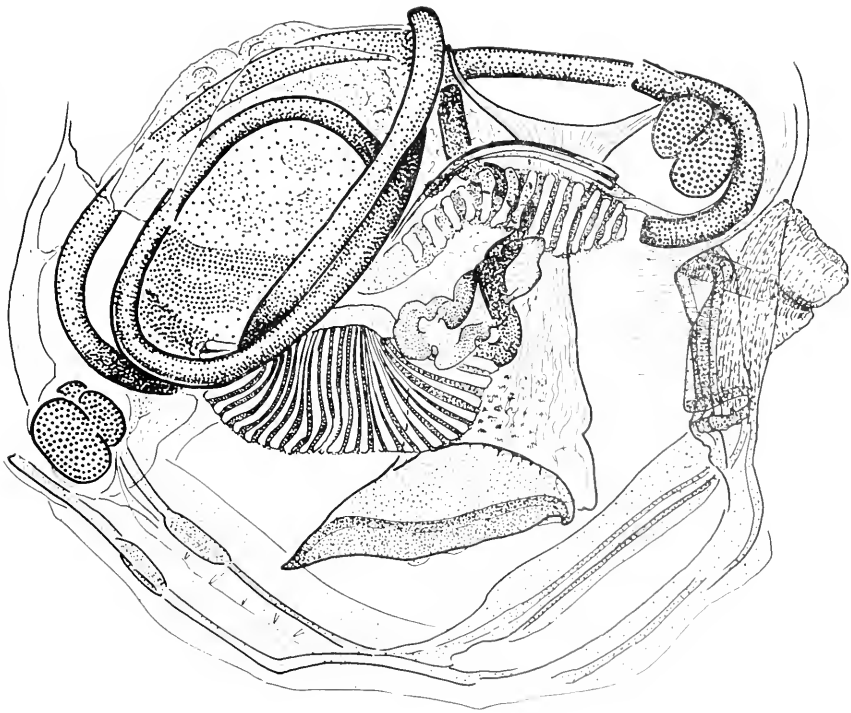
The palps are relatively larger than those of *Tindaria* with many more ridges (17 to 30). The mouth is close to the anterior adductor muscle and the palps extend more than half way across the body. The palp proboscides are relatively large. The foot is moderately large with a well-defined neck; the fringing papillae and heel are very small. A large 'byssal' gland is present, the hyaline central portion of which is elongate, cylindrical and different in shape from any of those described to date (Sanders and Allen, 1973; Allen and Sanders, 1973) (Fig. 35). As in other genera, there is a central sagittal strip of tissue dividing the gland in half, the gland opening just posterior to the sole of the foot.

The oesophagus extends dorsally, and posteriorly, opening into a relatively simple stomach which has a few low-crested sort-

→

Figure 32. *Pseudotindaria erebus* (Clarke). Semidiagrammatic drawings of the body and mantle organs as seen from the right and left sides.


viseral ganglion
gill
posterior adductor muscle
hind gut
kidney
combined siphons
anterior adductor muscle
anterior sense organ
palp
foot



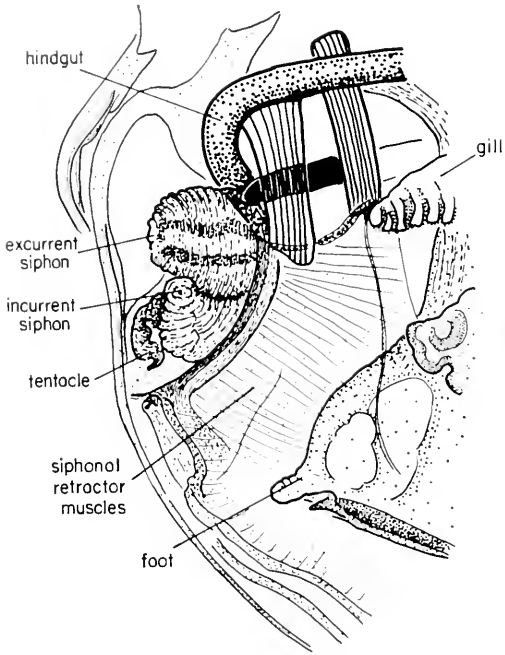


Figure 33. *Pseudotindaria erebus* (Clarke). Detail of siphonal region.

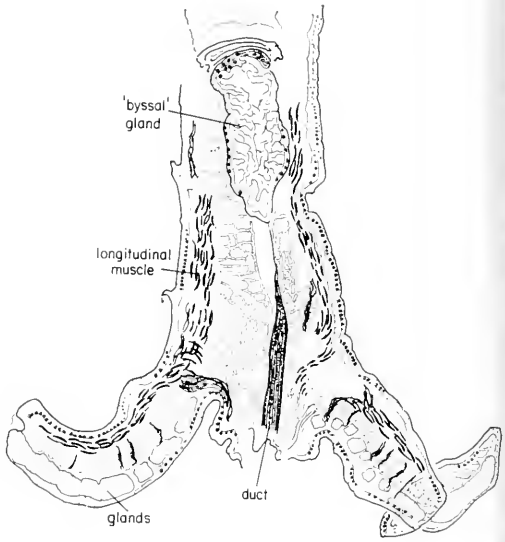


Figure 35. *Pseudotindaria erebus* (Clarke). Transverse section through the foot to show the position of muscles and gland.

ing ridges on the right side (Fig. 36). The long axis of the stomach and style sac is oblique to the body axis and directed postero-ventrally. The hind gut does not penetrate far into the foot before turning dorsally to the left ventral side of the body. Thereafter it passes to the right side of the body in front of the stomach (posterior to the oesophagus) forming a small loop before returning to the left where it outlines the periphery of the stomach and the digestive gland (Fig. 37). After forming this single

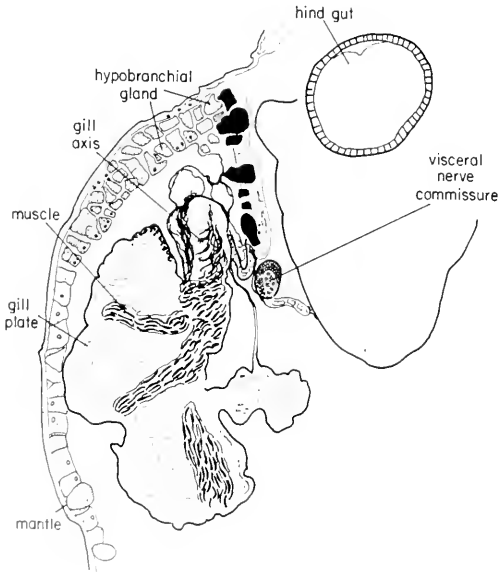


Figure 34. *Pseudotindaria erebus* (Clarke). Transverse section through gill and mantle to show musculature and glands.

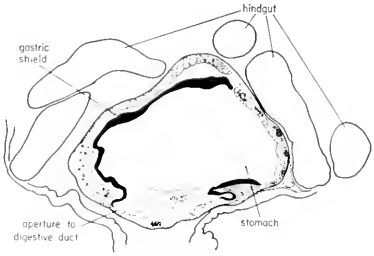


Figure 36. *Pseudotindaria erebus* (Clarke). Transverse section through body to show stomach and outline of hind gut sections.

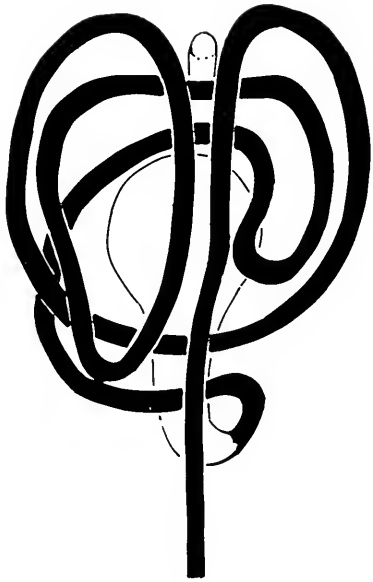


Figure 37. *Pseudotindaria erebus* (Clarke). Dorsal diagrammatic view of stomach and hind gut.

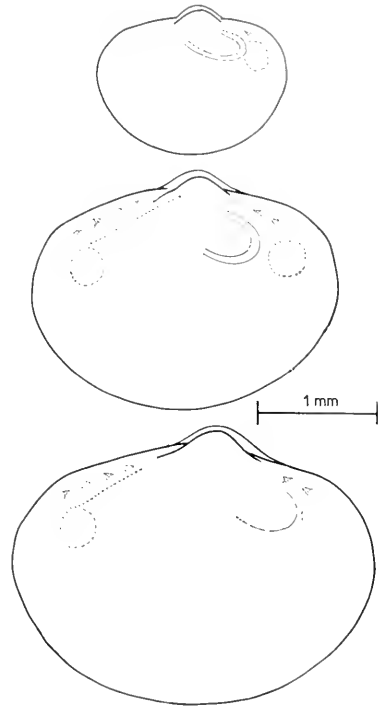


Figure 39. *Pseudotindaria erebus* (Clarke). Growth series in lateral view.

coil it returns to the right side of the body passing dorsal to the style sac and the anterior part of the hind gut. Here it forms a second loop to the outside of the first before continuing to the anus via the mid-dorsal line. The second loop on the right side and the single coil on the left are approximately the same diameter and pass close to the posterior face of the anterior adductor muscle. No typhlosole is present nor does the hind gut penetrate the mantle.

The ganglia are not particularly large, the

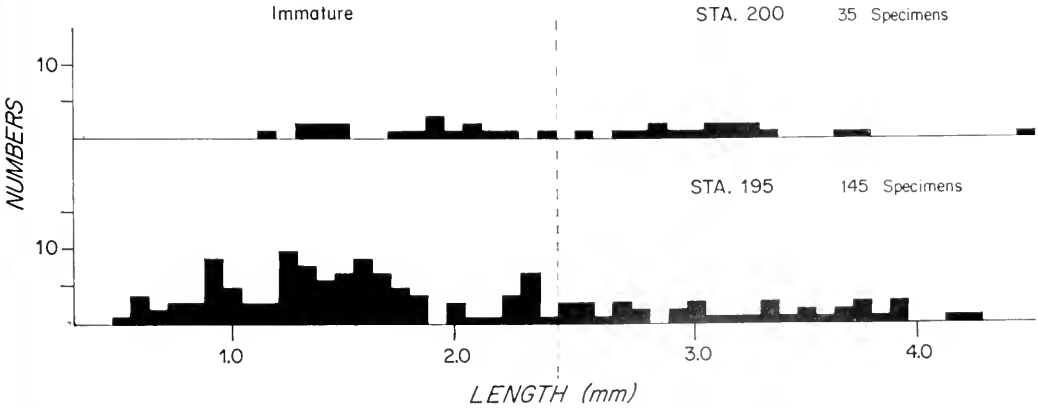


Figure 38. *Pseudotindaria erebus* (Clarke). Size frequency histograms of samples from two stations. The dashed lines indicate the size at which gametogenesis is evident.

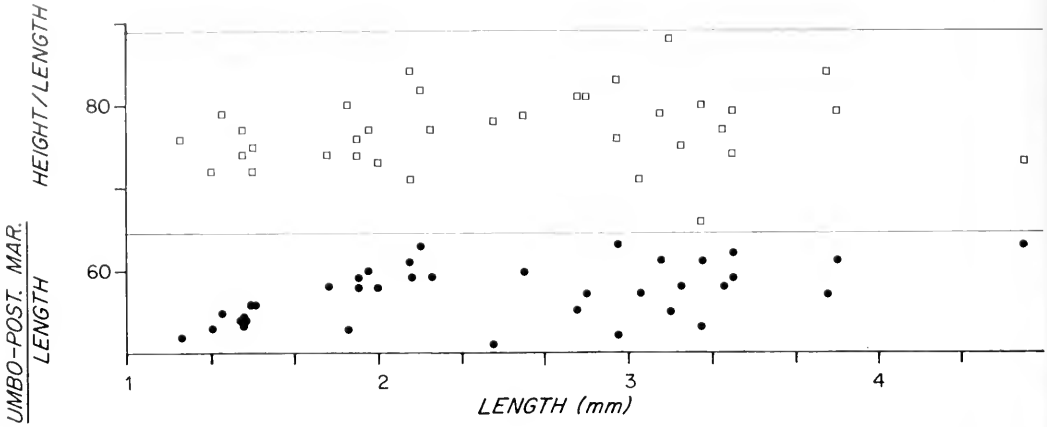


Figure 40. *Pseudotindaria erebus* (Clarke). Graph showing height/total length (□) and umbo to posterior margin/total length (●) plotted against total length.

visceral and cerebral are elongate, the pedal ganglia are positioned high in the foot, the visceral ganglia about the posterior adductor muscle (Fig. 32). Note that the foot can be extended backwards far into the posterior part of the mantle cavity and, as in other protobranch species, may well assist in pushing rejected faecal material out of the mantle cavity.

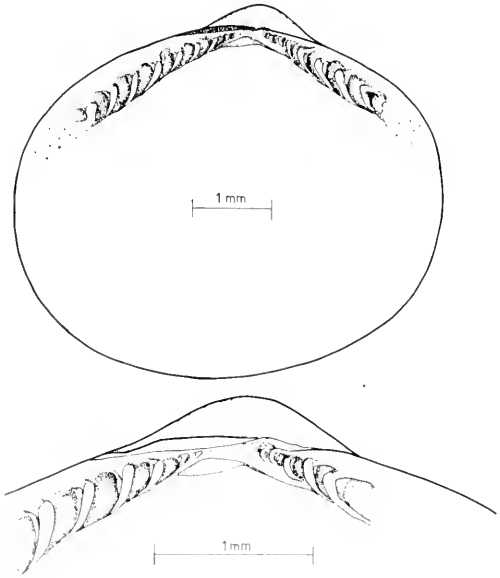


Figure 41. *Pseudotindaria championi* (Clarke). Internal views of left valve of type specimen No. 224957 Museum of Comparative Zoology, Harvard with enlarged detail of the umbonal region.

Size and Reproduction. The population histograms of stations 195 and 200 (Fig. 38) show that the skew to the left is not nearly so marked as it is in *T. callistiformis.* Specimens less than 2.5 mm in total length are all immature and those 3 mm or more show signs of gonad development. Sexes are separate, the sex ratio is even. Maturity increases with increasing size. A fully mature female measuring 6.0 mm total length contained approximately 800 ova having a maximum length of 142 μ. The gonads initially develop at the ventral perimeter of the body to the inside of the outer hind gut loop. Eggs mature simultaneously. On an average, 42 per cent of a given population is maturing, samples ranging from 33 per cent to 49 per cent.

As in *T. callistiformis,* there is a relatively high degree of variation in shell dimensions, particularly in respect to the height/total length ratio, which varies from 0.71 to 0.87. There is no relation between this variation and the increasing size of the shell. The lat-

ter also applies to the total length umbo-posterior margin length ratio. The umbo, although anterior, is not so far forward as it is in *T. callistiformis* (51–63 per cent of the total length). There is a slight trend for the posterior umbonal length to increase with increasing size although the variation remains wide throughout the size range (Figs. 39 and 40). Maximum total length recorded is 6.0 mm.

Pseudotindaria championi (Clarke, 1961)
Figures 41–43

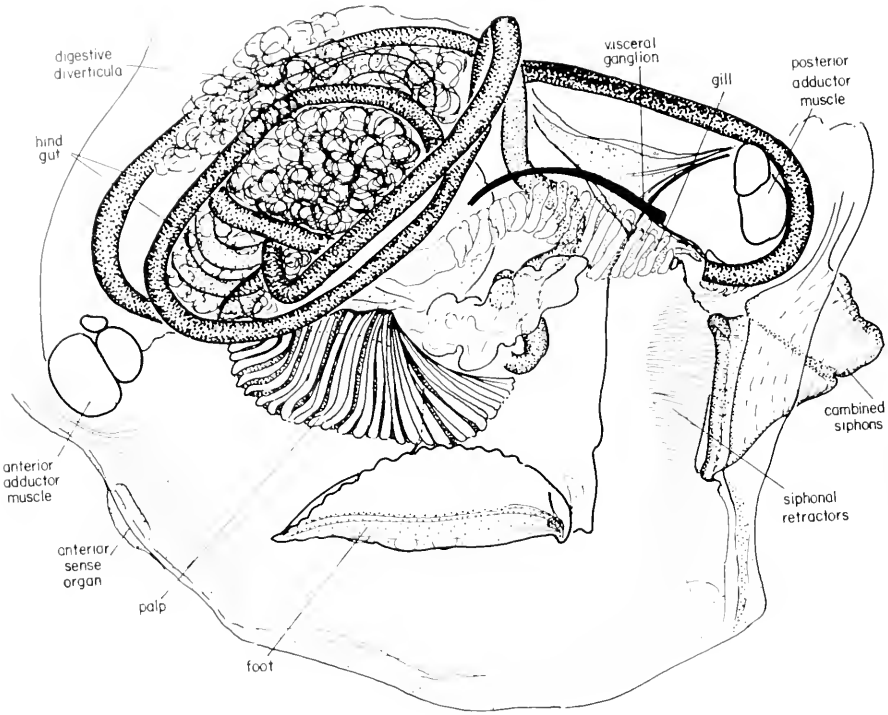
Tindaria championi, Clarke, 1961. Bull. M.C.Z. 125, 372. Plate 2, figs. 1 and 4. (Type locality: r v *Vema*, Biology Station 12, Lat. 38°58.5′S, Long. 41°45′W, type specimen M.C.Z. 224957).
Previous records: Depth range = 3116 to 5133 m.
Argentine Basin—1 station. Ref. Clarke, 1961.
Cape Basin—1 station. Ref. Clarke, 1961.
Present records:

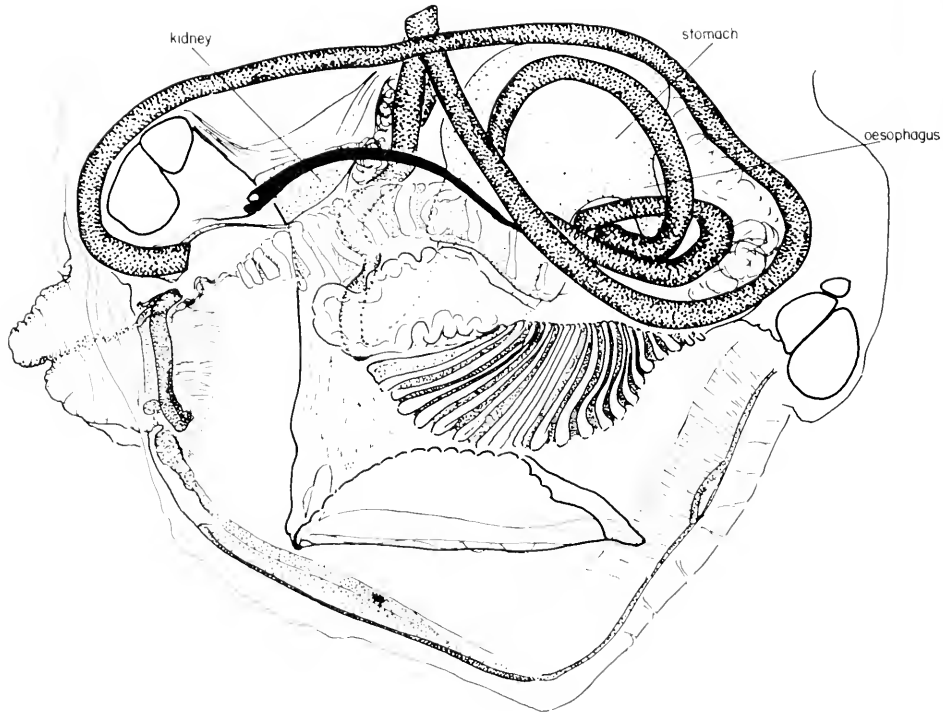
Cruise	Station No.	Depth (m)	No. of Specimens	Latitude	Longitude	Gear	Date
			Argentine Basin				
Atlantis II 60	269A	3305–3317	5	37°13.3′S	52°45.0′W	ES	26.3.71
Atlantis II 60	242	4382–4405	3	38°16.9′S	51°56.1′W	ES	13.3.71

Description of Shell. Since we are able to add a number of further observations to Clarke's (1961) very adequate description of the hard parts of *Pseudotindaria championi*, a fairly extensive redescription follows.

Shell stout, with strong concentric ridges, subovate in outline, and slightly extended posteriorly; umbos low, anterior in position, beaks moderately prominent and curved medially; escutcheon forms a shallow concavity; external ligament elongate, narrow, extends from about the insertion of fourth tooth on the posterior hinge plate to about second tooth of the anterior hinge plate; hinge plate strong and somewhat angular with moderately extensive edentulous gap below umbo; posterior hinge plate with about eight chevron-shaped teeth medial three teeth becoming progressively smaller and restricted to upper margin, distally teeth enlarge in size with bases almost spanning the width of the hinge plate, distalmost teeth rather massive; anterior hinge plate with about seven teeth, medial tooth small, rudimentary and confined to middle of hinge plate, more distal teeth chevron-shaped and progressively larger inserted progressively further from the dorsal shell margin; entire shell margin smoothly rounded in outline; postero-dorsal shell margin much more convex than short, almost straight antero-dorsal margin; posterior margin broad; ventral margin long and moderately convex. Total length of 3.56 mm. *Pseudotindaria championi* is readily distinguished from *P. erebus* by its more rounded outline, a more medial positioning of the umbo and its fewer teeth.

Morphology of the soft parts. The morphology of the animal is very similar to that of *P. erebus*; combined incurrent and excurrent siphons are present, the respective channels being separated by approximation of the tissues along the length of the midline of the siphon. Similarly the incurrent siphon is separated from the pedal gape by apposition of the right and left ventral edges. There is a shallow embayment formed by the extension of the mantle edge between the insertion of the pallial muscles and the outer part of the sensory lobe. Inserted on the right-hand side at the ventral limit of the embayment is a small single sensory tentacle (Figs. 42, 43). The food aperture is not very clearly defined in *P. championi*, and barely separates from the extensive pedal gape—its ventral limit is marked by the posterior edge of a well-marked ridge of glandular tissue to the inside of the inner muscular lobe of the mantle edge in the posterior half of the pedal gape (Fig. 42). A pair of well-developed anterior mantle sense organs are present below


digestive diverticula
hind gut
visceral ganglion
gill
posterior adductor muscle
combined siphons
siphonal retractors
anterior adductor muscle
anterior sense organ
palp
foot


kidney
stomach
oesophagus

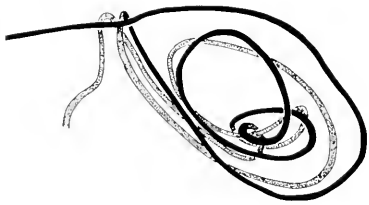


Figure 43. *Pseudotindaria championi* (Clarke). Lateral view of the course of the hind gut as seen from the right side. Stippled sections are positioned on the left side of body, blacked sections on the right.

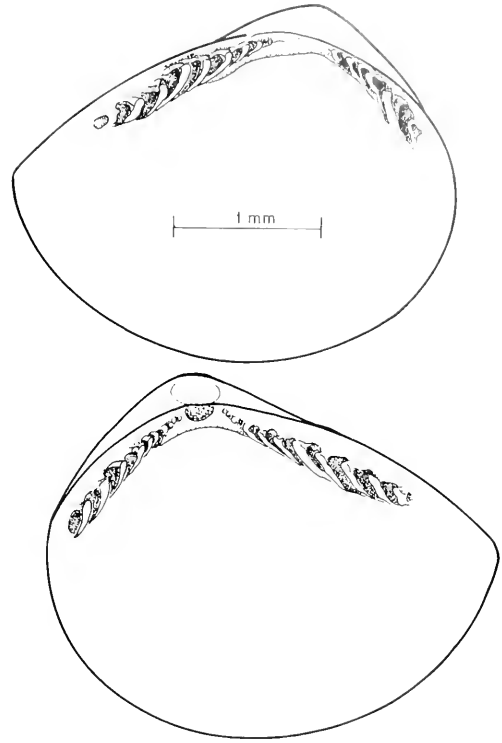


Figure 44. '*Tindaria*' *acinula* Dall. Internal views of the left and right valves.

the anterior adductor muscle. The adductor muscles are oval, equal in size, with the 'quick' and 'catch' portions clearly seen.

The gills are horizontal, each with 10 or 11 pairs of plates. The gill axis extends beyond the posterior plates to fuse with the siphonal tissue at the junction of incurrent and excurrent channels, and as in *T. erebus* there is no fusion between gill and mantle, body or opposite gill. It seems likely that as in other protobranchs, the posterior limits of the gill axes act as guide rails to facilitate the removal of bulky faecal rods. The palps are moderately large and extend from the mouth partly across the foot; the dorsal limit of the ridged area is attached to the body in front of the junction of the anterior edge of the muscular part of the foot to the viscera. The many ridges (approximately 25) spread fanwise, posteriorly. The retracted palp proboscides do not extend beyond the posterior margin of the foot. The foot is dorso-ventrally elongate, the sole is not exceptionally large, the tip is pointed, with the fringing papillae moderately small, rounded and low crowned. The heel is produced as a small, short process with a moderately large 'byssal' gland, similar to that described for *P. erebus*. The gut is also similar to that of *P. erebus* (Fig. 42), with the hindgut arranged in the same configuration. However, the relative diameter of the hind gut is greater in *P. championi*, in which the gut occupies much more of the body space (Figs. 32, 42).

DISTRIBUTION PATTERNS

Of the six species considered in this paper, four members of the genus *Tindaria* and two representatives of the genus *Pseudotindaria*, two are cosmopolitan while the remaining four appear to be confined to restricted regions of the Atlantic. The two widely distributed species *Tindaria callistiformis* and *Pseudotindaria erebus* are abyssal species and have been collected from the North America, Guina and Angola

←

Figure 42. *Pseudotindaria championi* (Clarke). Semidiagrammatic drawings of the body and mantle organs as seen from the left and right sides.

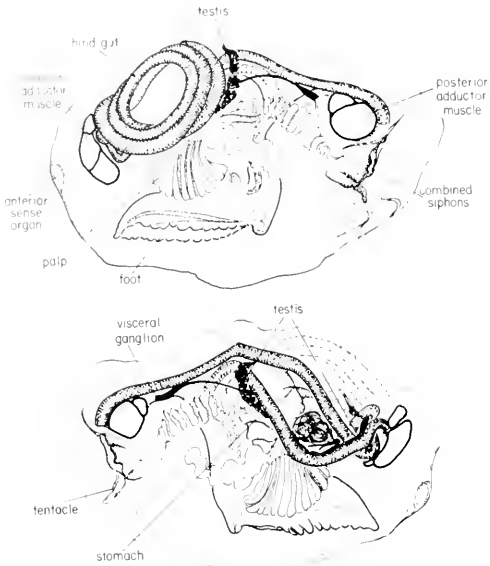


Figure 45. '*Tindaria*' *acinula* Dall. Semidiagrammatic drawings of the body and mantle organs as seen from left and right sides.

Basins. In addition, *P. erebus* has been taken in the Canaries, Cape Verde and Brazil Basins and *T. callistiformis* in the Argentine Basin. *Pseudotindaria erebus*, which occurs in shallower depths, has been found in about 2650 m in the Angola Basin, but *T. callistiformis* has never been collected shallower than about 3300 m. The only region so far examined where *P. erebus* has not been obtained is the West Europe Basin. However, the samples analysed to date from that region have been limited to depths less than 2380 m. Similarly, on the basis of depth distribution of *T. callistiformis*, there are only four stations of appropriate depths where it has not been found (two stations in the Angola Basin and two stations in the Brazil Basin). Probably these forms are present throughout the Atlantic wherever there are adequate depths. Our data suggest that *Tindaria callistiformis* may be numerically significant only in a small subset of its vertical and perhaps its horizontal range. In most samples where it is present, *T. callistiformis* makes up but a minor fraction of the protobranch fauna, 0.08 to 1.97 per cent at ten stations 4600 m or deeper. At the shallowest station, in 3305 to 3317 m of water, it constitutes 4.48 per cent. In the remaining six samples, taken in 3806, 3828, 3834, 3906 to 3917, 4417 to 4429, and 3825 to 3862 m, this species formed 20.84, 18.99, 13.80, 27.61, 3.82 and 0.74 per cent respectively of the protobranch specimens. The first three samples were taken from the North American Basin, the fourth was from the Argentine Basin, and the remaining two, from the Guiana Basin.

Despite its broad horizontal distribution, *Pseudotindaria erebus* must be a very rare animal at least in part of its range. Of more than 22,500 protobranchs collected from the Gay Head-Bermuda transect in the North America Basin, only four specimens of *P. erebus* have been taken. Alternatively, in the Angola Basin it may be numerically important, 19.05 per cent at station 200 and 20.03 per cent at station 195. The values found in the Canaries, Cape Verde, Guiana, Brazil and Argentine Basins fall between these extremes.

Of the remaining species, *Tindaria hessleri* appears to be a lower slope–upper abyssal rise inhabitant of the northeast Atlantic. We have taken it at a single station in the West Europe Basin and from five of the six stations in its depth range in the Cape Verde Basin. Thus it appears to be a constant faunal constituent within the appropriate depth range and in the latter basin comprises, numerically, nearly one to ten per cent of the protobranch bivalves.

Tindaria cytherea has a narrow depth range, restricted to intermediate slope depths in the northwest Atlantic. It has so far been reported from a few localities in the North America, Gulf of Mexico and Caribbean Basins. We have collected but a single specimen in 1000 m depth off Bermuda. It is probably not present at equivlent depths at the New England end of the Gay Head-Bermuda traverse, which have been extensively sampled.

Pseudotindaria championi is an abyssal species of the high southern latitudes known from three localities in the Argentine Basin and a single sample in the Cape Basin.

The remaining species, *Tindaria miniscula*, is probably limited to the deeper abyssal depths of the southeast Atlantic. We have found it at three stations in the Angola Basin where it formed 0.99, 2.04 and 3.29 per cent of the protobranch fauna.

PALEONTOLOGICAL RELATIONSHIPS

Pojeta (1971) has pointed out that all known 'nuculoids' from the early Paleozoic (Ordovician) lacked a resilifer but had instead a hinge plate continuous beneath the umbo. In addition, these forms possessed a continuous row of teeth rather than teeth that were separated into an anterior and posterior hinge series. Among the living protobranchs, the genera *Tindaria*, *Pseudotindaria* and *Neilonella* have a similar combination of morphological characters.

Most Ordovician nuculoids have been placed in the extinct family Ctenodontidae. However, the careful studies of Pojeta (1971) clearly show that the Ordovician nuculoids were a "highly varied and successful group," a fact masked by the pronounced conservatism of the systematics.

Earlier, Verrill & Bush (1897) noted that the ctenodont *Palaeoneilo* "agree in nearly all essential characteristics with the living genus Tindaria." Within the complex of Ordovician ctenodont shell morphologies cited by Pojeta (1971) can be found apparent homologues of *Tindaria* and *Pseudotindaria*; e.g., *Palaeoneilo fecunda* (Hall), and *Neilonella*; e.g., *Decaptrix* aff. *D. hartsvillensis* (Stafford) and *Decaptrix baffinense* (Ulrich).

In the present paper we have documented the profound differences in the soft part anatomy of *Tindaria* and *Pseudotindaria*, two genera which have almost identical shells. *Neilonella* is more elongate and rostrate but the soft part anatomy resembles that of *Pseudotindaria*, e.g., they have siphons, many gill plates and palp ridges and lack posterior papillae. Thus, these few modern genera also represent a varied complex of morphologies. Yet, on the basis of shell morphology, there is no reason why these living genera should not be the modern descendants of the Paleozoic ctenodonts, the oldest lineage of protobranchs with typical chevron-shaped teeth, representing a group or groups of bivalves with remarkably conservative shell features.

In comparison, we have pointed out elsewhere that the modern nontaxodont protobranchs such as the families Nucinellidae (Allen & Sanders, 1969), Lametilidae and Siliculidae (Allen & Sanders, 1973) are analogs of the Palaeozoic actinodonts and may, indeed, be direct derivatives.

DISCUSSION

The present paper, in addition to defining a morphology that stands apart from all other protobranchs, emphasizes more clearly than in any other group of the Protobranchia the danger of relying on shell character to define a taxon. Thus, *Tindaria* and *Pseudotindaria* on shell characters alone would have been (indeed were) placed in the same genus, but the soft parts show that they are greatly different. This has the unhappy consequence that anatomical studies must be made to confirm the placement of many of the species referred to the genus *Tindaria*.

Pseudotindaria is difficult to place in relation to other known protobranch genera at this stage in our researches. Some species of *Neilonella* described by Knudsen (1970) certainly resemble *Pseudotindaria* and it is our intention to analyze the "*Neilonella* complex" in a subsequent paper of this series. Similarly, so-called *Tindaria acinula* (a species that occurs in our samples) is an example of a species wrongly described in the literature as a tindariid which, like *Pseudotindaria*, has siphons, not tentacles, and a large palp with many ridges. The hind gut does not penetrate the mantle and

the large posterior adductor is not close to the shell margin (Figs. 44, 45). However, unlike *Pseudotindaria*, the hind gut crosses to the left side of the body *in front* of the mouth and there forms four coils, and the valves are posteriorly rostrate rather than oval. Again, this species will be considered in a later paper.

The species of *Tindaria* are characterized by the lack of posterior mantle fusion and, in this sense, as well as in having a gill placed obliquely across the mantle cavity, they are at first sight akin to the Nuculoidea. We hypothesize that the tindariids may have similar habits to some species of *Nucula* (see below). Nevertheless, the posterior mantle edge is highly specialized and, in addition to the pedal gape, it forms functional posterior incurrent, excurrent and feeding apertures. The apertures are formed by the apposition or overlapping of the inner and, sometimes, middle lobes of the mantle. The excurrent region is particularly circumscribed, the space between the adductor muscle and the first papillae being only wide enough to allow the passage of the faecal rod. Knudsen (1970) reports a simple flap-like extension of the mantle on the dorsal side of the aperture in two Pacific species. In *T. bengalensis* and *T. compressa*, at the ventral limit of the excurrent region and extending across the mantle edge on each side is a shallow ridge which might possibly be considered to be the first stage in the development of a siphon, to which the attenuate part of the gill axis attaches. The anus opens opposite this channel. In many specimens the dorsalmost papilla on each side of the incurrent region point inwards, parallel to this channel. The number of papillae on either side of the aperture varies between species. An unpaired papilla or tentacle, which in some cases is longer than the other papillae, may be present on the right or left side at the ventral limit of the inhalent region. This may or may not be equivalent to the unpaired siphonal tentacle of other nuculanids. Histologically there is no difference between the two. The papillae consist of a central pair of longitudinal muscle bands with a haemocoele between the muscles and the outer epithelium. There are no major nerves supplying the papillae and innervation is probably in the form of a number of fine fibers. There are also no concentrations of gland cells, thus the papillae are in no way comparable to the feeding tentacles of the deep sea carnivorous Verticordiidae (Allen & Turner, 1974). We can only assume that the papillae have a generalized sensory function and possibly act as a coarse filter for the incurrent flow generated by the pumping action of the gills.

We have been able to keep *T. callistiformis* alive for approximately one month. The soft parts are virtually colorless in life. Although the metabolism of these animals was clearly affected by their long journey to the surface, to reduced pressure and through the varying changes of temperature of the water column, their condition was sufficiently good to confirm that the papillate region defines the incurrent area and that the palp proboscides are extended from the feeding aperture. The inner mantle folds are extended beyond the shell margin in this region. Although gross movements of the gills occurred, no definite pumping rhythm was observed. Ciliary movement was particularly languid and we hesitate to say more than that the ciliary patterns within the mantle cavity are similar to those described by Yonge (1939) for more shallow-living nuculanids.

The stomach takes up much of the body space and it may be that the extension of the hind-gut into the mantle is in part related to the lack of space between the body wall and the stomach. Undoubtedly the refractile nature of the food (diatom frustules, etc.) to enzyme action is correlated with the considerable extension of the gut in deep-sea deposit feeding bivalves (Allen & Sanders, 1966; Allen, 1971, 1973). One of the many strategies used by the deep-sea protobranch for housing the hind gut is exemplified in the tindariids by their utiliza-

tion of mantle space. Exploitation of mantle space occurs in other bivalves, as for the gonads of mytilids—but deep-sea protobranchs are unique in the accomodation of the hind-gut in this manner. There is much evidence that material entering the stomach in deep-sea protobranchs is less rigorously sorted than that in shallow-water species. Thus the ciliated sorting ridges are reduced in number and size. The large tooth of the gastric shield deserves mention because it presumably does not act in the same manner as in the Lamellibranchia. The material coming forward from the style sac in the protobranchs is a soft particulate mixture and not a hard crystalline style. Hence it is difficult to imagine that the tooth either serves as a stop to the forward movement of the style or as a cutting surface which 'turns' the head of the style with subsequent release of style material. We believe that it may act here as a barrier to the encroachment of space immediately posterior to the oesophageal aperture by the style and/or acts as a 'breakwater' in front of the ducts to the digestive diverticula preventing material from being forced into the ducts. It may also act as a baffle to enhance the mixing of the stomach contents in a fashion analogous to the blade in a cement mixer. There is evidence that selection of particles does occur because a high proportion of the stomach contents consists of diatom frustules.

We believe that it is possible to deduce something about the habits of the genus *Tindaria*. The strong robust concentrically ornamented shell and rounded shape, together with an attached growth of hydroids on many of the specimens, indicate a surface dwelling rather than the infaunal habit for the genus. The presence of tentacles around the inhalent region and a pumping gill can also be correlated to a stationary habit close to the surface. The foot is by no means as highly developed as in the smooth, glossy, thin-shelled genera without epifauna such as *Silicula* and *Spinula*, which have all the hallmarks of fast-burrowing infaunal bivalves (Allen & Sanders, 1973). Nevertheless, the foot is moderately developed and, in addition to any cleansing function, it may well be involved in occasional rapid movement, necessitated by predators or for reorientation.

Tindaria species do not show an inverse relationship between the size of the palp and the size of the gill with increasing depth, first shown in *Abra* (Allen & Sanders, 1966) and later for some genera of Protobranchia (Allen, 1973). We think that a possible explanation is that gill size is critical in relation to efficient pumping action. Elsewhere (Allen & Sanders, 1966) we have also shown that hind gut length is much greater in deep water species as compared with related shallow water forms. In this, *Tindaria* is more consistent with the general pattern. Thus, estimations of hind gut volume per unit animal volume shows that gut volume is half as large again in *T. callistiformis* (3305 to 5042 m) as compared with *T. hessleri* (1739 to 2339 m). However, *T. miniscula* (3797 to 4566 m) is an exception for it has a similar gut volume/animal volume ratio, as in the two shallower-dwelling tindarid species (see below). This anomaly may be explained by the small size of *T. miniscula* as compared with the other species. Perhaps of more significance is the fact that the gut volume of *Pseudotindaria* (2644 to 5007 m) is similar to that of *Tindaria*, i.e., that irrespective of the great difference in hind gut configuration the volume is not significantly different in the two genera.

	Gut volume/unit shell volume	
T. cytherea	1000 m	1.005
T. hessleri	1739–2339 m	0.903
T. miniscula	3797–4546 m	0.954
T. callistiformis	3305–5042 m	1.413
P. championi	3305–4405 m	?
P. erebus	2644–5007 m	0.915

The reproductive strategies of the genera *Tindaria* and *Pseudotindaria* are greatly different. *Pseudotindaria* follows the typical

deep-sea pattern of approximately 50 per cent of the population maturing at any one time. The largest animals are the most mature and the sex ratio is 1:1 (Sanders & Allen, 1973; Allen and Sanders, 1973; Scheltema, 1972). (It must be noted that both dioecious and hermaphroditic species occur in the deep sea.) Our collections of *Tindaria callistiformis* differ in the extremely low percentage of the population that was maturing and also in the male-female ratio of 5:1. However, it appears that the largest animals are the most mature. We have argued elsewhere (Sanders & Allen, 1973) that, in the sparsely populated abyss, it is an advantage to have large numbers of sperm produced (and have a free planktonic larva, even though of a short duration). We may be observing, in this case, an exceptional condition even for *Tindaria* and if so we have fortuitously encountered a remarkably successful and isolated larval settlement. However, there are reasons to doubt this; not only is the pattern maintained at three widely spaced stations but also the analysis of the *T. miniscula* specimens indicates that this species is showing a similar population structure, i.e., that these are features common to the genus. It is our intention to re-investigate these stations at a different time of year following an interval of some years to see whether the structure has been maintained. More striking and less easily explained is the small number of eggs present in the ovary, which conflicts with the dominance of this species in the samples and the large number of small specimens in the sample.

SUMMARY

A new family of the Protobranchia, the Tindariidae, is erected and included in the Order Nuculanoidea. As of present, the family is monogeneric; previously associated genera, namely *Pseudoglomus*, *Neilonella* and *Malletia* are not included because of their markedly different morphologies.

Two new species are described—*Tindaria hessleri* and *T. miniscula*.

The species of *Tindaria* described here show a number of common anatomical features that are of particular note.

1) The posterior mantle edge bears papillae on either side of the non-siphonate incurrent aperture, the number varying according to the species and to the size of the animal.

2) The single loop of the hind gut and associated visceral tissue penetrates the right mantle to a greater or lesser extent. In *T. callistiformis* the loop approaches close to the mantle margin immediately above the anterior mantle sense organ while in *T. cytherea* it barely penetrates the mantle.

3) Palp ridges are few in number.

4) Gametogenesis was observed in less than 5 per cent of the specimens of *T. callistiformis* (the most common species in our collection), males outnumbering females by 5:1. In only the largest specimens could gonads be recognized.

A new genus, *Pseudotindaria* (not included in the family Tindariidae), is descibed. This includes species with shell morphologies very similar to those of *Tindaria* but with soft parts that are markedly different. The taxonomic affinities of *Pseudotindaria* will be discussed in a later paper.

Pseudotindaria is siphonate. The hind gut is arranged in a complex series of loops and coils on either side of the body and does not penetrate the mantle. Palp ridges are numerous. In the case of *P. erebus*, the most common species in our samples, more than 40 per cent of the specimens have recognizable gonads and the sex ratio is even.

Shell morphologies indicate that *Tindaria* and *Pseudotindaria* could well be considered as recent descendants of the Paleozoic ctenodont Protobranchia.

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The American Butterflies of Genus Euptychia, Satyrinae, Nymphalidae, with Revision of Some Other Neotropical Satyrinae

Lauren Pamela Pyrcz

VOLUME 160, NO. 4

PUBLISHED BY THE MUSEUM
CAMBRIDGE, MASSACHUSETTS, U.S.A.

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THE AMERICAN ORB-WEAVER GENERA *CYCLOSA*, *METAZYGIA* AND *EUSTALA* NORTH OF MEXICO (ARANEAE, ARANEIDAE)

HERBERT W. LEVI[1]

ABSTRACT. Five species of *Cyclosa*, three of *Metazygia* and thirteen of *Eustala* are found in the region. One species of *Cyclosa* is holarctic in distribution, others are temperate and tropical American. The rarity of the dwarf males of the tropical Florida *Cyclosa bifurca* suggests that the species may be parthenogenetic. *Metazygia* and *Eustala* are known from the Americas only, most species being tropical. The five temperate species of *Eustala*, especially the three eastern ones, are difficult to separate; possibly they hybridize in some areas. Two of the *Eustala* species are new, with the range of southern Florida and the West Indies.

INTRODUCTION

As with most orb-weaver genera, *Cyclosa*, *Metazygia* and *Eustala* have never been revised and until now only some common species could be determined with certainty.

A revisionary study such as this should report the results of the research; that is, it should summarize the diagnostic characters of the species and genera revised, indicate how to separate the species, and provide some general information on the natural history of the species studied.

Much previously unpublished data on natural history can be gleaned from collecting labels; the author's own experience and published literature (if the determinations are reliable) can supply more. A summary of this information is of as much general interest as are the keys and diagnosis.

On the other hand, detailed nondiagnostic morphological descriptions are of little interest, although they are frequently given in revisionary studies. Of still less interest, except to the writer, is the nomenclatural confusion that preceded the revision. In non-numerical, taxonomic research only the results, not the procedures, are usually given. If the specimens key out and the illustrations are useable, the study is demonstrated to be adequate. Nevertheless, in this paper I have indicated the procedures used to study *Eustala* as a partial answer to those who claim that taxonomic work might be hastened.

ACKNOWLEDGMENTS

I would like to thank the following persons for helping in these revisions. W. J. Gertsch generously made part of his unpublished manuscript on West Indian *Eustala* available to me. Two of the new species from the West Indies are described here as they also occur in southern Florida; Gertsch's manuscript names were adopted to avoid confusion in already labeled specimens. N. I. Platnick and F. R. Wanless went out of their way to find misplaced specimens in their collections. R. E. Buskirk, J. E. Carico, H. K. Wallace, W. Sedgwick, and M. Stowe reported observations. W. G. Eberhard, Y. D. Lubin, W. L. Brown, A. Moreton, R. E. Buskirk, V. Brach and J. E. Carico provided photographs. Specimens were loaned by P. H. Arnaud and R.

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X. Schick, California Academy of Sciences; J. A. Beatty (*Cyclosa* only); D. Bixler; The British Columbia Provincial Museum, Victoria; J. E. Carico; R. Crawford; C. D. Dondale, Canadian National Collections, Ottawa; H. Dybas and J. B. Kethley, Field Museum of Natural History, Chicago; W. G. Eberhard; S. Frommer; W. J. Gertsch; M. Grasshoff, Senckenberg Museum, Frankfurt; M. Hubert, Muséum National d'Histoire Naturelle, Paris; B. J. Kaston; R. E. Leech; W. R. Icenogle; W. W. Moss, Academy of Natural Sciences, Philadelphia; Mr. and Ms. J. Murphy; W. B. Peck, Exline-Peck Collection, Warrensburg, Missouri; N. I. Platnick, American Museum of Natural History and Cornell University collections; S. E. Riechert, University of Wisconsin; W. T. Sedgwick; W. A. Shear; M. Stowe; K. J. Stone; H. K. Wallace; C. A. Triplehorn and A. J. Penniman, The Ohio State University collections; F. R. Wanless, British Museum (Natural History), London; H. V. Weems, Florida Collection of Arthropods, and B. R. Vogel. E. Mayr made comments and suggestions for the introduction. Some outline maps were supplied by D. Quintero, L. Roth mapped the species, and D. Randolph typed numerous manuscript drafts and the final copy. L. R. Levi corrected the syntax. The study and its publication were supported in part by National Science Foundation grant BMS 75-05719. A grant from The Center for Field Research and Earthwatch Inc. made a trip and stay at the Archbold Biological Station, Lake Placid, Florida possible. K. Harris and J. Maluda, participants in the field work, helped with observations of *Eustala anastera*, *Metazygia wittfeldae* and some *Cyclosa* species.

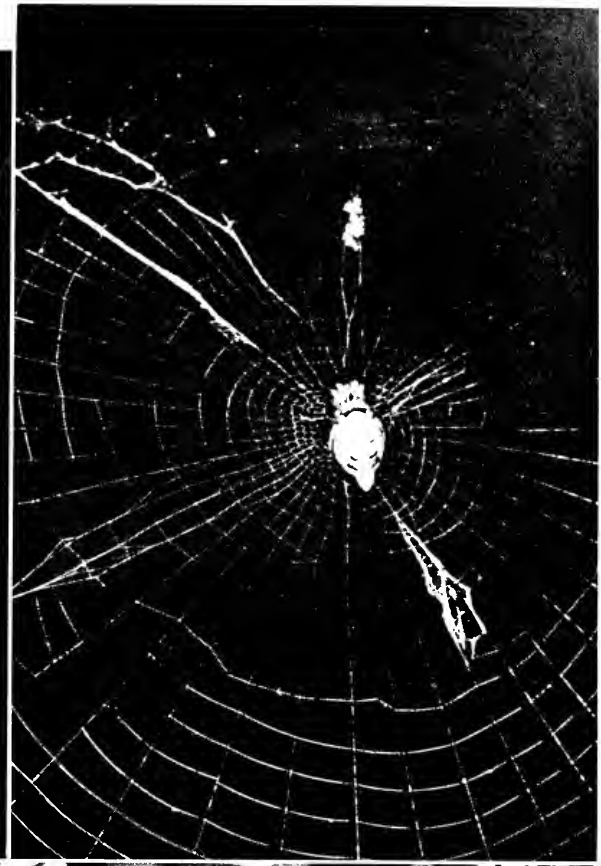
Cyclosa, Metazygia and *Eustala*

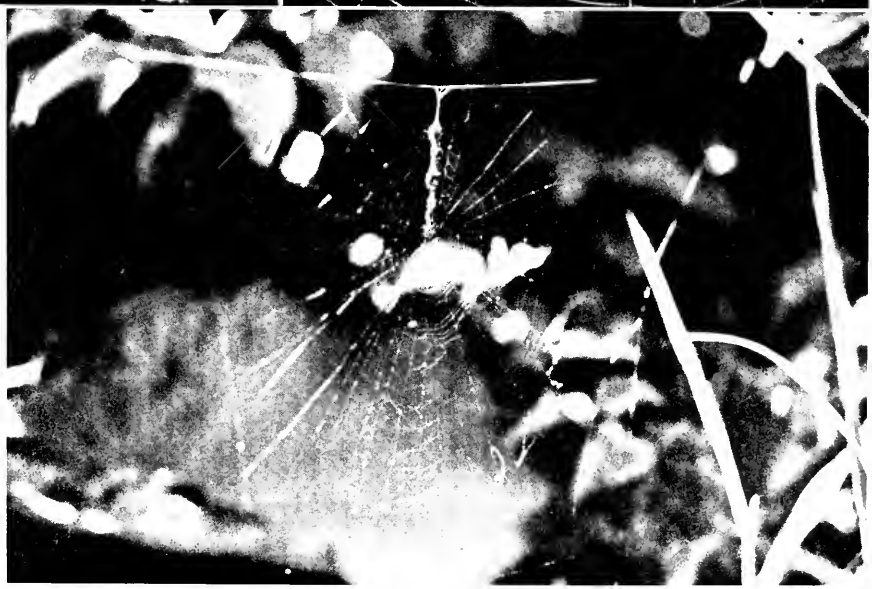
Cyclosa, like *Mecynogea* and *Cyrtophora* among the araneid orb-weavers, hangs its eggs on a radius of the web, perhaps as a camouflage device (Plates 1, 2). Juveniles make a line of debris. But *Cyclosa* remakes its web almost daily, as do most members of the family, while *Mecynogea* and *Cyrtophora* do not. *Cyclosa* renews the viscid

Plate 1. *Cyclosa conica* penultimate female and a web built by a penultimate female, New Hampshire.

→

Plate 2. *Cyclosa turbinata* female and her web. Upper photographs Virginia, lower one California (upper left photo J. Carico, upper right A. Moreton, lower B. Opell).





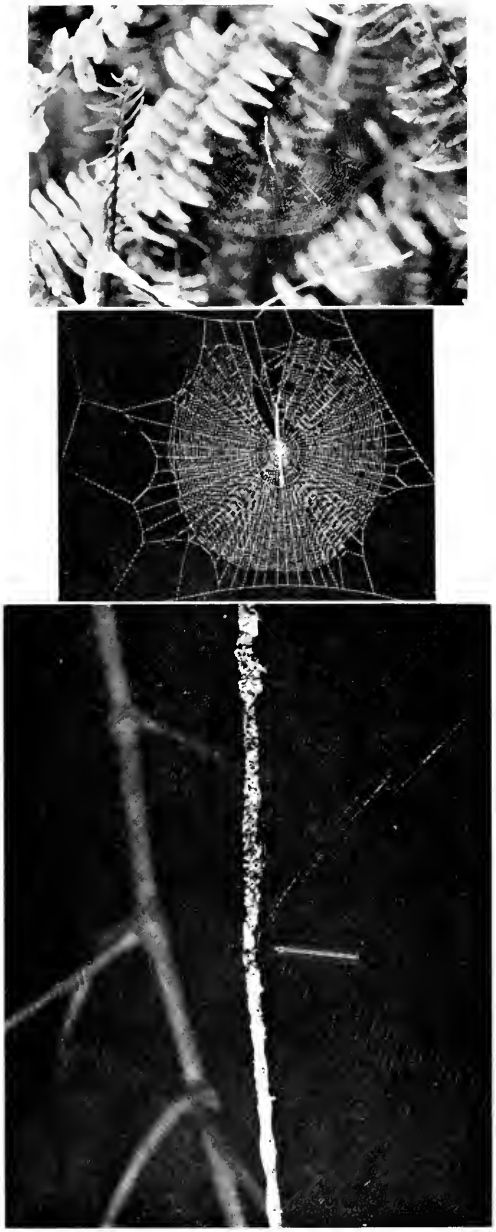


Plate 3. *Cyclosa caroli*, upper and middle photograph web, bottom detail with spider (arrow) in center of line of debris. Upper photograph south central Florida, middle and bottom Panama Canal Zone (upper photograph J. Maluda, middle one W. Eberhard, bottom Y. Lubin).

threads, leaving the egg-sacs hanging (Y. Lubin, personal communication, Plate 4). The holarctic *Cyclosa conica* is the exception. While it does hang debris and silk in the web, it places its egg-sacs on leaves, probably because of the short season in the northern parts of the range. *Uloborus*, a cribellate orb-weaver, also hangs its egg-sacs in the web. But cribellate silk owes its stickiness to its woolly nature, so the webs do not dry and have to be replaced. Females of both *Uloborus* and *Cyclosa* hang among their egg-sacs, head up in some *Cyclosa* species, and resemble their egg-sacs so closely as to be hard to find (Plates 1–5).

Cyclosa bifurca is the only colored species; both spider and egg-sac are green. The female genitalia are reduced secondarily, reverting almost to a haplogyne condition: there is no scape and no ventral opening. Of about 350 specimens examined, only two males were found. Is the species parthenogenetic? The male is dwarfed and the palpal structures are somewhat reduced. For instance, the paramedian apophysis is lacking and the conductor is small (Figs. 86, 87).

The accumulated errors in the literature of several generations posed several riddles. For instance, there has been much speculation as to how the "American" *Cyclosa oculata*, common in the Mediterranean area, was introduced to Europe (Lutz, 1915, Simon, 1928). But *Cyclosa oculata* (Figs. 21–23) is actually a European species which has never been found in America. Because its abdomen resembles that of the American *C. walckenaeri* (Plate 4), Simon (1900) confused and synonymized the two, leading later authors astray.

Besides the poorly known species from the Balkans, five species of *Cyclosa* are known from western and southern Europe (Roewer, 1942, Bonnet, 1956) (Figs. 21–37). Three of these are Mediterranean (*C. algerica*, *C. sierrae* and *C. insulana*). [*C. insulana* is found from France and Africa to India and the southwestern Pacific (Bonnet,

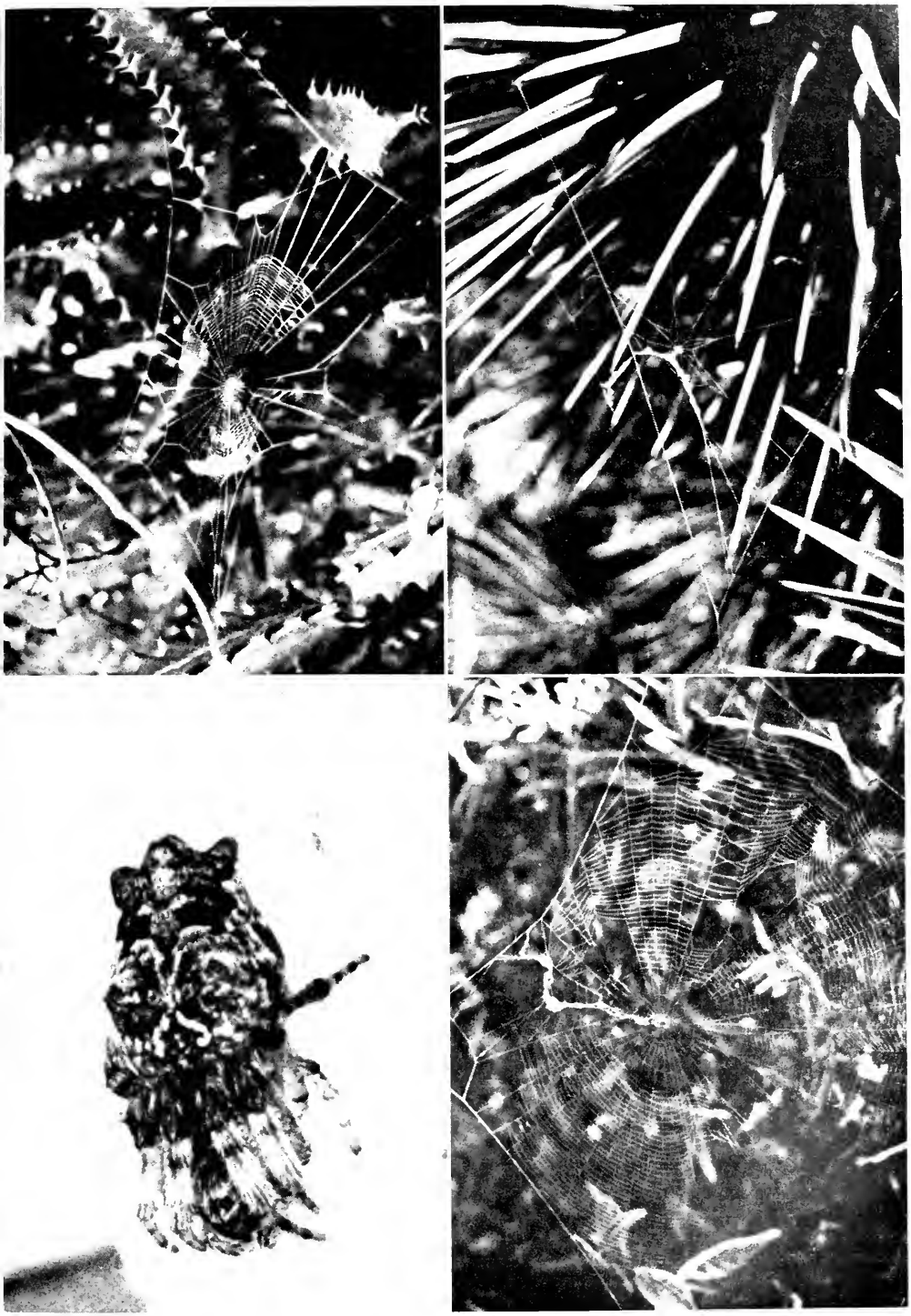


Plate 4. *Cyclosa walckenaeri*, upper left female, upper right horizontal web built by juvenile, 9 cm diameter; lower left web of adult with egg-sacs, 17 cm diameter; lower right incomplete web and egg-sacs.

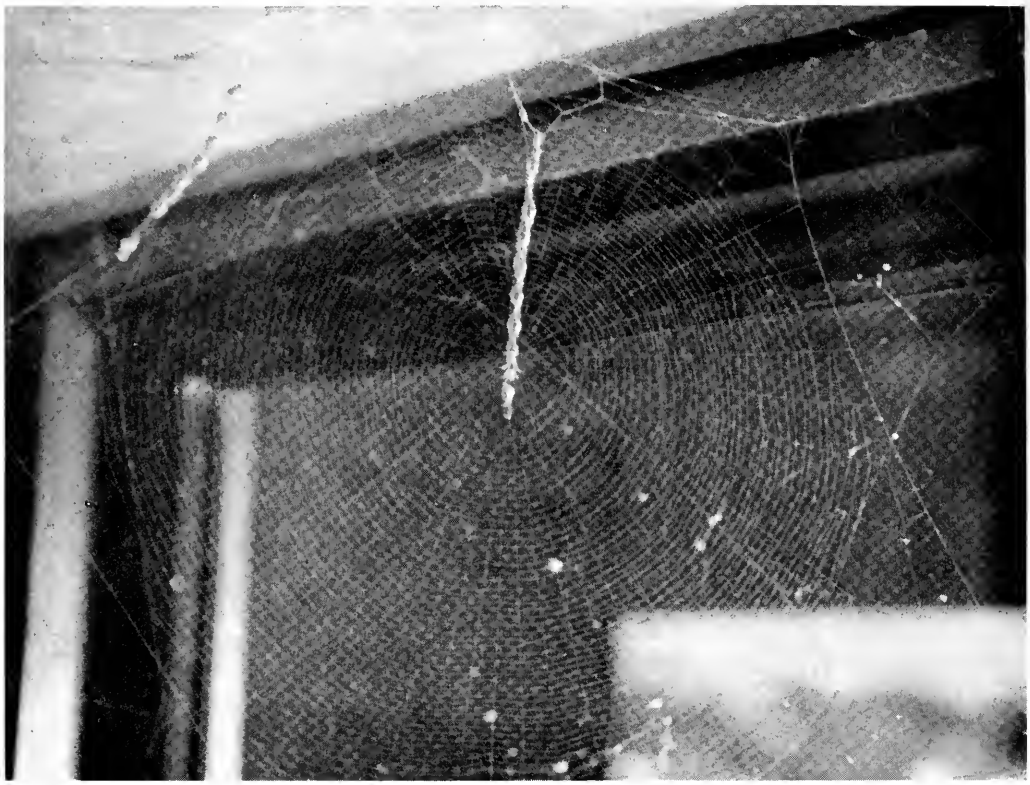


Plate 5. *Cyclosa bifurca* web with female and egg-sacs, 15 cm diameter, Florida (photo V. Brach).

1956).] All five species are closer to *C. conica* than to the other American species.

Metazygia is mostly made up of tropical American species. The orbs are loose with widely spaced spirals (Plate 6). They are usually left up during the day, while the spider rests in a retreat, and are replaced every evening after dark. *Metazygia wittfeldae*, which often makes its webs on bridges or buildings, occupies a niche similar to that of the more northern *Nuctenea cornuta* (Clerck), and is similar in appearance (Plate 6).

Eustala, although common, is not well-known. Various species are found resting on dead twigs of shrubs or trees. W. Eberhard (in letter) writes that some *Eustala* have their webs up during the day, but most (in southern Colombia) put them up in the evening and tear them down in the morning. The webs are characteristic with some variation. In construction they are more or less vertical and somewhat asymmetrical with the larger part usually below the hub. They have frame threads that do not span particularly large spaces, and a hub with several well-ordered loops and a medium hole in the center. They are often built in dead branches or tree trunks. In general they are undistinguished webs with nothing particularly remarkable about them. My own observations agree with Eberhard's. *Eustala anastera* in central Florida make their webs in the evening after dark. Usually the webs have disappeared by morning, but once in awhile a web is kept (Plate 7).

Eustala and *Metazygia* webs are similar and may be horizontal or vertical. Both are

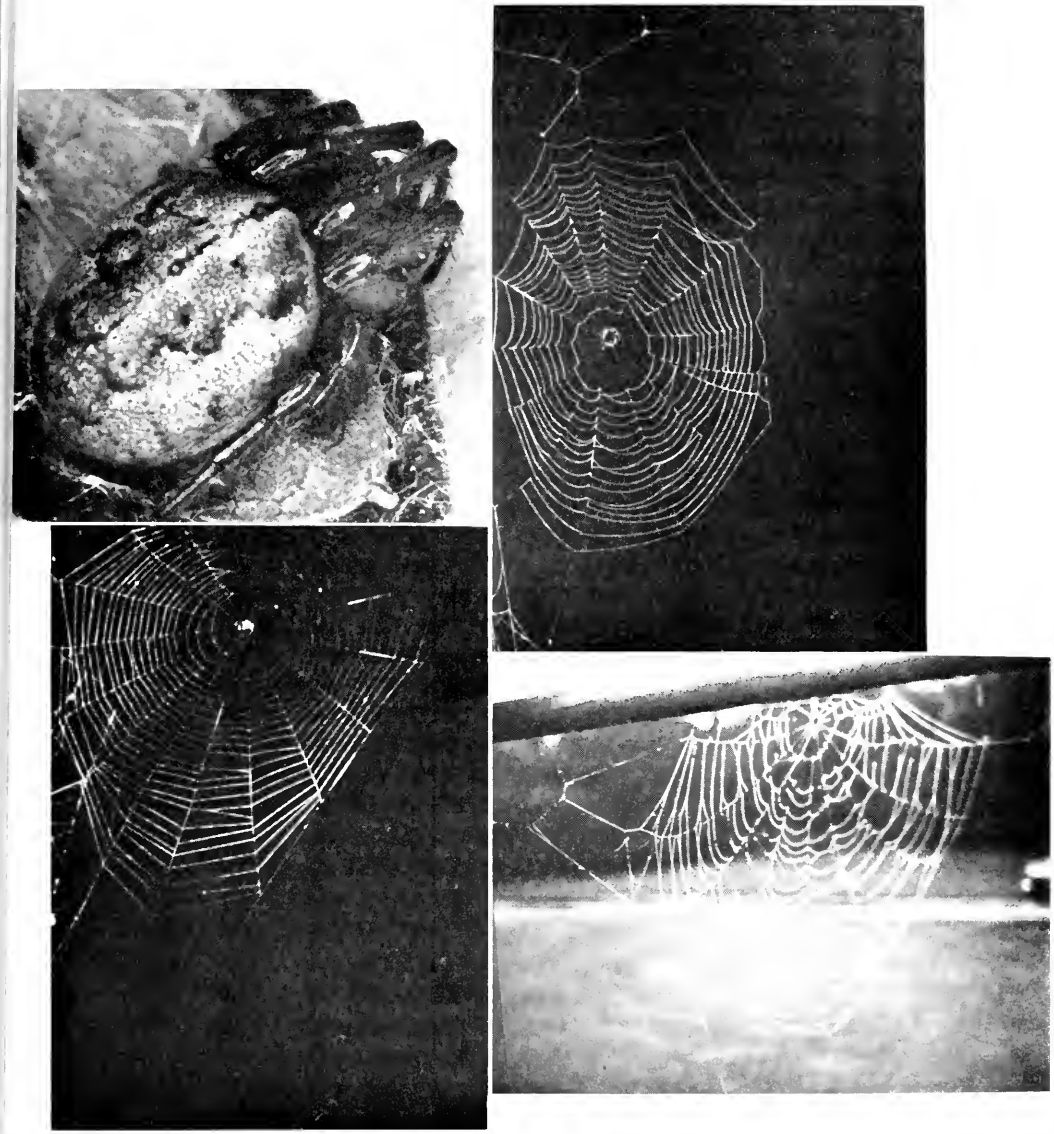


Plate 6. *Metazygia wittfeldae*, upper left female; upper right web 15 cm horizontal diameter; lower left 18 cm horizontal diameter; lower right web with dew, 25 cm horizontal diameter.

loose constructions with few threads. And both *Eustala anastera* and *Metazygia wittfeldae* are less likely than many other nocturnal orb-weavers to tear down the web when disturbed by artificial light or when the web is dusted with cornstarch to make it more visible in photographs.

METHODS

At the start of a revisionary study the taxonomist has in front of him perhaps hundreds of specimen collections. Are those collected together all the same species? Can species be separated readily by their genitalia, or by their size, coloration, eye ar-

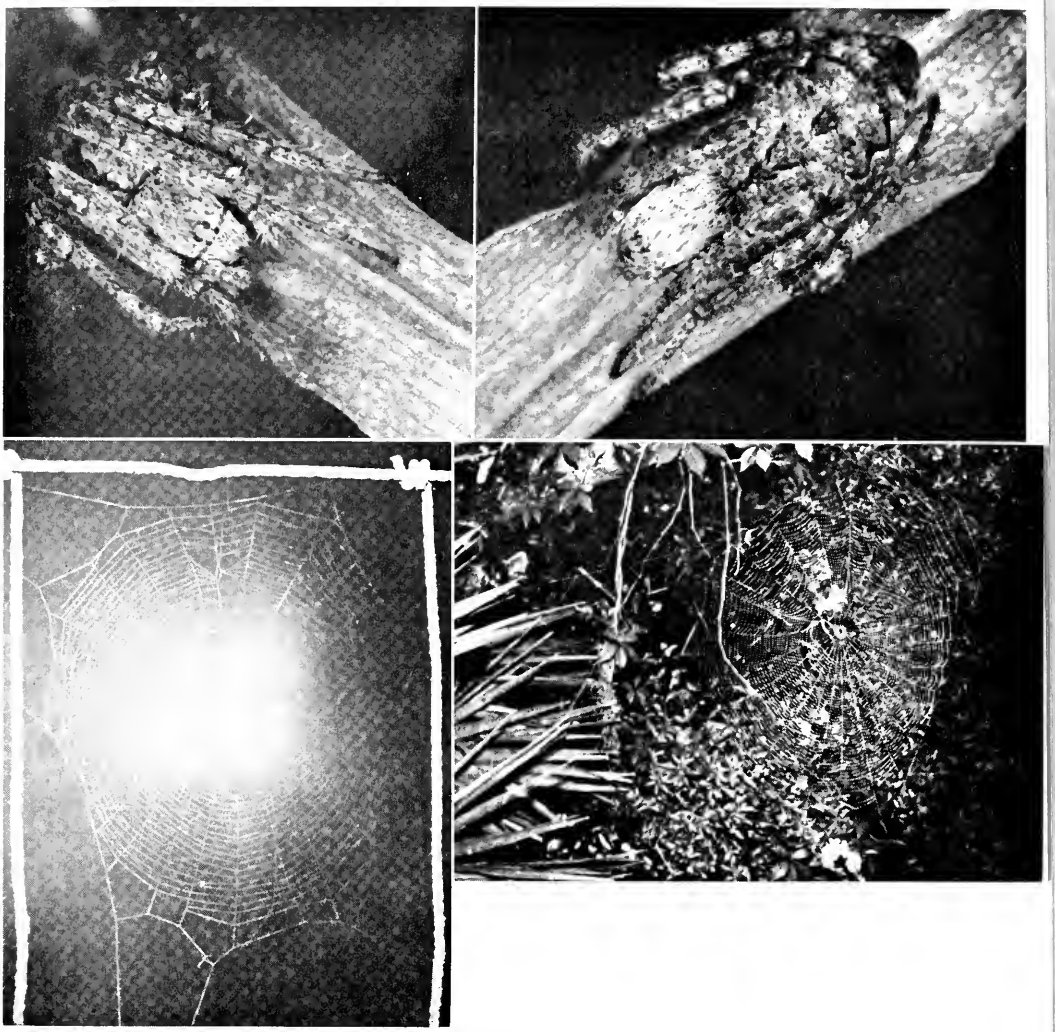


Plate 7. *Eustala anastera*, Florida; top row female; bottom webs: left with spider in web 13 cm diameter; right spider removed, 38 cm diameter.

rangement, or the shape of the abdomen? Perhaps a system could be based on each character like the one devised by Adanson, in the 18th century, but it might be unnatural, each character giving a separate classification. Some species are so distinct that the diagnostic characters are obvious, but more often the taxonomist has to sort out specimens and try various combinations of characters. Do all those that lack a hump on the abdomen also have distinct genitalic characters, and do all these fall within a certain size range? Might the smaller size, larger eyes, and lack of hump reflect merely fewer instars passed by a spider before maturity, or do they reflect a segregated breeding population for which we can predict also different behavior and habits? In both *Cyclosa* and *Eustala* the numerous genitalic differences between specimens usually represent individual variation of no taxonomic importance. To be diagnostic, differences

must characterize all members of the population.

The separation of populations from the mass of specimens cannot be done by intuition. Numerical and statistical methods are not applicable, as spiders grow allometrically and mature after a variable number of instars. Statistically significant measurements would make specimens maturing in the 8th instar distinct from those maturing in the 9th. This is very different among most mites, which have a fixed number of molts. My own method is to find the diagnostic characters for the population that is most distinct, and try to delineate the more difficult species on the basis of the same characters. But is it valid to assume that other members of the genus differ in the corresponding characters? In the *Cyclosa conica* group of species (Figs. 1–37), the median apophysis of the palpus is a useful character for classifying males, and differences in its shape correlate with differences in size, shape of abdomen, and other characters. The shape of the median apophysis is similarly useful in other American species of *Cyclosa*, but for separating species of *Larinia* and *Eustala*, it is useless. To find the most useful characters, I make numerous outline drawings to scale, few of which will be used in the final presentation of the research. The nontaxonomist, who sees only conclusions, remains puzzled as to the aims and methods of the study.

In *Cyclosa* the females of North American species could readily be separated by the shape of the abdomen as well as by the epigynum. Males of one species were all accompanied by females, and all came from the northern part of North America. But males of other species were much more difficult to separate. An occasional specimen matched females or accompanied females. At first the palpi could not readily be separated, but gradually differences were found in the median apophysis (Figs. 47, 60, 73).

Today's approach is vastly different from that of twenty to fifty years ago, when revisers used the smallest possible sample from a population, any specimen that differed would be described as new, and "difficult" specimens were ignored or discarded as abnormal. But these "difficult" specimens represent the variation that makes revisions challenging. The huge numbers of specimens in American collections embrace an enormous amount of variation, aside from abnormalities, making a sound basis for revisionary studies.

The *Eustala* species are difficult. Chamberlin and Ivie (1935) considered the California-Arizona populations distinct because of a series of humps on the posterior of the abdomen, selected a juvenile specimen as type, and named the species *rosae*. In 1944 in the controversial paper on the spiders of the Georgia region, the same authors listed three southeastern species, using (wisely in this instance) old Walckenarian names. *Eustala anastera* was characterized as having "a sharp conical tip to the abdomen. It occurs in a great variety of color patterns. . . ." Nothing was said about how to separate males. "*Eustala cepina* is smaller than *anastera*, the abdomen is less sharply angulate and is broad. It lacks the silky white hairs found on the top of the head of *anastera* and *triflex*, or at most are much reduced." *Eustala triflex* (= *emertoni*) "differs from *anastera* and *cepina* which occur in the same region by larking [sic] the terminal angulation on the abdomen, the abdomen being rounded behind. There are also differences in the male palpus." But what are these differences in the complicated palpus?

It is not surprising that Kaston (1948) in his discussion on *Eustala anastera*, does not list *cepina* and *triflex* in the synonymy, but indicates that "Chamberlin and Ivie prefer to maintain [*triflex*] as a distinct species. . . ." Chickering (1955), describing Central American *Eustala*, listed *cepina* as a synonym of *anastera*, but did not mention *triflex*. Archer (1951), however, considered *triflex* distinct and described a fourth species, *E. arkansana*,

citing differences of the epigyna (which I could not verify). For *arkansana*, Archer illustrated the epigynum, and for all the species he illustrated a palpal structure he called the "median apophysis." I cannot recognize the palpal structure illustrated; it may be the embolus. Archer did not indicate whether he illustrated the one from the left or the right palpus.

I started my investigation of *Eustala* with the American Museum collection. Gertsch, Archer and Ivie had used the Chamberlin and Ivie (1944) names on only a few specimens (most others were not determined), but Chickering, who examined a small part of the collection, labeled all specimens *E. anastera*. One locality, in eastern Pennsylvania, yielded a large series of males and females. These had labels of the three species (*anastera*, *cepina*, "*triflex*"), and I started to draw these and study their differences. But I could not find the differences when I tried to use them for separating other collections. Only one character, the ventral row of macrosetae on the second femur of *E. anastera*, remained constant (Fig. 214), and I subsequently sorted out all collections using these "spines." However, such large setae could reflect allometric growth, as the *anastera* were also the largest specimens. I removed all *E. rosae* because they seemed distinct and similar in size to *anastera*, lacked the femoral macrosetae in males, had humps on the abdomen, and had a distinctive epigynum (Fig. 193). To get some new ideas, I examined *E. californiensis*, a distinct North American species. The diagnostic genitalic characters were a differently shaped terminal apophysis and median apophysis in the male palpus (Figs. 147, 148), and the shape of the posterolateral plates of the epigynum (Fig. 139). The embolus of the palpus, which I had previously carefully examined and illustrated was not significantly different. Because it is soft, the median apophysis is a more difficult character to work with. With this new knowledge I returned to *E. rosea* and confirmed that all females with extra abdominal humps (Fig. 196) also had the extra dorsal lobe on the posterior face of the epigynum (Fig. 193). The males had very distinct "half-spear-shaped" terminal apophyses (Figs. 202, 203, 313) and lacked the ventral setae on the second femur (Fig. 201), characteristic of *anastera*. I returned to *anastera* only to find that it had a similar but less distinct "half-spear-shaped" terminal apophysis (Figs. 215, 216). One specimen, determined by Ivie to be *anastera*, was an exception (Fig. 315). (It turned out to be one of many males with this character.)

Could the bubble-shaped transparent subterminal apophysis (sa in Fig. 232), which differed also in *E. californiensis*, be used? Sketches and comparisons indicated not. But the combined characters of terminal apophysis shape, femoral setae, large size and heavy pigmentation, facilitated sorting out *anastera*. Only one specimen with an *anastera* palp lacked femoral setae. And, several specimens had filamentous terminal apophyses, but were large, dark, and had femoral setae. Do these exceptional specimens represent a new species, intermediates, or perhaps products of introgression? Adopting introgression as a temporary working hypothesis, I began to doubt that I could separate most males of this species. The disturbing thought occurred to me that Ivie, in working through the three large collections from one locality in Pennsylvania, might not have kept difficult-to-place intermediate specimens with the labeled collections.

I decided to re-examine "*triflex*" males. Preliminary examination had shown the palpus to have an especially long tail on the conductor (Figs. 266, 309–311). Careful examination indicated that the long tail usually was associated with a relatively short terminal apophysis (Figs. 309–311). But there were specimens with a half-spear-shaped embolus. Was *triflex* merely a small *E. anastera* that failed to grow the femoral macrosetae? Some specimens had the char-

acteristic long tail of the conductor but had a long terminal apophysis, as does *A. cepina*. Are these separate species or hybrids? The females associated with these males had the oval abdomen (Fig. 258) described by Chamberlin and Ivie, and also had an epigynum distinct from that of *anastera*, but apparently not from *cepina* (as far as I could tell at this point). My confidence increased and I decided to work on a new, very distinct species found in the West Indies and Florida (*E. cazieri*) to find some new characters to use before returning to the male *E. anastera* for measurements and recording collecting data.

Examination of the new species provided evidence that the main pattern of macrosetae is not merely the result of allometric growth: the large *E. rosae* has no macrosetae ventrally on the second femur (Fig. 201), the small *E. cazieri* has many (Fig. 135).

The next problem was to separate females of *E. cepina*. By making numerous drawings and clearing epigyna, I found that in *cepina* the base of the epigynum has a tiny sclerotized scale dorsally (Figs. 286–290). The scale is absent in *E. "triflex"* and *E. anastera*, and absent or transparent in Florida specimens believed to belong to the species. This character was abandoned late in the study as it is not consistent.

To make sure that these Florida females, which are much smaller than *E. anastera* from the rest of the range, really are the same species, I decided to study the associated males. I went back to various other West Indian species, and found that the males of some differed in the shape of the conductor. I now made outline drawings of the conductor, only to discover that the long tail of *E. "triflex"* was more distinct than I previously thought and, more importantly, that of these three species, *E. cepina* lacked the distal ventral lobe of the conductor (upper right in Figures 303–308), providing an additional diagnostic character. It also reaffirmed the differences previously noted and compounded the problem that *E. anastera* comes with short (Fig. 315) and long (Fig. 314) terminal apophyses. It seemed that if two species are collected together, specimens are easy to separate, but lone individuals often cannot be placed.

In consulting type specimens and Abbot illustrations, I found that the illustrations labeled *Epeira triflex* were contrastingly marked (Figs. 219, 222), a coloration found only in *E. anastera*, not in any specimen I had available of *E. "triflex."* The name was changed to *E. emertoni*, the next oldest name available.

After the first triumph of finally figuring out that there are differences and the species can be told apart, there comes doubt about being able to place all specimens. If all specimens can be determined, new doubts arise: now that I have finally discovered the obvious, is it worth publishing? But after the doubts are overcome, there comes the challenge to put the conclusions into a form that a nonspecialist can use for separating species. The last generation's specialists indulged in a kind of gamesmanship, just stating that there are differences, but failing to describe them, or hiding them in drawings that made comparison impossible.

After examining, measuring and determining the contents of a few hundred vials, most with many specimens, I found determinations getting easier. I had unconsciously used the relative size of the conductor in males and found now that not only does *E. "triflex"* (= *emertoni*) have a relatively large conductor (Figs. 309–311), but also that *anastera* has a relatively small conductor (Figs. 298–302).

While determining specimens and recording data, I took measurements of specimens from all parts of the range and found that the genitalia of *anastera* and the similar *cepina* do not overlap in size (Figs. 283–290 and 298–308). That the area of the conductor "above" the embolus is larger in *anastera* than in *cepina* and *emertoni*, I did not re-

alize until finishing the illustrations (Figs. 298–311).

But a few problem specimens remained: the male *anastera* with the terminal apophysis short (Fig. 315), and those lacking macrosetae on the second femur; a few *emertoni* (= "*triflex*") with the terminal apophysis long; and a few *cepina* with a distal lobe on the conductor. Problem females may have been overlooked due to relatively arbitrary decisions in separating specimens with fewer characters.

At the end, when determining various borrowed collections, I found that *Eustala anastera* from Nova Scotia and some from Quebec have smaller abdominal humps, males have a much smaller conductor (Fig. 298), and females have the middle piece of the epigynum larger (Fig. 229). Are they a distinct species? One male from Ontario had one Nova Scotia-like palpus and one "normal" *anastera* palpus. I decided that perhaps one palpus was more dehydrated and shrivelled.

A single collection, from Jefferson Co. in northern Florida, included both small females of the central Florida type, and larger sized females similarly marked. Are the smaller ones a distinct species? Adult females collected at Archbold Biological Station in February and March 1976 were all considerably larger than females from the same population collected in July and August 1975 by M. Stowe. The winter ones were predominantly brown, the summer ones green on the abdomen.

Character displacement. Eastern Canadian specimens of *E. anastera* are of slightly smaller size—the males having few macrosetae and a smaller conductor (Fig. 298) and the females having a smaller hump and larger epigynal middle piece (Fig. 229)—resemble *E. cepina* and *E. emertoni*, and are more distinct in the shared range of all three species because of character displacement. Perhaps the Mexican specimens of this group all belong to *E. anastera* but look different in the absence of competing species.

Remaining questions. Other questions remain unresolved. Is *Eustala conchlea* (Figs. 269–279) just a western form of *E. emertoni* with a large abdominal hump? It was arbitrarily decided to keep them separate.

Among the puzzling specimens are the asymmetrical ones. The macrosetae on left and right femora of the same specimens often differ, or there may be one ventral macroseta on one second femur, none on the other. (In the *E. anastera* group of species these were all considered *E. anastera*.) An interesting epigynum is that of an *E. cepina* female from Emmet County, Michigan (A. M. Chickering, collector, in the Museum of Comparative Zoology) (Fig. 248). Only the epigynum is asymmetrical, not the rest of the animal. More startling is the left palpus of a male *E. anastera* from Kisatchie National Forest, Grant Parish, Louisiana (A. F. Archer, collector, in the American Museum of Natural History). The left palpus has a unique bulbous terminal apophysis, the right one a normal, short, pointed one (Fig. 231).

Several collections of the *Eustala anastera* group might be new species, but I am hesitant to name them until more specimens are available. One collection, consisting of two females and a male that appears to be a small *E. anastera*, comes from Black Mesa State Park, Cimarron County, Oklahoma (16 August 1964, H. Fitch in the American Museum of Natural History). The females have three posterior humps in a row on the abdomen, and the epigynum in posterior view has a very small middle piece (Fig. 230). The male lacks macrosetae on the venter of the second femur; the conductor of the palpus is like that of *E. cepina*, and lacks the large lateral conductor lobe present in most specimens of *E. anastera*.

Another new species may be represented by two females, one from Cologne (? Goliad Co.), Texas (7 June 1937, S. Mulaik in the American Museum of Natural History) and another from Little Pine Key, Florida

(27 March 1939 in the American Museum of Natural History). Both look like very large *E. anastera* with the more common spotted patchy pattern, but more contrasting. The females have two posterior humps and, in the epigynum, a very heavy, large scape with parallel sides (Fig. 228). The Texas female, whose epigynum was illustrated (Fig. 228), was 14.0 mm in total length, carapace 4.9 mm long, 4.1 wide. Several very large *E. anastera* males from southern Florida (as compared with the small *E. anastera* from central Florida) may belong with these females. But the question remains whether they represent a separate species or large-sized populations.

After all was completed, the "easy" *Metazygia* illustrated and determined, I felt that I had to return to these difficult *Eustala* specimens. Perhaps I had overlooked characters seen in ventral view of the median apophysis, the paracymbium and sculpturing of the tegulum of the palpus. But no new characters were found. However, on reexamination, the Oklahoma male turned out to be *E. cepina*, the females (Fig. 230) are perhaps a new species to be named when additional specimens are available. I also reexamined most Texas and southern Florida specimens of *E. anastera* in search for additional large females having an epigynal scape with parallel sides (Fig. 228), and perhaps for males, but found only intermediates, all in the collection from Raven Ranch, Kerr County, Texas. The intermediate specimens (Figs. 226, 227) dissuaded me from describing the two specimens as a new species.

While revision of *Eustala* is now completed, I would not be surprised to find additional sibling species among the *Eustala anastera* collections.

Cyclosa Menge

Cyclosa Menge, 1866, Schrift. naturforsch. Gesellsch. Danzig, neue Folge, 1: 73. Type species *C. conica* (Pallas) by monotypy. The name is feminine.

Parazygia di Caporiacco, 1955, Acta biol. Venezuelica, 1: 345. Type species *P. accentonotata* di Caporiacco [= *C. caroli* (Hentz)] by monotypy. NEW SYNONYMY.

Diagnosis. *Cyclosa* species differ from those of other Araneidae genera and especially from *Araneus* in the narrow head region of the carapace, often separated by shallow grooves from the thoracic region (Figs. 10, 12, 29, 48). The eyes are closely spaced, posterior median eyes almost touching (Figs. 10, 12, 14). *Cyclosa* differs from *Larinia*, which also has the posterior median eyes close, in having banded legs, and in the shape and coloration of the abdomen. There are dorsal, paired, black or gray patches on white (Figs. 10, 29, 48, 61, 74) and a characteristic pair of ventral white spots surrounded and separated by a black band running from epigynum to spinnerets and posteriorly surrounding the spinnerets (Figs. 11, 49, 62, 75). The posterior dorsal end of the abdomen is extended beyond the spinnerets in the female and there may be shoulder humps or additional posterior humps (Figs. 2, 10, 28, 29, 39, 48, 52, 61, 65, 74, 78, 88). *Cyclosa* further differs from *Araneus* and *Larinia* in that the male palpal patella has only one macroseta (Fig. 1).

The web is diurnal, its form diagnostic; lightly spun with few frame threads, it has a stabilimentum containing debris or a vertical row of egg-sacs through the center; the spider rests at the lower end or in a gap in the decoration and is often difficult to find (Plates 1–5).

Description. The head region of the brown carapace is narrow and lighter in color than the thoracic region; the thoracic depression is round (Figs. 10, 29, 48, 61, 74). The carapace is covered with down. The anterior median eyes are slightly larger than the others, which are subequal in size (Fig. 16). The anterior median eyes are their diameter apart, usually one, but not more than two and one-half diameters from laterals. Posterior median eyes touching or less than their diameter apart, one and one-half to three diameters from laterals (Figs. 10, 29, 48, 61, 74, 88). The clypeus height

equals about the diameter of the anterior median eyes (Fig. 16). The sternum is dark brown, often enclosing white pigment patches. The coxae are light, sometimes with dark marks. The legs are light with dark bands with short setae and macrosetae. The spinnerets are usually dark brown. *Cyclosa bifurca* departs from the drab coloration of other species by being green. The widespread *C. insulana* (Fig. 29) of Eurasia and Africa to the Pacific has a silvery abdomen, perhaps an adaptation to the open sunny areas it frequents (M. H. Robinson *et al.*, 1974).

Males are smaller than females, more sclerotized, darker in color, and have the abdomen almost spherical with humps only faintly indicated. The markings are dark with few paired light spots, but with some indications of the humps (Figs. 1, 12, 38, 50, 51, 63, 64, 76, 89). The endites have a lateral tubercle facing a minute cone on the palpal femur (lacking in the small male of *C. bifurca*). The first coxa of the male has a small hook (also lacking in *C. bifurca*) that fits into a groove of the male second femur. In addition, the fourth coxae of *C. conica* are armed with two macrosetae (Fig. 15). The second tibia is only slightly thicker than the first with a few more macrosetae (Figs. 1, 12, 50, 51, 63). The male of *C. bifurca* is dwarfed (Fig. 89).

Genitalia. The epigynum has a small weak scape, the shape of which may be diagnostic: straight and pointed in *C. conica* (Fig. 4), oval in *C. turbinata* (Fig. 41), almost circular in *C. caroli* (Fig. 54), and usually with parallel sides in *C. walckenaeri* (Fig. 67). The scape is absent in *C. bifurca* (Fig. 80). The seminal receptacles of all are sclerotized (Figs. 3, 5, 40, 42), but the connecting ducts and their openings to the outside are so thin-walled that they are hard to find, and once found their course is difficult to follow. They open in a fold on the venter of the base on each side of the scape (Figs. 40, 53), except that in *C. bifurca* they open on the posterior not far from the fertilization ducts (Figs. 79, 81), a peculiar, probably secondary modification approaching haplogyne condition. Some material may be found in the depression having the openings of the epigynum, but I believe that these are an epigynal plug formed from mucus and not a part of the palpus left behind. (It is not known whether males or females can mate several times.)

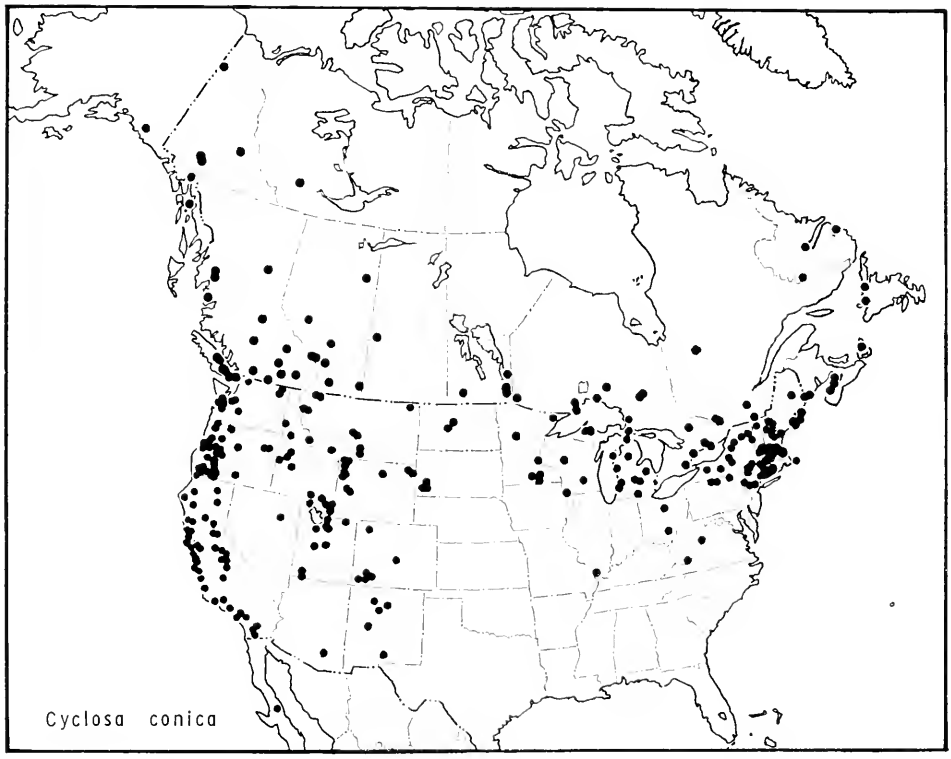
The palpal patella has one macroseta (Fig. 1). The bulb has a large conductor holding the tip of the embolus ("c" in Figs. 7, 17, 20), a small terminal apophysis ("a" in Figs. 17, 20), and a paramedian apophysis (pm), the latter apparently absent in *C. bifurca*. The embolus (e) is thread-shaped in all and the median apophysis has moved to the ventral side in all except *C. bifurca* ("m" in Figs. 8, 17, 20, 46). The complex median apophysis is species specific (Figs. 9, 23, 27, 33, 37, 47, 60, 73, 87), apparently fitting the epigynal scape into which it hooks during mating.

Natural History. The web has few frame threads (Plates 1–5). That of *C. conica* is almost circular, with about 40 radii (Wiehle, 1931); in each sector are 20–30 viscid threads separated by 2 to 3 mm (Plate 1).

The spider hangs in the middle of the web; juveniles have a detritis-covered stabilimentum (Plates 1, 4). Adults place the egg-sacs in a vertical line in the center, the spider resting at one end or the middle (Plates 1–5). Only *Cyclosa conica* does not place her egg-sacs in the web, no doubt an adaptation to the short season of the more northern areas it frequents. The sacs are left hanging when the viscid threads of the web are renewed (Y. Lubin, personal communication).

Some *Cyclosa* species are known to hang with the head up rather than down, like the widespread Eurasian *Cyclosa insulana* (Wiehle, 1928).

The shape of the stabilimentum of young *Cyclosa* cannot be used to separate species as it may differ greatly even in successive webs of the same individual (Marson, 1947).



Map 1. Distribution of *Cyclosa conica* (Pallas) in North America.

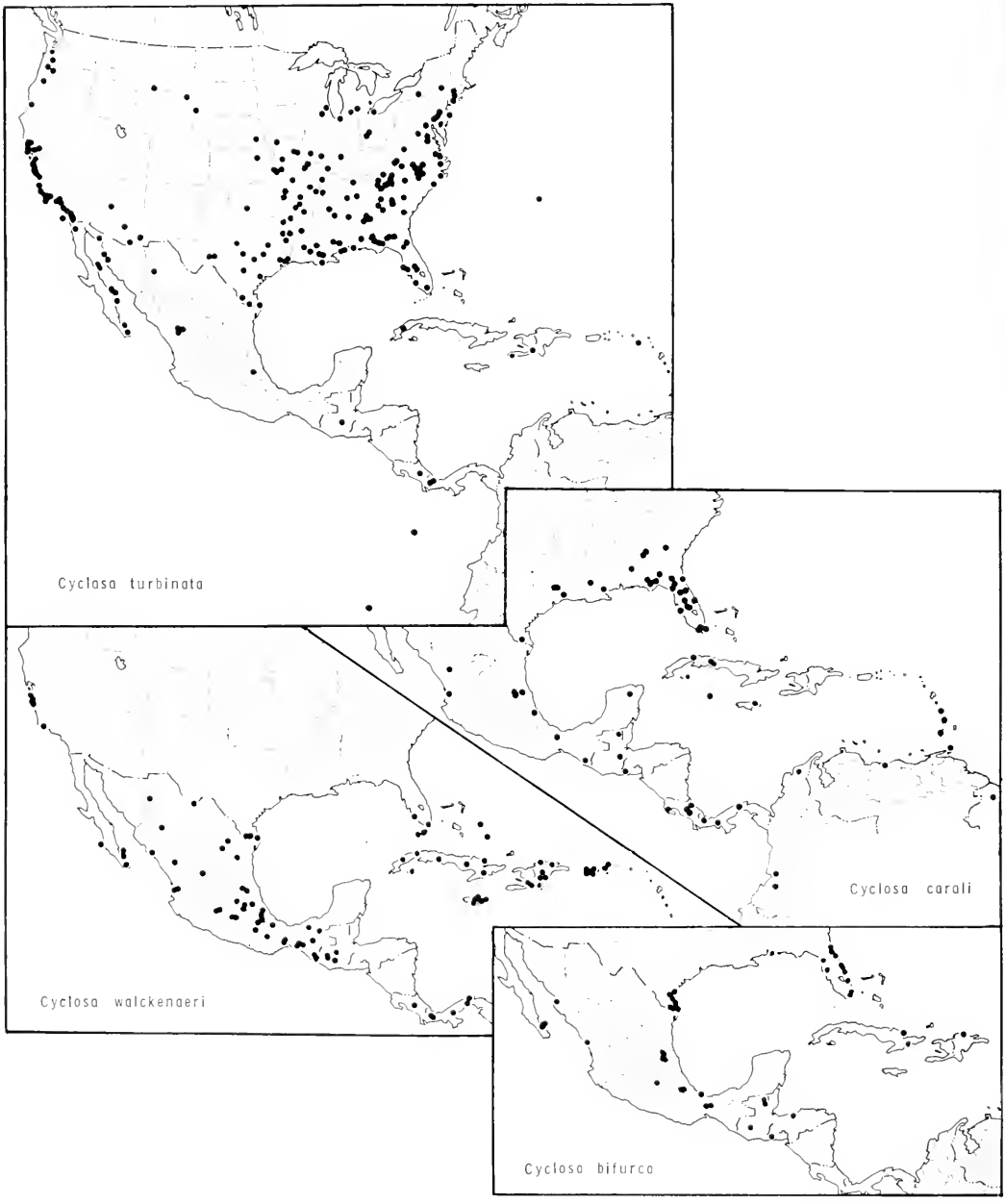
All species shake the web when disturbed, then may drop on a thread.

Species. Of the five species north of Mexico, *C. conica* is northern and holarctic, the remainder southern (Maps 1, 2). There are numerous tropical American species. The species north of Mexico can be separated by the shape of the abdomen of the female (Figs. 2, 39, 52, 65, 78), the shape of the epigynum, especially the scape (Figs. 4, 41, 54, 67), and the matching median apophysis of the palpus (Figs. 9, 47, 60, 73). It is ironic that A. Archer, who tried to separate all Araneidae species on the shape of the median apophysis alone, did not study *Cyclosa*, one genus in which the structure is of diagnostic importance.

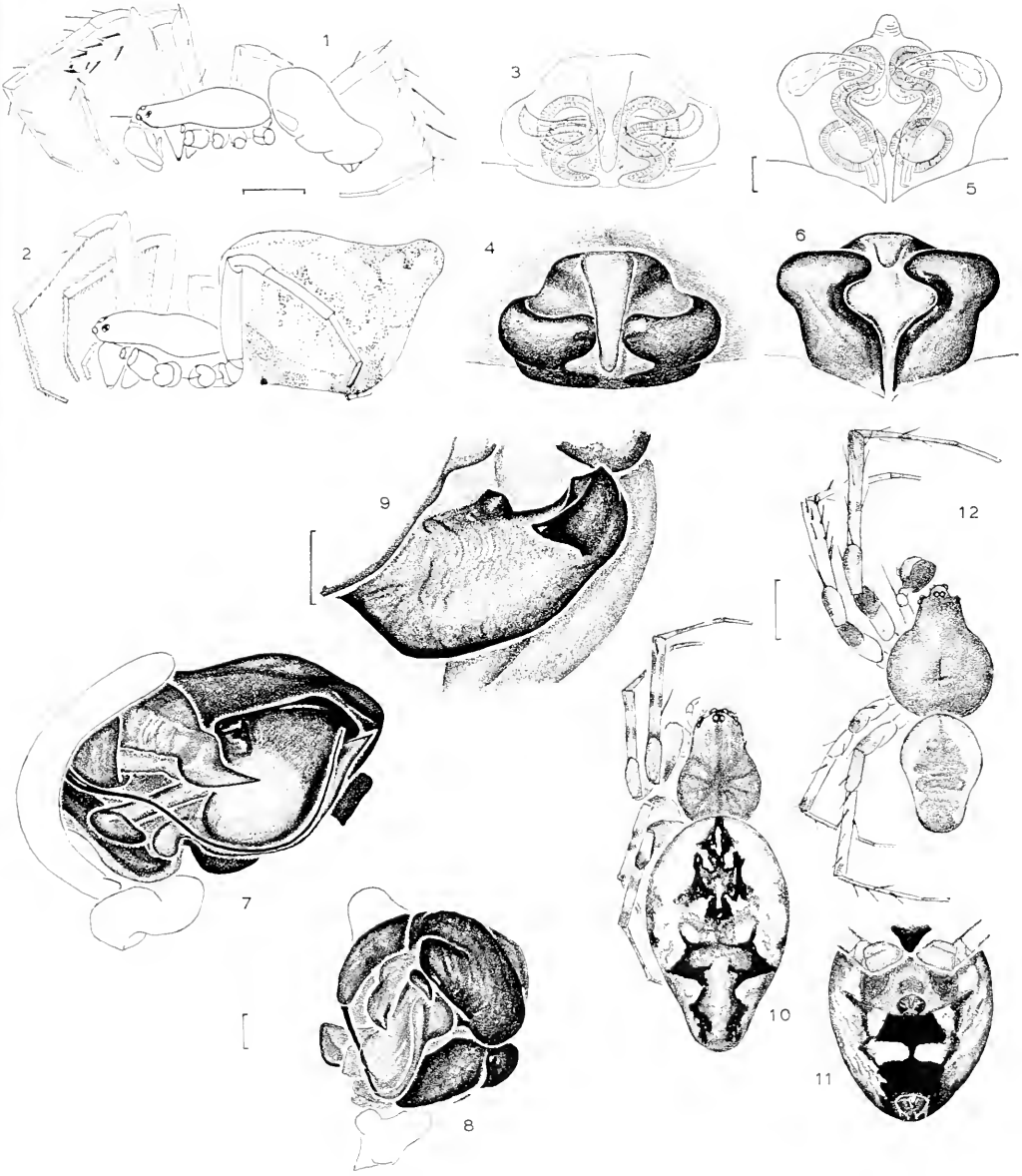
Distribution. *Cyclosa* species are found in all parts of the world.

KEY TO FEMALE *CYCLOSA* NORTH OF MEXICO

1. Posterior tip of abdomen biforked (Fig. 88); epigynum without scape (Figs. 80, 84); Florida, Alabama coast and southern Texas ..... *bifurca*
– Abdomen with a single posterior hump (Fig. 10) or four posterior tubercles (Fig. 74) 2
2(1) Epigynum with sclerotized lobe on each side of scape (Fig. 4); Alaska, south to Virginia, Arizona and California ..... *conica*
– Epigynum base without sclerotized lateral lobes (Figs. 41, 67); Connecticut to Washington and south 3
3(2) Abdomen with a pair of dorsal tubercles on anterior half of abdomen (Figs. 39, 65) 4
– Abdomen without dorsal tubercles; abdomen posterior to spinnerets longer than part in front of spinnerets (Fig. 62), epigynum scape an oval to circular lobe (Fig. 54); Georgia to Texas ..... *caroli*
4(3) Abdomen with a single posterior hump (Fig. 39), epigynal scape a rounded lobe



Map 2. Distribution of *Cyclosa turbinata* (Walckenaer), *C. caroli* (Hentz), *C. walckenaeri* (O.P.–Cambridge) and *C. bifurca* (McCook).



Figures 1–12. *Cyclosa conica* (Pallas). 1. Male from side. 2. Female from side. 3–6. Epigynum: 3, 4. Ventral, 5, 6. Posterior. 3, 5. Cleared. 7–9. Left male palpus: 7. Mesal. 8. Ventral. 9. Median apophysis, ventral. 10. Female, dorsal. 11. Female abdomen, ventral. 12. Male, dorsal.
Scale lines. 0.1 mm, except Figs. 1, 2, 10–12, 1.0 mm.

(Fig. 41); from Connecticut to Washington and south ..... *turbinata*

– Abdomen with four posterior humps (Fig. 65), epigynal scape usually with sides parallel (Fig. 67), southern Florida, southern Texas, California ..... *walckenaeri*

KEY TO MALE *CYCLOSA* NORTH OF MEXICO

1. Fourth coxae each with a pair of macrosetae (Fig. 15); palpus with median apophysis heavily sclerotized and its distal tip folded over (Fig. 9); Alaska south to Virginia, Arizona and California ..... *conica*

– Fourth coxae never with macrosetae (Fig. 77); median apophysis lightly sclerotized, tip not folded 2

2(1) Median apophysis mesal (Fig. 86); tip of abdomen biforked (Fig. 89); total length less than 2 mm; Florida, Alabama coast and southern Texas ..... *bifurca*

– Median apophysis almost hidden in mesal view (Figs. 45, 58, 71), posterior tip of abdomen with a tubercle or four tubercles; total length more than 2.1 mm 3

3(2) Abdomen usually extended beyond spinnerets (Fig. 51); median apophysis of the palpus short without a middle spine but with a rounded keel proximal to distal tip (Fig. 60); Georgia to Texas ..... *caroli*

– Abdomen with only a posterior hump, or four slight posterior humps (Figs. 38, 64); median apophysis with a spine in middle, with or without distal keel (Figs. 47, 73) 4

4(3) Posterior tip of abdomen usually with indications of four tubercles (Fig. 64); median apophysis long, with a tiny median spine and a more distal keel ending in distal tip (Fig. 73); southern Florida, southern Texas, California ..... *walckenaeri*

– Posterior of abdomen with at most a dorsal hump (Fig. 38); median apophysis with a large median spine but no keel distally in ventral view (Fig. 47), in subapical view keel extending from distal to median spine, from Connecticut to Washington and south ..... *turbinata*

Cyclosa conica (Pallas)

Plate 1, Figures 1–19, Map 1

Aranea conica Pallas, 1772, Spicilegia Zoologica, 9: 48, pl. 1, fig. 16. Female specimen from Germany, believed lost.

Epeira canadensis Blackwell, 1846, Ann. Mag. Natur. Hist. (ser. 1), 17: 81. Juvenile type from vicinity of Toronto, in the Hope Museum at Oxford, lost.

Cyclosa conica,—Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 321, pl. 34, fig. 3, pl. 38, fig. 11, ♀, ♂. Keyserling, 1893, Spinnen Amerikas, 4: 276, pl. 14, fig. 205, ♀, ♂. McCook, 1894, American Spiders, 3: 225, pl. 17, figs. 3–4, ♀, ♂. Emerton, 1902, Common Spiders, p. 183, figs. 428, 429, ♀, ♂. F.O.P.–Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 493, pl. 46, figs. 19, 20, ♀, ♂. Wiehle, 1931, in Dahl, Tierwelt Deutschlands, 23: 18, figs. 8, 17–21, ♀, ♂. Comstock, 1940, Spider Book, rev. ed., p. 465, figs. 463–464, ♀, web. Roewer, 1942, Katalog der Araneae, 1: 754. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist., 70: 236, figs. 711–713, fig. 2037, ♀, ♂, web. Locket and Millidge, 1953, British Spiders, 2: 166, fig. 111, ♀, ♂. Bonnet, 1956, Bibliographia Araneorum, 2: 1310.

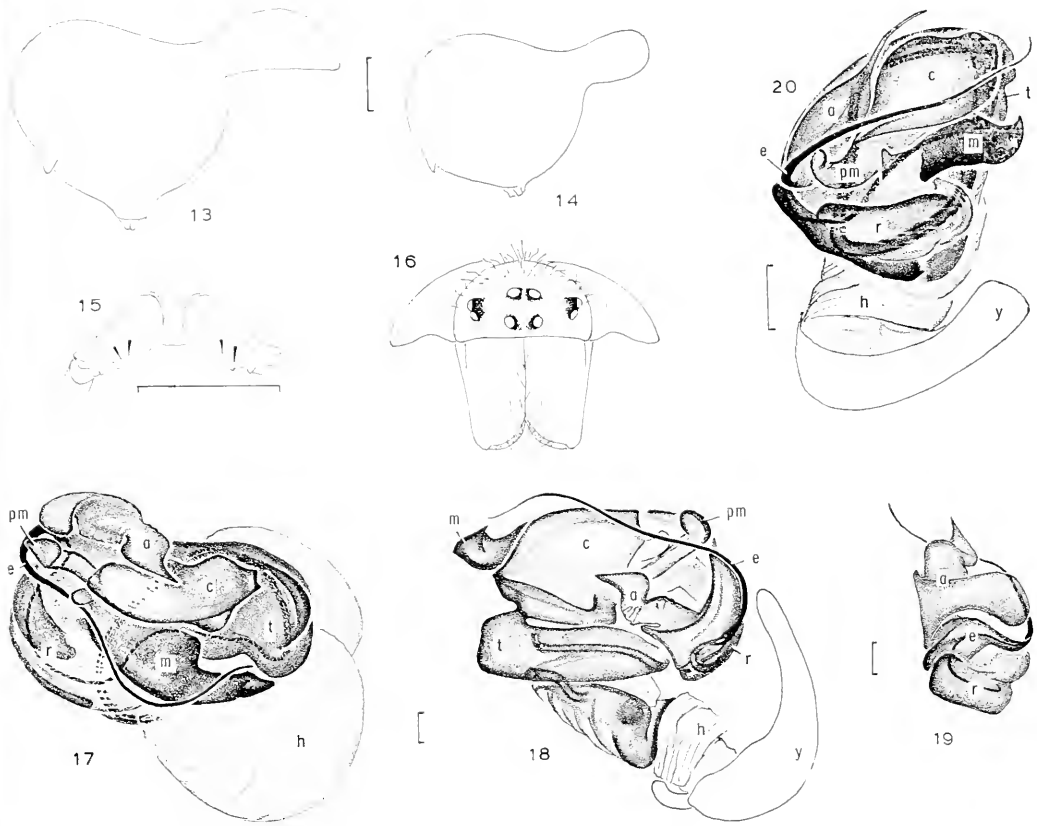
Note. Many specimens of *C. turbinata* in collections had been erroneously labeled as *C. conica*, thus literature citations of "*C. conica*" are not reliable, and records from the southern states, Mexico, Central and South America are all erroneous.

Measurements. Female from Wyoming: Total length 5.5 mm. Carapace 1.9 mm long, 1.4 wide. First femur, 2.1 mm; patella and tibia, 2.3; metatarsus, 1.4; tarsus, 0.7. Second patella and tibia, 2.0 mm; third, 1.3; fourth, 1.9.

Male from Wyoming: Total length 3.5 mm. Carapace 2.2 mm long, 1.6 wide. Head 0.7 mm wide. First femur, 2.6 mm; patella and tibia, 2.7; metatarsus, 1.6; tarsus, 0.7. Second patella and tibia, 2.1 mm; third, 1.4; fourth, 1.7.

Variation. Females vary in total length 3.6 to 7.9 mm, carapace 1.7 to 2.5 long, 1.3 to 1.7 wide. Males vary in total length 3.5 to 4.9 mm, carapace 2.0 to 2.3 long, 1.5 to 1.6 wide. The largest specimens came from the northeastern states. Specimens from Oregon and Washington had greater size variation than those from other parts of the range. The caudal hump varies in length and is quite long in some populations (Figs. 13, 14). Rarely are females almost all black. All long-tailed and black individuals came from the southernmost localities. One specimen (Fig. 13) had a long tail as well as a relatively long epigynal scape with its tip twisted.

Diagnosis. In North America *C. conica* is the only *Cyclosa* species over most of its range; only in the south does its range overlap with that of *C. turbinata*. *Cyclosa conica* is larger than *C. turbinata* and lacks the two anterior dorsal abdominal humps (Figs. 2, 10). The epigynum base in *C. conica* has a sclerotized lobe on each side of the scape (Figs. 4, 6), unlike *C. turbinata*, and the median apophysis of the palpus is



Figures 13–19. *Cyclosa conica* (Pallas). 13, 14. Female abdomen: 13. (Southern California) 14. (Minnesota) 15. Male, fourth coxae, ventral. 16. Eye region and chelicerae of female. 17–19. Left male palpus, expanded (17, 19, without cymbium). 17. Submesal view. 18. Subdorsal view. 19. Embolic division, dorsal.

Figure 20. *Cyclosa turbinata* (Walckenaer) male palpus, expanded, submesal view.

Abbreviations. a, terminal apophysis; c, conductor; e, embolus; h, hematodocha; m, median apophysis; pm, paramedian apophysis; r, radix; t, tegulum; y, cymbium.

Scale lines. Figs. 13–15, 1.0 mm; Figs. 17–20, 0.1 mm.

sclerotized, its distal tip folded over and pointed (Figs. 8, 9, 17). Two macrosetae on the fourth coxae of males (Fig. 15) are only rarely absent. In southern Europe *C. conica* can be confused with the very similar *C. sierrae* Simon (Figs. 30–33) and *C. algerica* Simon (Figs. 34–37). The males of these also have two macrosetae on the fourth coxa.

Natural History. The orb of *C. conica* is found on shrubs and understory of coniferous forests, sometimes deciduous, where it is the most common orb-weaver. According to Kaston (1948) the orb is wider than high, with 40 to 50 radii, and lacks a retreat, the spider resting in the center (Plate 1). When disturbed the spider shakes the web or may drop out of the web. There may or may not be a stabilimentum in webs of the same individual. Objects falling into the web and insect remains are incorporated into the stabilimentum. Mature males do not build orbs. The three to five egg-sacs of loose silk are elliptical, yellowish brown, 3 × 7 mm, and are attached to dead twigs or under leaves, but not to the orb. The egg-sacs contain 10 to 130 eggs (Kaston, 1948).

Males are mature from May to July in

New England and from March to June in California. Mature females can be found from June to late August in New England and from March to September in California. The species overwinters in juvenile stages.

Distribution. Holarctic, in America from Alaska to southern West Virginia, southern Illinois to southern New Mexico and Baja California Norte (Map 1).

Cyclosa turbinata (Walckenaer)
Plate 2, Figures 20, 38–50, Map 2

Epeira turbinata Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2: 140. Female types are figures no. 79 and 80 from Georgia in Abbot's Georgia Spiders manuscript in the British Museum, Natural History. Copy in the Museum of Comparative Zoology, examined.[1]

Epeira caudata Hentz, 1850, J. Boston Soc. Natur. Hist., 6: 23, pl. 3, fig. 14, ♀. Female types from United States in Boston Natural History Museum, destroyed.

Singa vanbruysselii Becker, 1879, Ann. Soc. Entomol. Belgique, 22: 78, pl. 1, figs. 4–6, ♂. Male holotype from Pascagoula, Mississippi in the Institut Royal des Sciences Naturelles de Belgique, Brussels, examined.

Cyclosa index O.P.–Cambridge, 1889, Biologia Centrali-Americana, Araneidea, 1: 51, pl. 6, fig. 6, ♀. Female holotype from Tamahu, Guatemala in the British Museum, Natural History, examined. F.P.–Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 496, pl. 47, fig. 12, ♀. NEW SYNONYMY.

[1] Note added in proof. C. Dondale made me aware recently that, according to Article 72 of the *International Code of Zoological Nomenclature*, the type has to be a specimen; thus the Abbot illustration cannot be the type. A neotype may be designated (Art. 75); this has not been done here.

Cyclosa caudata,—Keyserling, 1893, Spinnen Amerikas, 4: 279, pl. 14, fig. 206, ♀, ♂.

Cyclosa culta O.P.–Cambridge, 1893, Biologia Centrali-Americana, 1: 112, pl. 14, fig. 12, ♂. Two male syntypes from near Omilteme, Guerrero, Mexico in the British Museum, Natural History, examined. F.P.–Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 493, pl. 47, fig. 2, ♂. NEW SYNONYMY.

? *Cyclosa tuberculifera* O.P.–Cambridge, 1898, Biologia Centrali-Americana, Araneidea, 1: 269, pl. 36, fig. 10, ♂. Male holotype without palpi from Teapa, Mexico in the British Museum, Natural History, examined. F.P.–Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 493, pl. 47, fig. 1, ♂. Doubtful NEW SYNONYMY.

Cyclosa turbinata,—McCook, 1893, American Spiders, 3: 224, pl. 17, figs. 5, 6, ♀, ♂. Comstock, 1940, Spider Book, p. 468, fig. 467, ♀. Roewer, 1942, Katalog der Araneae, p. 761. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 237, fig. 710, ♀. Bonnet, 1956, Bibliographia Araneorum, 2: 1325.

Cyclosa nanna Ivie and Barrows, 1935, Bull. Univ. Utah, biol. ser. 3(2): 18, figs. 52, 53, ♀, ♂. Male holotype and female paratype from Naples, Georgia, lost. NEW SYNONYMY.

Note. Specimens of *C. nanna* are not in the American Museum or University of Utah or Ohio State University collections. The illustration shows the epigynum of *C. turbinata*.

Specimens in many collections of *C. turbinata* had been misidentified as *C. conica*. Many *C. conica* records appear to be this species.

Measurements. Female from Louisiana: Total length 4.3 mm. Carapace 1.5 mm long, 1.0 wide. First femur, 1.3 mm; patella and

→

Figures 21–37. Old-world *Cyclosa*.

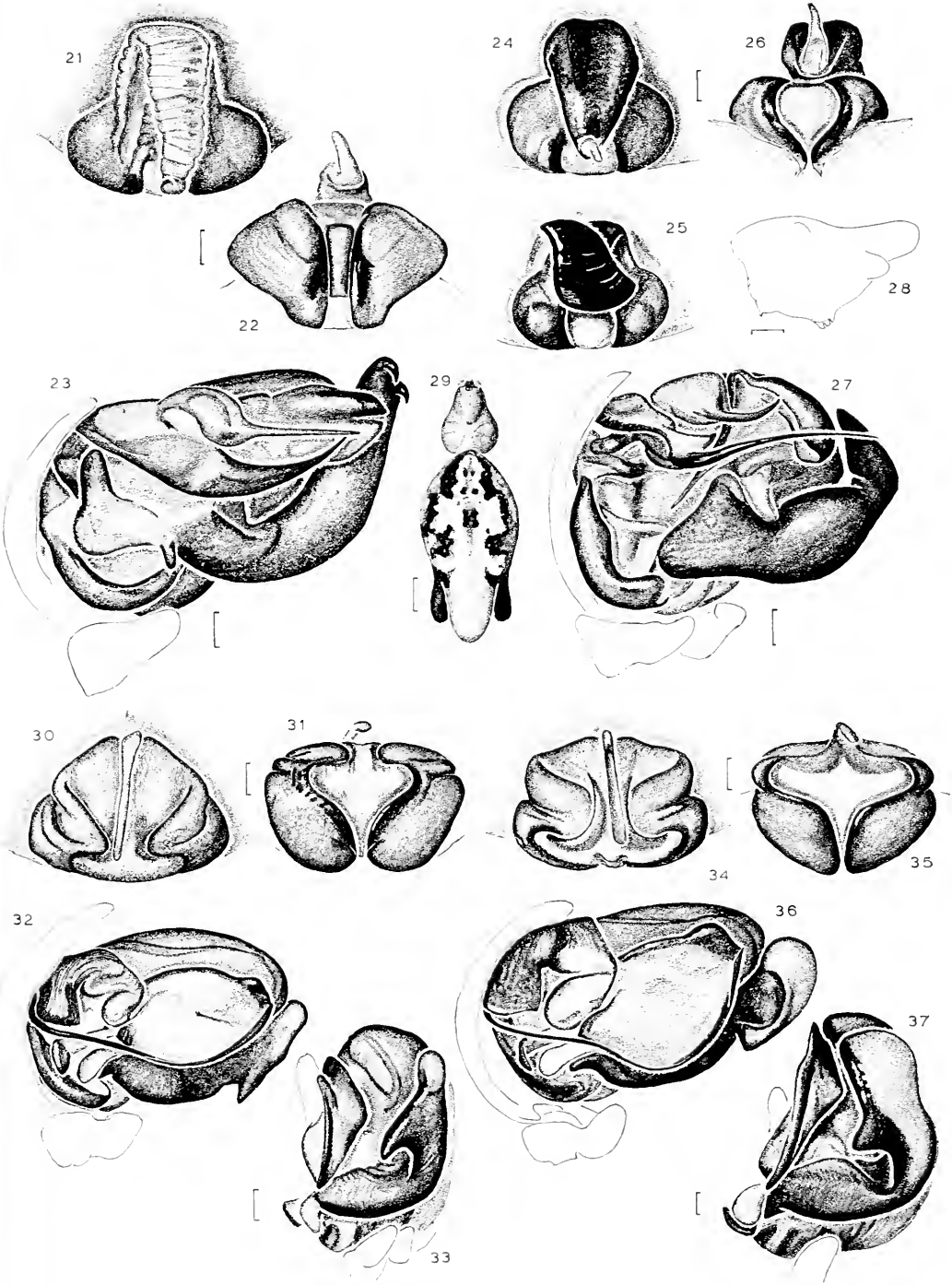
Figures 21–23. *C. oculata* (Walckenaer) (Central Europe): 21, 22. Epigynum. 21. Ventral. 22. Posterior. 23. Left male palpus, mesal view.

Figures 24–29. *C. insulana* (Costa): 24–26. Epigynum: 24, 25. Ventral. 26. Posterior. 27. Palpus, mesal view. 28. Female abdomen from side. 29. Female, legs removed. 24, 26, 28, 29. (Southern France). 25, 27. (New Guinea).

Figures 30–33. *C. sierrae* Simon (Central Italy): 30, 31. Epigynum: 30. Ventral. 31. Posterior. 32, 33. Palpus: 32. Mesal. 33. Ventral.

Figures 34–37. *C. algerica* Simon (Southern France): 34, 35. Epigynum: 34. Ventral. 35. Posterior. 36, 37. Palpus: 36. Mesal. 37. Ventral.

Scale lines, 0.1 mm, Figs. 28, 29, 1 mm.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tibia, 1.4; metatarsus, 0.8; tarsus, 0.5. Second patella and tibia, 1.2 mm; third, 0.8; fourth, 1.3.

Male from Louisiana: Total length 2.5 mm. Carapace 1.4 mm long, 1.1 wide. First femur, 1.2 mm; patella and tibia, 1.3; metatarsus, 0.7; tarsus, 0.4. Second patella and tibia, 1.1 mm; third, 0.7; fourth, 1.0.

Variation. Females vary in total length 3.3 to 5.2 mm, carapace 1.4 to 1.7 long, 0.9 to 1.3 wide. Males vary in total length 2.1 to 3.2 mm, carapace 1.3 to 1.6 long, 1.0 to 1.2 wide. Small and large individuals appeared in many collections, but Florida specimens are usually small. Some females from Central America have a much longer posterior tail.

Diagnosis. Female *C. turbinata* differ from *C. conica* by being smaller in size and having a pair of anterior dorsal humps (often indistinct) on the abdomen (Figs. 39, 48) and by the lightly sclerotized base of the epigynum (Fig. 41). In North America, females differ from other species by the abdomen shape and the details of the epigynum (Figs. 39, 41). The males differ from those of *C. conica* by lacking macrosetae on the fourth coxae, and by their smaller size (less than 3.3 mm total length); from *C. caroli* by usually having the abdomen only slightly overhanging the spinnerets (Fig. 38); and from the related *C. caroli* and *C. walckenaeri* by having a median apophysis in the palpus with a terminal hook and a large median proximally directed tooth (Figs. 46, 47). There is no such tooth in *C. caroli*, and that of *C. walckenaeri* is small and the median apophysis is relatively longer.

Natural History. The web with stabilimentum is illustrated in Plate 2. The cocoons are attached to the stabilimentum and are covered with insect remains. The lowest ones may have spiderlings while the upper one has only eggs (Kaston, 1948).

Specimens have been collected by sweeping lawns in West Virginia, by sweeping abandoned fields and in a garden in North Carolina, in a blueberry patch near Lake Michigan, from oak dunes in Indiana, by beating underbrush in Arkansas, from a roadcut in Missouri, in salt marshes, coastal oak woods and by sweeping a meadow in California. Judging by these notes, *C. turbinata* prefers more open areas than *C. conica*, but according to Berry (1970) *Cyclosa turbinata* has no clear habitat preferences in North Carolina. H. K. Wallace's field notes report specimens from a slope near a stream, the web attached to a stump, from a stream bottom, from a slope near a stream in Giles County, Virginia and in an old field on a stream bank and in a sterile area with fetterbush (*Leucothoë*) in Florida. I have collected specimens in central Florida in dry grassy "prairie." Males are mature from July to August in New York, Pennsylvania and Virginia, from June to September in the Southeast, from March to August in Florida, to October in Texas, and from March to September in California. Females have been collected from May to September in northern part of the range, in all seasons except December to February in Florida.

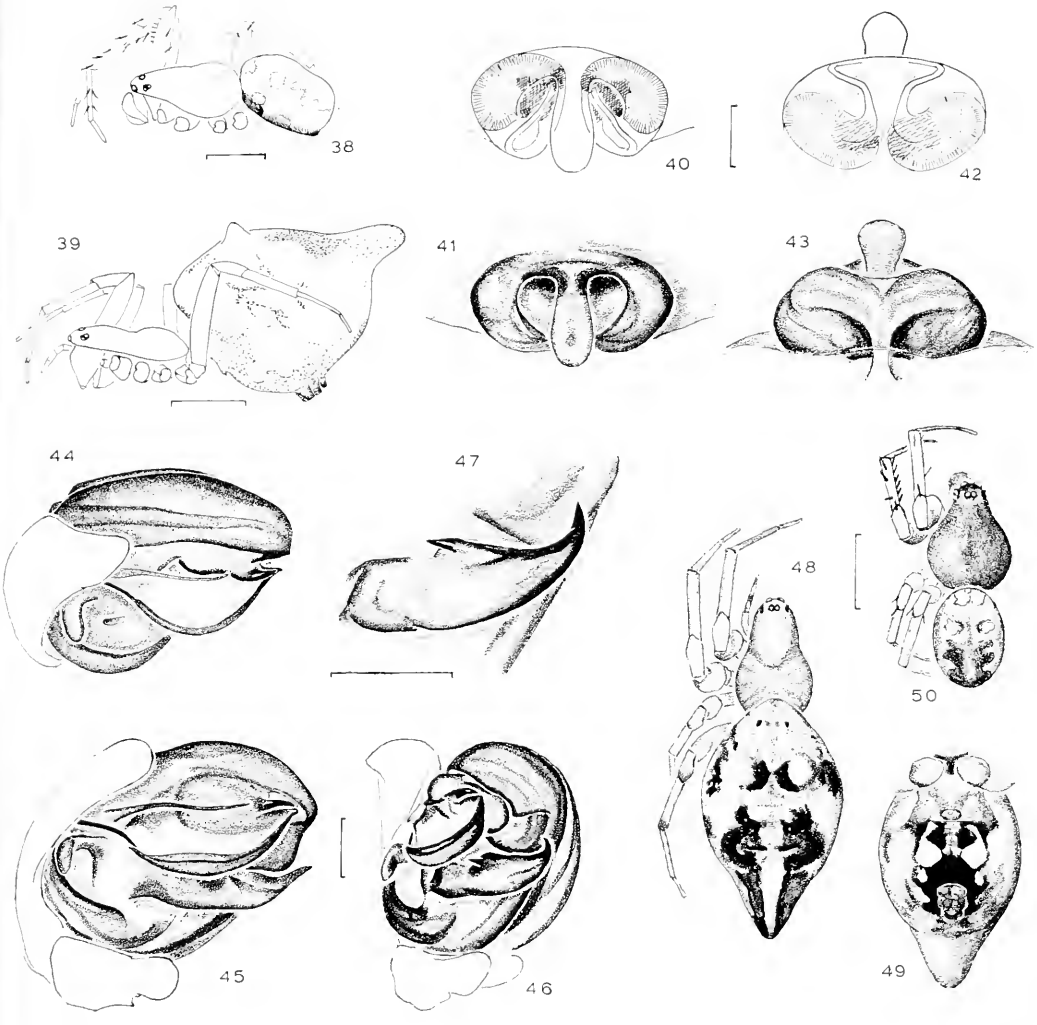
Distribution. Connecticut, central New York, southern Michigan to Washington, south to Central America, West Indies, and also Bermuda, Cocos Island and Galapagos Islands (Map 2).

Cyclosa caroli (Hentz)
Plate 3, Figures 51–63, Map 2

Epeira caroli Hentz, 1850, J. Boston Soc. Natur. Hist., 6: 24, pl. 3, fig. 15, ♀. Female type from Alabama, destroyed. Keyserling, 1863, Sitzungsber. Naturges. Isis Dresden, p. 137, pl. 6, figs. 17–19, ♀.

Cyclosa lacerta O.P.-Cambridge, 1889, Biologia Centrali-Americana, Araneidea, 1: 50, pl. 7, fig. 14, ♂ (as *Epeira lacerta*). Male lectotype here designated from Guatemala or Panama in the British Museum, Natural History, examined. Keyserling, 1893, Spinnen Amerikas, 4: 275, pl. 14, fig. 204, ♂. F.P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidae, 2: 494, pl. 47, fig. 3, ♂. NEW SYNONYMY.

Cyclosa caroli,—McCook, 1893, American Spiders, 3: 277, pl. 17, figs. 7, 8, ♀, ♂. Keyserling, 1893, Spinnen Amerikas, 4: 272, pl. 14, fig. 202, ♀.



Figures 38–50. *Cyclosa turbinata* (Walckenaer): 38. Male from side. 39. Female from side. 40–43. Epigynum: 40, 41. Ventral. 42, 43. Posterior. 40, 42. Cleared. 44–47. Male left palpus: 44. Apical. 45. Mesal. 46. Ventral. 47. Median apophysis, ventral. 48. Female, dorsal. 49. Female abdomen, ventral. 50. Male, dorsal. *Scale lines.* 0.1 mm, except Figs. 38, 39, 48–50, 1.0 mm.

♂. F.P.–Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 494, pl. 47, fig. 4, ♀. Comstock, 1940, Spider Book, rev. ed., p. 467. Roewer, 1942, Katalog der Araneae, 1: 761. Bonnet, 1956, Bibliographia Araneorum, 2: 1310.

Cyclosa conigera F.P.–Cambridge, 1904, Biologia Centrali-Americana, 2: 494, pl. 47, fig. 5, ♀. Ten female syntypes from Omilteme, Mexico in the British Museum, Natural History, examined. NEW SYNONYMY.

Cyclosa elongata Franganillo, 1930, Mem. Inst. Nac. Invest. Cient., 1: 68. Type specimens from Sierra Maestra and Montañas de Trinidad in Cuban Academy of Sciences, lost.

Parazygia accentonotata di Caporiacco, 1955, Acta biol. Venezuelica, 1: 345, fig. 30, ♂. Male holotype from Rancho Grande, Aragua, Venezuela in the collections of Universidad Central, Caracas, Venezuela, examined. NEW SYNONYMY.

Measurements. Female from Florida: Total length 6.0 mm. Carapace 1.7 mm

long, 1.1 wide. First femur, 1.4 mm; patella and tibia, 1.7; metatarsus, 0.9; tarsus, 0.4. Second patella and tibia, 1.4 mm; third, 0.9; fourth, 1.4.

Male from Florida: Total length 2.7 mm. Carapace 1.4 mm long, 0.9 wide. First femur, 1.3 mm; patella and tibia, 1.2; metatarsus, 0.7; tarsus, 0.4. Second patella and tibia, 1.1 mm; third, 0.6; fourth, 1.1.

Variation. Females vary in total length from 3.7 to 6.8 mm, carapace 1.3 to 1.9 long, 0.8 to 1.2 wide. Males vary in total length from 3.0 to 3.4 mm, carapace 1.5 to 1.7 long, 1.1 to 1.2 wide. The largest individuals came from Mississippi and Panama, the smallest from Florida and Trinidad. The tail of the female and especially of the male varies in length.

Diagnosis. Females of *C. caroli* found north of Mexico can be separated from other species by the shape of the abdomen (Figs. 52, 61). The epigynal scape of *C. caroli* is almost always oval to round (Fig. 54) and is lightest in the center, unlike the scape of Central and South American species with a similar abdomen. Male individuals almost always have a small abdominal tail (Fig. 51), lacking in *C. turbinata* males. Males differ from related species also in the shape of the short palpal median apophysis, which has a distal hook and a convexly curved distal keel below the hook (Figs. 59, 60). The middle spine present in *C. turbinata* and *C. walckenaeri* median apophysis is absent.

Natural History. Field notes of H. K. Wallace report it from dense palmettos in palmetto, in live-oak-hammock and in a ravine, both in Alachua Co., Florida. I have collected specimens in Baygall woods and mixed cypress forest in central Florida. Comstock (1940) observed the species in a "jungle near Miami, Fla. The orb of the adult is six inches in diameter. The female fastens her egg-sacs in a series which extend across the web from the hub to the upper margin like a stabilimentum, and looks like a dead twig caught in the web. This band of egg-sacs and the spider are of the same gray colour. When disturbed the spider rushes to the band and appears as if it were part of it. And here he will cling motionless even when the band is removed from the web. . . . I also observed smaller individuals shake their webs; these clung to the stabilimentum, projecting the body at right angles to it and in this position shook the web violently." (Plate 3.)

Ruth Buskirk, in a note with the collections, says she found the "species very common in woods and woods edge in Costa Rica. The orb has 25 radii, 22 spiral turns . . . a radius of 8–12 cm, always vertical orientation, debris and insect [remains] wrapped with silk into long straight lines, . . . ♀'s often with egg cases in upper line."

Adult males have been collected in February, July, September and December in Florida, in June and July in Central America. Females are mature in all seasons.

Distribution. Georgia, Florida, Gulf states, Mexico, Central America, West Indies, to southern Colombia, Venezuela and Guyana (Map 2).

Cyclosa walckenaeri (O.P.–Cambridge)
Plate 4, Figures 64–77, Map 2

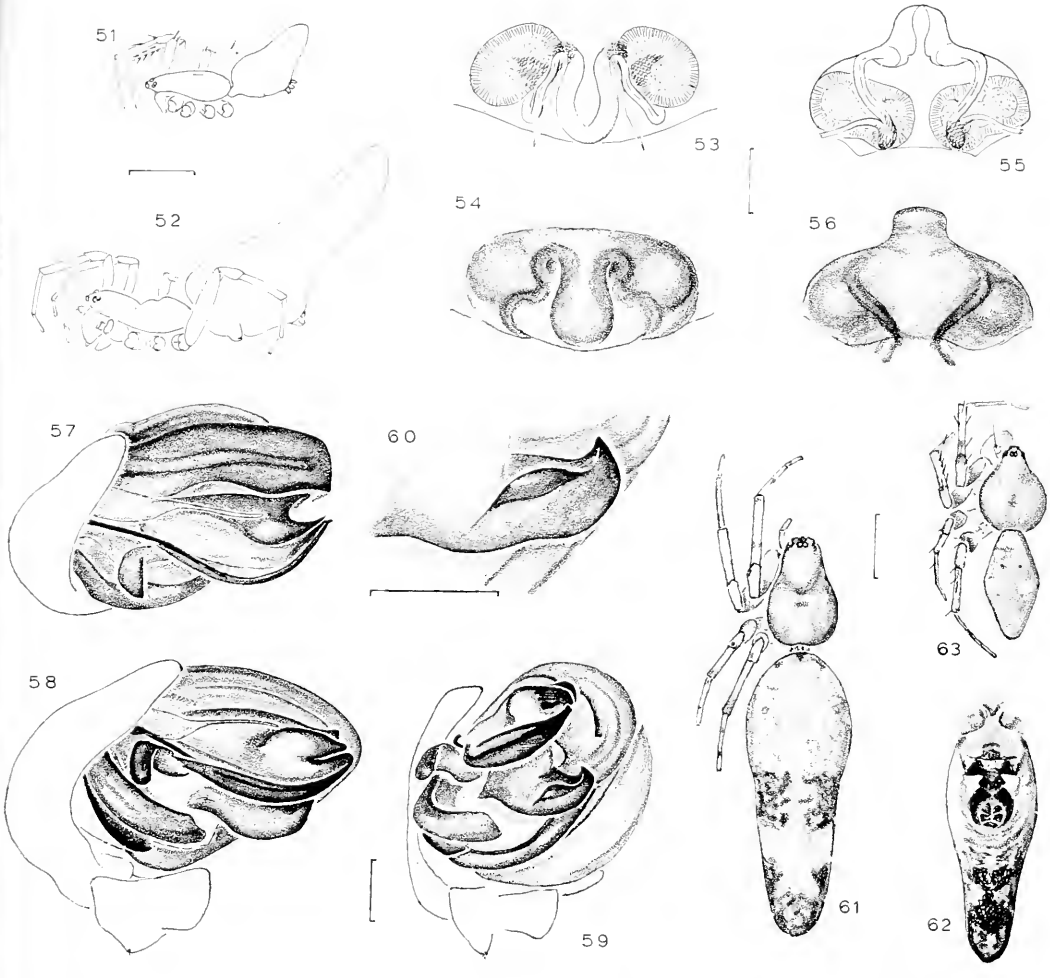
Epeira bifurcata,—Keyserling, 1863, Sitzungsber. Naturf. Gesell. Isis, Dresden, p. 142, pl. 6, figs. 22–23, ♀. Specimens from Bogota, Colombia. Not *Epeira bifurcata* Walckenaer, 1841.

Turckheimia walckenaerii O.P.–Cambridge, 1889, Biologia Centrali-Americana, Araneidea, 1: 47, pl. 8, fig. 6, ♀. Three female syntypes from Volcan de Fuego, Guatemala in the British Museum, Natural History, examined.

Epeira walckenaerii Keyserling, 1892, Spinnen Amerikas, 4: 98, pl. 5, fig. 73, ♀, ♂. Types from Bogota, Colombia, Guatemala, Taquara do Mundo novo and Rio Grande do Sul, Brazil in the British Museum, Natural History.

Cyclosa walckenaeri,—McCook, 1893, American Spiders, 3: 226, pl. 17, fig. 1, ♀, ♂. F.P.–Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 495, pl. 47, fig. 9, ♀. Petrunkevitch, 1930, Trans. Connecticut Acad. Sci., 30: 315, figs. 188, 189, ♀.

Cyclosa trifida F.P.–Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 495, pl. 47, fig. 7, ♀. Three female syntypes, slightly dam-



Figures 51–63. *Cyclosa caroli* (Hentz): 51. Male from side. 52. Female from side. 53–56. Epigynum: 53, 54. Ventral. 55, 56. Posterior. 53, 55. Cleared. 57–60. Male left palpus: 57. Apical. 58. Mesal. 59. Ventral. 60. Median apophysis. 61. Female, dorsal. 62. Female abdomen, ventral. 63. Male, dorsal.

Scale lines. 0.1 mm except Figs. 51, 52, 61–63, 1.0 mm.

aged from Cohabon, Guatemala, in the British Museum, Natural History, examined. NEW SYNONYMY.

? *Cyclosa cuadritubcrosa* Franganillo, 1936. Arácnidos de Cuba, p. 84. Juvenile holotype from Cuba in the Cuban Academy of Science, in poor condition, examined. It appears to lack lateral posterior tubercles.

Note. Specimens of this species and several similar South American species in both the American Museum and the Museum of Comparative Zoology had been labeled *Cyclosa oculata*. *Cyclosa oculata* (Walckenaer) (Figs. 21–23) is a European species not found in the Americas. The type specimens of the name came from Paris. This error dates from Simon (1900), who listed *C. oculata* as occurring in Hawaii, the United States, Antilles and Venezuela and indicated that *Epeira walckenaeri* Keyserling is probably a synonym. Simon did not examine genitalia carefully and the shape of the abdomen of the two species

is similar. E. B. Bryant (1940), skeptical of the synonymy, borrowed specimens of *C. oculata* from Paris and got specimens determined by Simon which were the same species as *C. walckenaeri*. Not surprisingly, they came from America: Hispaniola.

The three syntypes of *C. trifida* have the characteristic epigynum but the abdomen is flattened, apparently damaged when collected. They have the four posterior tubercles, but not the two anterior ones.

Measurements. Female from Texas: Total length 6.3 mm. Carapace 2.2 mm long, 1.5 wide. First femur, 2.0 mm; patella and tibia, 2.2; metatarsus, 1.1; tarsus, 0.6. Second patella and tibia, 1.9 mm; third, 1.0; fourth, 1.7.

Male from Texas: Total length 3.8 mm. Carapace 1.7 mm long, 1.4 wide. First femur, 1.7 mm; patella and tibia, 1.7; metatarsus, 1.0; tarsus, 0.6. Second patella and tibia, 1.2 mm; third, 0.7; fourth, 1.4.

Variation. Total length of females 3.8 to 6.8 mm, carapace 1.3 to 2.0 long, 1.0 to 1.2 wide. Total length of males 2.1 to 3.8 mm, carapace 1.1 to 1.7 long, 0.8 to 1.3 wide. The smallest females came from Florida, the largest individuals from Guatemala. Some specimens have the abdomen longer. Rarely, the sides of the scape of the epigynum are curved out and the scape slightly oval. One female from Oriente Province, Cuba had an epigynum like that of *C. walckenaeri*, but the abdomen was like that of *C. caroli*, with only faint indications of humps.

Diagnosis. The four humps on the posterior tip of the abdomen and two dorsal humps anterior of the middle separate the species from other *Cyclosa* in North America. Unlike *C. caroli* and *C. turbinata* the sides of the epigynum scape are usually parallel, making it a narrow rod (Fig. 67). Males can usually be readily separated by the indications of the four posterior abdomen humps (Figs. 64, 76). The median apophysis of the palpus is very long, but unlike that of *C. turbinata*, the middle spine is minute and the distal hook continues into a keel proximally (Figs. 72, 73). That of *C. caroli* lacks the middle tooth entirely and is short.

Natural History. Specimens of *C. walckenaeri* have been found on large aloe and in open shrubs at edge of woods in Jamaica, in dry shrubs in the Virgin Islands, in a garden in Cuba, on shrubby edge of woods along coast of Florida Keys, on mangroves in Baja California and in a pine-oak forest in Chiapas. The eggs are hung in the web. Webs of juveniles observed in Florida had a narrow stabilimentum of debris (Plate 4) and the only one containing egg-sacs had been destroyed and left unfinished.

Males have been collected in May, August, September and October in the southern states and northern Mexico and females in all seasons.

Distribution. Southern Florida, southern Texas, central California coast to Panama and West Indies (Map 2).

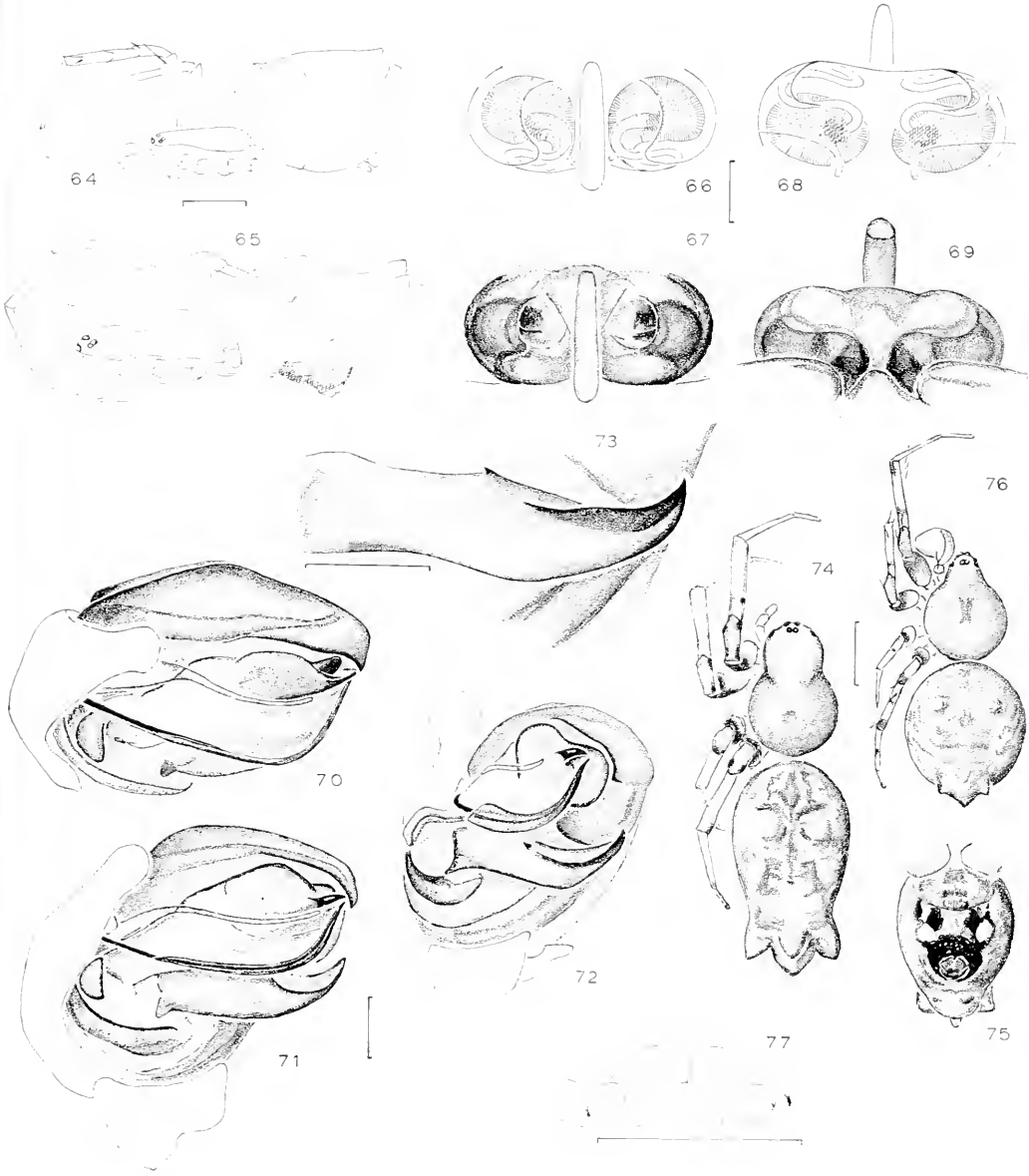
Cyclosa bifurca (McCook)
Plate 5, Figures 78–89, Map 2

Cyrtophora bifurca McCook, 1887, Proc. Acad. Natur. Sci. Philadelphia, 3: 342. Female, male syntypes from Fairyland, Merrit's Island on the Indian River, Florida in the Philadelphia Academy of Sciences, lost.

Cyclosa fissicauda O.P.–Cambridge, 1889, Biologia Centrali-Americana, Araneidea, 1: 49, pl. 8, fig. 7, ♀. Fifteen syntypes in two vials, from near Dolores, Guatemala in the British Museum, Natural History, examined. Keyserling, 1893, Spinnen Amerikas, 4: 274, pl. 14, fig. 203, ♀.

Cyclosa bifurca,—McCook, 1893, American Spiders, 3: 227, pl. 17, figs. 9, 10, ♀, ♂. F.P.–Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 495, pl. 47, fig. 8. Comstock, 1940, Spider Book, p. 467, figs. 465, 466, ♀, egg-sacs. Roewer, 1942, Katalog der Araneae, 1: 759. Bonnet, 1956, Bibliographia Araneorum, 2(2): 1309.

Description. Female from Florida: In alcohol, carapace yellow-white, sternum brown with a central longitudinal white band and white patches near base of anterior three coxae. Legs yellow-white with some indistinct dark bands distally. Dorsum of abdomen white with indistinct



Figures 64–77. *Cyclosa walckenaeri* (O.P.–Cambridge): 64. Male from side. 65. Female from side. 66–69. Epigynum: 66, 67. Ventral. 68, 69. Posterior. 66, 68. Cleared. 70–73. Male left palpus: 70. Apical. 71. Mesal. 72. Ventral. 73. Median apophysis. 74. Female, dorsal. 75. Female abdomen, ventral. 76. Male, dorsal. 77. Male coxae.

Scale lines. 0.1 mm except Figs. 64, 65, 74–77, 1.0 mm.

marks, sides with indistinct gray marks. Venter with a white square whose sides are lateral to the spinnerets. The legs are thick (Fig. 88). Total length 6.5 mm. Carapace 2.2 mm long, 1.7 wide. First femur, 2.5 mm; patella and tibia, 2.7; metatarsus, 1.6; tarsus, 0.8. Second patella and tibia, 2.2 mm; third, 1.2; fourth, 2.1.

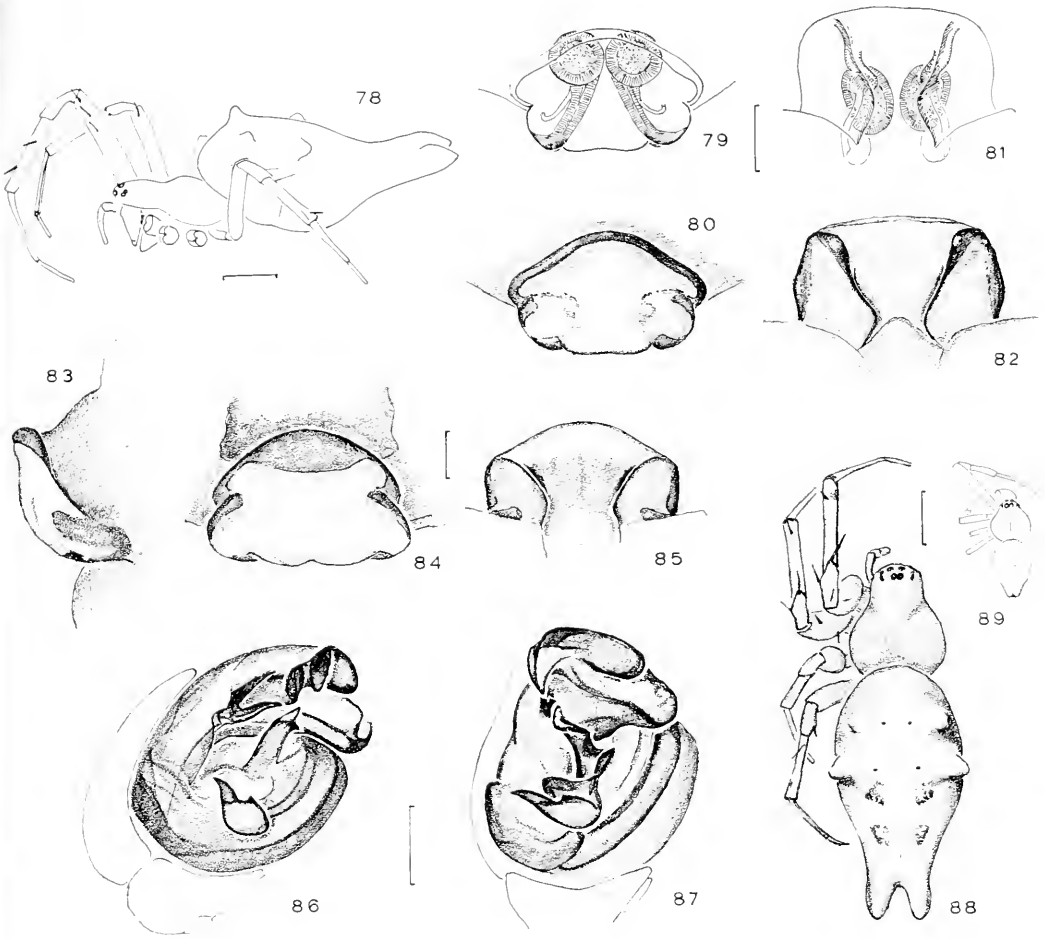
Male from Florida: Carapace and abdomen yellowish white with a median black longitudinal line on carapace, some indistinct black pigment spots on the abdomen. Posterior median eyes 0.6 diameter of anterior medians. Anterior laterals 0.5, posterior laterals 0.6 diameters. Anterior median eyes their diameter apart, 0.7 from laterals. Posterior median eyes their diameter apart, 1.5 from laterals. Neither coxae nor legs modified. The abdomen is like that of female, but the humps are barely visible. Total length 1.8 mm. Carapace 0.9 mm long, 0.7 wide. First femur, 1.0 mm; patella and tibia, 1.1; metatarsus, 0.9; tarsus, 0.4. Second patella and tibia, 0.8 mm; third, 0.4; fourth, 0.6. Another male measured 1.7 mm total length.

Note. The live spider and the egg-sacs are green, the venter of the abdomen having a bright red patch between epigynum and spinnerets (Comstock, 1940). The color washes out in alcohol. The egg-sac is an irregular octagon, and as many as 10–14 egg-sacs may be strung together (McCook, 1887). The male is minute. Only one male was found in a collection of 207 specimens. About another 130 specimens yielded only one more male.

Variation. Total length of females 5.1 to 9.0 mm long, carapace 2.0 to 2.9 mm long, 1.5 to 2.3 mm wide. Some individuals have more black pigment than others and have the legs ringed.

Diagnosis. North of Mexico no other American species of *Cyclosa* has a forked tail (Figs. 78, 88). *Cyclosa furcata* O.P.–Cambridge is similar in appearance but the epigynum has a scape and the base differs in shape.

Natural History. J. Boursot collecting in El Salvador reported on notes in the vial: "with contracted legs these spiders crouch at one end of the stabilimentum composed of rejected chewed food which they match identically. Discovered only on tarred surface of huge water tank." C. B. Worth (1940) reported on the shape and coloration of the animals whose vertical webs, six inches in diameter, he saw on the walls of a Florida house, parallel to the walls: "The egg-sacs are arranged in a row, occupying the position of the hands of a clock at exactly noon. The spider herself reposes at the center of the web, that is immediately below and touching the lowermost egg-sacs. She invariably faces the ground, so that her abdomen appears as an additional egg-sac in the row above her. . . ." The "mass of objects in the web is that of a catkin. . . . This appearance is heightened by the spider's disposition of captured food. Such prey is wrapped in silk and anchored below the spider, forming an uneven row of objects as a direct short continuation of the line of egg-sacs. The average length of the 'catkins,' i.e. egg-sacs, spider food-sacs . . . is from two-and-a-half to three inches, which means that they occupy about half the diameter of the web. The usual number of egg-sacs ranges from five to nine with eight on an average. But the most remarkable feature of all is the resemblance of the egg-sac to the abdomen of the female. The latter is light green with dark green central and lateral stripes and in these details the egg-sacs agree precisely with their maternal source. The spider's abdomen moreover bears a series of tubercles and projections, which again are reproduced faithfully in the egg-sacs even including the terminal bifurcation. The egg-sacs are finally deposited in the web in a shingled or overlapping series, and the spider takes a position at the center of the web so that her abdomen overlaps the lowermost egg-sac in an exact continuation of the series above her. . . . The spider's light green color and smooth integument give it a translucent appearance when seen close at hand. Even this quality of



Figures 78–89. *Cyclosa bifurca* (McCook): 78. Female from side. 79–85. Epigynum: 79, 80, 84. Ventral. 81, 82, 85. Posterior. 83. Lateral. 79, 81. Cleared. 79–83. (Florida). 84, 85. (Texas). 86, 87. Male left palpus: 86. Mesal. 87. Ventral. 88. Female, dorsal. 89. Male, dorsal.

Scale lines. 0.1 mm except Figs. 78, 88, 89, 1.0 mm.

translucence is duplicated in the smooth-woven texture of the egg-sacs." (Plate 5.)

The spider has been collected on a torn-down building in a wooded area of Australian pines (*Casuarina* sp.) and cabbage palms (*Sabal palmetto*) and on a saw palmetto leaf (*Serenoa* sp.) in Florida, from the nest of a wood rat (*Neotoma* sp.), and from a wasp nest. One record is from an arid, subtropical area in San Luis Potosí. Comstock (1940) found it in a "jungle near the shore" and also on the "ceiling of a veranda by the hundred." Mature females have been collected in every month in Florida and Texas.

Distribution. Florida, southern Alabama, southern Texas, Mexico to El Salvador, Cuba and Hispaniola (Map 2).

Metazygia F.P.–Cambridge

Metazygia F.P.–Cambridge, 1903, Biologia Centrali-Americana, Araneidea, 2: 501. Type species by original designation *M. wittfeldae* (McCook). The name is feminine.

Diagnosis. The abdomen is spherical (Fig. 108) to round and dorsoventrally flattened (Figs. 98, 109) as in *Nuctenea* and *Zygiella*, but differs from those two genera by having no pigment ventrally between genital groove and spinnerets (Figs. 99, 117). The carapace differs from that of *Nuctenea* by lacking fine setae (Figs. 96, 108), and the epigynum differs by lacking a scape. In place of the scape is a laterally flattened knob (Figs. 90–92), which can expand and project anteriorly in *M. zilloides* (Figs. 104–106) so as to resemble the epigynum of *Eustala* species. There is no such knob in *M. carolinalis* (Fig. 112).

Males differ from *Nuctenea* in having only one macroseta on the palpal patella, as in *Zygiella*, and differ from *Zygiella* in the very different structure of the palpus. *Metazygia*, unlike *Zygiella*, has a hook-shaped paracymbium (p in Fig. 103), a transparent subterminal apophysis (sa), and a knob-shaped median apophysis (m), ventrally attached (Figs. 101–103). *Metazygia* resembles *Zygiella* in having the tegulum (t) of the palpus modified; however, the modification is apical (Figs. 102, 111). The palpus is similar to that of *Eustala* but the median apophysis (m) is always knob-shaped (Figs. 101–103, 110, 111), not cone-shaped as in *Eustala*.

Description. Carapace smooth with few hairs, often darker anteriorly than posteriorly (Fig. 96), or with a median longitudinal pigment line (Fig. 108), with little or no thoracic depression.

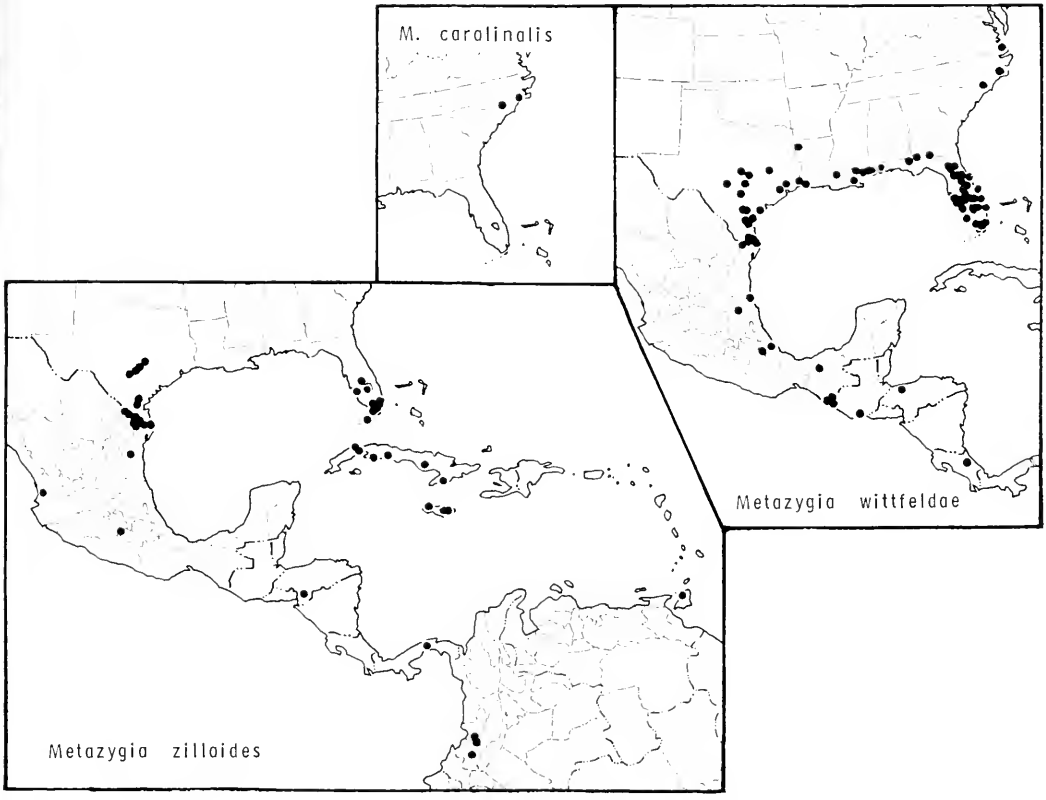
Eye sizes subequal (*M. carolinalis*) or anterior median eyes slightly larger than others (*M. wittfeldae*, *M. zilloides*). Laterals some distance from medians (Fig. 97) except in the small *M. zilloides* in which the eyes of the anterior row are equally spaced. Height of clypeus slightly less than diameter of anterior median eyes (Fig. 97). Chelicerae very strong, bulging proximally (Fig. 97), narrower distally, especially in *M. carolinalis*. Legs thick and strong (Figs. 96, 108), not banded, with many macrosetae and setae. First leg longest, legs 1,2,4,3. Abdomen oval to round, more or less dorsoventrally flattened (Figs. 96, 98, 108, 109, 116). In *M. carolinalis* the abdomen has dorsal sclerotized discs (Fig. 116). No black pigment on venter (Figs. 99, 117).

Males slightly smaller (Fig. 100) than females, with similar coloration and eyes. The chelicerae and fangs of some tropical species are modified, perhaps for copulation. Legs differ from those of females by being slightly longer and having more macrosetae (Fig. 100), especially on the second tibia. The distal margin of first coxa has a hook that fits into a groove on the second femur.

Genitalia. The base of the epigynum has a ventral, laterally compressed knob in place of the scape (Figs. 90–92, 104–106); the knob is absent in *M. carolinalis*; in *M. zilloides* it projects anteriorly if expanded, resembling that of *Eustala*.

The male palpus, similar to that of *Eustala*, differs in several ways. The terminal apophysis is a prong (a in Figs. 103, 110, 111), the subterminal apophysis often a transparent bubble (sa in Figs. 101–103, 110). The embolus (e), hidden in the temperate species, may have a piece that breaks off during mating and (in *M. zilloides*) remains in the epigynum. (But this is not certain, as the two common species north of Mexico have the embolus hidden behind the conductor and subterminal apophysis.) The conductor is a complex sclerite and the median apophysis (m) a simple knob (Figs. 102, 103, 110, 111), not a cone hanging down as in *Eustala*. The *Metazygia* palpus has a large sclerite mesally which may be the stipes (Figs. 101, 103, with texture in 110); it differs in shape in related tropical species.

Natural History. Unlike the related *Eustala*, *Metazygia* makes a retreat near the orb web. *Metazygia wittfeldae* is often found on bridges and buildings; *Metazygia witt-*



Map 3. Distribution of *Metazygia carolinalis* (Archer), *M. wittfeldae* (McCook) and *M. zilloides* (Banks).

feldae becomes active after dark, tearing down remnants of the old web and making new radii, scaffolding and viscid threads. The old web is usually left until a new one is built, which may not be every night. Threads coated with cornstarch (dusted by photographers the previous night) are hauled in, two sections at a time, balled up, and thrown horizontally away from the web, with some force, at the rate of a ball every minute or two. Silk not dusted is probably eaten. During the day the spider remains in a crevice; at night it hangs in the center of the web. The light from a flashlight may cause the spider to move away. The webs observed at the Archbold Biological Station, Lake Placid, Florida were loose with few frame threads and 10 to 18 radii. The number of viscid threads in several webs was 18, 16, 22, 25, 15 below the hub and 11, 3, 3, 17, 10 above the hub. The webs had solid hubs (Plate 6) and horizontal diameters ranging from 10 to 27 cm. Webs, as many as five next to each other in a suitable corner, were vertical between railings of a ramp 35 cm above the ground; at 2.7 m above the level of the ramp, under the ceiling, the webs were almost horizontal. The spiders avoided the area near a light fixture, but used areas some distance away, where they harvested insects attracted to the light.

Species. There are three species north of Mexico; most other species are tropical American (Map 3); none is known outside of America.

KEY TO FEMALE *METAZYGIA*

1. Epigynum without ventral median knob (Fig. 112); dorsum of abdomen with 4 pairs of sclerotized discs (Fig. 116); North Carolina ..... *carolinalis*
- Epigynum with a ventral median, laterally compressed knob (Figs. 90–92, 104–106); abdomen without sclerotized discs; Virginia south to Texas 2
2(1) Median knob very narrow, areas to side and anterior to it soft and expandable (Fig. 104); openings of epigynum on ventral face on each side (Fig. 104); dorsum of abdomen with a pair of anterior black marks (Fig. 108) ..... *zilloides*
- Median knob wide; areas to side and anterior to it not expandable (Fig. 90); openings of epigynum posterolateral of base (Figs. 91, 92); dorsum of abdomen with a series of dark brackets, farthest apart anteriorly, and a median dark line (Fig. 96) ..... *wittfeldae*

KEY TO MALE *METAZYGIA*
(*M. CAROLINALIS* MALE UNKNOWN)

1. Terminal apophysis prong of palpus pointed (Figs. 101–103) ..... *wittfeldae*
- Terminal apophysis prong of palpus with blunt tip, wider at tip than proximally (Figs. 110, 111) ..... *zilloides*

Metazygia wittfeldae (McCook)
Plate 6, Figures 90–103, Map 3

Epeira wittfeldae McCook, 1893, American Spiders, 3: 168, pl. 7, figs. 6, 7. Three female, two male and one male juvenile syntypes from Florida in the Academy of Natural Sciences, Philadelphia, examined.

Metazygia wittfeldae,—F.P.–Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 501, pl. 47, figs. 22, 23, ♀, ♂. Roewer, 1942, Katalog der Araneae, 1: 868. Bonnet, 1957, Bibliographia Araneorum, 2(3): 2820.

Description. Female from Florida: Carapace with head region much darker brown than thorax (Fig. 96). Sternum, legs orange. Dorsum of abdomen light brown with pairs of dark marks approaching each other posteriorly (Fig. 96). Total length 8.0 mm. Carapace 4.2 mm long, 3.0 wide. First femur, 3.6 mm; patella and tibia, 4.0; metatarsus, 2.7; tarsus, 1.2. Second patella and tibia, 3.7 mm; third, 2.3; fourth, 2.9.

Male: Total length 5.8 mm. Carapace 3.5 mm long, 2.4 wide. First femur, 3.6 mm; patella and tibia, 4.4; metatarsus, 3.4; tarsus, 1.4. Second patella and tibia, 4.0 mm; third, 2.2; fourth, 2.7.

Variation. Females varied in total length from 6.0 to 10.2 mm; carapace 2.9 to 4.2 long, 2.5 to 3.4 wide. Males varied, total length 5.0 to 7.0 mm; carapace 3.0 to 4.0 long, 2.2 to 3.1 wide.

Diagnosis. Females of *M. wittfeldae* differ from a similar West Indian species and from *M. dubia* (Keyserling) in Central and South America by the epigynum, which, in posterior view, has overhanging lateral bulges of the median area (Figs. 91, 92). Males differ by having the embolus hidden by the large subterminal apophysis (Figs. 101–103), a tooth at the base of the conductor (c in Figs. 102, 103) and a pocket at the distal edge of the tegulum (t in Figs. 102–103).

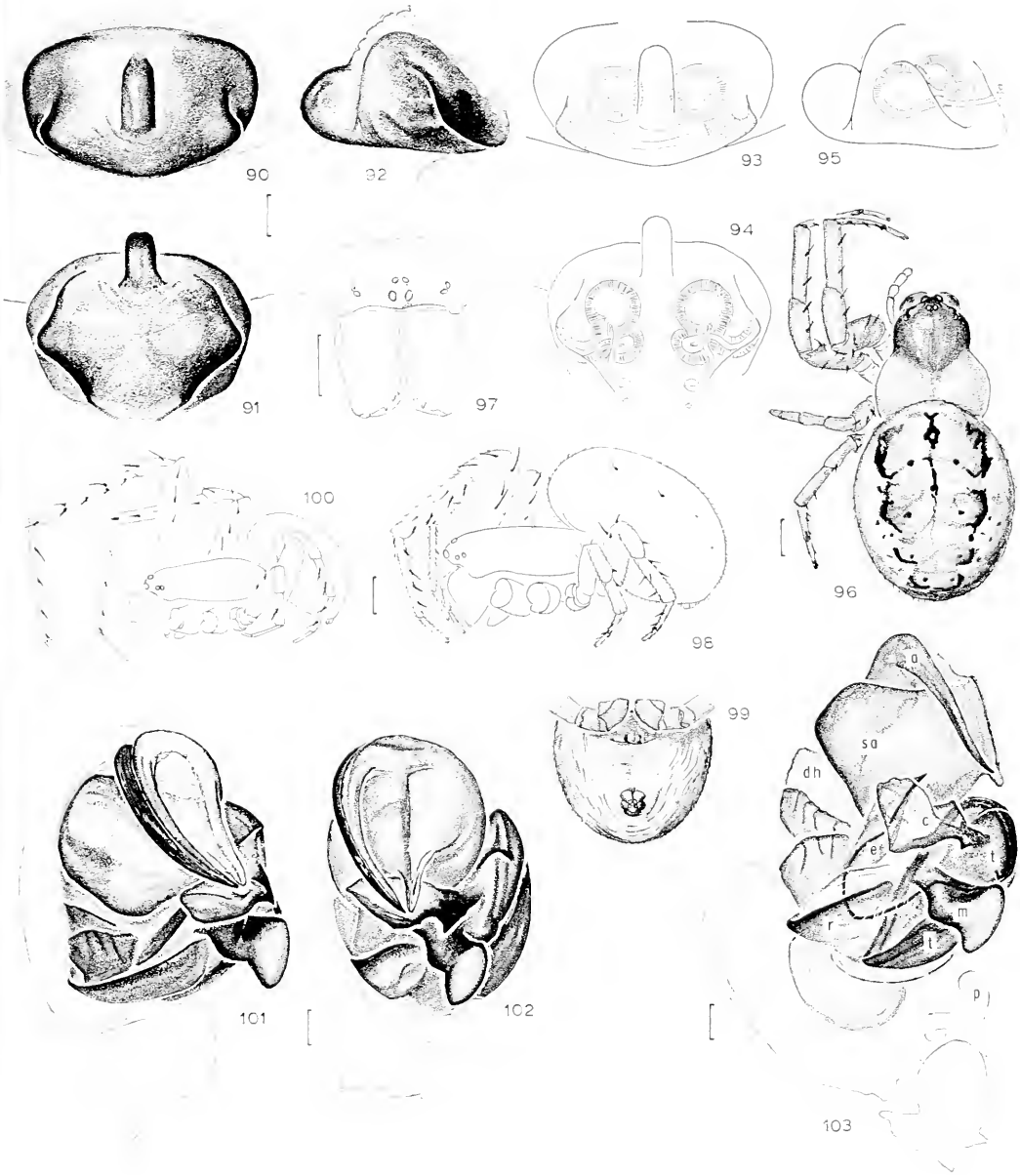
Natural History. This species is commonly found under the eaves of buildings from Virginia to Florida, and also on houses, and on and under bridges. In Florida, it has been found in cypress swamp, in tall grass, in citrus tree foliage, in vegetation bordering a canal, on canal banks with heavy cut grass and ragweed, and on slash pine (*Pinus elliottii*). Many specimens came from wasp nests. The web (Plate 6) is described above in the introduction to the genus *Metazygia*.

Distribution. From Norfolk, Virginia (numerous collections from buildings around Stumpy Lake) to Florida, Gulf states to Texas to Central America (Map 3).

Metazygia zilloides (Banks), new combination
Figures 104–111, Map 3

Epeira zilloides Banks, 1898, Proc. California Acad. Sci., 3 ser., 1: 255, plate 15, fig. 2, ♀, ♂. Three female, one male, one juvenile syntypes from Tepic, Mexico in the Museum of Comparative Zoology, examined.

Aranea dilatata F.P.–Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 513, pl. 49, fig. 9, ♂. Male lectotype here designated from [no locality] Guatemala in the British Museum, Natural History, examined. There are three



Figures 90–103. *Metazygia wittfeldae* (McCook): 90–94. Epigynum: 93–95. Cleared. 90, 93. Ventral. 91, 94. Posterior. 92, 95. Lateral. 96. Female, dorsal. 97. Female, eye region and chelicerae. 98. Female from side. 99. Female abdomen, ventral. 100. Male from side. 101–103. Left male palpus: 101. Mesal. 102. Ventral. 103. Mesoventral, expanded.

Abbreviations. a, terminal apophysis; c, conductor; dh, distal hematodocha; e, embolus; m, median apophysis; p, paracymbium; r, radix; sa, subterminal apophysis; t, tegulum.

Scale lines. 0.1 mm, except Figs. 96–100, 1.0 mm.

paralectotypes, of which one is *Metazygia incerta*. NEW SYNONYMY.

Metazygia keyserlingi Banks, 1929, Bull. Mus. Comp. Zool., 69: 94, fig. 63. Female holotype from Barro Colorado Island, Canal Zone, in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Metazygia albonigra,—Bryant, 1940. Bull. Mus. Comp. Zool., 86: 339, figs. 107–109, 111, ♀. ♂, erroneous determination, not *Larinia albonigra* Franganillo.

Araneus pallidulus,—Kraus, 1955, Abhandl. Senckenbergischen Naturf. Gesell., 493: 24, fig. 66, ♀. Erroneous determination.

Note. American Museum specimens had been labeled *Metazygia incerta*, Museum of Comparative Zoology West Indian specimens as *Metazygia albonigra* (Franganillo) and Florida and Texas specimens as *Epeira pallidula* (Keyserling) by Bryant, and as *M. keyserlingi* by Chickering. The name *Metazygia incerta* belongs to a different species. The name *Larinia albonigra* is a synonym of *L. directa* and the specimens were incorrectly determined by Bryant. *M. keyserlingi* is a synonym of *M. zilloides*.

Description. Female from Florida: Carapace light yellowish brown with a narrow, median, longitudinal dark band on carapace. Sternum, legs, light brownish. Dorsum of abdomen white with anterior pair of dark patches and four pairs of dark spots (Fig. 108). Total length 6.1 mm. Carapace 2.3 mm long, 1.8 wide. First femur, 2.2 mm; patella and tibia, 2.7; metatarsus, 1.8; tarsus, 0.8. Second patella and tibia, 2.2 mm; third, 1.3; fourth, 2.0.

Male from Florida: Total length 4.0 mm. Carapace 2.2 mm long, 1.7 wide. First femur, 2.7 mm; patella and tibia, 3.5; metatarsus, 2.7; tarsus, 1.0. Second patella and tibia, 2.8 mm; third, 1.4; fourth, 2.0.

Variation. Some specimens have the posterior of the abdomen dark and there are white rings around the black spots. Total length of females 3.6 to 7.4 mm, carapace 1.8 to 3.2 long, 1.4 to 2.4 wide. Total length of males 3.4 to 4.8 mm, carapace 1.7 to 2.6 long, 1.3 to 2.0 wide. Males from Cuba have the distal edge of the tegulum smooth, with no teeth.

Diagnosis. Most specimens have the anterior black patches on the abdomen and a series of dark spots (Fig. 108). Females differ from both *M. wittfeldae* and *M. incerta* (O.P.-Cambridge) by having anteroventrally directed openings on each side of the epigynal base (Fig. 104). Males differ from *M. wittfeldae* by the blunt terminal apophysis (Figs. 110, 111), and from *M. wittfeldae* and *M. incerta* by the shape of the (textured) stipes (Fig. 110), the shape of the conductor (under terminal apophysis, Fig. 111), and the toothed edge on the distal surface of the tegulum (Fig. 111).

Natural History. The species has been collected by sweeping flowers in Texas, in Florida in palmetto-poisonwood flats, among roadside weeds along a canal, in shrubs and vegetation, and on *Casuarina* (Australian pine). Males have been collected in Florida in June.

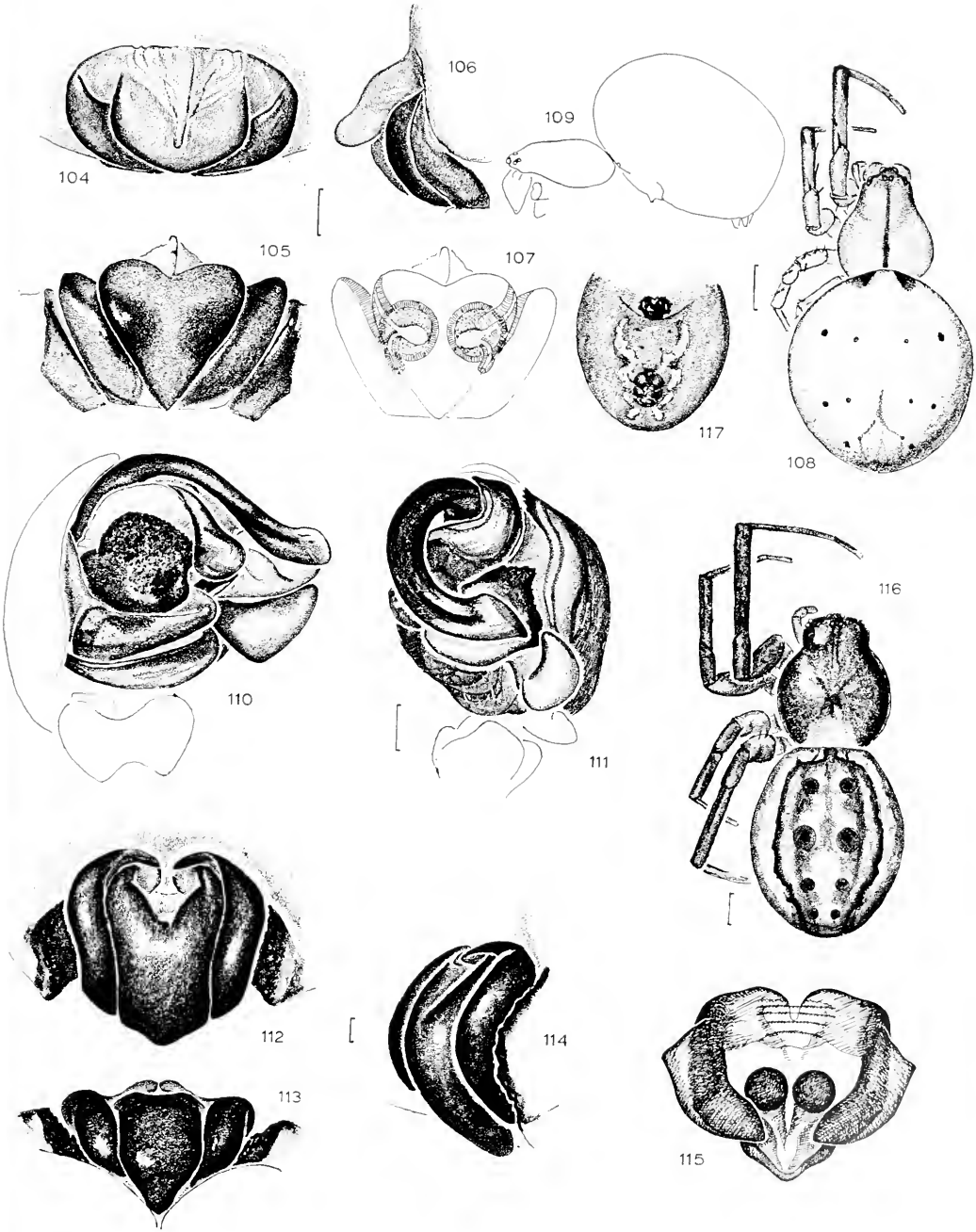
Distribution. Southern Florida, central and southern Texas to Colombia; Cuba, Jamaica and Trinidad (Map 3).

Metazygia carolinalis (Archer), new combination

Figures 112–117, Map 3

Epeira carolinalis Archer, 1951, Amer. Mus. Novitates, no. 1487: 40, fig. 57, ♀. Female holotype from White Lake, Bladen County, North Carolina, in the American Museum of Natural History, examined.

Description. Female: Carapace dark brown on sides, brown above. Legs brown. Sternum light brown. Dorsum of abdomen with sclerotized discs brown, white pigment spots, and two dark lines, one on each side, approaching each other anteriorly and posteriorly (Fig. 116). Venter with a pair of indistinct white brackets, no black pigment (Fig. 117). The carapace is flat and very low (Fig. 116). Abdomen oval, dorsoventrally flattened (Fig. 116). Total length 11.0 mm. Carapace 4.5 mm long, 3.7 wide. First femur, 3.7 mm; patella and tibia, 5.5;



Figures 104–111. *Metazygia zilloides* (Banks): 104–107. Epigynum: 104. Ventral. 105. Posterior. 106. Lateral. 107. Posterior, cleared. 108. Female, dorsal. 109. Female, lateral. 110, 111. Left male palpus: 110. Mesal. 111. Ventral.

Figures 112–117. *Metazygia carolinalis* (Archer): 112–115. Epigynum: 112. Ventral. 113. Posterior. 114. Lateral. 115. Dorsal, cleared. 116. Female, dorsal. 117. Female abdomen, ventral.

Scale lines. 0.1 mm except Figs. 108, 109, 116, 117, 1.0 mm.

metatarsus, 3.7; tarsus, 1.4. Second patella and tibia, 4.8 mm; third, 2.7; fourth, 4.3.

Diagnosis. Unlike other *Metazygia* species, *M. carolinalis* lacks a ventral knob (Fig. 112) on the epigynum.

Note. The placement of this species in *Metazygia* is doubtful. Archer thought *M. carolinalis* close to *Nuctenea cornuta* and placed it with *cornuta* in *Epeira*. He may have been right. But the following facts speak against this placement. *Nuctenea* is mainly a Palearctic genus with a few species in North America having a holarctic distribution. One of the main characters of *Nuctenea* females is the black venter with the comma-shaped white marks on each side. This is not present in *M. carolinalis*. The placement of the species will remain uncertain until the male is found.

Natural History. The flattened shape of the spiders, especially the low carapace, suggests that the spider has its retreat in crevices, probably under bark.

Records. North Carolina: Bladen Co., ♀ paratypes, Sept. 1929 (J. C. Beakley); Craven Co.: New Bern, May 1900, 2 ♀, 1 juv. (J. H. Emerton) (Map 3).

Eustala Simon

Eustala Simon, 1895, Histoire Naturelle des Araignées, 1: 795. Type species *Epeira anastera* Walckenaer by original designation. The name is feminine.

Diagnosis. Eustala differs from other Araneidae, especially from *Araneus*, by the epigynum, which has its scape projecting anteriorly (Figs. 118, 138, 140) instead of posteriorly as in all other genera, and by the male palpus, which has only one patellar macroseta, and has the median apophysis, a white cone-shaped structure, hanging down the venter of the palpus (Figs. 126, 147, m in Fig. 232).

The carapace has a deep longitudinal cleft in the thoracic region (Figs. 163, 183, 197). The abdomen is usually triangular, pointed above the spinnerets (Figs. 142–144, 209–210). Like *Larinia* and *Metepeira*, but unlike many other Araneidae genera, *Eustala* has a central, ventral white patch on the abdomen (Figs. 155, 173, 185, 211). The white patch is absent in those tropical *Eustala* that have the abdomen elongate, like that of *Larinia*. Juvenile *Eriophora*, which look like *Eustala*, lack the white patch and have a dark trapezoid on the venter.

The related *Metazygia* has the scape of the epigynum projecting ventrally (Figs. 90, 91) and the median apophysis is a soft knob (Figs. 101–103, 110, 111). The carapace is smooth (Figs. 96, 108), and the abdomen is oval, slightly flattened dorsoventrally, with indistinct ventral markings (Figs. 96, 98, 99, 108, 109).

Description. The carapace is shaped as in *Araneus*, but with a deep longitudinal thoracic cleft (Figs. 163, 183, 197). The carapace is covered with setae and the thoracic area is high in some species (Figs. 133, 154, 172). The posterior median eyes are slightly smaller than the anterior medians, sometimes equal, rarely slightly larger. The laterals are always smaller than the medians. Anterior medians are their diameter apart, or 1.5 diameters at most; the posterior medians are separated by about the same distance. The laterals (except in the smallest species) are two to several diameters from medians. The clypeus height equals the diameter of the anterior median eyes (Fig. 225) except in *E. clavispina* where it is about one and one-half the diameter of the anterior median eyes as a result of the projection of the eye area. There often is a dark transverse band between anterior median and anterior lateral eyes (Figs. 163, 210, 225). The legs are more or less banded. The abdomen is generally triangular with a posterior hump (Figs. 209, 210), but this may be absent (Figs. 122, 123, 257, 258) or there may be several humps (Figs. 163, 164, 196, 197, 223, 224). Most species are variable in coloration with dark and light individuals, but most have a folium pattern on the dorsum,

exceptions being some specimens of *E. anastera* that are contrastingly colored with black patches on white in alcohol (Figs. 219, 222). In most *Eustala* species, unlike most species of *Araneus*, the venter has a more or less distinct median ventral white patch (Figs. 185, 198). In a few species this white patch is as distinct and contrasting (Fig. 173) as in *Metepeira*. Living specimens of *E. anastera* from central Florida have a greenish abdomen, but the green washes out of alcohol-preserved specimens.

Males are smaller than females, slightly darker in color, their abdominal humps are less distinct than in females (Figs. 199, 212). The distal margin of the first coxa has a hook (Fig. 201) which fits into a groove on the second femur. Except for being longer and having stronger macrosetae, especially on the second tibia, the legs of *Eustala* are not modified. Some species have a ventral row of macrosetae on one or more femora (Figs. 125, 156, 189, 214). This is a species characteristic and has been illustrated. The males are exceedingly difficult to match with females: species with the (seemingly) most specialized palpi do not necessarily have the most specialized epigyna (e.g. *E. californiensis*, Figs. 138–148).

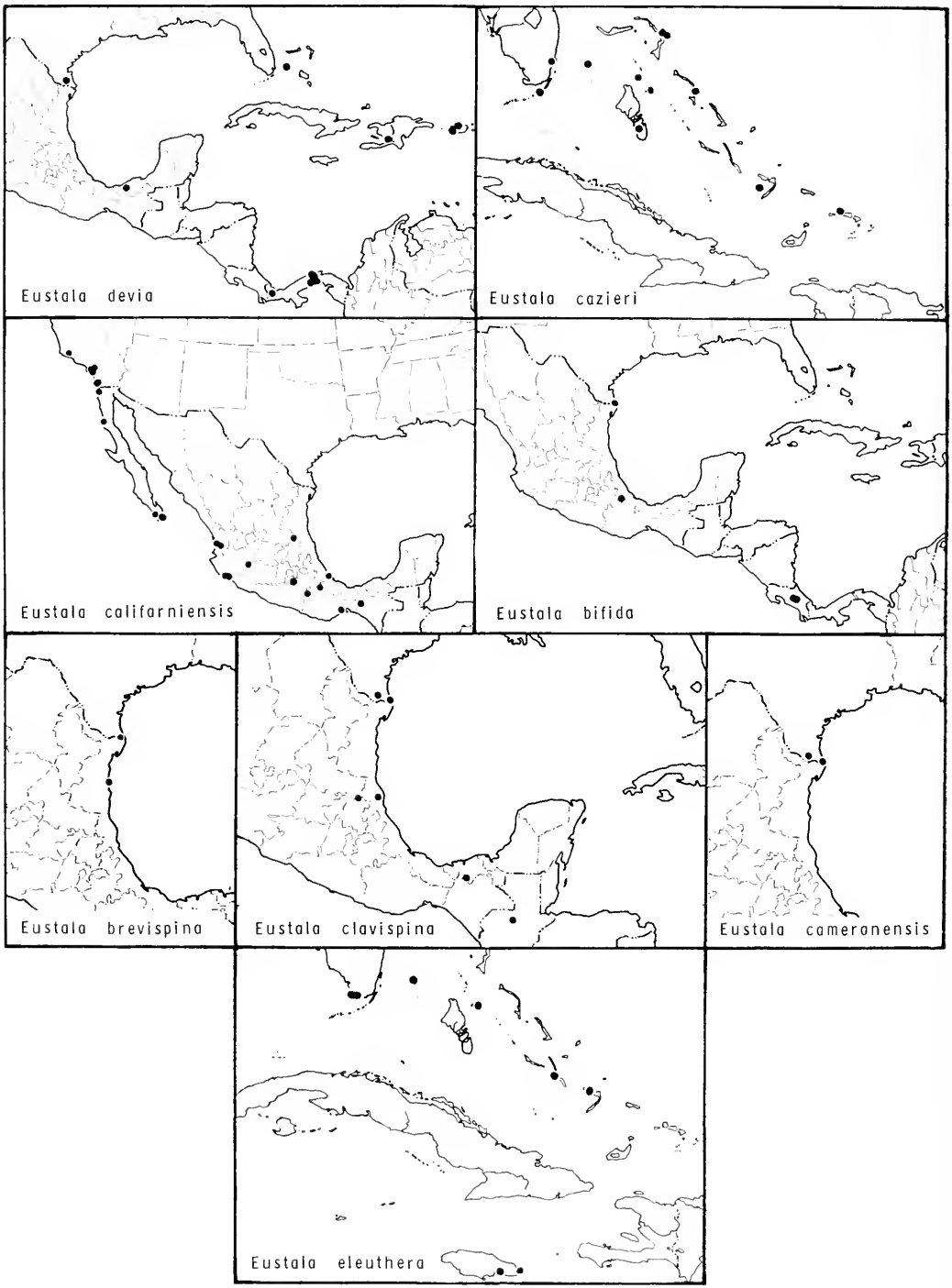
Genitalia. The epigynum has an unusual, anteriorly projecting scape, annulate in most species but smooth in *E. devia* (Fig. 118) and *E. cazieri* (Fig. 128). The three plates in posterior view of the epigynum are of diagnostic importance: the median and two laterals, varying in shape. The seminal receptacles are usually spherical; between the openings is another smaller spherical structure which appears to contain a winding duct (Figs. 208, 256).

The palpal patella has one macroseta (Figs. 217, 252). The bulb, which is similar to that of *Metazygia*, has a huge conductor (c), variously shaped in different species, and a white, soft, conical median apophysis (m), which hangs down on the venter of the bulb in all *Eustala* species (Fig. 232). The embolus (e) is a hook, similar in all species, and has a large sclerotized base, the stipes. The terminal apophysis is a sclerotized prong (a), slightly different in different species, resting on a bubble-like, transparent, spherical subterminal apophysis (a in Fig. 232). In some species the terminal apophysis is different in shape (Figs. 126, 136, 147, 157). The mesal side of the palpus faces ventrally, the ventral side laterally in resting position (Fig. 231).

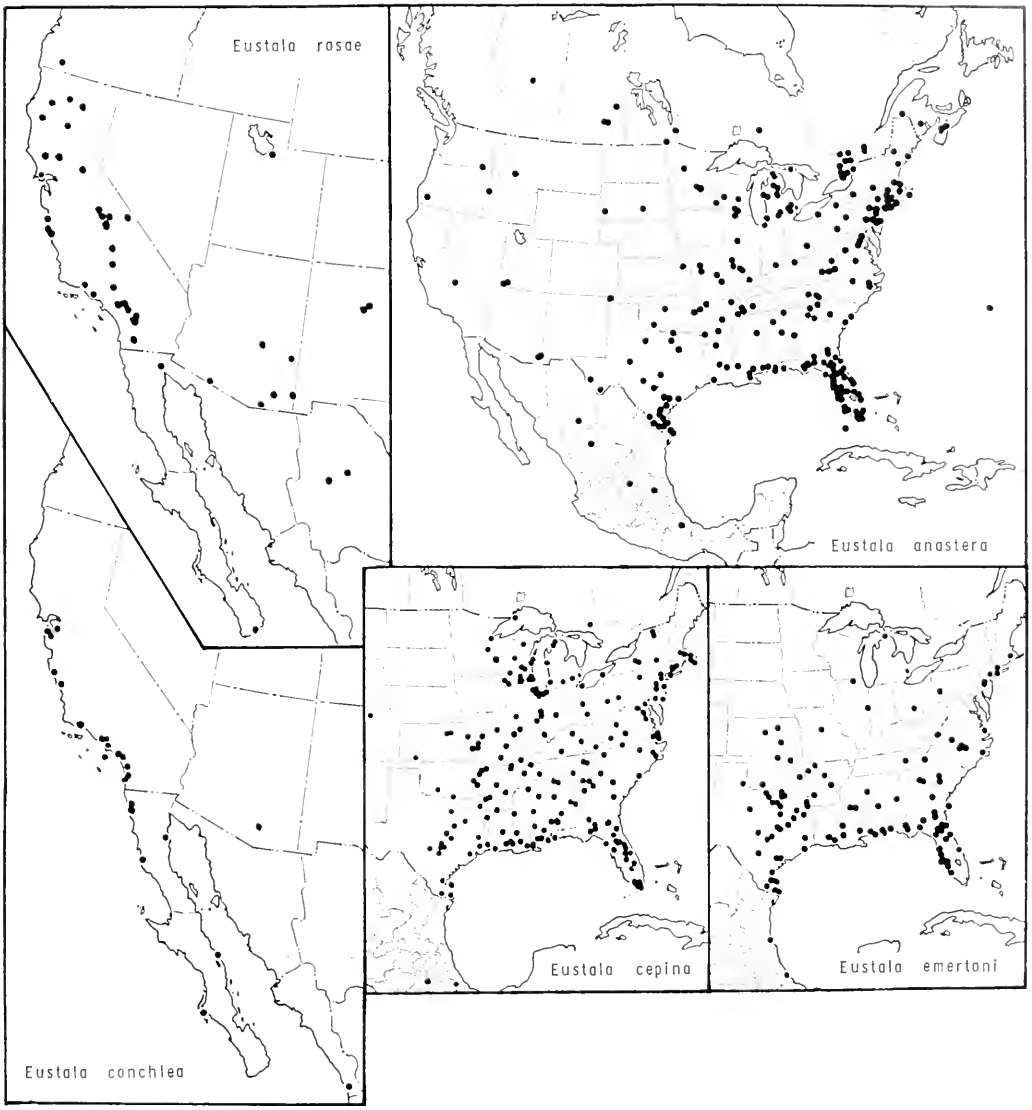
Natural History. Considering the common occurrence of many *Eustala* species, surprisingly little was known about them. *Eustala* apparently is nocturnal and removes its web at daytime. During the day it rests on a dead branch; there is no retreat. *Eustala* species are commonly collected by sweeping and are found also as prey in mud-dauber wasp nests.

Eustala anastera observed at the Archbold Biological Station, Lake Placid, Florida made webs every evening after dark. The webs usually had disappeared by the morning, but once in awhile the webs are not taken down. The webs of juveniles had 17 to 25 radii, that of an adult, 18 and 21. The webs of these juveniles had 28, 37, 41, 31 and 15 viscid threads below the hub and above the hub had 36, 38, 39, 28, 32. The web of an adult had 30, 33 below, 31, 28 above. The horizontal diameter of juveniles' webs ranged from 12 to 25 cm; of adults' webs 19 and 30 cm. There were few frame threads, the hub was solid (Plate 7). The webs were built in dead branches, usually away from leaves and within a wire fence, having vertical wires 15.5 cm apart. *Eustala* has no retreat; when not in the center of the web, it sits appressed to branches. Most webs are vertical but a horizontal web was seen. The lowest webs are 3 to 4 feet above the ground; the maximum height is not known.

Eustala anastera in central Florida feeds on a wide variety of medium-sized prey, and when resting in the web usually keeps its legs slightly spread like *Zygiella x-notata*,



Map 4. Distribution of *Eustala devia* (Gertsch and Mulaik), *E. cazieri* n. sp., *E. californiensis* (Keyserling), *E. bifida* F.P.–Cambridge, *E. brevispina* Gertsch and Davis, *E. clavispina* (O.P.–Cambridge), *E. cameronensis* Gertsch and Davis and *E. eleuthera* n. sp.



Map 5. Distribution of *Eustala rosae* Chamberlin and Ivie, *E. anastera* (Walckenaer), *E. cepina* (Walckenaer), *E. emertoni* (Banks), *E. conchlea* (McCook).

but unlike many other genera (M. Stowe, personal communication).

Species and Distribution. *Eustala* is only known from the Americas. Most species are tropical, and only five species are found in temperate North America. Another eight tropical species have been collected in southern Florida, southern Texas or southern California. The many species in the American tropics are probably very difficult to separate by morphological characters alone.

KEY TO *EUSTALA* FEMALES NORTH OF MEXICO

1. Tropical species, southern California, southern Texas, southern Florida (Map 4) 2
– Temperate species (Map 5) 9

2(1) Scape of epigynum without annulations (Figs. 118, 128) 3
– Scape with annulations (Figs. 138, 149) 4
3(2) Epigynum wider than long in both ventral and posterior view (Figs. 118, 119); lightly sclerotized; Texas to Panama, West Indies ..... *devia*
– Epigynum as wide as long in ventral view (Fig. 128), longer than wide in posterior view (Fig. 129); sclerotized; Florida, West Indies ..... *cazieri*
4(2) Middle piece of epigynum wide and large, almost hiding framing parts to the sides (Figs. 167, 168); Texas to Costa Rica ..... *bifida*
– Middle piece of epigynum narrower (Figs. 139, 150, 160) 5
5(4) Abdomen setae dilated at base; eye region projecting slightly (Fig. 163); scape of epigynum in side view unusually deep (Fig. 161); Texas to Guatemala ..... *clavispina*
– Abdomen setae not modified, eye region not projecting; scape of epigynum not deep (Figs. 140, 151) 6
6(5) Epigynum in posterior view with lateral constrictions ventrally (Figs. 139, 150) 7
– Epigynum without such lateral constrictions (Figs. 180, 206); if constricted, constriction dorsally (Fig. 193) 8
7(6) Epigynum in posterior view with lateral pieces dorsally expanded, middle piece wide ventrally (Fig. 139); abdomen with one hump; California, Mexico ..... *californiensis*
– Epigynum in posterior view with lateral pieces not so expanded (Fig. 150), middle piece narrow (Fig. 149); abdomen with two or three large humps (Figs. 153, 154); Texas ..... *brevispina*
8(6) Scape thick, finger-shaped with rounded tip (Figs. 179, 181); epigynum in posterior view long and middle piece small (Fig. 180); tropical Florida, West Indies ..... *eleuthera*
– Scape tapering to a point (Figs. 192, 205, 228); epigynum in posterior view more or less square in outline with middle piece larger (Figs. 193, 206, 234, 254); whole region 9
9(1) Epigynum in posterior view with dorsal, lateral lobes (Fig. 193); abdomen with three humps in a row (Figs. 196, 197); California to New Mexico ..... *rosae*
– Epigynum in posterior view without the dorsal lobes (Figs. 206, 234, 254) 10
10(9) Middle piece of epigynum in posterior view larger than each lateral area (Fig. 270) and abdomen with a distinct hump (Figs. 273, 274); California, Arizona, northwestern Mexico ..... *conchlea*
– Middle piece of epigynum smaller or as large as lateral area (Figs. 206, 244); if middle piece of epigynum in posterior view larger than lateral area, abdomen without hump; eastern and central United States and Canada 11
11(10) Abdomen longer than wide with a distinct posterodorsal hump (not in Florida) (Figs. 209, 210); posterior median piece of epigynum smaller in area than either lateral one (Figs. 206, 280–285); total length 5.7 to 10.0 mm, of southern Florida specimens 5.4 mm, 0.36 (Florida), 0.44 to 0.58 mm wide ..... *anastera*
– Abdomen, if longer than wide, posterior tubercle indistinct (Figs. 257, 258), or almost as wide as long (Figs. 237–241); area of posterior median piece of epigynum of same size or larger than either lateral one (Figs. 286–295); total length less than 7.6 mm, epigynum less than 0.5 mm wide 12
12(11) Abdomen egg-shaped, longer than wide, without tubercle, with pattern as in Figs. 258, 260; middle piece of epigynum in posterior view distinctly larger than each lateral one (Figs. 254, 262, 291–295). Total length 3.4 to 7.6 mm; southern Florida specimens 5.0 to 6.1 mm; epigynum 0.35 to 0.5 mm wide ..... *emertoni*
– Abdomen almost as wide as long, subtriangular, with small posterior dorsal tubercle, with variable pattern (Figs. 237–241); middle piece of epigynum about the same area as lateral ones or slightly larger; epigynum with a minute posterodorsal sclerotized scale (Figs. 234, 244–247, 286–290); total length 3.4 to 7.9 mm; southern Florida specimens the smallest; epigynum 0.28 to 0.38 mm wide ..... *cepina*

Key to *Eustala* males north of Mexico

1. Conductor of palpus very large with a tail (Figs. 232, 250, 266, 297–312); temperate and tropical 2
– Conductor of palpus without a tail and usually small (Figs. 126–127, 136–137, 147–148, 157–158, 165, 174, 187, 190); subtropical (southern Florida, southern Texas, southern California only, Map 1) 7
2(1) Second femur with a ventral row of macrosetae or at least one macroseta (Fig. 214); whole region ..... *anastera*
– Second femur never with a ventral macroseta (Figs. 201, 249, 265) 3
3(2) Pacific states and southwestern states (Map 5) 4
– Eastern states and central states (Map 5) 5

4(3) Terminal apophysis shorter than bubble-like subterminal apophysis (Fig. 277), conductor very large with a tail more than twice as long as visible part of embolus (Figs. 277, 312, 318) ..... *conchlea*

– Terminal apophysis overhanging bubble-like subterminal apophysis (Fig. 202); conductor small with tail, equal in length to visible part of embolus (Figs. 202, 297, 313) ..... *rosae*

5(3) Conductor with tail shorter than embolus height (Figs. 215, 298–302, 314–315); total length 3.9 to 9.5 mm, Florida males smallest; palpus 0.9 to 1.6 mm wide ..... *anastera*

– Conductor with its tail as long or longer than embolus height (Figs. 303–311). Total length less than 5.0 mm; palpus less than 1.2 mm wide 6

6(5) Terminal apophysis shorter than bubble-like subterminal apophysis (Figs. 266, 309–311, 317); conductor bulging "above" embolus and with a tail about 5 times as long as wide and much longer than embolus is high (Figs. 309–311). Total length 3.8 to 5.0 mm; palpus 0.8 to 1.2 mm wide ..... *emertoni*

– Terminal apophysis as long or longer than bubble-like subterminal apophysis, overhanging it (Figs. 250, 303–308, 316); conductor not bulging "above" embolus, with a tail less than 4 times as long as wide (Figs. 303–308), equal in length or slightly longer than embolus height (Figs. 303–308). Total length 2.5 to 4.3 mm; southern Florida specimens smallest; palpus 0.65 to 0.72 mm wide ..... *cepina*

7(1) Palpus with bubble-like semitransparent subterminal apophysis below stylet-shaped terminal apophysis (Figs. 165, 174, 187, 190) 11

– Palpus lacking bubble-like semitransparent subterminal apophysis or if present, distal to ("above") stylet-shaped terminal apophysis (Figs. 126, 136, 147, 157) 8

8(7) Second femur without ventral row of macrosetae (Fig. 146); palpus as in Figures 147, 148; southern California, Mexico ..... *californiensis*

– Second femur with a ventral row of macrosetae (Figs. 125, 135, 156); palpus not as in Fig. 147; southern Texas and Florida 9

9(8) Terminal apophysis covering embolus, subterminal apophysis distal in palpus (Figs. 126, 127); Texas to Panama and West Indies ..... *devia*

– Subterminal apophysis not distal and terminal apophysis not hiding embolus (Figs. 136, 157) 10

10(9) Terminal apophysis of palpus a non-transparent lobe overhanging embolus (Fig. 136); Florida, West Indies ..... *cazieri*

– Terminal division of palpus as in Fig. 157; Texas ..... *brevispina*

11(7) Embolus twisted with embolus base extending beyond tip (Fig. 174); Texas to Costa Rica ..... *bifida*

– Embolus hook-shaped (Figs. 165, 187, 190) 12

12(11) Terminal apophysis with a constricted neck, and knife-blade-shaped tip (Fig. 165); conductor large (Figs. 165, 166); Texas to Guatemala ..... *clavispina*

– Terminal apophysis otherwise (Figs. 187, 190); conductor small (Figs. 187, 190) .. 13

13(12) Embolus partly hidden by bubble-like subterminal apophysis (Fig. 190); Texas ..... *cameronensis*

– Embolus below bubble-like subterminal apophysis (Fig. 187); Florida ..... *eleuthera*

Eustala devia (Gertsch and Mulaik), new combination
Figures 118–127, Map 4

Neosconella devia Gertsch and Mulaik, 1936, Amer. Mus. Novitates, no. 863: 16, fig. 38, ♀. Female holotype from Edinburg, Texas, in the American Museum of Natural History, examined.

Eustala minima Chickering, 1955, Bull. Mus. Comp. Zool. 112: 471, figs. 94–96, ♀. Female holotype from Barro Colorado Island, Panama Canal Zone, in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Note. The epigynum of specimens of *E. minima* from Panama differs some from that of specimens from the Bahama Islands and the holotype of *E. devia* (Figs. 118, 119).

Description. Female holotype: Carapace yellowish with some black patches. Posterior median eye area black and lateral eyes on black spots. Sternum yellow, legs yellow with black patches and rings. Dorsum of abdomen light and with folium. Venter of abdomen with white pigment spots behind epigynum and a gray trapezoid and a gray transverse band in front of spinnerets (Fig. 124). The abdomen is almost as wide as long and without humps. Female from South Bimini: Total length 3.6 mm. Carapace 1.5 mm long, 1.2 wide. First femur

2.0 mm; patella and tibia, 2.3; metatarsus, 1.5; tarsus, 0.6. Second patella and tibia, 1.9; third, 1.1; fourth, 1.6.

Male from South Bimini: Total length 2.8 mm. Carapace 1.4 mm long, 1.2 wide. First femur, 2.1 mm; patella and tibia, 2.4; metatarsus, 1.6; tarsus, 0.7. Second patella and tibia, 1.8; third, 0.8; fourth, 1.5.

The illustrations were made from the female holotype and from a South Bimini male.

Diagnosis. The abdomen of the female lacks a distinct hump (Figs. 122, 123). As in *E. cazieri*, the epigynum has a smooth scape without annuli, but unlike that of *E. cazieri*, the scape is tipped by a knob (Figs. 118, 120). The male differs from other species of *Eustala* in having the terminal apophysis covering the embolus in mesal view (Fig. 126), and the subterminal apophysis apical. The similar West Indian *E. perdita* Bryant has a differently shaped terminal apophysis.

Distribution. Southern Texas to Panama, Bahamas, Hispaniola, Puerto Rico (Map 4).

Records. Mexico. Tabasco. 2 mi. NE of Comalcalco, ♂. *Panama.* Boquete; Arraijan; El Valle; Porto Bello; all ♀♀. *Canal Zone.* Barro Colorado Island; Ft. Randolph; Chilibre; Madden Dam; Forest Reserve; all ♀♀. *Bahamas.* South Bimini, ♀, ♂. *Haiti.* Kenskoff, ♀. *Puerto Rico.* Mayagüez; Cambalche Forest east of Arecibo.

Eustala cazieri new species
Figures 128–137, Map 4

Holotype. Female from Plantation Key, Monroe County, 4 miles south of Tavernier, Florida, 11 March 1963 (H. and L. Levi), edge of hardwood forest, in the Museum of Comparative Zoology. The species is named after Prof. M. A. Cazier, collector of many specimens of this species in South Bimini.

Description. Female from Bimini: Carapace orange-brown with paired black patches and white down. Legs orange-brown, indistinctly banded. Dorsum of abdomen with lines outlining the folium and sometimes with a black longitudinal band (Fig. 132). Venter with little black pigment (Fig. 134). Thoracic depression a median longitudinal line. Posterior median eyes 0.9 diameter of anterior, laterals 0.8 diameter. Anterior median eyes 1.5 diameters apart, posterior median eyes 1.5 diameters apart. The abdomen is triangular, pointed above spinnerets. Total length 5.4 mm. Carapace 2.2 mm long, 1.9 wide. First femur, 2.5 mm; patella and tibia, 3.0; metatarsus, 1.9; tarsus, 0.7. Second patella and tibia, 3.0 mm; third, 1.4; fourth, 2.5.

Male from Miami: Coloration like that of female. Eye sizes about as in female, anterior median eyes slightly larger. Anterior median eyes their diameter apart, posterior median eyes slightly more than their diameter apart. First coxa with a hook. Total length 4.7 mm. Carapace 2.4 mm long, 1.9 wide. First femur, 3.6 mm; patella and tibia, 4.3; metatarsus, 2.8; tarsus, 1.1. Second patella and tibia, 3.0 mm; third, 1.5; fourth, 2.4.

Female illustrated came from South Bimini, male from Miami.

Variation. Females may lack a pattern on the dorsum of the abdomen, and some have a median longitudinal dark band. Total length of Florida females, 5.2 to 6.8 mm, carapace 2.0 to 2.5 long, 1.8 to 2.0 wide. Males vary in total length 3.3 to 4.7 mm, carapace 2.1 to 2.4 long, 1.7 to 1.9 wide.

Diagnosis. Females differ from other

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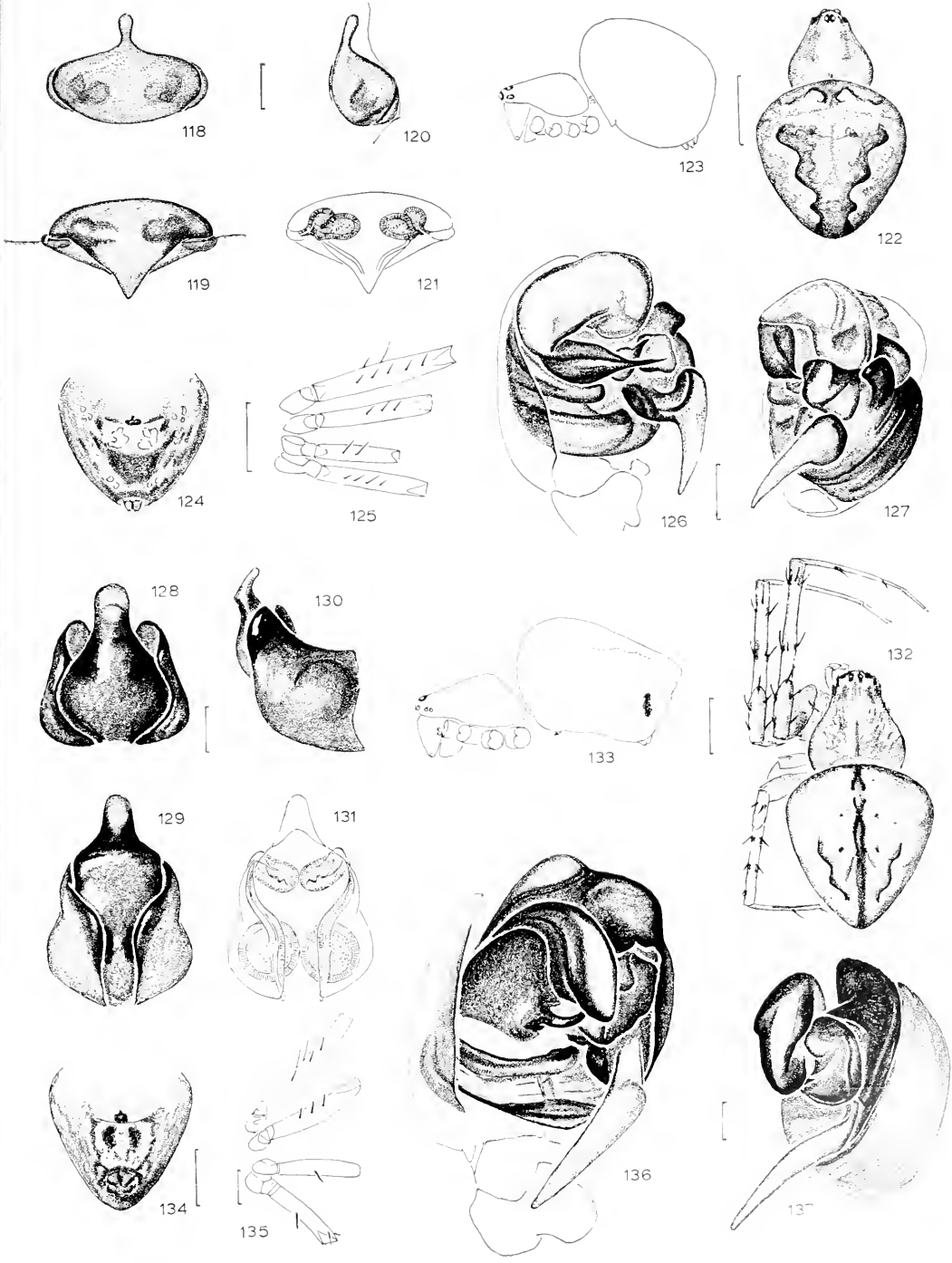
Figures 118–127. *Eustala devia* (Gertsch and Mulaik): 118–121. Epigynum: 118. Ventral. 119. Posterior. 120. Lateral. 121. Posterior, cleared. 122. Female carapace and abdomen, dorsal. 123. Female, legs removed, lateral. 124. Female abdomen, ventral. 125. Male, ventral macrosetae on left femora. 126, 127. Left male palpus: 126. Mesal. 127. Ventral.

Figures 128–137. *Eustala cazieri* n. sp.: 128–131. Epigynum: 128. Ventral. 129. Posterior. 130. Lateral. 131. Posterior, cleared. 132. Female, dorsal. 133. Female, legs removed, lateral. 134. Female abdomen, ventral. 135. Male, ventral macrosetae of left femora. 136, 137. Male palpus: 136. Mesal. 137. Ventral.



Scale lines. 0.1 mm except Figs. 122–125 and 132–135, 1.0 mm.

Florida species by the angular abdomen (Figs. 132, 133) and by lacking annuli on the smooth, anteriorly directed scape of the epigynum (Figs. 128–130). The scape lacks the knob present in *E. devia*. Unlike males of most *Eustala* species, those of *E. cazieri* have no bubble-like transparent subterminal apophysis (Fig. 136); they have an ovoid terminal apophysis overhanging the embolus (Figs. 136, 137).

Distribution. Southern Florida and Bahama Islands (Map 4).

Records. Florida. Dade Co.: Miami; Miami Beach. Monroe Co.: Tavernier. *Bahama Islands.* North Bimini; South Bimini; Crooked Isl.; Eleuthera; Great Abaco Isl.; North Caicos Isl.; Berry Isl.; Andros Isl.; New Providence.

Eustala californiensis (Keyserling), new combination
Figures 138–148, Map 4

Cyrtophora californiensis Keyserling, 1885, Verhandl. Zool. Bot. Ges. Wien, 34: 525, pl. 13, fig. 24, ♀. Female holotype from "California" in the Museum of Comparative Zoology, examined. Keyserling, 1893, Spinnen Amerikas, 4: 263, pl. 13, fig. 196, ♀. Roewer, 1942, Katalog der Araneae, 1: 751. Bonnet, 1956, Bibliographia Araneorum, 2(2): 1361.

Araneus diegensis Schenkel, 1950, Verh. Naturf. Gesell., Basel, 61: 67, fig. 23, ♀. Female holotype from Missions Bay, San Diego, California, in the Natural History Museum, Basel, examined. NEW SYNONYMY.

Eustala abdita Chickering, 1955, Bull. Mus. Comp. Zool., 112: 410, figs. 19–23, ♂. Male holotype from Huajuapan, Oaxaca, Mexico in the American Museum of Natural History, examined. NEW SYNONYMY.

Eustala mexicana Chickering, 1955, Bull. Mus. Comp. Zool., 112: 465, figs. 88–89, ♀. Female holotype from Lo Bajo, Guerrera, Mexico in the American Museum of Natural History, examined. NEW SYNONYMY.

Description. Female from Oaxaca: Carapace light brown with paired dark brown patches and dark longitudinal mark in thoracic cleft. Legs light brown with some black rings, more distinct ventrally. Dorsum of abdomen whitish with folium (Fig. 142). Sides with gray lines. The abdomen is triangular, narrow with a dorsal posterior hump (Figs. 142–144). Total length 5.4 mm. Carapace 2.2 mm long, 2.0 wide. First femur, 3.2 mm; patella and tibia, 3.7; metatarsus, 2.0; tarsus, 0.9. Second patella and tibia, 3.0 mm; third, 1.5; fourth, 2.6.

Male from Oaxaca: Coloration as in female. Total length 3.6 mm. Carapace 1.8 mm long, 1.5 wide. First femur, 2.9 mm; patella and tibia, 3.0; metatarsus, 1.9; tarsus, 0.9. Second patella and tibia, 2.0 mm; third, 1.1; fourth, 1.9.

Female illustrated was from Oaxaca and males from Colima and Veracruz.

Variation. Females usually have the abdomen narrow (Fig. 142), but it may be wider and may have a dorsal triangular dark mark (Fig. 143). Total length of females is 3.9 to 7.0 mm, carapace 1.6 to 2.6 long, 1.4 to 2.1 wide. Total length of males 3.0 to 4.3 mm, carapace 1.6 to 2.3 long, 1.3 to 1.9 wide.

Diagnosis. Females can be separated from all related species by the posterior view of the epigynum, which shows a ventral constriction with laterally expanded dorsolateral lobes on each side (Fig. 139). The terminal apophysis of the palpus (Figs. 147, 148), lacking the usual sclerotized

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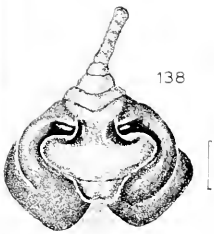
Figures 138–148. *Eustala californiensis* (Keyserling): 138–141. Epigynum: 138. Ventral. 139, 141. Posterior. 140. Lateral. 141. Cleared. 142. Female, dorsal (Mexico). 143. Female abdomen, dorsal (California). 144. Female, legs removed, lateral. 145. Female abdomen, ventral. 146. Male, ventral macrosetae on left femora. 147, 148. Male left palpus: 147. Mesal. 148. Ventral.

Figures 149–158. *Eustala brevispina* Gertsch and Davis: 149–152. Epigynum: 149. Ventral. 150. Posterior. 151. Lateral. 152. Posterior, cleared. 153. Female carapace and abdomen. 154. Female, legs removed, lateral. 155. Female abdomen, ventral. 156. Male, ventral macrosetae of left femora. 157, 158. Male palpus: 157. Mesal. 158. Ventral.

Scale lines. 0.1 mm except Figs. 142–146, 153–156, 1.0 mm.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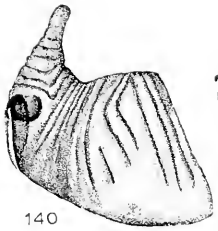
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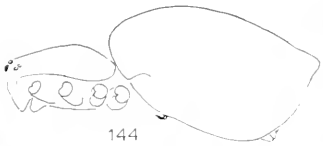
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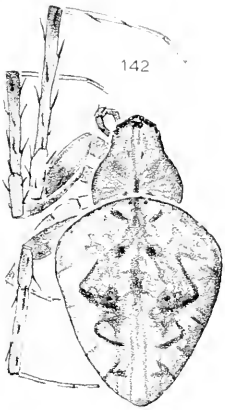
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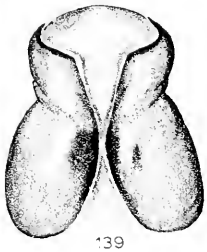
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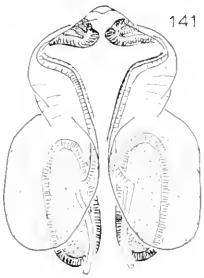
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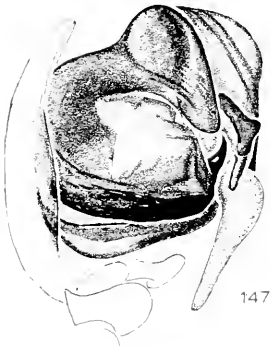
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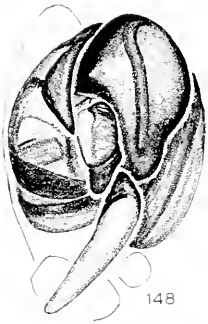
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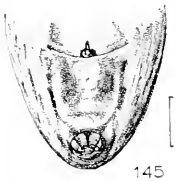
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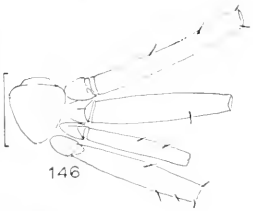
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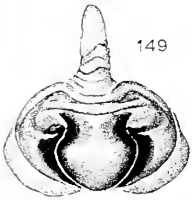
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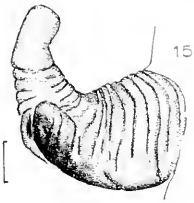
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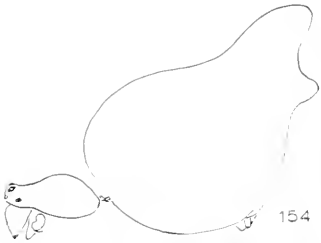
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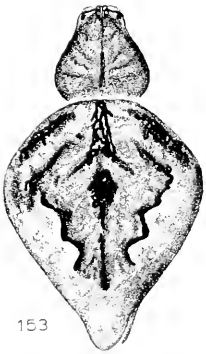
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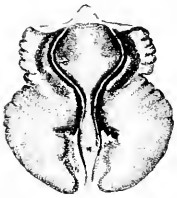
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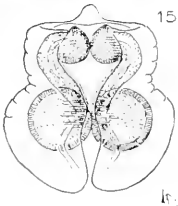
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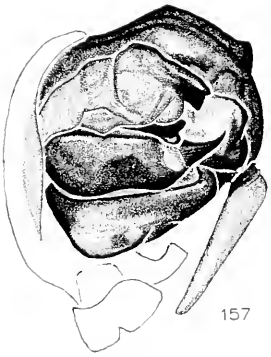
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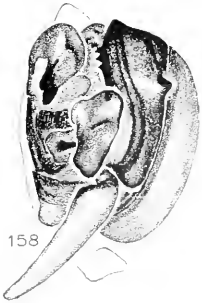
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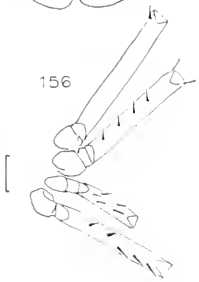
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prong, is distinct from that of related species.

Distribution. Southern California, San Luis Potosí south to Chiapas (Map 4).

Eustala brevispina Gertsch and Davis
Figures 149–158, Map 4

Eustala brevispina Gertsch and Davis, 1936, Amer. Mus. Novitates, 881: 12, figs. 9, 10, ♀, ♂. Male holotype from Cameron Co., Texas in the American Museum of Natural History, examined.

Description. Female: Carapace brown with black marks and white setae. Legs brown with narrow black bands on distal articles. First, second and fourth femora mostly black. The abdomen is contrastingly marked and has two posterior humps (Figs. 153, 154). Total length 8.5 mm. Carapace 2.7 mm long, 2.4 wide. First femur, 3.2 mm; patella and tibia, 3.9; metatarsus, 2.5; tarsus, 1.0. Second patella and tibia, 3.5 mm; third, 1.7; fourth, 2.9.

Male holotype: Total length 5.8 mm. Carapace 3.0 mm long, 2.6 wide. First femur, 4.1 mm; patella and tibia, 4.7; metatarsus, 3.0; tarsus, 1.2. Second patella and tibia, 4.0 mm; third, 2.1; fourth, 3.6.

Diagnosis. This large species can be told from related species by the large abdominal humps (Figs. 153, 154) not present in *E. californiensis*. Like *E. californiensis* the epigynum in posterior view has a diagnostic constriction (Fig. 150), but the lateral pieces are differently shaped from those of *E. californiensis*. Unlike most *Eustala* species the male lacks the transparent subterminal apophysis. The shape of the terminal apophysis of the palpus (Figs. 157, 158) is unlike that of related species.

Distribution. Texas. Cameron Co.: Brownsville, 25 May 1934, ♀ allotype; 1 June 1934, 3♀; 8 June 1934, 3♀ (J. N. Knull). *Tamaulipas.* La Pesca, 17 May 1952, 1♀ (W. J. Gertsch).

Eustala clavispina (O.P.–Cambridge)
Figures 159–166, 176–177, Map 4

Epeira clavispina O.P.–Cambridge, 1889, Biologia Centrali-Americana, Araneidea, 1: 37, pl. 7, fig. 11, ♀. Two female syntypes from Cubilguitz in Vera Paz, Guatemala, in the British Museum, Natural History, examined. Keyserling, 1892, Spinnen Amerikas, 4: 102, pl. 5, fig. 75, ♀.

Amamra nigromaculata O.P.–Cambridge, 1895, Biologia Centrali-Americana, Araneidea, 1: 155, pl. 19, fig. 5. Female holotype from Teapa, Tabasco, Mexico in the British Museum, Natural History, examined.

Eustala clavispina,—F.P.–Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 509, pl. 48, fig. 19, ♀. Roewer, 1942, Katalog der Araneae, 1: 764. Chickering, 1955, Bull. Mus. Comp. Zool., 112: 428, figs. 45–48, ♀.

Eustala rosae,—Gertsch and Davis, 1936, Amer. Mus. Novitates, no. 881: 14, fig. 11, 12, ♀, ♂. Not *E. rosae* Chamberlin and Ivie.

Note. This name is not a synonym of *E. conchlea* McCook as thought by Bonnet (1955, Bibliographia Araneorum, 2(2): 1839).

Description. Female from Texas: Carapace brown with dark brownish black Y (Fig. 163). Posterior median eyes surrounded by black. Sternum maculated with black and white pigment. Legs with contrasting bands on femora, spots and dark patches on distal articles. Dorsum of abdomen with indistinct folium (Fig. 163). Median eye area of carapace swollen. There are lateral abdominal humps, the second pair indistinct, and three pairs of posterior humps in a row (Figs. 163–164). Total length 11.5 mm. Carapace 4.0 mm long, 3.0 wide. First femur, 4.7 mm; patella and tibia, 6.0; metatarsus, 3.9; tarsus, 1.3. Second patella and tibia, 5.3 mm; third, 2.6; fourth, 4.6.

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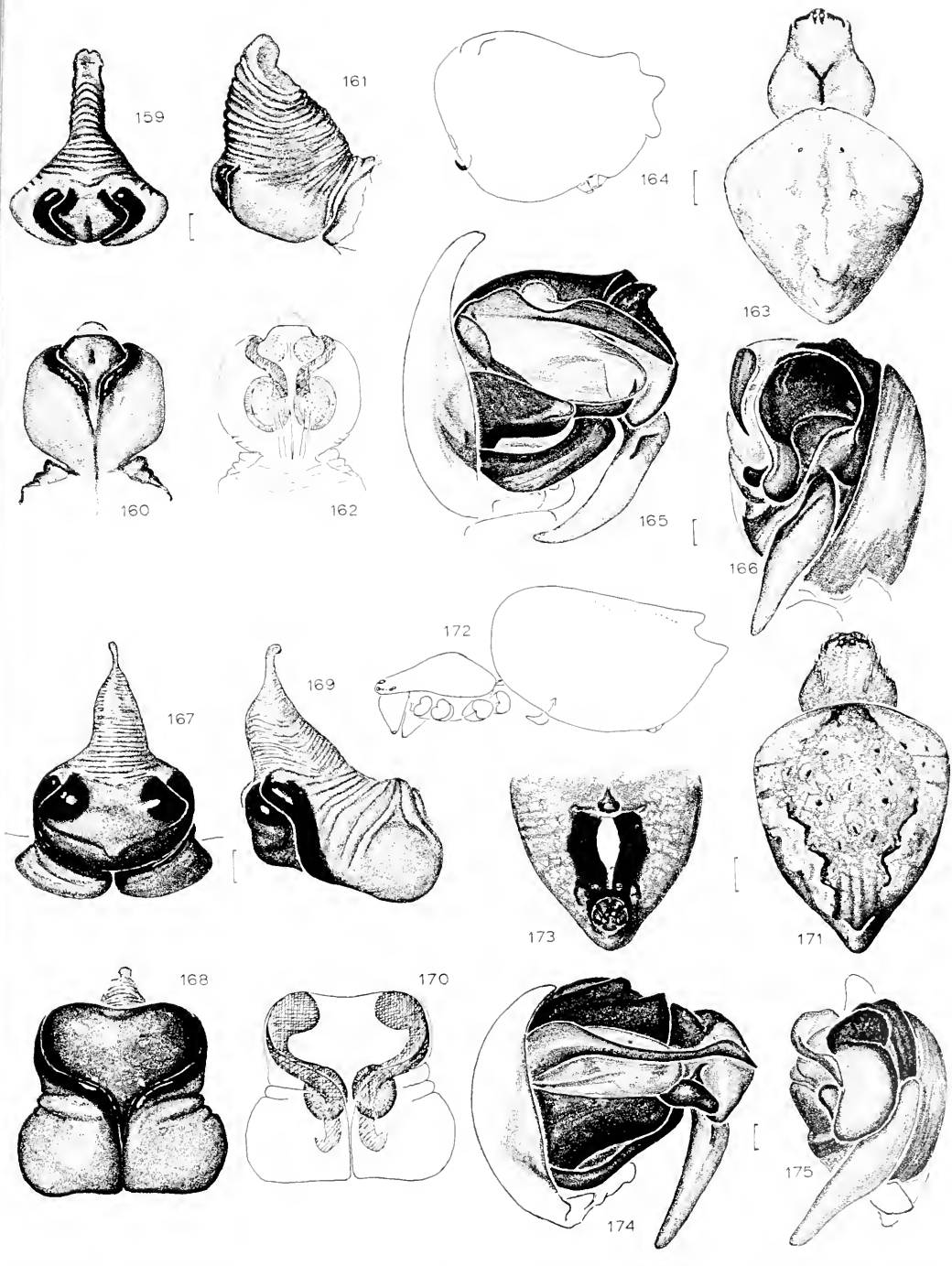
Figures 159–166. *Eustala clavispina* (O.P.–Cambridge): 159–162. Epigynum: 159. Ventral. 160. Posterior. 161. Lateral. 162. Posterior, cleared. 163. Female carapace and abdomen. 164. Female abdomen, lateral. 165, 166. Male left palpus: 165. Mesal. 166. Ventral.



Figures 167–175. *Eustala bifida* F.P.-Cambridge: 167–170. Epigynum: 167. Ventral. 168. Posterior. 169. Lateral. 170. Posterior, cleared. 171. Female carapace and abdomen. 172. Female, legs removed, lateral. 173. Female abdomen, ventral. 174, 175. Male palpus: 174. Mesal. 175. Ventral.

Scale lines. 0.1 mm except Figs. 163, 164, 171–173, 1.0 mm.

Male from Texas: Coloration like that of female. Carapace with two setae within median eye quadrangle. The abdomen has some strong macrosetae on dorsum and there are two posterior humps on the triangular abdomen only. Total length 6.7 mm. Carapace 3.1 mm long, 2.5 wide. First femur, 4.4 mm; patella and tibia, 5.8; metatarsus, 4.0; tarsus, 1.4. Second patella and tibia, 4.3 mm; third, 2.2; fourth, 4.0.

Specimens illustrated came from Texas.

Variation. The leg banding is less distinct in some specimens. Some lack the characteristic basally dilate macrosetae on the abdomen; perhaps they were broken off in collecting. The eye region projects more in southern specimens, little in northern ones. Specimens from Teapa, Mexico have paired black patches on the dorsum of the abdomen, and have indications of a dorsal fold on the posterior side of the epigynum, as in *E. rosae*. Total length of females 8.4 to 11.5 mm, carapace 3.4 to 4.0 long, 2.6 to 3.1 wide. Total length of males 6.7 to 7.3 mm, carapace 3.1 to 3.7 long, 2.5 to 2.7 wide.

Diagnosis. This is the only *Eustala* species of the area having a projecting eye region (Fig. 163) and basally expanded setae on the abdomen. (The setae may be broken off and the eye region projects only little in northern specimens.) Unlike all other species, the scape of the epigynum appears laterally compressed, thus deeper than wide (Fig. 161). The embolus of the palpus is partly hidden by the subterminal apophysis and the terminal apophysis is kitchen-knife-blade-shaped (Fig. 165).

Distribution. Southern Texas to Guatemala (Map 4).

Records. Texas. Hidalgo Co.: 7 mi. E. of Edinburg; Edinburg. Cameron Co.: Rangerville. *Mexico. San Luis Potosí.* Tamazunchale. *Veracruz.* Cerro Azul. *Tabasco.* Teapa. *Guatemala. Vera Paz.* Cubilguitz.

Eustala bifida F.P.–Cambridge
Figures 167–175, 178, Map 4

Eustala bifida F.P.–Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 507, pl. 48, figs. 9, 10, ♀, ♂. Female, male syntypes from San José, Costa Rica in the British Museum, Natural History, examined. Roewer, 1942, Katalog der Araneae, 1: 764. Chickering, 1955, Bull. Mus. Comp. Zool., 112: 421, figs. 35–40, ♀, ♂. Bonnet, 1956, Bibliographia Araneorum, 2(2): 1839.

Description. Female syntype: Carapace brown, sternum brown with white pigment in center. Legs brown, banded with blackish brown. Dorsum of abdomen with indistinct folium, black and gray marks (Fig. 171). Venter black between epigynum and spinnerets with a median white longitudinal line through the center, widest anteriorly, fading out behind (Fig. 173). Abdomen triangular with two posterior humps in a row (Figs. 171, 172). Total length 9.0 mm. Carapace 4.0 mm long, 3.1 wide. First femur, 4.2 mm; patella and tibia, 5.8; metatarsus, 3.6; tarsus, 1.3. Second patella and tibia, 5.0 mm; third, 2.5; fourth, 4.4.

Male syntype: Coloration like that of fe-

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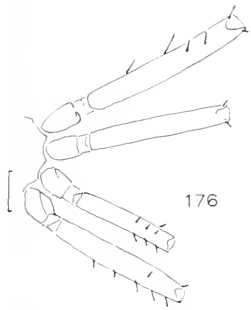
Figures 176, 177. *Eustala clavispina* (O.P.–Cambridge): 176. Male, ventral macrosetae of left femora. 177. Female abdomen, ventral.

Figure 178. *Eustala bifida* F.P.–Cambridge. Male ventral macrosetae.

Figures 179–188. *Eustala eleuthera* n. sp. 179–182: Epigynum: 179. Ventral. 180. Posterior. 181. Lateral. 182. Posterior, cleared. 183. Female carapace and abdomen. 184. Female, legs removed, lateral. 185. Female abdomen, ventral. 186. Male, ventral macrosetae of left femora. 187, 188. Male left palpus: 187. Mesal. 188. Ventral.

Figures 189–191. *Eustala cameronensis* Gertsch and Davis, male: 189. Ventral macrosetae of left femora. 190, 191. Palpus: 190. Mesal. 191. Ventral.

Scale lines. 0.1 mm except Figs. 176–178, 183–186, 189, 1.0 mm.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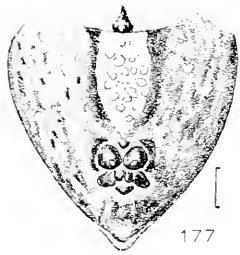
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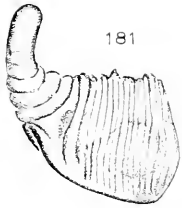
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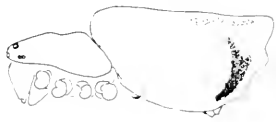
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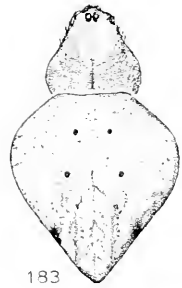
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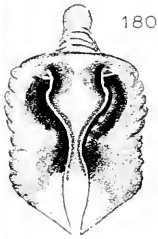
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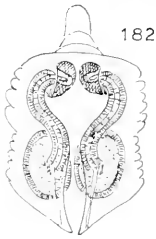
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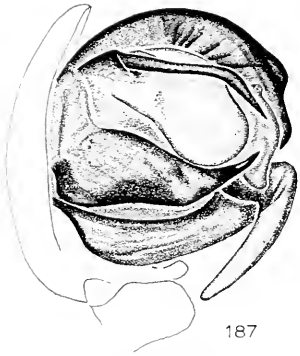
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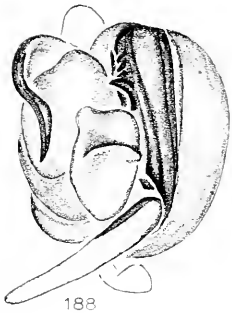
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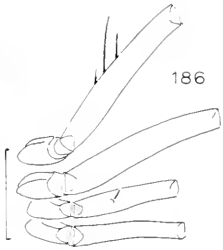
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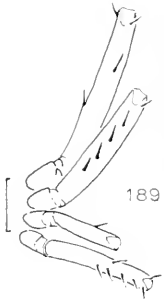
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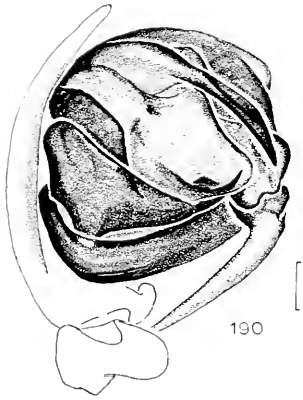
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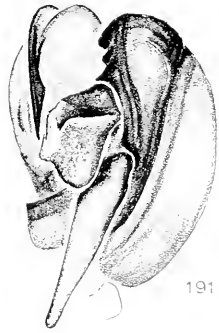
191

male. Total length 6.3 mm. Carapace 3.4 mm long, 2.8 wide. First femur, 4.5 mm; patella and tibia, 5.5; metatarsus, 3.7. Third patella and tibia, 2.2; fourth, 3.9.

The illustrated specimens came from Costa Rica except Fig. 175 from Panama.

Diagnosis. The venter of the abdomen of females is more contrastingly colored than that of other species; it has a white mark framed by black (Fig. 173). Unlike all other species north of Mexico, *E. bifida* has the middle piece of epigynum bulging in both ventral and posterior view (Figs. 167, 168); the lateral areas are about as long as wide (Fig. 168). Unlike all other species north of Mexico, *E. bifida* has the embolus of the male palpus different; it is twisted (Fig. 174) and the terminal apophysis is a long prong widest near the tip and extending to the outer edge of the conductor (Fig. 174).

Distribution. Southern Texas to Costa Rica (Map 4).

Records. Texas. Cameron Co.: most southern Palm Grove, 16 Feb. 1941, ♀ (L. I. Davis). *Veracruz.* Río Blanco, 6 Nov. 1957, ♀ (R. Dreisbach). *Costa Rica.* La Verbena, ♀♀ (Tristan).

Eustala eleuthera new species
Figures 179–188, Map 4

Holotype. Male from Cape Sable, Monroe County, Florida, 4 April 1958, H. V. Weems, collector, in the Museum of Comparative Zoology. The specific name is a noun in apposition after the Bahamian Island Eleuthera.

Description. Female from South Bimini: Carapace yellow with white hairs in cephalic region. Sternum, legs yellow. Dorsum of abdomen speckled with black marks. There is an outline of folium, sometimes a black line (Fig. 183). Venter with a central white spot, longer than wide, black on each side; spinnerets dark brown (Fig. 185). Posterior median eyes 1.2 diameters of anterior medians, laterals 0.6 diameter of anterior median eyes. Anterior median eyes 1.8 diameters apart, posterior medians their diameter apart. The abdomen is triangular with a pointed posterior dorsal hump, and a second smaller hump between the dorsal hump and spinnerets (Figs. 183, 184). Total length 6.3 mm. Carapace 2.2 mm long, 2.0 wide. First femur, 2.7 mm; patella and tibia, 3.4; metatarsus, 2.0; tarsus, 0.9. Second patella and tibia, 2.7 mm; third, 1.5; fourth, 2.5.

Male: Coloration slightly darker than in female. Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.7, posterior laterals 0.6 diameters. Anterior median eyes 1.3 diameters apart, posterior median eyes their diameter apart. Total length 3.4 mm. Carapace 1.9 mm long, 1.6 wide. First femur, 2.5 mm; patella and tibia, 3.0; metatarsus, 2.0; tarsus, 0.7. Second patella and tibia, 2.2 mm; third, 1.2; fourth, 1.9.

Specimens illustrated came from South Bimini.

Variation. Some individual females are much darker than others. Total length of females 4.1 to 6.3 mm, carapace 1.7 to 2.2 long, 1.5 to 2.0 wide. Total length of males 2.7 to 4.0 mm, carapace 1.5 to 2.1 long, 1.2 to 1.6 wide.

Diagnosis. Many females can be separated from other species by the speckled abdomen (Fig. 183) and by the short, finger-shaped scape of the epigynum (Fig. 179). Unlike that of *E. brevispina*, the epigynum

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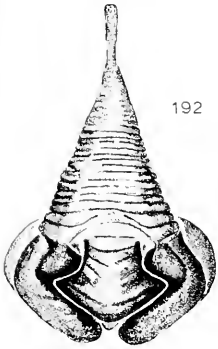
Figures 192–204. *Eustala rosae* Chamberlin and Ivie: 192–198. Female: 192–195. Epigynum: 192. Ventral. 193. Posterior. 194. Lateral. 195. Posterior, cleared. 196. Lateral. 197. Dorsal. 198. Abdomen, ventral. 199–204. Male: 199. Lateral, legs removed. 200. Dorsal. 201. Ventral macrosetae on left femora. 202–204. Left palpus: 202. Mesal. 203. Apical. 204. Ventral.

Scale lines. 0.1 mm except Figs. 196–201, 1.0 mm.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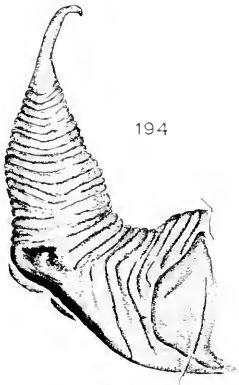
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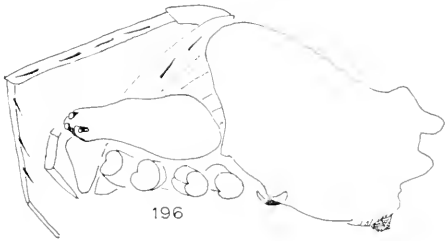
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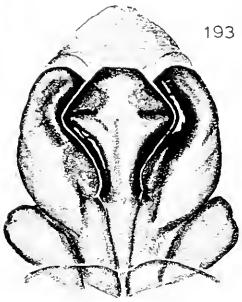
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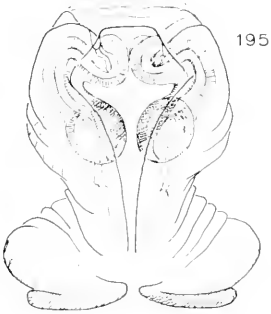
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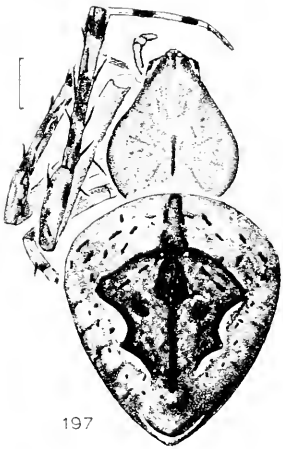
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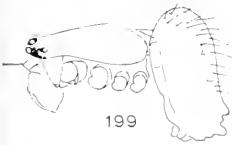
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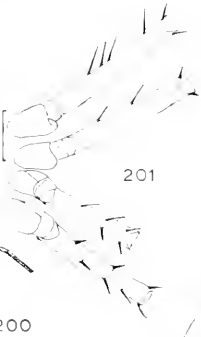
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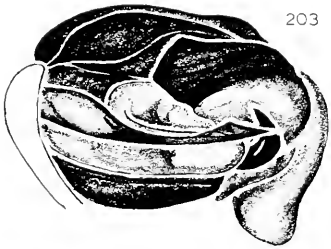
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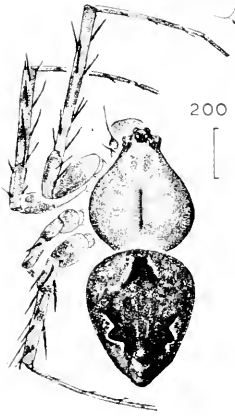
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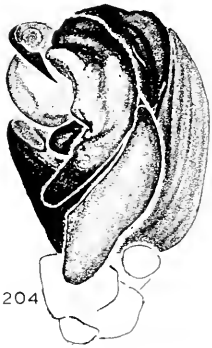
204

of *E. eleuthera* lacks a constriction in posterior view (Fig. 180), and the median piece is relatively small (Fig. 180). The male has a unique, bent, half-spear-shaped terminal apophysis (Fig. 187) and a very small conductor with a proximally facing pocket in lateral view (Fig. 188).

Distribution. Southern Florida, Bahamas, Jamaica (Map 4).

Records. Florida. Monroe Co.: 2 mi. north of Flamingo; Cape Sable. *Bahama Islands.* South Bimini; Long Island; Crooked Island; New Providence. *Jamaica.* St. Andrew Parish: Hope Gardens. St. Thomas Parish: Holland Bay. St. Ann Parish: Claremont.

Eustala cameronensis Gertsch and Davis
Figures 189–191, Map 4

Eustala cameronensis Gertsch and Davis, 1936, Amer. Mus. Novitates, 881: 13, fig. 13, ♂. Male holotype from Cameron Co., Texas in the American Museum of Natural History, examined.

Description. Male holotype: Carapace yellow-brown with dark patches and some tiny black pigment spots posteriorly. Sternum with black pigment spots. Legs yellow-brown. Third and fourth legs banded, the first two unbanded. Dorsum of abdomen with a black-bordered folium. Abdomen is oval with posterior hump indistinct. Total length 4.0 mm. Carapace 2.0 mm long, 1.7 wide. First femur, 3.4 mm; patella and tibia, 3.6; metatarsus, 2.1; tarsus, 0.8. Second patella and tibia, 2.4; third, 1.2; fourth, 2.1.

Diagnosis. The male palpus (Figs. 190, 191) resembles that of *E. clavispina.* As in *E. clavispina* the embolus is partly hidden by the transparent subterminal apophysis (Fig. 190), the terminal apophysis has a wider neck, and the conductor is of very different shape (Figs. 190, 191). The female is unknown.

Record. Texas. Hidalgo Co.: 7 mi. E. Edinburg, 3 Sept. 1953, ♂ (S. Mulaik).

Eustala rosae Chamberlin and Ivie
Figures 192–204, 297, 313, Map 5

Eustala rosae Chamberlin and Ivie, 1935, Bull. Univ. Utah, biol ser., 2(8): 22, fig. 124, abdomen. Juvenile female holotype from Roosevelt Dam, Arizona, lost.

Description. Female from Trinity County, California: Carapace yellow-brown with tiny dark dots. Sternum brown with black spots and some irregular white spots. Legs contrastingly banded, black on brown. Dorsum of abdomen white, brown and black with a distinct folium and a median longitudinal dark line from anterior to posterior (Fig. 197). Sides with thin longitudinal black lines. The abdomen is triangular, pointed behind, with a hump in front of the point and a hump halfway between the point and spinnerets; three humps in a row (Figs. 196, 197). Total length 7.5 mm. Carapace 3.2 mm long, 2.7 wide. First femur, 4.5 mm; patella and tibia, 5.2; metatarsus, 3.2; tarsus, 1.4. Second patella and tibia, 4.5 mm; third, 2.5; fourth, 3.7.

Male from San Diego Co., California: Carapace, legs and sternum much darker than in female. Legs with indistinct light spots. Venter of abdomen black with transverse colorless area behind genital groove (Fig. 198). Abdominal humps as in female (Figs. 199, 200). Dorsum of abdomen has scattered macrosetae. Total length 4.3 mm. Carapace 2.5 mm long, 1.9 wide. First femur, 3.4 mm; patella and tibia, 4.0; metatarsus, 2.6; tarsus, 1.0. Second patella and tibia, 3.0; third, 1.7; fourth, 2.7.

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Figures 205–217. *Eustala anastera* (Walckenaer): 205–211. Female (Pennsylvania). 205–208. Epigynum: 205. Ventral. 206. Posterior. 207. Lateral. 208. Posterior, cleared. 209. Lateral. 210. Dorsal. 211. Abdomen, ventral. 212–217. Male (Pennsylvania): 212. Lateral, legs removed. 213. Dorsal. 214. Ventral macrosetae on left femora. 215–217. Left palpus: 215. Mesal. 216. Apical. 217. Ventral.

Scale lines. 0.1 mm except Figs. 209–214, 1.0 mm.


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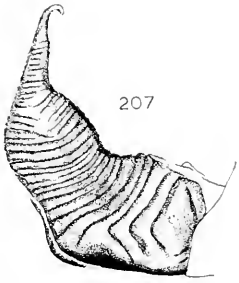
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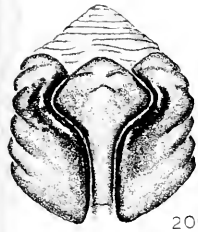
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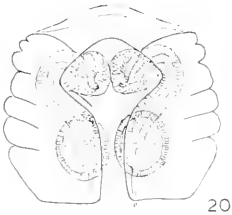
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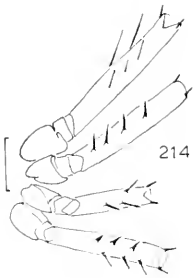
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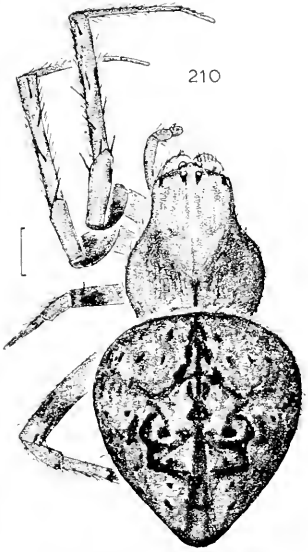
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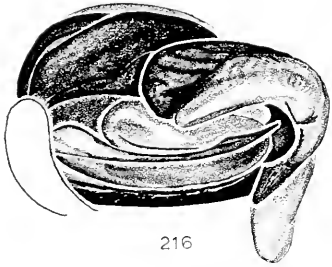
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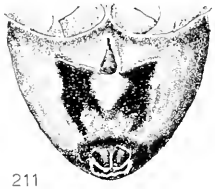
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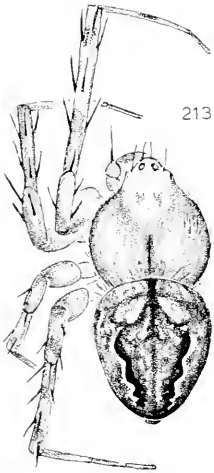
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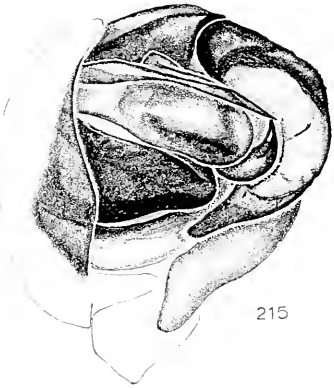
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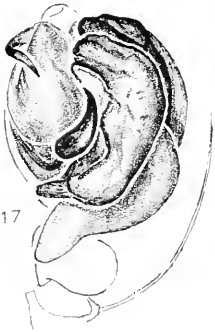
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Variation. Total length of females 6.8 to 9.0 mm, carapace 2.3 to 3.6 long, 1.9 to 3.1 wide. Total length of males 5.0 to 5.9 mm, carapace 2.6 to 3.0 long, 2.2 to 2.7 wide.

Diagnosis. Females differ from those of related species by having three posterior tubercles in a row on the abdomen (Fig. 196), and by the extra lateral lobe on the base of the epigynum (Figs. 193, 195) in posterior view. Males differ from most related *Eustala* species by the half-spear-shaped tip of the terminal apophysis of the palpus, much wider than its stalk (Figs. 202, 203, 297, 313). Males differ from *E. anastera*, which have a similar terminal apophysis, by lacking macrosetae on the venter of the second femur (Fig. 201).

Natural History. Specimens have been collected from montane forest and juniper woodland, and creosote brush scrub in California. Most mature individuals were collected from April to August.

Distribution. Oregon, Utah to Baja California, New Mexico and Chihuahua (Map 5).

Eustala anastera (Walckenaer)
Plate 7, Figures 205–232, 280–285, 298–302, 314, 315, Map 5

Epeira anastera Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2: 33. Type, Abbot manuscript, Spiders of Georgia, in the British Museum, Natural History, drawing no. 381. Copy of manuscript in the Museum of Comparative Zoology, examined.[1] McCook, 1893, American Spiders, 3: 172, pl. 8, figs. 1–4, ♀, ♂.

Epeira eustala Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2: 37. Type, Abbot manuscript, Spiders of Georgia, in the British Museum, Natural History, drawing no. 119. Copy of manuscript in the Museum of Comparative Zoology, examined.

Epeira apotroga Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2: 43. Type, Abbot manuscript, Spiders of Georgia, in the British Museum, Natural History, drawing no. 371. Copy of manuscript in the Museum of Comparative Zoology, examined.

Epeira spatulata Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2: 44. Type, Abbot manuscript, Spiders of Georgia, in the British Museum, Natural History, drawing no. 366. Copy of manuscript in the Museum of Comparative Zoology, examined.

Epeira illustrata Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2: 45. Type, Abbot manuscript, Spiders of Georgia, in the British Museum, Natural History, drawing no. 186. Copy of manuscript in the Museum of Comparative Zoology, examined.

Epeira decolorata Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2: 49. Type, Abbot manuscript, Spiders of Georgia, in the British Museum, Natural History, drawing no. 345. Copy of manuscript in the Museum of Comparative Zoology, examined.

Epeira triflex Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2: 60. Type, Abbot manuscript, Spiders of Georgia, in the British Museum, Natural History, illustration no. 112. Copy of original in the Museum of Comparative Zoology, examined.

Epeira trinotata Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2: 75. Type, Abbot manuscript, Spiders of Georgia, in the British Museum, Natural History, illustration no. 272. Copy of original in the Museum of Comparative Zoology, examined.

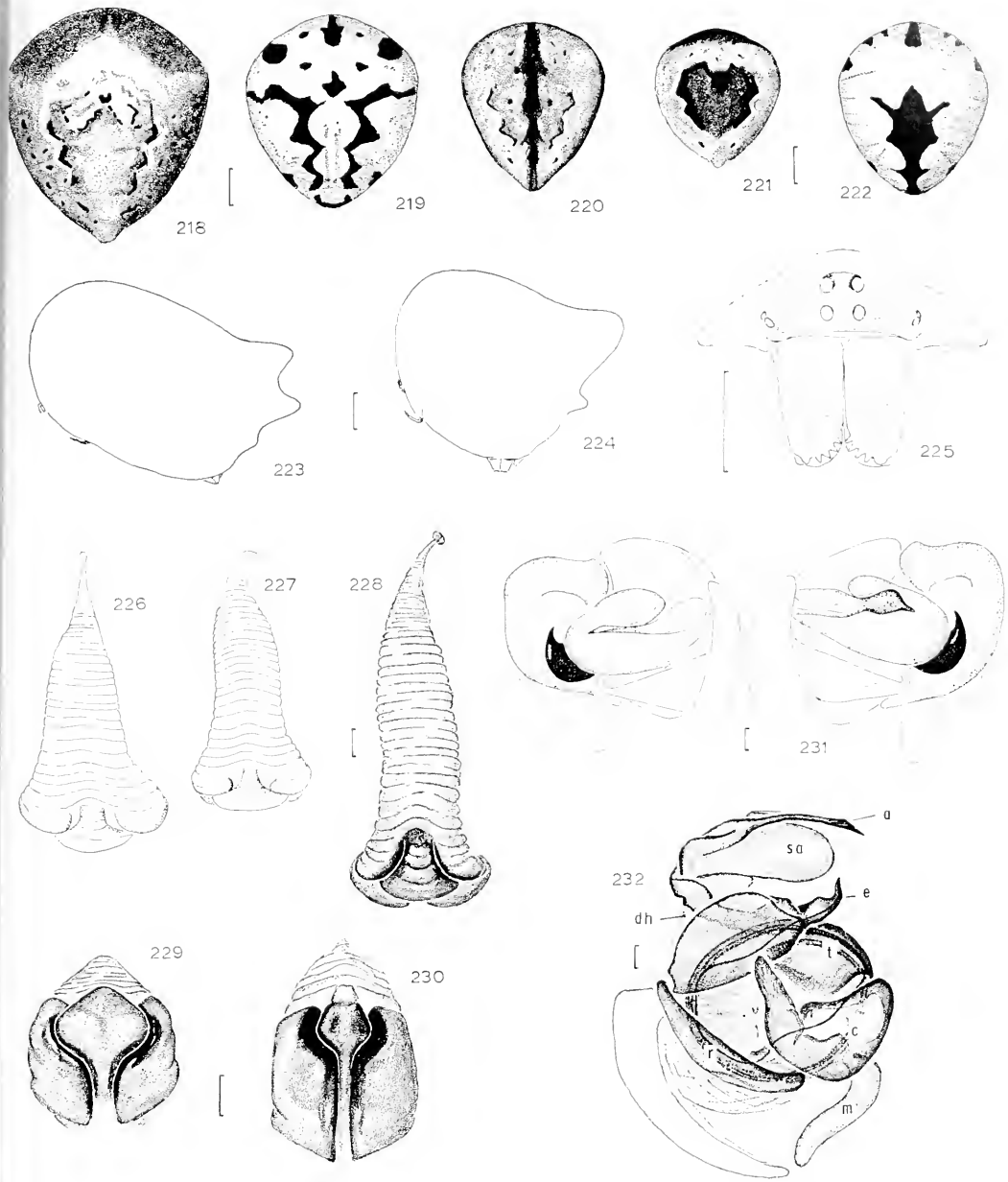
Eustala anastera,—Chamberlin and Ivie, 1944, Bull. Univ. Utah, biol. ser., 7(5): 102, fig. 4. Kaston, 1948, Bull. Connect. Geol. Nat. Hist. Surv., 70: 233, figs. 706–709, 727, ♀. Bonnet, 1956, Bibliographia Araneorum, 2(2): 1837 (in part only).

Note. I have listed only the first Abbot figure cited by Walckenaer for each name. *Epeira circulata* Walckenaer, 1841, p. 79, may have been an *Eriophora*, probably not *Eustala* as indicated by Chamberlin and Ivie (1944).

Description. Female from Pennsylvania: Carapace brown, sides of thorax darker. Thorax covered with white hairs and down. Legs dark, banded. Dorsum of abdomen with folium or longitudinal dark line. Abdomen triangular, longer than wide with a distinct posterior dorsal hump (Figs. 209, 210). Total length 7.5 mm, carapace 2.7 mm long, 2.4 wide. First femur, 3.4 mm; patella and tibia, 4.2; metatarsus, 2.4; tarsus, 0.9. Second patella and tibia, 3.6 mm; third, 1.7; fourth, 3.2.

Male from Pennsylvania: Coloration as in female. Total length 4.8 mm. Carapace

[1] See footnote under *Cyclosa turbinata*.



Figures 218–232. *Eustala anastera* (Walckenaer): 218–222. Dorsal patterns of female abdomen. 218. (Pennsylvania). 219. (West Virginia). 220. (Michigan). 221, 222. (Florida). 223, 224. Female abdomen, lateral. 223. (Georgia). 224. (southern Texas). 225. Female eye region and chelicerae. 226–230. Epigynum. 226–228: Ventral. 229, 230. Posterior. 226, 227. (Kerr Co., Texas). 228. (Goliad Co., Texas). 229. (Nova Scotia, Canada). 230. (Cimarron Co., Oklahoma). 231. Left and right palpi from same individual (Grant Par., Louisiana). 232. Left palpus expanded.

Scale lines. 0.1 mm except Figs. 218–225, 1.0 mm.

Abbreviations. a, terminal apophysis; c, conductor; dh, distal hematodocha; e, embolus; m, median apophysis; r, radix; sa, subterminal apophysis; t, tegulum.

2.5 mm long, 2.2 wide. First femur, 3.6 mm; patella and tibia, 4.3; metatarsus, 2.9; tarsus, 1.2. Second patella and tibia, 3.0 mm; third, 1.8; fourth, 2.8.

Variation. The pattern is variable although most specimens are dark. Some specimens have a folium on the abdomen (Figs. 210, 218, 221), some have black patches on white (Figs. 219, 222), others only a longitudinal median line (Fig. 220). Females from Texas have two humps in a line (Fig. 224), as do occasional females from other areas (Fig. 223); one from Cimarron, Oklahoma, had three. The hump is smaller in the northeastern part of the range, where *E. emertoni* is not found, and the epigynum has a larger middle piece in posterior view (Fig. 229) and resembles that of *E. emertoni.*

Males sometimes have a short and pointed terminal apophysis (Fig. 315). Such males included those collected and determined by W. Ivie from eastern Pennsylvania, one each from Alabama (Mobile), Mississippi (Jefferson City), West Virginia, Virginia, South Dakota, Idaho, Texas, Oklahoma, Mississippi, Ontario, Connecticut (New Canaan), and all males from Michigan. The smaller males in Florida may have only one macroseta on the second femur, sometimes only on one side. But several very large males lacked these macrosetae entirely: one from Calhoun Co., Arkansas, one from Boston, Mass., one from Lebanon State Forest, New Jersey and one from Center Harbor, New York. Most males from the northeastern part of the range, where *E. emertoni* and *E. cepina* are not found, lack these macrosetae and the outer, "upper," bulge of the conductor is smaller (Fig. 298).

Total length of females 5.4 to 10.0 mm, carapace 2.5 to 3.3 long, 2.3 to 2.6 wide. Total length of males 3.9 to 9.5 mm, carapace 2.2 to 4.8 long, 1.8 to 4.0 wide. The smallest specimens all came from central and southern Florida.

Diagnosis. The species differs from the related *E. emertoni* and *E. cepina* by being darker and larger. Females differ from *E. cepina* by size, color and shape of the abdomen (Figs. 209, 210), from *E. emertoni* by having the median area of the base in posterior view smaller than each lateral area (Figs. 280–285) (but in eastern Canada where *emertoni* is absent, the epigynum may resemble that of *E. emertoni*). The abdomen is longer than wide with a distinct posterior hump (unlike *E. emertoni*). The epigyna are larger, 0.36 (Florida), to 0.58 mm wide (the smallest from south central Florida) than those of *E. cepina.* Females differ from the western *E. rosae* and *E. conchlea* by the shape of the epigynum in posterior view. The contrasting black and white pattern (Figs. 219, 222) found in some individuals is diagnostic; it is not found in related species.

Males differ from *E. rosae*, *E. emertoni* and *E. cepina* by having a row of three to five short macrosetae on the venter of the second femur (Fig. 214); rarely, in small Florida specimens, there is only one. (These macrosetae may be absent in individual males and always absent in those from eastern Canada.) The conductor is smaller and its tail shorter than that of *E. triflex* and *E. cepina* (Figs. 298–302). Most of the conductor is "above" the embolus, the portion "below" the embolus is less in length than the embolus height. The terminal apophysis

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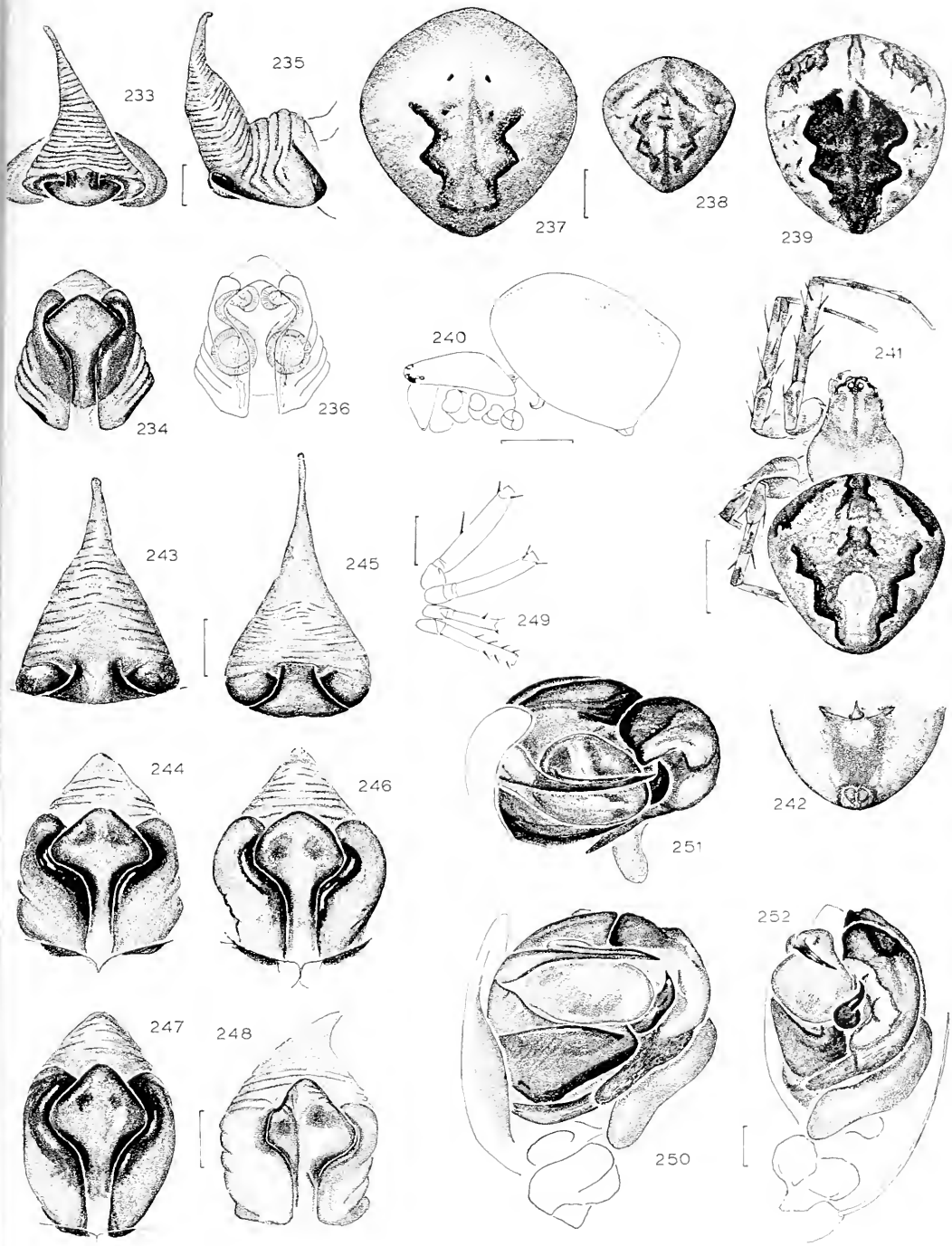
Figures 233–252. *Eustala cepina* (Walckenaer): 233–236. Epigynum. (Pennsylvania): 233. Ventral. 234. Posterior. 235. Lateral. 236. Posterior, cleared. 237–239. Dorsal patterns of female abdomen (all Texas): 240–242. Female (Pennsylvania): 240. Lateral, legs removed. 241. Dorsal. 242. Abdomen, ventral. 243–248. Epigynum: 243, 245. Ventral. 244–248. Posterior. 243, 244. (New Jersey). 245, 246. (Missouri). 247. (Kansas). 248. (Emmet Co., Michigan). 249–252. Male (Pennsylvania): 249. Ventral macrosetae of left femora. 250–252. Left palpus: 250. Mesal. 251. Apical. 252. Ventral.

Scale lines. 0.1 mm except Figs. 237–242, 249, 1.0 mm.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tip is usually (but not always) "half-spear-shaped" and wider than its neck (Figs. 215, 314), but not so wide as that of *E. rosae*. In both *E. triflex* and *E. cepina*, the terminal apophysis tip is only rarely wider than its neck. In *E. rosae* it is wider but, as in the other two species, lacks the line of ventral macrosetae on the second femur. The conductor of the palpus, unlike that of *E. cepina*, has an "upper, outer" lobe (seen upper right in Figs. 299, 302); the palpus is much larger (0.91 to 1.6 mm wide in mesal view) than that of *E. cepina*.

Natural History. *Eustala anastera* is commonly found as prey in *Trypoxylon* and *Trypargilum* mud-dauber wasp nests. The species is found in diverse habitats. Collecting sites are goldenrod (*Solidago*) fields, chokeberry, an apple tree in Ontario, a tamarack bog (*Larix occidentalis*) in Manitoba, a balsam fir tree (*Abies balsamea*) in New Brunswick, a white spruce (*Picea glauca*) in New Brunswick, maple woods in Wisconsin, and tamarack (*Larix occidentalis*). Specimens have also been collected by sweeping a marsh, in xeromesic woods, by beating dead oak branches, by sweeping *Poa pratense*, in a web in dead twig in Michigan, in loblolly pine (*Pinus taeda*) in Arkansas; in oak-pine flatwoods, by sweeping turkey oak (*Quercus laevis*) scrub, by sweeping cypress (*Taxodium*) swamp edge, in palm-cypress (*Taxodium*), in red mangrove (*Rhizophora*) hammock, along a road, in a web in Spanish moss (*Tillandsia usneoides*), on *Pinus clausa*, and near scrub oak in Florida. I think one requirement for *Eustala anastera* is dead branches in a relatively open wooded area or along wood borders. Comstock (1940) reports vertical webs from low bushes. The spider does not make a retreat but sits on bark or dead branches to the side of the web, "the spider closely resembling the bark of the tree or other plant on which it rests; and they act as if conscious of this protection, running only a short distance when disturbed and then crouching down close to the bark." Kaston (1948) reports *Eustala anastera* as being one of the few orb-weavers overwintering in the penultimate instar. Males are found throughout the season but, even in Florida, are more common in spring. The web illustrated by Plate 7 is described in the introduction as belonging to *Eustala*.

Distribution. Throughout southern Canada and the United States, except perhaps within the range of the similar *E. rosae* in California. The southern limits are unknown but are believed to be Central America (Map 5).

Eustala cepina (Walckenaer)
Figures 233–252, 286–290, 303–308, 316, Map 5

Epeira cepina Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2: 37. Type, Abbot manuscript, Spiders of Georgia, in the British Museum, Natural History, drawings no. 173 and 175. Copy of original in Museum of Comparative Zoology, examined.

Epeira parvula Keyserling, 1863, Sitzungsber. Naturf. Gesellsch. Isis, Dresden, p. 131, pl. 6, figs. 9, 10, ♀. Female lectotype here designated from Baltimore in the British Museum, Natural History. One female, one male paralectotypes are *E. cepina*, another female *E. anastera*; one juvenile female paralectotype from Peoria is *E. anastera*. NEW SYNONYMY.

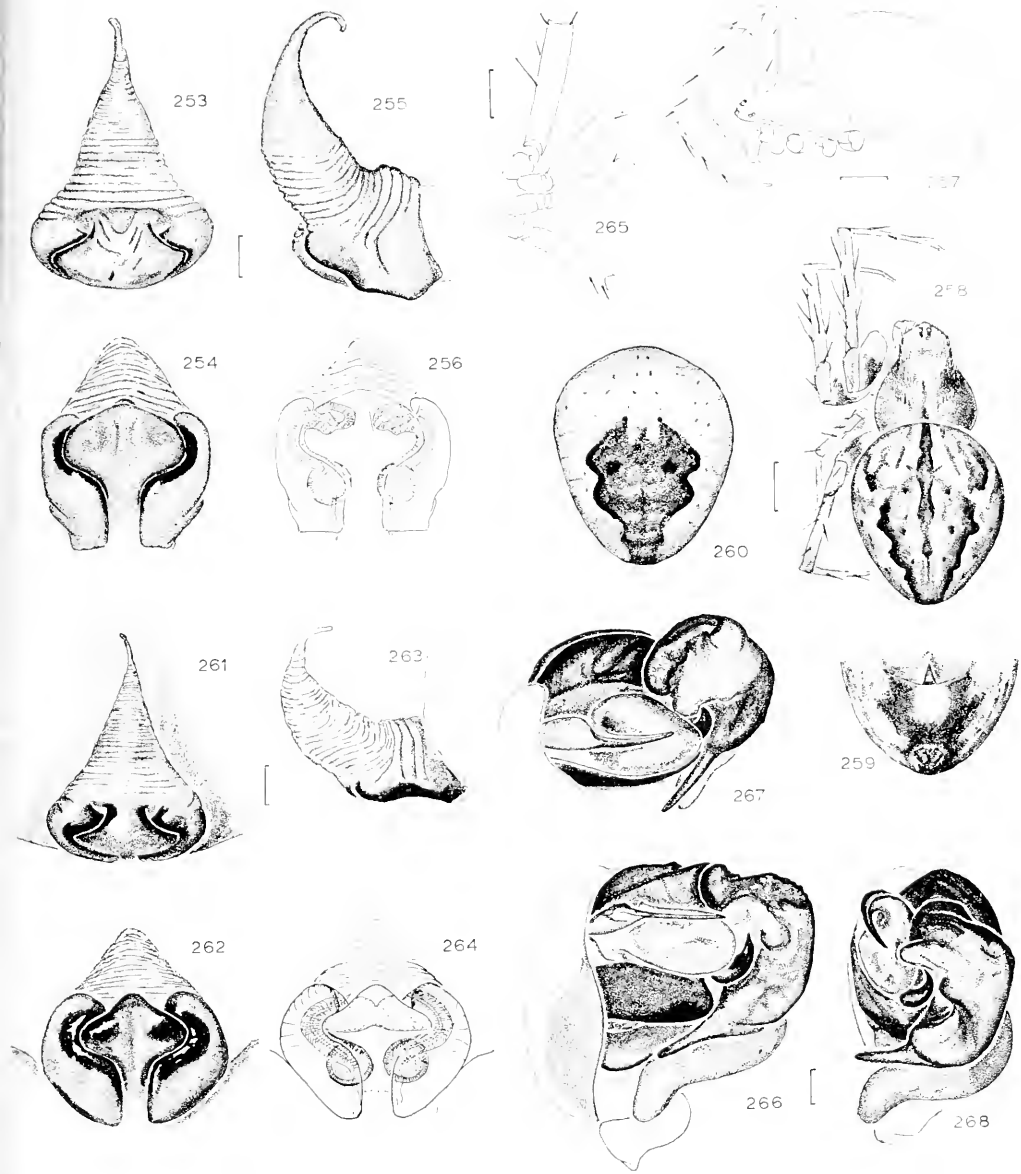
Eustala cepina,—Chamberlin and Ivie, 1944, Bull. Univ. Utah, biol. ser., 7(5): 103.

Eustala arkansana,—Archer, 1951, Amer. Mus. Novitates, no. 1487: 19, fig. 47, ♀. Female allotype not male holotype.

Note. Most specimens in collections had been labeled *E. anastera*, but A. F. Archer called this species *A. triflex*.

Description. Female from Pennsylvania: Carapace orange-brown. Sternum orange-brown with some white spots. Legs orange-brown, slightly banded. Dorsum of abdomen with a folium. The abdomen is triangular, almost as wide as long (Figs. 237–241). Total length 5.5 mm. Carapace 2.3 mm long, 1.7 wide. First femur, 3.2 mm; patella and tibia, 3.6; metatarsus, 1.9; tarsus, 0.8. Second patella and tibia, 2.6 mm; third, 1.4; fourth, 2.2.

Male: Coloration as in female. The abdomen is oval, triangular. Total length 3.3



Figures 253–268. *Eustala emertoni* (Banks): 253–259. Female (Pennsylvania): 253–256. Epigynum: 253. Ventral. 254. Posterior. 255. Lateral. 256. Posterior, cleared. 257. Lateral. 258. Dorsal. 259. Female abdomen, ventral. 260. Dorsal pattern of female abdomen (Texas). 261–264. Epigynum (Connecticut): 261. Ventral. 262. Posterior. 263. Lateral. 264. Posterior, cleared. 265–268. Male (Pennsylvania): 265. Ventral macrosetae of left femora. 266–268. Left palpus: 266. Mesal. 267. Apical. 268. Ventral.

Scale lines. 0.1 mm except Figs. 257–260, 265, 1.0 mm.

mm. Carapace 1.7 mm long, 1.5 wide. First femur, 2.2 mm; patella and tibia, 2.7; metatarsus, 1.8; tarsus, 0.8. Second patella and tibia, 2.3 mm; third, 1.0; fourth, 1.8.

Variation. The color variation of the abdomen is less than that of *E. anastera*, a black median longitudinal line is common (Figs. 237–241). Total length of females 3.4 to 7.9 mm, carapace 1.4 to 2.9 long, 1.3 to 2.2 wide. Total length of males 2.5 to 4.3 mm, carapace 1.5 to 2.4 long, 1.2 to 2.0 wide. The smallest specimens, females measuring total length 3.4 to 4.5 mm, epigynum less than 0.38 mm wide, all came from southern Florida. Some specimens appear intermediate with *E. emertoni* and perhaps *E. anastera*.

Diagnosis. The abdomen is triangular (Figs. 237–241), almost as wide as long, and may lack a dorsal pattern. The middle area of the epigynum in posterior view is larger or subequal to the lateral (unlike *E. emertoni*) (Figs. 236, 244, 247, 286–290). The epigynum is much smaller in size (0.28 to 0.38 mm wide) than that of *E. anastera*. The male differs from *E. emertoni* in that the longer terminal apophysis overhangs the bubble-like subterminal apophysis (Figs. 303–308, 316). The conductor lacks the lobe (to the upper right in Figs. 303–308) present in both *E. anastera* and *E. emertoni*. The conductor is smaller (Figs. 303–308) than that of *E. emertoni* and *E. anastera*. The embolus sits in the middle of the conductor, not in the "lower" half as is common in *E. anastera*. The palpus is also always smaller in size (about 0.65 to 0.72 mm wide) than in *E. anastera* and *E. emertoni*.

Natural History. *Eustala cepina* is commonly found as prey in mud-dauber wasp nests, of *Chalybina* wasps in Oklahoma. It has been found on lake shores in Michigan and Wisconsin, in dune grass and mixed forest in Wisconsin, by sweeping weeds in Illinois, in pine dunes in Indiana, by sweeping around a pond in Pennsylvania, in a garden in North Carolina, on pecan trees in South Carolina, in low grass and an urban area in Alabama, in pond vegetation, on wheat and cotton in Arkansas, on weeds beside a road in Mississippi, by beating cedar (*Taxodium*) branches on a slope near a stream in Georgia; in oaks along a beach, in grasslands, and on a small oak in an open area in mesic hammock in Florida. The spiders also probably rest on dead branches next to the web without retreat. It seems to prefer wetter areas than does *E. anastera*.

Distribution. New England south to Florida, Ontario, Wisconsin, Colorado, central Texas to Mexico (Map 5).

Eustala emertoni (Banks)
Figures 253–268, 291–295, 309–311, 317, Map 5

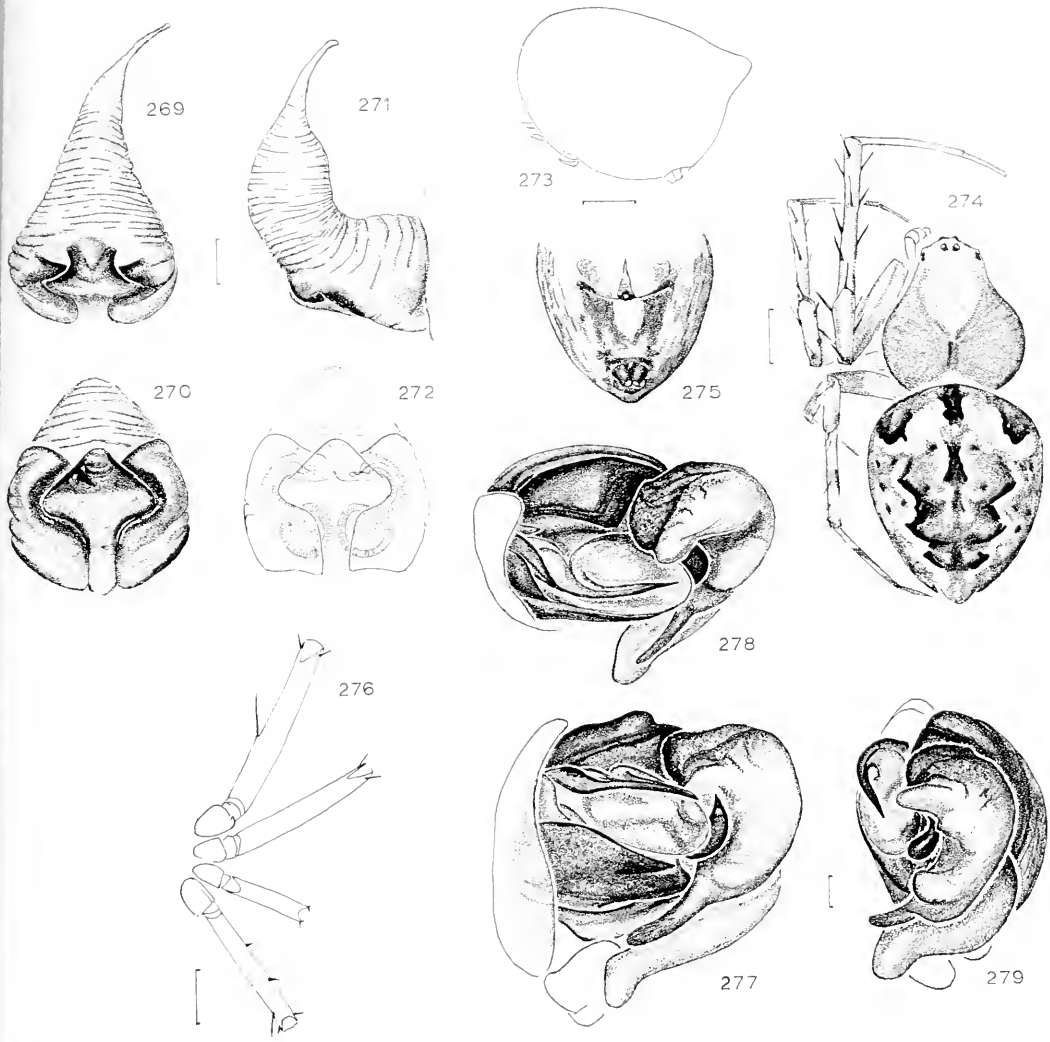
? *Epeira petasata* Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2: 70. Type, Abbot manuscript, Spiders of Georgia, in the British Museum, Natural History, illustration no. 135. Copy of original in Museum of Comparative Zoology, examined. Doubtful name.

Epeira emertoni Banks, 1904, J. New York Entomol. Soc., 12: 111. Female syntypes from Sea Cliff, N.Y., Washington, D.C., and Auburn, Alabama, lost.

Eustala triflex,—Chamberlin and Ivie, 1944, Bull. Univ. Utah, biol. ser., 8(5): 103 (not *E. triflex* Walckenaer).

Eustala arkansana Archer, 1951, Amer. Mus. Novitates, no. 1487: 19, fig. 44, ♂, not ♀. Male holotype from Berryville, Carroll Co., Arkansas, in the American Museum of Natural History, examined. NEW SYNONYMY.

Note. This species, called *Eustala triflex* by Chamberlin and Ivie (1944), is not *E. triflex* Walckenaer. *Eustala triflex*, fig. no. 112 of Abbot's manuscript, Spiders of Georgia, is contrastingly white and black as in Figures 219, 222, a coloration not found in this species. The same comment applies to the name *E. trinotata* Walckenaer, Abbot's fig. no. 272. Chamberlin and Ivie believed Hentz's *bombycinaria* to be this species. The light shoulder spots of *bombycinaria* Hentz are found, as in fig. 16, plate 31, but they are not white as shown by Hentz in the figures and in a colored manu-



Figures 269–279. *Eustala conchlea* (McCook): 269–275. Female: 269–272. Epigynum: 269. Ventral. 270. Posterior. 271. Lateral. 272. Posterior, cleared. 273. Abdomen, lateral. 274. Dorsal. 275. Abdomen, ventral. 276. Male ventral macrosetae on left femora. 277–279. Male left palpus: 277. Mesal. 278. Apical. 279. Ventral.

Scale lines. 0.1 mm, except Figs. 273–276, 1.0 mm.

script illustration at Harvard University. Banks was the first to describe the species and give diagnostic characters.

Description. Female from Pennsylvania: Head region much lighter than sides of thorax. Carapace with white down. Sternum with some black pigment marks. Legs with only femora banded. Dorsum of abdomen with very distinct contrasting folium (Fig. 258). The abdomen is oval without hump (Figs. 257, 258). Total length 5.6 mm. Carapace 2.3 mm long, 2.0 wide. First femur, 3.0 mm; patella and tibia, 3.6; metatarsus, 1.9; tarsus, 0.7. Second patella and tibia, 2.9 mm; third, 1.5; fourth, 2.5.

Male from Pennsylvania: Coloration and

shape as in female. Total length 4.3 mm. Carapace 2.3 mm long, 1.7 wide. First femur, 3.0 mm; patella and tibia, 3.4; metatarsus, 2.0; tarsus, 0.8. Second patella and tibia, 2.4; third, 1.4; fourth, 1.9.

Variation. The abdominal pattern is similar in most specimens (Fig. 258), some have a dark triangle on the dorsum (Fig. 260). Total length of females 3.4 to 7.6 mm, carapace 1.7 to 3.5 long, 1.5 to 2.9 wide. Total length of males 3.8 to 5.0 mm, carapace 2.4 to 2.6 long, 1.8 to 2.2 wide. Southern Florida females measure 5.0 to 6.1 mm total length, carapace 2.0 to 2.3 long, 1.7 to 2.0 wide.

Diagnosis. The abdomen of females is egg-shaped, widest anteriorly, the posterior hump absent; the median area of the epigynum in posterior view is distinctly larger than the small posterior lateral areas (Figs. 254, 262, 291–295), unlike that of *E. anastera* and, usually, of the smaller *E. cepina.* The epigynum is 0.4 to 0.5 mm wide, larger than that of *E. cepina.* It is similar to the epigynum of *E. conchlea* in the west, but the abdominal hump of *E. conchlea* is lacking in *E. emertoni.*

Males lack macrosetae on the venter of the second leg femora (Fig. 265). The tip of the terminal apophysis of the palpus is shorter than the bubble-like subterminal apophysis, unlike that of *E. cepina.* The conductor is much larger than that of *E. cepina* and *E. anastera* and, unlike that of *E. cepina,* is bulging "on top" and has a thin tail, about five times as long as wide (Figs. 266, 309–311, 317). The palpus is 0.8 to 1.2 mm wide.

Natural History. Specimens have been collected as prey by *Chalybion* wasps in Oklahoma and other mud-dauber wasps, in button woods (*Platanus* sp.) in Rhode Island (the northernmost locality), in wheat and in alfalfa in Arkansas, in a broom-sedge (*Andropogon virginicus*) field and bottomland pine-hardwood forest in North Carolina, in pinewoods and salt marsh in Georgia, in roadside low weeds and grass in Mississippi, in a wooded area in Texas, in pine-flatwoods, bottomland, palmetto flatwoods, and around a swamp in Florida.

Distribution. Rhode Island, Michigan to Florida, Kansas, central Texas and northeastern Mexico (Map 5).

Eustala conchlea (McCook)
Figures 269–279, 296, 312, 318, Map 5

Epeira parvula var. *conchlea* McCook, 1888, Proc. Acad. Sci. Philadelphia, p. 199, fig. 6, ♀. Specimens from Wisconsin and California. Female lectotype from California, here designated, and numerous female and male paralectotypes of the same species and one female paralectotype which is *E. californiensis,* all in the Academy of Natural Sciences, Philadelphia, examined. Wisconsin specimens do not survive.

Epeira anastera var. *conchlea* McCook, 1893, American Spiders, 3: 174, pl. 8, fig. 1n.

Eustala anastera buliafera Chamberlin, 1924, Proc. Calif. Acad. Sci., 4 ser., 12: 650. Female holotype from Isla Partida, Gulf of California in the California Academy of Sciences, examined. NEW SYNONYMY.

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Figures 280–296. Epigyna of the *E. anastera* group.

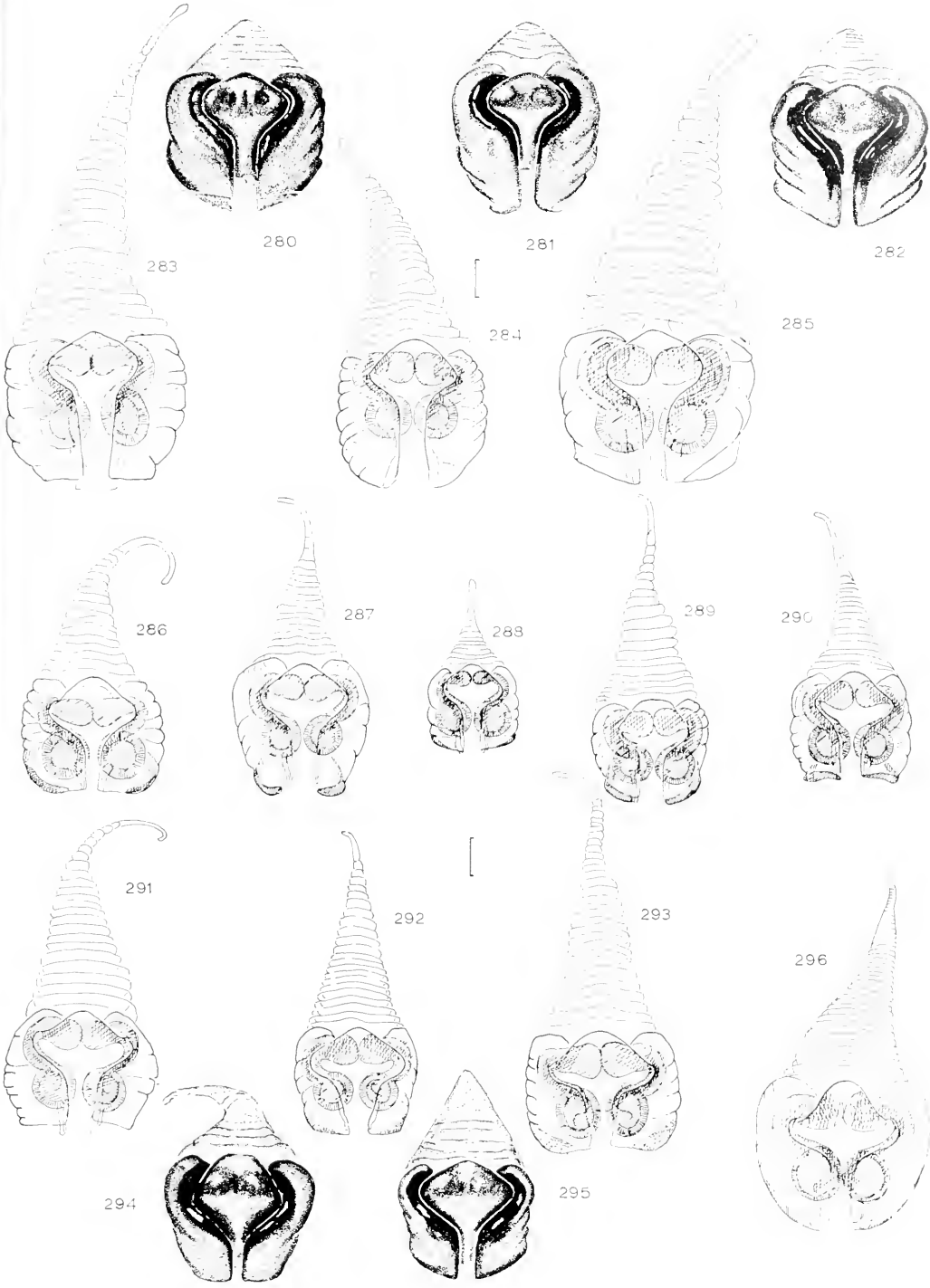
Figures 280–285. *Eustala anastera* (Walckenaer): 280–282. Posterior: 283–285. Mounted and cleared on a microscope slide: 280. (Michigan). 281. (northern Florida). 282. (Texas). 283. (Pennsylvania). 284. (Highland Co., Florida). 285. (Texas).

Figures 286–290. *Eustala cepina* (Walckenaer) mounted and cleared: 286. (New Jersey). 287. (Pennsylvania). 288. (Florida). 289. (Missouri). 290. (Kansas).

Figures 291–295. *Eustala emertoni* (Banks): 291–293. Mounted and cleared: 291. (Pennsylvania). 292. (Florida). 293. (Texas). 294, 295. Posterior: 294. (Florida). 295. (Texas).

Figure 296. *Eustala conchlea* (McCook).

Scale line. 0.1 mm.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Eustala anastera leuca Chamberlin, 1924, Proc. Calif. Acad. Sci., 4 ser., 12: 650. Female holotype in poor physical condition from Santa Inez Island, Gulf of California in the Academy of Sciences, examined, NEW SYNONYMY.

Note. In 1935 (p. 22), Chamberlin and Ivie compared the new *E. rosae* to *E. conchlea*, presumably considering them sympatric. In 1944, however, they consider "*Epeira anastera* var. *conchlea* McCook, Ibid., 173 (in part, including type)" a synonym of *E. anastera*.

Description. Female from Laguna Beach, California: Head region yellow-brown, thoracic region darker. Black rings around posterior median eyes. Sternum with black pigment. Legs banded. Dorsum of abdomen with folium and median longitudinal dark line (Fig. 274). The abdomen has one posterior dorsal hump. Total length 5.3 mm. Carapace 2.4 mm long, 1.9 wide. First femur, 3.3 mm; patella and tibia, 3.9; metatarsus, 1.9; tarsus, 0.9. Second patella and tibia, 3.0 mm; third, 1.6; fourth, 2.6.

Male from Los Angeles, California: Carapace more evenly brown than in female and legs less banded. The posterior dorsal tubercle of the abdomen is distinct. Total length 5.2 mm. Carapace 2.7 mm long, 2.2 wide. First femur, 4.1 mm; patella and tibia, 4.5; metatarsus, 2.9; tarsus, 1.1. Second patella and tibia, 3.5 mm; third, 1.9; fourth, 3.0.

Variation. The variation is less than in other species. One female had a second tubercle below the posterior dorsal hump. Females measure total length 4.6 to 7.9 mm, carapace 2.2 to 3.2 mm long, 1.8 to 2.6 wide. Males, total length 4.3 to 5.0 mm, carapace 2.2 to 2.6 long, 1.9 to 2.2 wide. Specimens from Baja California and Arizona tend to be larger; a male from Tucson, Arizona, 6.4 mm long, carapace 3.4 long, 2.7 wide.

Diagnosis. The shorter, pointed terminal apophysis of the palpus (Figs. 277, 278, 312, 318), the posterior view of the epigynum (Fig. 270), and the single posterior dorsal hump (Fig. 273) separate *E. conchlea* from the sympatric *E. rosae*. *Eustala conchlea* is very similar to the eastern North American *E. emertoni*. Specimens differ from *E. emertoni* by having a posterior dorsal hump on the abdomen, while the abdomen of *E. emertoni* is egg-shaped, narrow behind without hump.

Natural History. This species has been collected from grassy fields, from tall weeds, and from reeds along a lagoon.

Distribution. Central California coast, Arizona, Baja California and Sinaloa.

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Figures 297–312. Conductor (stippled), embolus and terminal apophysis tip (black) and median apophysis (white) of left palpus of *E. anastera* group. (Note different enlargements.)

Figure 297. *Eustala rosae* Chamberlin and Ivie.

Figures 298–302. *Eustala anastera* (Walckenaer): 298. (Nova Scotia, Canada). 299. (Michigan). 300. (Missouri). 301. (Florida). 302. (southern Texas).

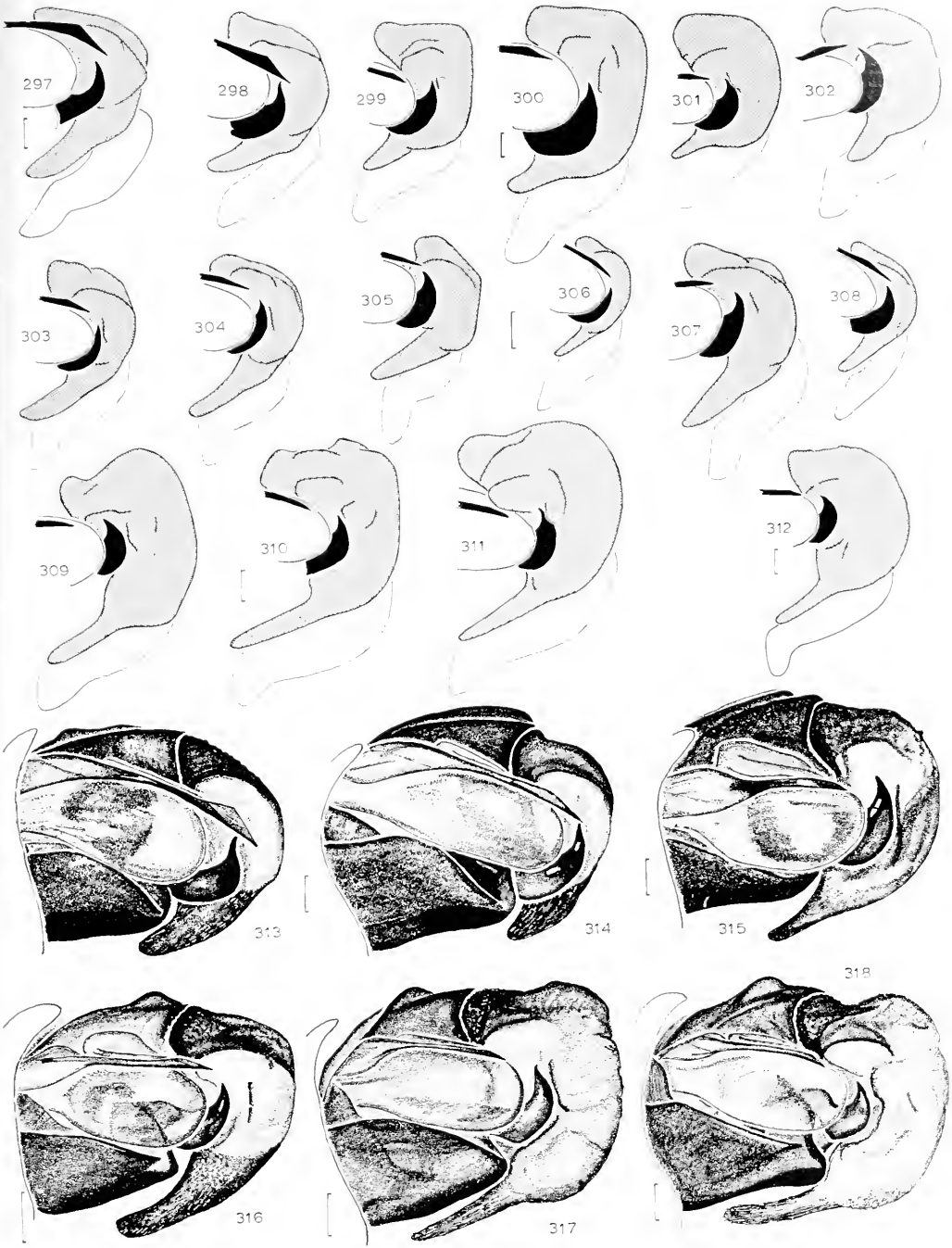
Figures 303–308. *Eustala cepina* (Walckenaer): 303. (Massachusetts). 304. (Wisconsin). 305. (Missouri). 306. (southern Florida). 307. (Alabama). 308. (southern Texas).

Figures 309–311. *Eustala emertoni* (Banks): 309. (Georgia). 310. (northeastern Texas). 311. (southern Texas).

Figure 312. *Eustala conchlea* (McCook).

Figures 313–318. Distal parts of palpus of the *E. anastera* group. (Note different enlargements.) 313. *Eustala rosae*. 314, 315. *Eustala anastera*. 314. (New Jersey). 315. (Pennsylvania). 316. *Eustala cepina* (Pennsylvania). 317. *Eustala emertoni* (Florida). 318. *Eustala conchlea*.

Scale lines. 0.1 mm.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Bulletin of the
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VOLUME [illegible]
[illegible]

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

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Bulletin 1863–
Memoirs 1864–1938
Johnsonia, Department of Mollusks, 1941–
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A CLASSIFICATION OF THE TYRANT FLYCATCHERS (Tyrannidae)

MELVIN A. TRAYLOR JR.[1]

CONTENTS

ABSTRACT. The classification of the Tyrannidae is re-examined, using available morphological, anatomical, behavioral and zoogeographic data. The usual seven subfamilies are reduced to three, and these are defined primarily on cranial characters. The former subfamily Myiarchinae is divided between the Fluvicolinae and Tyranninae, and the remaining "subfamilies" are lumped into one subfamily, the Elaeniinae. Thirty-five genera recognized in the last complete list of flycatchers (Hellmayr, 1927) are synonymized, one is resurrected, and two new ones are recognized, of which one is here described.

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INTRODUCTION

This investigation of the classification of the New World flycatchers, Tyrannidae, was undertaken as the first step in the preparation of a list of the family for inclusion in vol. 8 of the continuation of Peters' *Check-list of the Birds of the World* (here usually referred to as "Peters"). The last classification of the whole family was that of Hellmayr (1927), and in the intervening 50 years much that requires assimilation has been learned about the family. David Snow of the British Museum (N.H.) has made similar studies of the Cotingidae and Pipridae, and his results have been published in two recent papers (Snow 1973, 1975).

Before his death in 1957, John T. Zimmer almost completed a manuscript of the Tyrannidae for Peters' *Check-list*. However, Zimmer was concerned almost entirely with species and subspecies, and, with only minor exceptions explained in his earlier published "Studies of Peruvian Birds" (1936–1941), he followed the classification of Hellmayr. While Zimmer's manuscript is invaluable for defining the limits of species and subspecies and their geographical ranges, he had little to say about the genera and higher categories. The present paper deals with those higher categories, and presents the rationale for the classification that will be followed in Peters. A subsequent paper will consider problems at the species level.

No study of a major family such as the Tyrannidae would be possible without the active assistance and cooperation of one's colleagues. Ernst Mayr, one of the editors of Peters' *Check-list*, first suggested that I edit volume 8, which includes the Tyrannidae, and he has been a source of constant support and encouragement throughout. I have also been fortunate in having Emmet R. Blake as a colleague in residence at Field Museum, with whom I could discuss the innumerable knotty points that arose. In order to examine the genera and species not available in Chicago, I have visited several museums and I would like to thank for their unfailing courtesy: Wesley Lanyon and Lester Short of the American Museum of Natural History, Raymond A. Paynter, Jr. of the Museum of Comparative Zoology, and Frank Gill and James Bond of the Academy of Natural Sciences, Philadelphia. Kenneth Parkes of the Carnegie Museum, Pittsburgh, and George Lowery and John O'Neill of the Museum of Zoology, Louisiana State University, generously lent me necessary material for examination. I was fortunate in having David Snow accept responsibility for the Cotingidae and Pipridae, for we were able to reach complete accord on the limits of our respective families. François Vuilleumier, John Fitzpatrick and John Weske, in both correspondence and personal coversations, have given me the benefit of their field experience with many of the flycatchers, particularly the Andean forms, and W. John Smith has not only done the same, but has given me a copy of his notes on his own flycatcher study. John Fitzpatrick allowed me to see a copy of his manuscript on the genus *Todirostrum* and allies before publication, and has given me permission to reprint one of the figures from the published (1976) version. I have benefited greatly from conversations and correspondence with Allen Phillips, primarily concerning the species of the genus *Tyrannus*. And finally, I am especially grateful to Stuart Warter for permission to freely use his Ph.D. thesis on the classification of the Tyrannoidea—one of the few papers actually defining the Tyrannid subfamilies—and to publish, as Appendix D, some of his figures and tables.

Eugene Eisenmann and John Fitzpatrick were kind enough to critically read the entire manuscript, and to make numerous suggestions for both form and content. I deeply appreciate their efforts to make this a more literate and comprehensive publication. David Snow also read it, to make sure our concepts of the Cotingidae and Tyrannidae were reconciled. I also owe thanks to my wife Marjorie who read the manuscript from the point of view of the intelligent layman and made many helpful suggestions, and to Dianne Maurer who typed it more times than we care to remember.

MATERIALS AND METHODS

External Morphology. During this study I attempted to use evidence from every available source—external morphology, anatomy, behavior and distribution. I personally examined and measured specimens of every genus recognized by Hellmayr, and of those described since the publication of his list. For every genus and for 279 out of 374 ± 1 recognized species, I have plotted the ratios tail/wing, culmen/wing, tarsus/wing and culmen/tarsus as functions of wing length. I selected these ratios as those best suited for comparing the proportions of different sized birds. While wing length is by no means an exact measure of absolute size, it seems the most reliable of the standard measurements.

The different states of various other characters were tabulated for all species. These were: the presence or absence of abnormal primaries, and, if present, in which sex; presence or absence of wing-bars and some measure of their contrast; presence or absence of a dark patch at the base of the secondaries; wing shape, measured by noting the inner primaries to which the 10th and 9th are equal in length, and by calcu-

lating the ratio of the wing tip (longest minus shortest primary) to the wing length; type of tarsal scutellation; type of nest; weight by sex; and presence or absence of a bright crest.

Besides the individual characters listed above, the degree of overall resemblance based on plumage color and pattern, general form and size, shape of bill, extent of rictal bristles, etc., is still important in any classification. Such resemblances and differences have been implicit in previous classifications and revisions, even though often subordinated to more artificial key characters. However, convergence in plumage and form is a constant problem, particularly among the smaller, forest-living species, and general resemblance alone is unreliable for diagnoses of genera in this family.

Distribution. The geographic and altitudinal distributions of each genus were plotted on outline maps and tabulated according to the following ecological and geographical divisions:

I. Lowland humid forest
   a) Amazonia, including Venezuela and the Guianas
   b) southeast Brazil
   c) Colombian-Pacific: the humid forests of Central America, western Colombia and northwestern Ecuador

II. Other lowland tropical
   a) woodland/campo/savanna, south of Amazonia
   b) woodland/llanos, north of Amazonia
   c) arid: Caribbean coast, Pacific coast of Peru, etc.

III. Montane forest

IV. Temperate savanna/puna/paramo
   a) montane
   b) lowland Chile and Argentina

V. Specialized: lacustrine, marsh, streams, etc.

VI. Central America, including tropical Mexico

VII. North America, including temperate Mexico

Literature. Considering that fifty years have passed since the publication of Hellmayr's list, the literature relevant to the higher classification of the Tyrannidae is surprisingly sparse. Zimmer (1936–1941) discussed in great detail the species of flycatchers occurring in Peru, which include a surprisingly large percentage of those of South America, but his concern was almost entirely with species and subspecies. In his 1955 manuscript, he followed Hellmayr's sequence, although he dropped the subfamilial classification. Zimmer's unpublished list was the basis of Meyer de Schauensee's treatment of the family in his *The species of birds of South America* (1966). In his *A guide to the birds of South America* (1970), Meyer de Schauensee transferred to the Tyrannidae a few genera formerly in the Cotingidae, but otherwise made no changes.

Ames (1971), in his study of the syrinx of passerine birds, examined 128 species in 86 genera of Tyrannidae. He worked within the framework of Hellmayr's classification, that is, he chiefly compared each genus with others in the same subfamily. In his taxonomic conclusions, Ames outlined seven groups of genera (Appendix C) whose members were more closely related to each other than to any genus outside the group, and in some cases he was able to indicate the degree of relationship between the groups. However, he did not attempt to place the groups in a taxonomic hierarchy, and he was left with a residue of thirty-one genera that were neither part of nor allied to any group.

The single paper that directly concerns

itself with the classification of the Tyrannidae as a whole is Stuart L. Warter's (1965) unpublished Ph.D. thesis on the cranial osteology of the Tyrannoidea. Warter examined the skulls of 160 species in 84 genera of the flycatchers. He concluded that cranial characters alone did not support the subdivision of the Tyrannidae into subfamilies, but he combined these characters with the external morphological classification of Hellmayr to produce a tentative classification that differed in several significant ways from Hellmayr's.

A number of authors have dealt with one or the other of Hellmayr's subfamilies, or parts thereof. Meise (1949) reviewed the subfamily Tyranninae, and separated them into three groups of genera primarily on the type of nest. W. John Smith (1966) reviewed the genus *Tyrannus* (including *Muscivora*) primarily from a behavioral point of view, and in 1971 did the same for Hellmayr's Serpophaginae. Smith and François Vuilleumier (1971) reviewed the ground-tyrants, *Ochthoeca*, *Xolmis* (including *Myiotheretes*, *Cnemarchus* and *Ochthodiaeta*), *Neoxolmis*, *Agriornis* and *Muscisaxicola*; in their study Smith emphasized the behavioral characters while Vuilleumier used the morphological and distributional evidence. Most recently, John Fitzpatrick (1976) has reviewed that part of Hellmayr's Euscarthminae including *Todirostrum* and its close allies.

Information on behavior and nest types is scattered through the literature, the one exception being Alexander Skutch's (1960) life histories of Central American birds. Records of weights are even more scattered, although a fair amount of data was gleaned from specimen labels.

The value of the various lines of evidence cited above proved extremely variable when applied to the higher classification of the flycatchers. No single character or group of characters was consistent throughout the family. Proportions—particularly the relative length of the tarsus, which was one of the original characters used in defining subfamilies—vary so much within Hellmayr's subfamilies that they are without value above the generic or generic group level. Such characters as abnormal primaries, bright coronal crests, wing shape, and wing-bars may be regular in some genera or groups of genera, but appear sporadically and irregularly in others.

The type of tarsal scutellation, which was used by both Sclater (1888: 2) and Ridgway (1907: 328 ff.) as a key family character, proves so variable that by itself it cannot even be used to define genera. Only when this scutellation correlates well with other characters can it be said to have taxonomic value. Plotnick and Pergolani de Costa (1955) examined the tarsi of some 12,500 passeriform specimens, and published figures showing that the classical exaspidean, pycnaspidean, taxaspidean and holaspidean tarsal types are not discrete entities, but blend into each other through various intermediate forms.

The importance of the syrinx as a taxonomic character is most difficult to assess. According to Ames (1971: 158), the groups of genera he defines show a high degree of syringeal homogeneity and each possesses certain features not found elsewhere in the family. I believe the homogeneity shown within these groups is real and a true indicator of relationship, because these genera groups correlate well both with the traditional classification and with certain innovations suggested by Warter (1965) on the basis of cranial characters. On the other hand, some genera, which on almost every other character belong in a given group, have syringes that are unlike those of their apparent relatives. *Arundinicola* is not included in the *Fluvicola* group by Ames, even though the two genera are so close that I merge them; *Todirostrum* stands by itself, although *Idioptilon*, with which Short (1975) merges it, is designated by Ames as a member of the *Colopteryx* group; and *Sublegatus*, which is distinguishable from *Elaenia* only by the swollen bill and lack of a white crest, stands completely

apart on syrinx from the *Elaenia* group. While close resemblance in the syrinx may be accepted as indicating phylogenetic relationship, the lack of such resemblance apparently does not negate relationship.

The cranial characters used by Warter, the forms of the nasal and interorbital septa, and of the palatines and the cranium, seem to show the greatest consistency in defining taxa above the generic level. These characters not only correlate with each other but with many other characters as well. In only a few cases does the preponderance of evidence from other sources cause me to go against the evidence of the cranial characters. However, the different cranial characters vary in importance from group to group, and no one of them is consistent throughout the family. For example, among the Fluvicolinae and Tyranninae the form of the nasal septum is almost 100 per cent consistent, but among the smaller flycatchers it is quite variable, and the form of the orbital septum is diagnostic.

Methods. Because of the variability shown by all the available criteria, I have not been able to quantify their values in any consistent way. In any given situation, I attempted to use those characters showing the strongest correlations and to ignore single contradictory characters, even though in a different situation the latter might be diagnostic. In other words, my approach has been intuitive, even though I believe it has also been objective. Whether the resulting classification is a valid one can only be determined by time and by many more detailed anatomical studies of the whole family.

In the following discussion I used, for the sake of simplicity, the generic names accepted by Meyer de Schauensee (1966), even though the authors cited have used different ones. I used Meyer de Schauensee's work in preference to Hellmayr's, because the former's names are now in general use and are more familiar to the majority of ornithologists. Appendix B lists all generic names whose status has changed at all since Hellmayr (1927) and names that have been proposed since that date. Use of the appendix should resolve most confusion.

LIMITS OF THE FAMILY

In the most recent widely-used classification of the perching birds, Passeriformes (Wetmore, 1960), the Tyrannidae are a family within the super-family Tyrannoidea, suborder Tyranni, order Passeriformes. They share their superfamily with the New World Cotingidae, Pipridae, Oxyruncidae, and Phytotomidae, and with the Old World Pittidae, Acanthisittidae and Philepittidae. This is also the classification of Mayr and Amadon (1951), except the latter authors use the name "Passeres" for the order, and make the Oxyruncidae a subfamily of the Tyrannidae. Ames (1971: 153), on the evidence of the syrinx, removed the three Old World families to a position "sedis incertae," and placed the Tyrannidae, Cotingidae, Pipridae, Oxyruncidae and Phytotomidae in their own suborder Tyranni. Despite the shifts in higher classification the limits of the latter five families have been remarkably persistent, remaining essentially the same since the mid-nineteenth century.

Mayr and Amadon merged *Oxyruncus* in the Tyrannidae in a parenthetical aside, and did not discuss any characters. Ames (1971: 163) treated the Oxyruncidae as a separate family. He found that *Oxyruncus* had a typically tyrannid syrinx, but no close resemblance to any particular tyrannid genus. The musculature was similar to that of *Pachyramphus* in the Cotingidae, but the cartilages showed substantial differences. Warter was even more positive in keeping *Oxyruncus* out of the Tyrannidae. He stated, "The uniqueness of the highly specialized [*Oxyruncus*] skull argues against the inclusion of the genus in an otherwise so relatively homogeneous a family as the Tyrannidae." I shall follow

Ames and Warter in keeping *Oxyruncus* in a separate family.

Although the families of New World Tyrannoidea have remained essentially the same for the past century, there has been some transference of genera and species between them. In 1907 Ridgway (p. 339) transferred several taxa from the Tyrannidae to the Cotingidae and Formicariidae because they had types of tarsal scutellation other than the exaspidean that he considered characteristic of the Tyrannidae. These genera were *Stigmatura*, *Hapalocercus* (= *Euscarthmus*), *Habrura* (= *Polystictus*), *Muscigralla*, *Culicivora*, *Syristes*, *Idiotriccus* (= *Acrochordopus*), *Elainopsis* (= *Myiopagis gaimardii*), *Tyrannulus*, *Microtriccus* and *Hylonax* (= *Myiarchus validus*). However, Hellmayr recognized, as did Ridgway (1907: 336, ftn.) in another context, that the forms of the tarsal envelope were of dubious value beyond the classification of genera, and sometimes not even there, and he returned (1927) all these genera to the Tyrannidae. Both Warter (1965: 37) and Ames (1971: 162) supported Hellmayr's conclusions.

More recently Ames (1971) and Snow (1973) recommended transferring from the Cotingidae, where they have traditionally resided, to the Tyrannidae the genera *Attila*, *Pseudattila*, *Casiornis*, *Laniocera* and *Rhytipterna*. Ames believed syringeal characters linked these genera into a closely related group, of which the flycatcher genus *Myiarchus* was an integral part. Snow concurred that the five genera did not belong in the Cotingids, although he recognized that so little was known of their behavior, except for *Attila*, it was difficult to reach any conclusions. Warter (1965: 37) also placed *Rhytipterna* in a natural group with *Myiarchus*. However, he considered *Attila*, while definitely not a Cotingid, sufficiently distinct from the other flycatchers as to form a subfamily of its own within the Tyrannidae. Warter did not examine *Casiornis* or *Laniocera*, but he assumed the former was allied to *Attila*, and the latter to *Rhytipterna*. These five genera, based on the then unpublished work of Ames and Warter, were included in the Tyrannidae by Meyer de Schauensee (1970) in his *Guide to the Birds of South America*, and by Wetmore (1972) in his *Birds of the Republic of Panama*; in both cases they were placed next to *Myiarchus*.

Wetmore (1972: 446) also included the Cotingid genus *Lipaugus* in the flycatchers. The genera *Laniocera*, *Rhytipterna* and *Lipaugus* show a remarkable parallelism in the geographical distribution of plumage types. Each genus has a gray species inhabiting Amazonia, and a representative rufous species in Central America and western Colombia. The three genera have always appeared together in linear lists, except for that of Meyer de Schauensee (1970). Snow (1973: 8) remarked on this parallelism, but felt that on behavioral and other plumage characters, *Lipaugus* should be retained in the Cotingas. Ames lacked adequate material of this genus. Warter (1965: 137) found the skulls of *Lipaugus* typically Cotingid, and placed the genus in the subfamily Querulinae. I include *Attila*, *Pseudattila*, *Casiornis*, *Laniocera* and *Rhytipterna* in the Tyrannidae, but leave *Lipaugus* in the Cotingidae.

The final genus added to the Tyrannidae since Hellmayr (1927) is *Corythopis*. *Corythopis* has been considered to form with *Conopophaga* a separate family, Conopophagidae, allied to the Formicariidae and Rhinocryptidae, and included with them in volume 7 of Peters' *Check-list* (1951). Ames, Heimerdinger and Warter (1968) introduced evidence from the sternum, the syrinx, the pterylosis and the antorbital osteology showing *Corythopis* belongs in the Tyrannoidea—not with *Conopophaga*, or with the Formicariids, with which the authors unite *Conopophaga*. Within the superfamily, the syrinx, pterylosis and external appearance are far more typical of the Tyrannidae than of any other family. The authors did not determine the precise relationships of *Corythopis* within

the Tyrannids, but the pterylosis resembles that of Hellmayr's Euscarthmines. Meyer de Schauensee (1970: 326) included *Corythopis* in the Tyrannidae, but placed it at the end of the family because he was uncertain of its position. Ames (1971: 67) inserted *Corythopis* between *Euscarthmus* and *Pseudocolopteryx*, but he described the syrinx as "unlike any of the above," meaning the subfamily Euscarthminae.

A difficult genus and species to place is *Xenopsaris albinucha*, which has been transferred back and forth between the Cotingids and Tyrannids several times. The species *albinucha* was originally described in the Cotingid genus *Pachyramphus* (Burmeister, 1869), and was recognized as a Cotingid by Sclater (1893), after he had unaccountably omitted it from his *Catalogue of Birds* (1888). In the meantime, *albinucha* became the type of two new genera, *Xenopsaris* Ridgway, 1891, which the author considered Cotingid and near the genus *Casiornis*, and *Prospoeitus* Cabanis, 1892, which that author considered Tyrannid and near the genus *Serpophaga*. Berlepsch (1907) and Hellmayr (1927) kept *Xenopsaris* in the Tyrannidae, but Zimmer, in his Peters manuscript, removed it to the Cotingids as a subgenus of *Pachyramphus*. Meyer de Schauensee (1966) placed *Xenopsaris* next to *Pachyramphus* but as a separate genus. Finally Smith (1971) tentatively placed it again in the Tyrannidae, in the subfamily Serpophaginae, as did Snow (1973). Unfortunately, neither Ames nor Warter had specimens.

The characters of *Xenopsaris* that most suggest relationship to the Cotingids are its taxaspidean tarsus and the glossy black crown in the male, which is like that of many *Pachyramphus*. Parkes (*in litt.*) considers that its slightly swollen bill with pale cutting edge suggests *Pachyramphus*, and that its sexual dimorphism is similar to that of *Pachyramphus* but has no counterpart among the Serpophagine flycatchers. On the side of Tyrannid relationship, *Xenopsaris* males lack the shortened and pointed 9th primary that is characteristic of [illegible] of all *Pachyramphus* species; in size *Xenopsaris* is smaller than any *Pachyramphus*, much nearer the size of the Serpophagines; it builds a cup-shaped nest rather than a large globular structure with side entrance characteristic of the Becards; its vocalizations are unlike those of *Pachyramphus*; and the white outer edge of its outermost rectrix is a common condition in Tyrannids, but not found in *Pachyramphus*. *Xenopsaris*' palustrine habitat would be unique among the Cotingids, but obviously not impossible.

I believe the differences in the 9th primary and in the nest form remove *Xenopsaris* from any close relationship to *Pachyramphus*, and that plumage similarities are, therefore, the result of convergence. This leaves only the taxaspidean tarsus and the bill form and color noted by Parkes (*in litt.*) as characters linking *Xenopsaris* with the Cotingids. While taxaspidean tarsi are characteristic of the Cotingids, they are also found in some Tyrannid genera such as *Culicivora*, *Stigmatura* and *Inezia*. The bill of *Xenopsaris* is more slender than that of *Pachyramphus*, which is the reason Ridgway and Cabanis placed it near *Casiornis* and *Serpophaga* respectively, and the color of the bill is much like that of some species of the Tyrannid genus *Knipolegus*, although unlike any of the Serpophagines. I consider *Xenopsaris* a Tyrannid, but because of the differences in sexual dimorphism and bill color I believe the resemblance to the Serpophagines, particularly to *Serpophaga cinerea*, is due to convergence. Since *Xenopsaris* is of uncertain relationship within the Tyrannids, I shall place it at the end of the family *incertae sedis*.

Warter (1965: 97–100; 138–140) discusses the cranial characters of the Cotingid Tityras [*Tityra* and *Erator*, the latter a genus not recognized by Meyer de Schauensee (1966: 320)] and Becards (*Pachyramphus* and *Platypsaris*). Both groups have essentially Tyranno-Myiarchine skulls, but differ from any of the recognized Tyran-

nids in a number of characters associated with the nasal capsule. The two *Tityras*, *cayana* and *semifasciata*, are the most aberrant. According to Warter (p. 99), "The peculiar structure of the tityrine bill and nasal capsule . . . provides a character which, by its very uniqueness, constitutes a radical departure from an essentially conservative pattern that obtains throughout the tyrannoid series." The skull of *Erator inquisitor*, however, despite the very close resemblance of that species to *Tityra* in plumage, external morphology, voice and nesting habits, is not so extreme, and shows more resemblance to the Becards. The latter, in turn, seem more closely related to the Tyrannids. Ames (1971: 163) also found that the syringes of the Becards had several Tyrannid features not found in the Cotingas.

Warter (pp. 139–140) suggested a number of alternatives for treating the Tityras and Becards. The first possibility was to emphasize their distinctiveness from the remainder of the Cotingas by recognizing them as a family Tityridae. If further study should show a closer link between the Becards and the Tyrannidae, the former could be made a subfamily, Pachyramphinae of the Tyrannidae, and the separate family Tityridae maintained for *Tityra* and *Erator*. However, he thought the "most logical" action would be to ally the subfamily Tityrinae to the Tyrannidae, recognizing within it two tribes, Tityrini and Pachyramphini. Although I accept his conclusions that the Tityrinae may be closer to the flycatchers than to the Cotingas, I do not consider them the hierarchical equivalent of the other Tyrannid subfamilies that I do recognize, the Elaeniinae, Fluvicolinae and Tyranninae. The skull uniformity among the Tyrannidae of Hellmayr and previous authors does not support the recognition of subfamilies on cranial characters alone (Warter 1965: 131), and the Elaeniinae, Fluvicolinae and Tyranninae are based on a combination of cranial, syringeal, external morphological and behavioral characters. The Tityrinae, however, are tentatively allied to the Tyrannidae only because their crania more nearly resemble those of the Tyrannids than those of the Cotingids. In Peters' *Check-list*, the Tityrinae will be placed at the end of the Tyrannidae, and they will not be considered further in the discussion of subfamilies below.

Two genera of Pipridae have recently been suggested as possible members of the Tyrannidae. Warter (1965: 133) felt that *Neopelma* should properly be in the Tyrannids, and Ames (1971: 160) recommended placing *Piprites* with his *Myiobius* group of Tyrannids. Warter considered *Neopelma* one of several Piprid genera that seemed intermediate between Pipridae and Tyrannidae, and the one most closely resembling the Tyrannids. He did not, however, ally it to any given genus or subfamily. Ames did ally *Piprites* to his *Myiobius* group, including *Myiobius*, *Terenotriccus*, *Pyrrhomyias* and *Onychorhynchus*; this syringeal type was so distinctive that Ames (p. 122) placed his *Myiobius* group in a different structural division from the remainder of the Tyrannidae, along with *Piprites* and the majority of the Cotingas. However, *Piprites*, with its short, deep bill, stout build, short tail and sexual dimorphism, is so unlike any members of his *Myiobius* group, that I think the syrinx resemblance is due to convergence. Unfortunately Ames did not have a specimen of *Neopelma*, nor did Warter have a skull of *Piprites*, so it is not possible to determine if there is a correlation between the syringeal and cranial characters. Snow (1975: 22) recognized that *Piprites* might be related to the Tyrannids, but he preferred to keep it in the piprids for the time being. In view of the uncertainty in both cases, I shall leave *Neopelma* and *Piprites* in the Pipridae, where they are both readily retrievable.

CLASSIFICATION TO SUBFAMILIES

Hellmayr (1927) divided the Tyrannidae into seven subfamilies: Fluvicolinae, Tyranninae, Myiarchinae, Platyrinchinae, Eus-

carthminae, Serpophaginae and Elaeniinae. Hellmayr did not define his taxa, and before they are critically examined, some attempt must be made to determine what criteria he had in mind. This is not an easy task, nor possibly even a profitable one. As Warter (1965: 130) remarked when discussing family group taxa, "Either the originality of, or the precedent for, the taxa used is often impossible to ascertain." However, a brief history of the development of Hellmayr's subfamilies since Sclater (1888) —the last author to review the whole family and to characterize his subfamilies—may give us some idea of what the former had in mind.

FLUVICOLINAE – This is the one subfamily that has descended with comparatively little change from Sclater. He characterized it as "Feet strong, tarsi stout, elongated; habits more or less terrestrial; coloration gray, white and black." Morphologically it is extremely heterogeneous, but the species agree in being non-forest types with their center of distribution south of the Amazon and in the temperate zones of the Andes, Argentina and Chile. Ihering (1904: 320) suggested removing *Sayornis* because of its North American distribution, but this was ignored by Berlepsch (1907) and Hellmayr.

TYRANNINAE – Sclater characterized this subfamily as "Feet strong; tarsi short but strong; habits arboreal but frequenters of more open spaces; coloration olive, gray, white or yellow." Although the name persists, the composition of the family has changed drastically. It originally contained only four of Hellmayr's Tyranninae genera, the remainder of which were in the Elaeniinae, but it also had all the genera of Hellmayr's Myiarchinae. Ihering (1904: 318) recognized a subfamily Pitanginae (Hellmayr's Tyrannine genera *Legatus* through *Pitangus*), which he moved from the Elaeniinae to the vicinity of the Tyranninae, with which they were incorporated by Berlepsch (1907: 473) and Hellmayr (1927). Ihering's reasons for the shift were the wide distribution and aggressive behavior of the Pitanginae. Hellmayr's Tyranninae took final shape when Berlepsch removed those genera now in the Myiarchinae.

MYIARCHINAE – Set up as a new subfamily by Berlepsch (1907: 476), but nowhere characterized; composed of genera formerly placed by Sclater in the Tyranninae.

PLATYRINCHINAE – Characterized by Sclater as "Feet weak, tarsi thin; forest dwellers; coloration olive and yellow; bill depressed; rictus bristled." Of the 20 genera included by Sclater, only the nominate genus appears in Hellmayr's subfamily! Ihering (1904: 318, 321) dismembered Sclater's family, placing those genera that made a pendent, pyriform nest in a new subfamily, Euscarthminae, and those making a cup-shaped nest in another new subfamily, Serpophaginae. Berlepsch (1907: 482) recognized Ihering's Euscarthminae, although calling it Platyrinchinae, but extracted from it three genera for which he created a new subfamily, Rhynchocyclinae. It was the latter family, to which was added *Platyrinchus*, that became Hellmayr's Platyrinchinae.

EUSCARTHMINAE – As noted above, this family was first recognized by Ihering as those genera of Platyrinchinae that made pendent, pyriform nests and were primarily forest forms. It was called Platyrinchinae by Berlepsch and then Euscarthminae again by Hellmayr when he removed *Platyrinchus*. Unfortunately, the name Euscarthminae was there incorrect, because Ihering's type genus *Euscarthmus* was called *Euscarthmornis* by Hellmayr, and he used the name *Euscarthmus* for the taxon known as *Hapalocercus* by Ihering, a cup-nest builder!

SERPOPHAGINAE – A family created by Ihering for the genera of Sclater's Platyrinchinae that built open, cup-shaped nests and inhabited open country or the Andes. It was accepted by Berlepsch (he actually called it *subfam. nov.*) and by Hellmayr.

ELAENIINAE – The last of Sclater's subfamilies, which he characterized as, "Feet

TABLE 1.

	Sclater	Ihering	Berlepsch	Hellmayr
Fluvicolinae	"Feet strong; tarsi stout, elongated; habits more or less terrestrial."	suggested removing *Sayornis* to the Tyranninae	as Sclater	as Sclater
Tyranninae	"Feet strong; tarsi short but strong; habits arboreal, but frequenters of more open spaces."	recognized the Pitanginae, Hellmayr's Tyranninae genera *Legatus* through *Pitangus* and placed them near the Tyranninae	incorporated Ihering's Pitanginae; removed the Myiarchinae to a new subfamily	as Berlepsch; only four of Sclater's 17 genera remain
Myiarchinae	(in the Tyranninae)	(in the Tyranninae)	created a new subfamily, but nowhere diagnosed it	as Berlepsch
Platyrinchinae	"Feet weak; tarsi thin; forest dwellers; bill depressed; rictus bristled."	divided it into two new subfamilies—Euscarthminae making pendent, pyriform nests, and Serpophaginae making cup-shaped nests	Ihering's Euscarthminae; created a separate subfamily Rhynchocyclinae for *Rhynchocyclus*, *Tolmomyias* and *Ramphotrigon*	Berlepsch's Rhynchocyclinae plus *Platyrinchus*, the oldest name. Only the nominate genus remains from the 20 included by Sclater
Euscarthminae	(genera in Platyrinchinae)	created for those genera of Sclater's Platyrinchinae making pendent, pyriform nests; also included *Rhynchocyclus* from the Elaeniinae	(called Platyrinchinae)	called Euscarthminae, but Hellmayr's genus *Euscarthmus* was actually Ihering's *Hapalocercus*, a cup-shaped nest builder
Serpophaginae	(genera in Platyrinchinae)	created for those genera of Sclater's Platyrinchinae making a cup-shaped nest	as Ihering	as Ihering
Elaeniinae	"Feet weak; tarsi thin; forest dwellers; bill compressed; rictus smooth	removed the Pitanginae, Hellmayr's Tyranninae from *Legatus* through *Pitangus*, to near the Tyranninae; removed *Rhynchocyclus* to the Euscarthminae	as Ihering	as Ihering

weak; tarsi thin; forest dwellers; coloration olive and yellow; bill compressed; rictus smooth." After Ihering (1904: 318) removed the Pitanginae—"large birds with strong bills that biologically much approximate to true Tyranninae"—and *Rhynchocyclus*, because of its pendent nest, the subfamily was accepted unchanged by Berlepsch and Hellmayr.

These changes are summarized in Table I.

The families of Sclater, except for the Fluvicolinae, have been so strongly revised that his original characters are no longer pertinent. Even Sclater's characters for the Fluvicolinae are irrelevant, for such genera as *Muscipipra* have among the shortest tarsi in the family instead of "stout, elongated." The Myiarchinae were never defined, and it is hard to know what Berlepsch had in mind, because they vary from some of the larger *Myiarchus*, with wings 90–100 mm to *Terenotriccus* with wing 52 mm, and from the small, round winged, forest haunting *Myiobius*, to the large, open-country, pointed winged *Hirundinea*. Ihering's separation of the Euscarthminae from the Serpophaginae on the basis of nest type was a major advance, because this character correlated well with proportions of bill and tarsi, but there were, and still are, so many problem genera for which the nest type is unknown, that its usefulness is limited.

Certainly mensural characters do not in any way define the present subfamilies. Taking wing length as a criterion of size, all the Tyranninae are larger than any of the Euscarthminae and Serpophaginae; otherwise there is overlap among all the subfamilies. The same is true of proportions. A species with a wing 62 mm, tail 52 mm, culmen 14 mm and tarsus 18 mm would fit in any subfamily except the Tyranninae without distorting the present limits of the taxon. It is clear that the present subfamilies are based on such qualitative characters as the form of the bill, the extent of the rictal bristles, the shape of the wing and tail, habitat, distribution, color and pattern. This does not imply that such a classification is valueless; Sclater, Ihering, Berlepsch and Hellmayr were all highly capable and experienced ornithologists, and the classification they developed improved at each stage. However, it is futile to search their work for key mensural or morphological characters that would clearly define their subfamilies.

In the literature since Hellmayr, there have been no attempts to evaluate his subfamilies. Ames (1971) used the subfamilies of Hellmayr as the framework within which he conducted his investigation of the syrinx. His genus-to-genus comparisons were almost all intra-subfamily, and although he set up groups of related genera, he expressly avoided equating them with subfamilies. Zimmer (1936–1941) in his *Studies of Peruvian Birds*, and also in his preliminary manuscript for Peters, ignored subfamilies. He could hardly have studied the Peruvian flycatchers, which include over half the known species, without forming some ideas about subfamilies. However, no hint of them appears in his works, and he followed the order of genera in Hellmayr's list without change. In one instance one gets the impression that he doubted the reality of some of the subfamilies completely. When he (1940b: 19) transferred *Mecocerculus superciliosus* and *Leptopogon nigrifrons* to the genus *Phylloscartes*, he merely stated "there are no positively distinguishing characters between these two species and various species of *Phylloscartes*," and he did not mention the fact that the genera had been assigned by Hellmayr to three different subfamilies, Serpophaginae, Elaeniinae and Euscarthminae respectively.

The one study that discusses the Tyrannidae at the subfamily level is that of Warter (1965). Although his cranial characters alone did not support the separation of the Tyrannidae into subfamilies they did, when combined with the classification of Hellmayr based on biological and external

morphological characters, suggest a revised classification that Warter (p. 131) presented "merely as a model for other workers."

In his study of the Tyrannoidea, Warter used five cranial characters:

a) nasal septum – six forms of the nasal septum were recognized (only five occurred in the Tyrannidae), which were determined by the type of supporting structure and by the presence and form of the transverse plate.

b) interorbital septum – five states of the interorbital septum were recognized (only four in the Tyrannids), characterized by the number and extent of the fenestrae.

c) prepalatines – three states, determined by their flattening and curvature.

d) cranium – three forms of the cranium depending on overall configuration.

e) palatomaxillaries – presence or absense recorded.

In his Figures 2 and 3 (Appendix D), Warter illustrates the states of his cranial characters.

Warter examined the crania of 850 specimens of flycatcher, representing 160 species in 84 genera. In his Table II (Appendix D) he lists the state of each of his five characters by genus. The Tyrannidae as a whole are homogeneous and there were too few long series to adequately investigate individual variation at species level; therefore his treatment had to be at the genus or group of genera level (p. 93). This problem did not exist among the more heterogeneous Cotingas, where single skulls of the genera and even some of the species, may be readily identified. In his Table II, Warter lists the genera in the order of Hellmayr.

Warter's Table II as reprinted here (Appendix D) differs slightly from the form in which it appeared in his dissertation. With his permission, I have included several ambiguous entries from an earlier draft that were eliminated from the final copy. These additions have been enclosed in parentheses; figures outside the parentheses, including the question marks, are those of his final version. The ambiguities are consequent upon the difficulty of assigning characters to a given type because of 1) shot damage, 2) careless cleaning, 3) overly zealous dermestids or 4) a continuum of form requiring arbitrary assignment to one type or the other. These ambiguous states are included here to help evaluate which data are equivocal, and which relatively certain.

When Warter's characters are compared with Hellmayr's classification, there is a strong correlation between the individual character states, and sometimes complexes of states, and the broad groupings of genera. This inspires confidence that both the evolved classification of Hellmayr and Warter's cranial characters reflect real relationships among the Tyrannidae, and not just superficial resemblance or convergence. The most striking example is found in the Tyranninae, all species of which have a character complex including type 1 or 2 nasal septum without basal plate, and types 1 interorbital septum, palatines and cranium. It is highly improbable that such a complex of four characters would have evolved independently more than once, thus the Tyranninae are almost certainly a monophyletic group. Since the cranial characters do correlate so well overall with what is known of Tyrannid relationships, they should be given considerable weight when they diverge from the old classification.

Warter (p. 94) found that the three subfamilies of "larger" flycatchers, Fluvicolinae, Tyranninae and Myiarchinae, lent themselves better to characterization than the four remaining subfamilies of "smaller" flycatchers. Although, as noted before, there is overlap in size among almost all subfamilies, the latter four of Hellmayr—Platyrinchinae, Euscarthminae, Serpophaginae, and Elaeniinae—have a preponderance of small species, for which skeletal material is less common, and, being deli-

cate, are frequently damaged. Warter (p. 96) stated, "Perhaps largely as a result of insufficient material, the adequate characterization of the smaller flycatchers, is, at the present time, impossible."

Within the larger flycatchers, there is a clear dichotomy. The Tyranninae of Hellmayr are a distinct group as outlined above. Belonging to this group, as shown by identical cranial characters, are the genera *Myiarchus* and *Eribates* of Hellmayr's Myiarchinae, and *Rhytipterna*, placed by Hellmayr and his predecessors in the Cotingidae. Presumably part of the same complex, although Warter had no material of them, are *Hylonax*, which has been synonymized with *Myiarchus* by Lanyon (1967b: 339); *Deltarhynchus*, which is a *Myiarchus* with a short broad bill; and *Laniocera*, which has been considered a close relative of *Rhytipterna* except by Ridgway (1907), who placed it in the Pipridae while leaving *Rhytipterna* in the Cotingidae. The second group of large flycatchers is composed of the Fluvicolinae of Hellmayr and most of the remaining genera of that author's Myiarchinae, the genera *Nuttallornis* through *Myiophobus*. This group is characterized by a type 6 nasal septum with horizontal baseplate, and either types 2 or 3 of at least two of the remaining three characters; the type 2 interorbital septum occurs almost exclusively in this group, although types 1 and 3 occur as well. Warter (p. 95) considers that the second group's two subgroups, the Fluvicolinae and the remainder of the Myiarchinae respectively, may be distinct on characters too minor to justify separation at the subfamily level. They merge insensibly together through such genera as *Ochthoeca*, *Ochthornis* and *Entotriccus* and may represent terrestrial or semi-terrestrial and arboreal divisions of the same stock.

A third group that Warter (pp. 95, 140) feels should be attached to the section of large flycatchers, either as a subfamily or "subfamily-equivalent" group are *Attila* and the probably closely related *Pseudattila* and *Casiornis*, two genera not available to him. Skulls of *Attila* were essentially Tyranno-Myiarchine, but with the following differences: interorbital septum less completely ossified (type 5, not found elsewhere in the Tyrannidae); nasal septum incomplete, shallow, along its entire length; prepalatines narrow, slightly convergent, nearly straight. In themselves, the *Attila* skulls were a distinct type. Warter's suggestion was to recognize among the large tyrant flycatchers three "subfamily-equivalent" groups: Attilinae, Tyranninae and Fluvicolinae.

Warter, as noted before, did not consider that cranial characters permitted the classification of Hellmayr's four subfamilies of small flycatchers at this time. He did believe (p. 131) the Euscarthminae graded into the Platyrinchinae via *Todirostrum* and *Oncostoma*, and the Serpophaginae graded into the Elaeniinae via *Serpophaga*. He also included in this section the genus *Onychorynchus*, which, like *Platyrinchus*, has a type 3 nasal septum and does not belong in either section of the Myiarchinae, the subfamily where Hellmayr placed it.

Warter's (p. 131) final tentative classification of the Tyrannidae was a compromise between the cranial evidence and the subdivisions of Hellmayr based on biological and external morphological features. It included five subfamilies, three of them divided into tribes:

- Attilinae (see Warter, pp. 95 and 140)
- Tyranninae
- Fluvicolinae
  - Fluvicolini
  - Alectrurini
  - "Contopini"
- Platyrinchinae
  - Onychorhynchini
  - Platyrinchini
  - Euscarthmini
- Elaeniinae
  - Elaeniini
  - Serpophagini

The classification adopted in this paper

is essentially that of Warter at the subfamily level, except that I do not recognize his Attilinae, and I consider that all of the small flycatchers, his Platyrinchinae and Elaeniinae, belong in a single subfamily for which Elaeniinae is the oldest name. The use of tribes, however, does not seem warranted. The three Fluvicoline tribes are uneven, both in numbers of genera and degree of difference, and the Fluvicolini and "Contopini" may not be so distinct as previous classifications would suggest. The tribes of Elaeniinae, which Warter recognized in deference to previous classifications, seem to merge into each other so insensibly that no divisions can be recognized.

The brief history of the evolution of Hellmayr's subfamilies showed that none of them was maintained on clear-cut characters, and that the Myiarchinae had never been diagnosed, not even by the original describer. The dismemberment of the Myiarchinae, therefore, may upset our sense of familiarity with a subfamily of 70 years' standing, but it does not do violence to any known diagnostic characters. The more important question is how well do the segments of Myiarchinae fit into the Tyranninae and Fluvicolinae respectively.

Myiarchus, with the closely related *Eribates*, *Hylonax* and *Deltarhynchus*, fits easily into the Tyranninae. It is a highly successful genus, like so many of those in the Tyranninae, with a geographical range equal to that of *Tyrannus* itself, from temperate North America to temperate South America. Form and proportions are typically "flycatcher," with a long, broad and moderately flattened bill and about average development of rictal bristles. The tarsi are longer than those of most of the Tyranninae, but still short enough that Sclater put them in with the "tarsus short, stout" Tyranninae. The hole nesting habits of *Myiarchus* are shared for the most part with *Myiodynastes*. There are no evident reasons for keeping *Myiarchus* out of the Tyranninae, and the cranial evidence for placing it there is compelling. The latter statement is also true for *Rhytipterna* and presumably *Laniocera*, and the transfer of these two genera to the vicinity of *Myiarchus* on other grounds by Snow (1973) and Ames (1971) reinforces the cranial evidence. Meyer de Schauensee (1970) and Wetmore (1972) followed Ames and Warter, whose theses they had seen before publication.

The recognition of Warter's subfamily Attilinae, *Attila* and *Casiornis*, must be considered here, because the above authors all included those genera, previously included in the Cotingidae, with *Rhytipterna* and *Laniocera* next to *Myiarchus*. Externally, there is nothing that keeps *Attila* and *Casiornis* separate from *Rhytipterna*, *Laniocera* or *Myiarchus*. Internally, there is strong evidence from the syrinx that they are closely related. The above five genera make up Ames' (1971: 160) *Myiarchus* group. Speaking of the former Cotingid genera compared to *Myiarchus*, Ames says, "Without assuming interdependence of several syringeal features, it is difficult to see how two groups of birds could evolve both external and internal similarities to such a degree." If this is true when *Attila*, *Casiornis*, *Laniocera* and *Rhytipterna* are compared to *Myiarchus*, it is equally true when *Attila* is compared to *Rhytipterna* and the others. Despite the fact that *Attila* has a partially ossified interorbital septum not found elsewhere in the Tyrannidae, which caused Warter to put it in a separate subfamily, I consider Ames' *Myiarchus* group to be monophyletic, and I keep it together in the Tyranninae.

The transfer of the remainder of the Myiarchinae, Warter's "Contopini," to the Fluvicolinae suggests some relationships not considered before. Both are presumably old lineages with a high degree of sympatry in the larger genera, numerous monotypic genera and relict species, and a high degree of phenetic variability. Warter's Fluvicolini contains all the truly terrestrial flycatchers and is usually thought of

as a long-legged group. However, there are a number of arboreal Fluvicolines, such as *Ochthoeca* and *Knipolegus*, and these are very close in proportions to the Contopines. When the two are treated as related, certain cases of resemblance between genera and species that were previously thought of as convergence may turn out to show close relationship. A striking example is the Fluvicoline *Ochthoeca diadema* and the Contopine *Myiophobus flavicans*. Both are bright olive green flycatchers, identical in wing length and shape, bill form, and rictal bristles; they can be separated only by the slightly longer tarsus and yellow superciliaries of *diadema*, and the yellow crest of *flavicans*. Their resemblance may be due to the persistance of the characters of an early common ancestor.

The Fluvicolines of Sclater and Hellmayr are a heterogeneous assemblage united by their dry country or temperate center of distribution in South America. Their great phyletic age has produced such unlike forms as the long-legged, long-billed terrestrial *Muscisaxicola* and the short-legged, short-billed arboreal *Muscipipra*. It is encouraging, and a tribute to Sclater's intuition, that Warter's cranial characters support the present classification. Warter's Contopines on the other hand, are a lineage that has had its most successful radiation in North and Central America. While there was a proliferation of species in the Fluvicoline genera *Muscisaxicola*, *Agriornis* and *Xolmis* in the south temperate and subtropical regions, there was a similar proliferation in the Contopine *Contopus*, *Empidonax* and *Sayornis* in the north temperate regions and Middle America. The Fluvicolines are still virtually all South American, with only one species reaching eastern Panama, while only a few genera of Contopines are primarily South American. These are mostly small, lowland forms, such as *Myiobius* and *Terenotriccus*, or montane forest genera such as *Myiotriccus*, *Pyrrhomyias* and *Myiophobus*. These South American genera may have separated from the North and Central American group fairly early, because some at least have a distinctive type of syrinx, as discussed below. However, in general form all these genera are fairly close, being "typical" small flycatchers with broad, depressed bills and moderate to heavy rictal bristles.

Three of Ames' genera groups are included in the expanded Fluvicolinae. The first of these, his *Fluvicola* group, belongs to what might be called the core of Warter's Fluvicolini: *Xolmis*, *Neoxolmis*, *Agriornis*, *Muscisaxicola*, *Fluvicola*, *Gubernetes*, *Knipolegus*, *Muscipipra* and *Phaeotriccus*. With the possible exception of *Gubernetes* and *Muscipipra*, one would expect these genera to be alike. What is surprising is the absence of *Arundinicola*, *Entotriccus* and *Yetapa*, which are in all morphological characters except the syrinx very close to *Fluvicola*, *Phaeotriccus* and *Gubernetes* respectively. Ames' second group is the *Nuttallornis* group—*Nuttallornis*, *Sayornis*, *Contopus*, *Blacicus*, *Empidonax*, *Aechmolophus*, and *Aphanotriccus*—which according to Ames is closest to the *Fluvicola* group in syringeal structure. It is this group that has been so successful in North and Central America.

The members of Ames' *Myiobius* group —*Myiobius*, *Terenotriccus*, *Pyrrhomyias* and *Onychorhynchus*—appear more closely related to each other than to any other group, and Ames placed them in a separate major structural division of the syrinx from the rest of the flycatchers. This is the group that is primarily of South American forest distribution. The inclusion of *Onychorhynchus* with the *Myiobius* group agrees with the traditional classification of Hellmayr, but differs from that of Warter, who considered the genus an aberrant "small" flycatcher in his subfamily Platyrinchinae. The status of *Onychorhynchus* is considered in more detail below.

The remainder of the family, which Warter, in deference to previous classifications, divided into two subfamilies and five tribes, seems to me incapable of such subdivision.

Consider first the cranial characters. The nasal septum, which has proved an important conservative character in the Fluvicolinae and Tyranninae, is extremely variable in the Elaeniinae, and lacks any correlation with other characters. On the other hand, his tribes Platyrinchini, Euscarthmini and Serpophagini, and some genera of the Elaeniini, all show a type 4 interorbital septum, which does not occur at all in the large flycatchers. Of those Elaeniini genera that lack the type 4 interorbital septum and that might be set apart on that account, three are linked to the Serpophagini by their type 5 nasal septum, which is unique to these two groups. As Warter said (p. 112) characterization of the smaller flycatchers on the basis of their cranial characters is impossible.

The external morphological and biological evidence for subdividing the small flycatchers is little better, despite the four subfamilies usually recognized. *Onychorhynchus*, with its striking ornamental crest, long, flat bill, and long rictal bristles, is out of place in any group; it fits no better with the small flycatchers than with the Myiarchinae, where Hellmayr placed it. It is seemingly related to *Platyrinchus* by the type 3 nasal septum, which is found only in these two genera, but *Platyrinchus* has a short, broad, flattened bill, a modest concealed crest, and makes a simple cup-shaped nest rather than the elaborate, pendent, pyriform nest of *Onychorhynchus*. *Platyrinchus* is somewhat out of place in its own tribe because of its peculiar nasal septum and simple cup-shaped nest. Warter (p. 131) found that on cranial characters the Platyrinchini and Euscarthmini intergraded through *Todirostrum* and *Oncostoma*, and that the Serpophagini and Elaeniini were related through *Serpophaga*. On external morphological and biological characters I can find no way to characterize family-level groups. There are certain core groups that are quite distinct, such as the flat-billed *Rhynchocyclus* type, the tody-flycatchers *Todirostrum* and allies, and the small-billed generalized *Elaenia* group, but there are more genera falling between these groups than within them.

Ames' two genera groups from this part of the family are essentially two of these core groups. His *Colopteryx* group—*Colopteryx*, *Oncostoma*, *Idioptilon*, *Hemitriccus*, *Myiornis* and *Lophotriccus*—are all members of what I call *Todirostrum* and allies, although *Todirostrum* itself has a distinctive syrinx and is not placed with the others. His *Elaenia* group includes *Elaenia*, *Sniriri*, *Camptostoma*, *Tyrannulus* and *Phaeomyias*, all part of what I call the small-billed generalized *Elaenia* group. However, the *Rhynchocyclus* type, that I mention as a core group, is considered by Ames as an artifact of convergence. Speaking of *Platyrinchus*, *Tolmomyias* and *Rhynchocyclus*, he (p. 161) says that they, "differ so strongly in their syringeal structure that one may seriously question the reliability of bill shape as a common character for the five genera" [including *Cnipodectes* and *Ramphotrigon*, which he had not seen]. Ames' evidence agrees with that of the nasal septum and nesting habits to show that *Platyrinchus* is out of place even in the restricted subfamily where Hellmayr put it.

The recognition of any Elaeniinae subdivisions, either the earlier subfamilies or Warter's tribes, would give a sense of certainty about the reality of these entities that is non-existent.

The sequence of subfamilies and of genera in the family lists for Peters' *Checklist* ideally go from primitive or generalized to advanced or specialized. Historically, the lineal list of the flycatchers has begun with the Fluvicolinae, and ended with the Tyranninae (Sclater, 1888) or the Elaeniinae (Berlepsch, 1907; Hellmayr 1927). Although there is little solid evidence, the flycatchers seem most nearly related to the Pipridae, with Elaeniine flycatchers and the sexually monomorphic Piprids nearest the ancestral line. Warter

(p. 111) found the skulls of the Piprids *Tyranneutes* and *Neopelma* flycatcher-like, and intermediate between the flycatchers and typical Piprids. This suggested an intermediate position for the Pipridae between the Cotingidae and Tyrannidae. Ihering (1904: 319) came to a similar conclusion many years before when he considered that the Pipridae and Tyrannidae descended from a common ancestor whose closest relatives were among the Elaeniinae (*sensu stricto*) in the Tyrannids and the Ptilochlorinae (including *Tyranneutes* and *Neopelma*) in the Piprids. The ancestral form was presumably small, olive green, arboreal and forest-living, with a short, somewhat compressed and bristled bill; a description that fits many genera among the Elaeniinae. Ames (1971: 150) did not find syringeal characters useful taxonomically in determining relationships among the higher categories of Tyrannoidea. As he says (p. 157), "Except for the *Piprites-Myiobius* complex and *Ilicura*, the few manakins examined show little syringeal similarity to the typical members of either the Tyrannidae or Cotingidae."

Assuming that the Elaeniine flycatchers are the most generalized or primitive, then the Fluvicolinae, with their many terrestrial forms, are the most specialized, and the Tyranninae are the most "advanced." I use "advanced" in the sense of most successful and presumably most recently evolved, for not only are the genera widely spread geographically, from North America or Mexico to southern South America, but many individual species are equally widespread. Fitzpatrick (*in litt.*) points out that wide distributions in the Tyranninae are almost always associated with open country and edge habitats, and bear no relation to recent speciation. However, the extreme uniformity in cranial characters among the Tyranninae, and the similarity in external morphology among them compared to the diversity in the Fluvicolinae, suggest to me a more recent proliferation. The sequence of the subfamilies for Peters' *Check-list* will therefore be: Elaeniinae
Fluvicolinae
Tyranninae

SEQUENCE AND RELATIONS OF GENERA

The sequence of genera that follows (Appendix A) relies heavily on tradition when there is no strong evidence to suggest a change. If I had started *de novo*, I might well have made considerable changes. However, they would have been based on characters no more conclusive than those of Berlepsch or Hellmayr. There being no advantage in producing a new sequence just for the sake of change, much of the following list follows Hellmayr, but in reverse.

ELAENIINAE

Just as the subfamilies were placed in the sequence of primitive or generalized to advanced or specialized, so should the genera be within a subfamily. While the concepts of primitive and advanced are difficult to apply with confidence to many of the flycatcher taxa, it should be possible to recognize certain groups as generalized or specialized. If we accept the concept of the manakins and flycatchers as evolving from a common stem, then some of the small green flycatchers of the restricted subfamily Elaeniinae are probably closest to the ancestral stock. They are generally olive green above, with the crown sometimes gray or dusky; paler below, whitish, yellow or olive; two pale wing-bars and pale edgings on remiges; bill short and constricted, and light rictal bristles. Genera that fall naturally into this group are *Xanthomyias*, *Phyllomyias*, *Tyranniscus*, *Oreotriccus* and *Acrochordopus*. They have almost certainly diverged some from the common primitive stock between manakins and flycatchers, because that was presumably a humid forest form as are many of the manakins today, and the above genera are found in drier, woodland habitats or in the

subtropical zone. They are, however, unspecialized, at least morphologically.

The characters used to define the above genera are minor. *Phyllomyias* has a broader, more triangular bill and heavier rictal bristles than *Xanthomyias*; *Oreotriccus* is considered to have an exaspidean tarsus while the others are pycnaspidean or "quasi-exaspidean"; *Tyranniscus* has a short, compressed bill; *Acrochordopus* has the most pointed wing and a pycnaspidean tarsus with the distal scutella roughened; *Oreotriccus* has a rounded wing. Plumage patterns, however, cut directly across the generic lines. *Acrochordopus burmeisteri*, *Phyllomyias fasciatus*, and *Xanthomyias virescens* are virtually identical in plumage; they can only be distinguished by the morphological characters listed above; the same is true of the pairs *Oreotriccus plumbeiceps* and *Tyranniscus cinereiceps*, and *Xanthomyias sclateri* and *Phyllomyias* (*Oreotriccus*) *griseocapilla*. The last named species, *griseocapilla*, was transferred from *Phyllomyias* to *Oreotriccus* by Zimmer (1955: 23) because of its exaspidean tarsus. However, *Phyllomyias fasciatus* shows individual variation from exaspidean to taxaspidean (Zimmer called it pycnaspidean, but with birds this size the tarsal types are difficult to distinguish), and the tarsal scutellation is not a valid generic character. With the exception of a group of species now in *Tyranniscus* that I separate below, I unite in one genus *Xanthomyias*, *Phyllomyias*, *Tyranniscus* (*nigrocapillus*, *uropygialis*, and *cinereiceps* only), *Oreotriccus* and *Acrochordopus*. *Phyllomyias* and *Tyranniscus* are equally available (both described by Cabanis and Heine, 1859: 57) as the oldest name; I select *Phyllomyias* since I split the present genus *Tyranniscus*, and the use of that name might cause confusion.

Zimmer (1955: 24) pointed out that the species of *Tyranniscus* fall into two groups on wing pattern. The species *nigrocapillus* (type of genus), *uropygialis* and *cinereiceps* have the common wing pattern of two wing-bars, pale edgings on the flight feathers, and a contrasting black patch at the base of the secondaries. The remaining species, *vilissimus*, *bolivianus*, *cinereocapillus*, *gracilipes* and *viridiflavus*, have a pattern unique among the tyrannids. The median and greater coverts are edged along the outer webs with yellow or white, rather than having the pale coloring at the tips producing a wing-bar; the secondaries and four or five subexternal primaries are edged with yellow, but the outermost and the four or five inner primaries are black. This produces a distinctive black stripe (wedge) down the wing when it is spread. Correlated with this type of wing is a longer bill and a much less accentuated black speculum on the secondaries. Zimmer believed both types had quasipycnaspidean tarsi, but in my notes on the tarsi, made before I was aware of the plumage types, I called *nigrocapillus*, *uropygialis* and *cinereiceps* "pycnaspidean/taxaspidean" and *vilissimus*, *bolivianus*, *cinereocapillus*, *gracilipes* and *viridiflavus* "exaspidean, some pycnaspidean proximally." Ames (1971: 162) noted a distinction in the syrinx. He found *nigrocapillus* like *Ornithion*, and *chrysops* (a race of *viridiflavus*) like nothing else. His comment (p. 162) was, "The two species of *Tyranniscus* examined differ so strikingly in syringeal morphology that I felt it necessary to verify the identity of the specimens through comparison with skins. One cannot help wondering if a thorough analysis of structural and behavioral characters of these and other species of *Tyranniscus* would not result in dividing the genus." Warter (1965: 157) examined specimens of *Tyranniscus acer* (a race of *gracilipes*), *chrysops* and *vilissimus*. They had the type 6 nasal septum, otherwise found only in the Fluvicolinae and the aberrant *Polystictus*. *Xanthomyias virescens*, the only other member of my *Phyllomyias* group that he examined, had a type 1 nasal septum, also found in several other genera of the enlarged Elaeniinae.

Published behavioral data on *Tyranniscus* are virtually non-existent. However,

John Weske (*in litt.*) says *nigrocapillus* forages like a kinglet, but *bolivianus* perches and sallies like a typical flycatcher. Distributionally the three barred-wing forms, *nigrocapillus et al.*, are all Andean subtropical; the "edged" forms are divided, *vilissimus* occurring in Central America, and Caribbean Colombia and Venezuela, and *gracilipes* in Amazonia, while *bolivianus*, *cinereicapillus* and *viridiflavus* are found in the Andean subtropics, sympatric with the *nigrocapillus* group. In the Vilcabamba Range in Peru, Weske (*in litt.*) found the range of the edged-winged *bolivianus* overlapped those of the two barred-winged species *nigrocapillus* and *uropygialis*, while the last two replaced each other altitudinally without overlap. Only two nests have been recorded—Snethlage (1935: 538) reported the nest of *acer*, a race of *gracilipes*, as large, triangular, retort-shaped and hung from the tree branches at middle height, and Skutch (1960: 465) described that of *vilissimus* as a cozy ovoid structure with a side doorway, found in hanging mosses or bromeliads. Unfortunately, *acer* and *vilissimus* have the same wing type and there is no comparative material of *nigrocapillus et al. Phyllomyias griseocapilla* and *burmeisteri*, however, both build cup-shaped nests.

Despite the superficial similarity, I believe the group of *Tyranniscus* species with the unique wing pattern, syrinx and aberrant nasal septum, should be separated generically from the typical group of species. Surprisingly, there is no name available, so I propose:

Zimmerius gen. nov., type *Tyrannulus chrysops* Sclater, 1858.

Diagnosis. Superficially most like *Tyranniscus* Cabanis and Heine, 1859, but differs as follows: has a unique wing pattern in which the median and greater coverts, the secondaries and four or five subexternal primaries are edged with yellow, while the outermost and four or five internal primaries are blackish, producing a black wedge when the wing is spread; tail proportionately longer, greater than 80 per cent of wing length instead of less than 80 per cent, and bill proportionately longer, greater than 18 per cent of wing length; tarsus basically exaspidean with a few scutes on the proximal half of the plantar surface, compared to taxaspidean/pycnaspidean in *Tyranniscus*; syrinx unlike any others in the Elaeniinae, lacking intrinsic muscles; nasal septum of Warter's (1965: 34) type 6 with transverse plate, a type found elsewhere only in the Fluvicolinae and in the unrelated *Polystictus* of the Elaeniinae. When *Tyranniscus* is merged with *Phyllomyias* (incl. *Xanthomyias* and *Oreotriccus*) the wing pattern, syrinx and nasal septum of *Zimmerius* remain as diagnostic characters, but the different proportions and tarsal envelopes are covered by variation in *Phyllomyias*.

The species included in *Zimmerius*, all formerly in *Tyranniscus*, are *bolivianus*, *vilissimus*, *cinereicapillus*, *gracilipes* and *viridiflavus* (including *chrysops*). The genus is named for the late John Todd Zimmer in belated recognition of his enormous contribution to the systematics of Neotropical birds, and his recognition of the unique wing pattern in this new genus.

Although I have *Zimmerius* follow *Phyllomyias* in the lineal list, I am not convinced they are closely related. There is, however, no other genus to which they seem more nearly related, so leaving them together will at least retain the benefit of familiarity.

Ornithion (including *Microtriccus*) is a genus of quite small flycatchers with disproportionately short tails. In plumage pattern, *O. inerme* is not unlike *Phyllomyias* (*Tyranniscus*) *nigrocapillus*, but much smaller; the other two species lack any wing-bars. *Ornithion inerme* is intermediate in tail length between "*Microtriccus*" *brunneicapillum* and *semiflavus* and the shortest tailed *Phyllomyias* in its size range. The values of the tail wing ratios are: *brunneicapillum* and *semiflavus*, 54 per cent and

57 per cent; *inerme*, 70 per cent; and *P. griseiceps*, 87 per cent respectively. The tarsi are taxaspidean/pycnaspidean, but the tarsi are so variable in this whole Elaeniine group of flycatchers, that they are not good indicators of relationship. Ames found the syrinx of *semiflavus* to be near *P. nigrocapillus* and probably related to *Elaenia*. In cranial characters *Ornithion* seems typical of many small flycatchers. Although there are no really trenchant characters to diagnose *Ornithion*, the included species are a cohesive group, and I recognize it.

Tyrannulus elatus is a small genus and species, similar to the smaller *Zimmerius* in size and proportions, but nearer *Phyllomyias nigrocapillus* in plumage pattern. It has generally been included with these genera in lineal lists, but it differs from both of the above in having a partially concealed bright yellow crest. Bright crests are common in the flycatchers, and have undoubtedly arisen independently in a number of different lineages. However, they are not known to occur in only one species of an otherwise crestless genus, and I do not think that *elatus* belongs in either *Phyllomyias* or *Zimmerius*. On the other hand, *elatus* is almost a miniature of *Myiopagis gaimardii*, and I believe that is where its relationships lie. Both genera have taxaspidean tarsi, and Ames (1971: 161) included *Tyrannulus* and *Myiopagis* in his *Elaenia* group on syringeal characters. Warter (1965: 34), however, found that *T. elatus* and *M. gaimardii* (which he included in *Elaenia*) differed in their types of nasal septum, interorbital septum and cranium. The relationship of *elatus* with *M. viridicata* was closer, but both skulls were damaged, so that the evidence was inconclusive. *Tyrannulus* should be placed next to but not in *Myiopagis*.

Camptostoma, *Phaeomyias*, *Sublegatus*, *Suiriri*, *Myiopagis* and *Elaenia* are a group of closely related genera. They are more successful than the genera previously discussed in the sense that all except *Suiriri* are found throughout the tropical lowlands of South America, and three reach Mexico or the southwestern United States. With the exception of *Sublegatus*, all are included in Ames' *Elaenia* group on syringeal characters.

Phaeomyias is basically a monotypic genus for the type, *murina*, but Hellmayr and Zimmer added or subtracted other species. Hellmayr (1927: 453) included *tenuirostris*, a species that Zimmer (1955: 2) properly removed to *Inezia*. Prior to that, Zimmer (1941b: 10) added *Elaenia leucospodia* because of its partially taxaspidean tarsus. The latter character, however, is of little value by itself; in some species, such as *Phyllomyias fasciatus*, the tarsi can vary from taxaspidean to exaspidean with every gradation in between. *Leucospodia* has a partially concealed white crest, similar to those of *Elaenia* or *Myiopagis*, and should not be placed in a crestless genus without more substantial evidence. Actually, in every available character of size, proportions, pattern and nest-type, *leucospodia* is a typical *Myiopagis*; the only difference is that all *Myiopagis* have at least some yellow or olive in their plumage (as does *Phaeomyias murina*), while *leucospodia* is plain dull brown, whitish below. This latter coloration is not unusual in species endemic to the arid coast of Peru, and I place *leucospodia* in *Myiopagis*.

Phaeomyias murina is about as "typical" a dull brownish flycatcher with yellowish belly as one could visualize; its only distinctive external character is a fairly broad, whitish superciliary. *Camptostoma* is a smaller version of the same, but with a compressed, arched bill. Both are members of Ames' *Elaenia* group, along with *Suiriri*, *Myiopagis* and *Elaenia*, but *Phaeomyias* and *Camptostoma* have type 2 nasal septa, without the transverse plate, while *Suiriri* and *Elaenia* have type 5 with plate. The situation in *Myiopagis* is uncertain, with *gaimardii* having type 5, *viridicata* probably type 1, and the others not examined.

Camptostoma and *Phaeomyias* agree in general form and color, and in all syringeal and most cranial characters; however, they differ strongly in voice and behavior according to both Eisenmann and Fitzpatrick (*in litt.*). One of the most marked differences between them is in the form of their nests. *Camptostoma* builds a globular nest with a side entrance, placed in branches of low trees, while *Phaeomyias* builds a neat cup, typical of the *Elaenia* group of genera. Ihering considered the nest of *Camptostoma* transitional between the cup-shaped nest of his Elaeniinae and Serpophaginae, and the pendant nest of his Euscarthminae. However, *Camptostoma* itself shows no relation to the Euscarthmines, being a typical member of the *Elaenia* group in color, form and syringeal characters. Despite its close resemblance to *Phaeomyias*, I keep it separate because of the differences in behavior and nest form.

The genus *Sublegatus* is composed of three parapatric species (to be discussed in a separate paper) found throughout practically all of lowland South America, although probably not resident in the rain forest. It differs from most *Elaenia* only in the lack of a white crest, and its somewhat swollen bill with wholly black mandible; it can be told from *E. cristata* only by the bill characters. It builds a shallow cup-shaped nest like *Elaenia*, and Warter (1965: 34) records them as having similar, but not identical, crania. In fact, there is little besides intuition that leads me to keep *Sublegatus* out of *Elaenia*, and the fact that the three species of *Sublegatus* form a different speciation pattern from that of any *Elaenia*.

Suiriri is composed of two hybridizing taxa, which Zimmer (1955: 18) thought should be treated as a single species, but which Short (1975: 283), presumably working with the same material, maintains as two species. They differ from *Elaenia* in lacking a white crest, and in having a longer bill with solid black mandible. The eastern species *affinis* differs from any *Elaenia* in having the rump and proximal quarter of the rectrices pale yellow in contrast to the olive back and blackish tail; however, it differs from the congeneric (possibly conspecific) *suiriri* in the same way. The most distinctive character shown by *Suiriri* is the white spotting of the juvenal plumage. All the grayish-brown dorsal feathers of the juvenal plumage have a wedge-shaped white tip, as do the wing coverts and three inner secondaries. When viewed from above, the juvenal bird shows a startling resemblance to juvenal Old World flycatchers of the genus *Muscicapa*; the pattern is unique in the Tyrannidae, except that juvenal *Sublegatus* has white spotting on the crown, according to Fitzpatrick (*in litt.*).

Although *Myiopagis* has always been associated with *Elaenia*, and many authors have followed Hellmayr (1927: 401) in uniting the two, Zimmer (1941a: 20) considered them distinct genera. He kept them separate because of the pycnaspidean or taxaspidean tarsus of *Myiopagis*, and the usually yellow (white in some subspecies of *gaimardii*) rather than the usually white crown in *Elaenia*. Ames found the syrinxes alike, but Warter (1965: 37) recorded *M. viridicata* (the type of the genus) as having a type 2 nasal septum, while *gaimardii* had a type 5 like *Elaenia*. As pointed out by Eisenmann (*in litt.*), *Elaenia* species prefer open habitats where they are relatively conspicuous, and *Myiopagis* species prefer denser foliage where they are relatively inconspicuous. I recognize *Myiopagis*, but with the knowledge that further anatomical research may suggest either merging it with *Elaenia*, or transferring species between them.

Elaenia is the largest and most "successful" of the Elaeniine genera, with 19 species occurring from southern Mexico to Tierra del Fuego, and from both humid and arid lowlands to above 3000 meters in the Andes. Although there is no single character by which to diagnose the genus, it is a natural assemblage whose limits are generally accepted. In size, the species range

from medium to large for this group of genera, wings 70 mm to 91 mm, with relatively short bills, 16–18 per cent of wing except for *cristata* in which it is 20 per cent and short to medium tarsi, 20–26 per cent of wing. The bill is short, moderately broad at the base and deep throughout, rictus lightly bristled, and wing usually fairly pointed, 10th primary equal to 4th to 6th. Plumage is generally dull olive above, except for males of *strepera*, which are dark slate gray, and the underparts are pale yellowish to olive to whitish; the majority of species have a concealed white crest. As far as recorded, all species build a neat cup-shaped nest, frequently covered with lichens.

The genera thus far discussed make up Warter's tribe Elaeniini, with the exception of *Leptopogon*, *Mionectes* and *Pipromorpha*, which will be inserted in the lineal list further on. The adjoining tribe of Warter, the Serpophagini, I consider to merge into the Elaeniini without the slightest break. *Serpophaga* and *Myiopagis* have been confused in the past, *M. caniceps* having been described in both genera, and as recently as 1957 Dorst described a population of *Myiopagis gaimardii* as *Serpophaga berliozi* (see Mayr, 1971: 313). *Mecocerculus* is also an obvious bridge. *Mecocerculus* species are remarkably close in plumage to *Phyllomyias* species. Intergeneric pairs showing especially close resemblance are *M. hellmayri* and *P. uropygialis*, *M. minor* and *P. plumbeiceps*, and *M. poecilocercus* and *P. sclateri*. The only plumage character that consistently distinguishes *Mecocerculus* is the distinct white superciliary. On the other hand, Ames (1971: 73, 74) found the syrinx of *Mecocerculus* like that of *Serpophaga* and *Anairetes*. Smith (1971: 285), on the basis of his behavioral studies of Hellmayr's Serpophaginae, considered *Mecocerculus* closely related to *Serpophaga* (incl. *Inezia*), *Anairetes* (incl. *Uromyias*) and *Stigmatura*. Finally Warter (1965: 34) recorded *Mecocerculus* as having a type 5 nasal septum, which it shared only with *Elaenia* and its closest relatives, and with *Serpophaga*, *Inezia*, and *Anairetes*. There seems little question that the former subfamilies or tribes were artifacts.

The genus *Inezia* is similar to *Serpophaga* in size, proportions and general plumage pattern. Hellmayr's *Inezia* consisted only of the species *subflava*, but Zimmer (1955: 1) added to it *Serpophaga inornata* and *Phaeomyias tenuirostris*. Smith (1971: 266) included *Inezia* in *Serpophaga* because of similarities in appearance and behavior. However, Parkes (1973: 249) has pointed out that the *Inezia* species differ from *Serpophaga* in lacking a white crest, and in having taxaspidean instead of exaspidean tarsi, pale instead of black mandibles, and a distinctive juvenal plumage rather than one like the adult plumage. I consider this combination of characters sufficient to define the two genera. There is also a close resemblance in plumage between *Inezia subflava* and the two species of *Stigmatura*. The latter are characterized by greater size, proportionately long tails and a nasal septum without a basal plate. The relative tail lengths compared to wing lengths of *Stigmatura budytoides* and *napensis* are 121 per cent and 113 per cent respectively, compared to 98 per cent in *subflava*. The plumage pattern of the three species is basically the same, upperparts olive brown, with a prominent white or pale yellow superciliary stripe running to well behind the eye; underparts pale yellowish; two distinct white wing-bars, and flight feathers edged white. The tails of both are rounded, but those of *budytoides* and *napensis* are elaborately patterned with white, while that of *subflava* is only narrowly tipped. Although the resemblance is close, I recognize *Inezia* and *Stigmatura* as distinct genera, primarily because of the difference in nasal septa, the former having a type 5 and the latter a type 2.

Anairetes, *Uromyias* and *Yanacea* are a closely related group of genera. They are composed of long-tailed, long-legged spe-

cies, found in the upper subtropical and temperate zones of the Andes and south through Chile and Patagonia to Tierra del Fuego. *Yanacea alpinus* and *Uromyias agraphia* are practically unstreaked, recalling *Stigmatura*, but *Uromyias agilis* is heavily streaked on throat and breast, similar to *Anairetes* species. *Uromyias* was separated from *Anairetes* because of its long tail with pointed rectrices, and *Yanacea* was recognized because of its relatively shorter bill and tarsus. These characters do not seem of great importance in an otherwise closely related group, and I merge *Yanacea* and *Uromyias* in *Anairetes*. Zimmer (*Ms.*) had already merged *Yanacea* and *Anairetes*, as he suggested in an earlier discussion (1940b: 10); Smith (1971: 275) merged *Uromyias* and *Anairetes*.

Tachuris, the brilliantly colored *Siete Colores*, has regularly been associated with *Serpophaga*. Smith (1971: 284) says it probably belongs with the Serpophagines, but it may have closer relatives in the Euscarthmines. He did not specify which of the latter, but possibly it is near *Pseudocolopteryx*, which also has marsh-living forms. However, the color and patterning of *Tachuris* are unique, particularly the blue auriculars, and there is no way to relate it closely to any of the other smaller flycatchers. The combination of orbital septum, palatines and cranial type are found throughout the Elaeniinae, and the nasal septum was undetermined (Warter 1965: 34); Ames found the syrinx unlike any other. I shall leave *Tachuris* in the vicinity of *Serpophaga*, but it could equally well be *sedis incertae*.

Colorhamphus parvirostris was placed in the genus *Ochthoeca* by Berlepsch (1907: 470), but was kept in its monotypic genus near *Serpophaga* by Ridgway (1907: 396) and Hellmayr (1927: 400). I agree with Berlepsch, and discuss *parvirostris* in more detail under *Ochthoeca*.

Culicivora, *Polystictus*, *Pseudocolopteryx* and *Euscarthmus* have been kept at the end of the Euscarthminae since Berlepsch (1907). The subfamily Euscarthminae was created by Ihering (1904) for a group of genera making pendant, pyriform nests, and its type genus *Euscarthmus* had at that time for its type species *Euscarthmus nidipendulus* Wied, a species now in the genus *Idioptilon*. *Culicivora* and allies show no particular resemblance to the typical *Todirostrum/Idioptilon* group, and are in some ways nearer *Serpophaga*. All but *Euscarthmus* have one or more species with whitish or streaked crests as in *Serpophaga*, they all have weak rictal bristles, and all make cup-shaped nests. In bill length they are intermediate between the long-billed *Todirostrum* and the shorter-billed Serpophagas. They seem to form a natural group, with their center of distribution in the dryer country of southeastern Brazil and northern Argentina and, except for *Culicivora*, with isolated populations in dry country north of the Amazonian forest. *Pseudocolopteryx* has penetrated the more temperate zones in Patagonia and the southern Andes, and three of the four species are sympatric in the Chaco. The four genera seem worth recognizing. *Culicivora* has a most peculiar rounded tail, with only 10 rectrices, and the barbs are stiff and decomposed, recalling *Synallaxis* in the Furnariidae. *Polystictus* has an aberrant cranium, with nasal septum, interorbital septum and palatines characteristic of *Fluvicola* rather than the Elaeniinae. *Pseudocolopteryx* is a natural assemblage of predominantly yellow species with marked sympatry among them, suggesting a long phylogenetic history; three of the four species have aberrant primaries. The two species of *Euscarthmus* are rich browns and buffs with rufous crests; they have frequently been allied to *Pseudocolopteryx*, but I hesitate to unite them because the latter is so uniform without *Euscarthmus*.

Leptopogon, *Mionectes* and *Pipromorpha* were placed at the end of the restricted Elaeniinae by Berlepsch (1907: 492). *Pipromorpha* had been merged in *Mionectes* for many years until Ridgway (1907: 354)

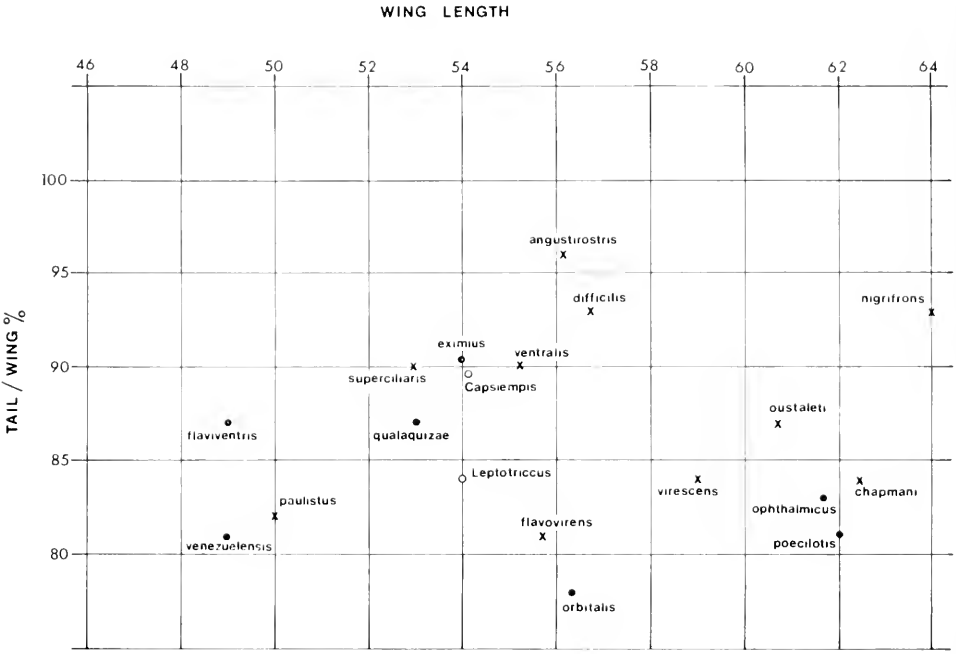

Figure 1. Proportions of tail/wing plotted as functions of wing length for species of the genera *Phylloscartes*, *Pogonotriccus*, *Leptotriccus* and *Capsiempis*. Although these genera were originally separated because of differing proportions, the points fall into a continuum. Closed circles, "●", are *Pogonotriccus*, crosses, "×", are *Phylloscartes*, and open circles, "○", are the types of the monotypic genera *Leptotriccus* and *Capsiempis*.

resurrected it because of the different shapes of the 9th primaries in adult males. This is a trivial character in a family where, in a single genus such as *Pseudocolopteryx*, three species have different sets of primaries aberrant, and the fourth has them all normal. In all other morphological and anatomical characters—size and proportions, bill shape and lack of rictal bristles, syrinx and cranial characters—*Pipromorpha* and *Mionectes* are virtually identical, and I again merge them. *Leptopogon* is close to *Mionectes* in size and proportions except for its longer tail, and both genera make pendent, globular nests, usually hung under logs or cut banks in the vicinity of water; this is unlike the nests of any Elaeniine flycatcher. According to Monroe (1975), they also share the behavioral trait, unusual among the Tyrannids, of single-wing flicking. Besides the peculiar nest, *Leptopogon* differs from the Elaeniine group in having fairly heavy rictal bristles, but this character is not shared with *Mionectes*. *Leptopogon* differs from *Mionectes* in having a much more rounded wing, longer tail, heavier rictal bristles, and normally shaped primaries; in all *Mionectes* species but *rufiventris*, males have either the 9th or 10th primary notched, shortened or attenuated. According to published accounts, there seems to be little difference in behavior.

The section of the subfamily where *Leptopogon* and *Mionectes* seem most at home is with *Phylloscartes*, *Pogonotriccus* and allies. In plumage and pattern, *Leptopogon* is particularly close to *Phylloscartes* and *Pogonotriccus*, in fact four of the species in the latter genera were originally described in *Leptopogon*. Superficially, there is little difference between *Leptopogon* and *Phyl-*

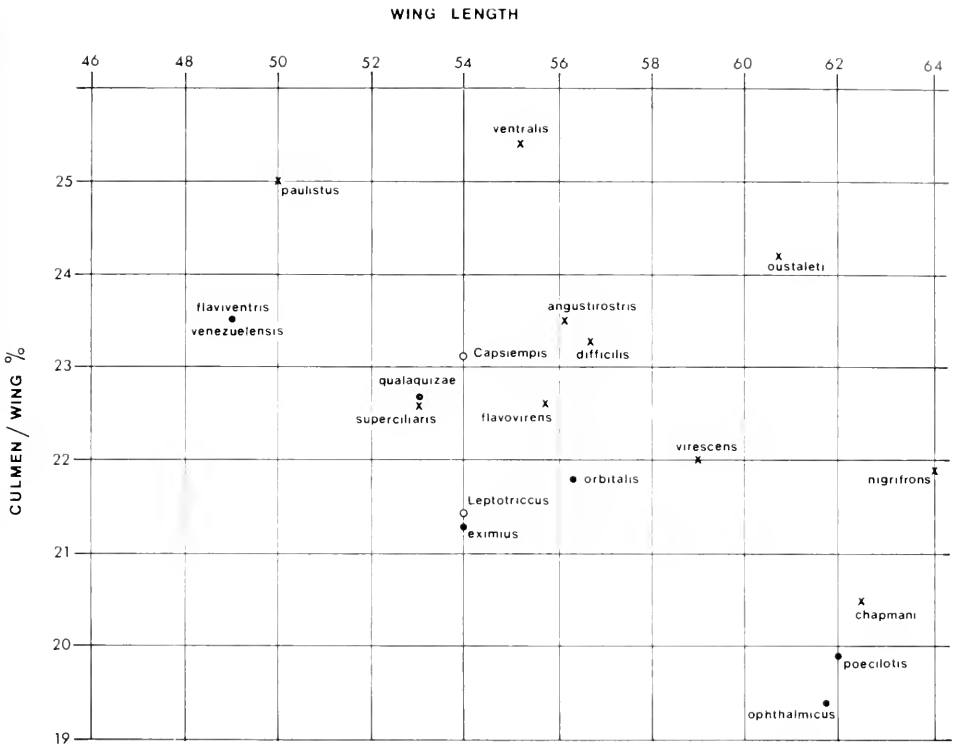

Figure 2. Proportions of culmen/wing plotted as functions of wing length. (See Fig. 1. legend.)

loscartes, but the former has a shorter tarsus, a type 3 nasal septum found otherwise only in the unrelated genera *Platyrinchus* and *Onychorhynchus*, and the peculiar nest type and single-wing flicking mentioned above. The importance of the nest type cannot be evaluated, since the nest type of only one of the 17 species in *Pogonotriccus* and *Phylloscartes* is known; *Phylloscartes ventralis* builds a partially domed, somewhat globular structure in the fork of a bough, according to Ihering (1904: 314).

Phylloscartes, *Pogonotriccus* and the two monotypic genera *Leptotriccus* and *Capsiempis* are a closely related group of genera placed by Berlepsch and Hellmayr in the Euscarthminae. They are all similar in appearance—small greenish and yellowish flycatchers, mostly with two well marked wing-bars, and several with gray crowns and patterned faces. All four were described as monotypic genera by Cabanis and Heine (1859: 52–56) for the type species *Phylloscartes ventralis*, *Pogonotriccus eximius*, *Leptotriccus sylviolus* and *Capsiempis flaveola*. The first three were defined primarily on mensural characters; *Phylloscartes* with a long bill and tarsus, *Pogonotriccus* with a long wing and short bill, and *Leptotriccus* by a "*Serpophaga*-like" bill and long tail. *Capsiempis* was considered more like *Tolmomyias flaviventer*, with a broad bill. During the next hundred years 15 species were added to this complex, seven by original description and eight by transfer from other genera, primarily *Leptopogon* and *Mecocerculus*. Within the group, two species, originally described in *Leptotriccus* and *Capsiempis* respectively, were moved to *Pogonotriccus*.

When the proportions of tail, culmen and

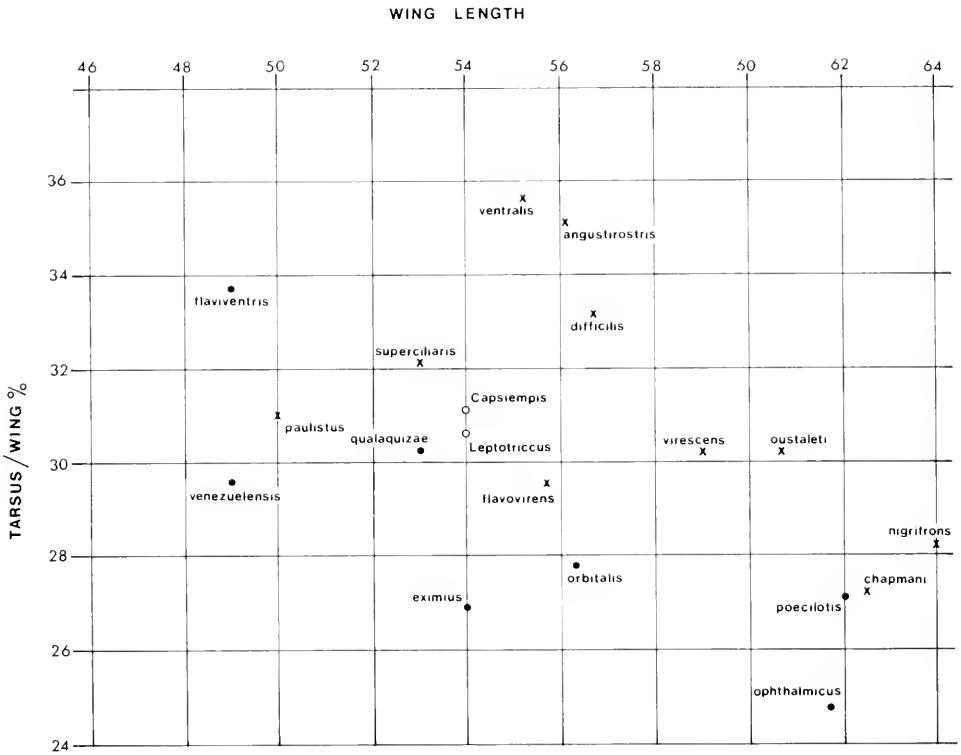

Figure 3. Proportions of tarsus/wing plotted as functions of wing length. (See Fig. 1. legend.)

tarsus to wing length are plotted as functions of wing length (Figs. 1–3), it is clear that on mensural characters the present genera overlap widely. There is a general trend within the group for species with longer wings to have proportionately shorter bills and tarsi, but this is true of all the currently recognized taxa. Even though some species are obviously separated from their nearest relatives by the present allocation to genera—the representative species *chapmani* and *poecilotis* being in *Phylloscartes* and *Pogonotriccus* respectively—no shifting of species between genera would segregate out two or more taxa. Warter (1965: 33) found the cranial characters similar in all four genera. Ames (1971: 67–72) considered the syrinxes different from each other and from all other genera, but as noted before negative syringeal evidence is inconclusive. I unite the four genera into a single genus. All the names were introduced at the same time in the same publication, and are equally available under the Rules [Art. 24(a)]. I select *Phylloscartes* as the name for the combined genus.

The geographical distributions of the species are most peculiar, but shed little light on relationships. Five species of *Pogonotriccus* are found in the subtropics of the Andes from Venezuela to Bolivia, but the sixth, the type *eximius*, is confined to the southeastern forest region of Brazil and adjoining Paraguay and Misiones, Argentina. On the other hand, four *Phylloscartes* species and *Leptotriccus sylviolus* are endemic to the southeastern forest region, and only the type, *ventralis*, has an isolated population in the Andean subtropics. The remaining species of *Phylloscartes* are found in the Guianan forests, the tepuis of

Venezuela, and in eastern Central America. Despite the fact that these are all forest forms, no species of this complex occurs in the Amazonian forests.

The one species that is out of place on ecological grounds is *Capsiempis flaveolus*, which has adapted to shrubs and bushes in clearings, and is found in the drier parts of tropical South America, north and west to Nicaragua. Eisenmann (*in litt.*) says that where *Capsiempis* overlaps the range of *Phylloscartes flavovirens* in Panama, the two are unlike in habits and do not appear closely related. However, as Zimmer (1940b: 2) pointed out, *flavovirens* and the closely related *virescens* are unusual among the *Phylloscartes* species in having more pointed wings, with the 10th primary equal to or greater than the 4th, rather than equal to or less than the 1st. *Pogonotriccus* species and *Leptotriccus* also have rounded wings with a short 10th primary. Practically nothing has been published about the habits of any *Phylloscartes* or *Pogonotriccus*, so it is not possible to say if *flavovirens* is typical of the rest of the genus. The only nests that have been described are *flaveolus* nests, which are cup-shaped, and *ventralis* nests which are partially covered. Although *Capsiempis* may later prove worthy of recognition as a distinct genus, I keep it in the enlarged *Phylloscartes* on morphological grounds.

Although the species of *Phylloscartes* do not have the long, spatulate-type bill characteristic of *Todirostrum* and *Idioptilon*, the bill is proportionately longer, and the rictal bristles more developed, than in the genera discussed so far. Their plumage pattern is typical of the "small green flycatchers" such as *Phyllomyias* and *Mecocerculus*, and they with *Leptopogon* represent the primitive stock from which the *Todirostrum* group evolved. Figure 4 is a schematic diagram showing the probable origin of the three best defined lineages within the Elaeniinae—the *Elaenia* group, the Tit-tyrants (*Anairetes*) and the Tody-tyrants. The position of *Pseudocolopteryx*

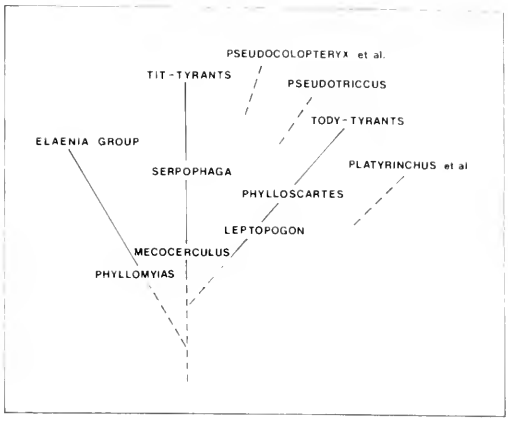

Figure 4. Schematic diagram showing probable relationships among the Elaeniinae. The three clearest lineages, *Elaenia* group, Tit-tyrants and Tody-tyrants, arose from *Phyllomyias*, *Mecocerculus*, and *Leptopogon* and *Phylloscartes*, respectively, genera that share a basic, "little green flycatcher" plumage pattern. The positions of genera not part of these lineages can only be suggested.

and allies, and of *Pseudotriccus* is probably somewhere between the Tit-tyrants and the Tody-tyrants, although not part of the lineage of either; the position of the Flatbills, *Platyrinchus* and allies, is even less clear. *Phyllomyias*, *Mecocerculus*, and *Leptopogon* and *Phylloscartes*, the presumably primitive genera, resemble each other closely, although they lead into three distinct groups.

Pseudotriccus, including *Caenotriccus ruficeps* (Zimmer, 1940a: 22), is a peculiar genus of three species, confined to the subtropics of the Andes and extreme eastern Panama, that seems to have no close relatives among the genra of Hellmayr's Euscarthminae. It has generally been associated with *Hemitriccus* at the end of the *Todirostrum* group, but there is little real resemblance. The colors of *Pseudotriccus* are dull olive, olive brown or rufous, and the birds are without any embellishments such as streaking, superciliary stripes, eye rings, wing-bars or contrasting edgings to the flight feathers. All of the *Todirostrum* group and *Phylloscartes* have yellow under wing coverts that come around the edge of

the wing, giving a bright spot at the bend when the wing is folded. In *Pseudotriccus* the under wing coverts are like the body plumage, with no contrast. The one genus to which *Pseudotriccus* may be allied is *Corythopis*, which has only recently been admitted to the Tyrannidae and which is without obvious relatives. The two genera share a proportionately long tarsus, relatively as long as those of the much smaller *Todirostrum/Idioptilon* species; the scutes of the tarsi are almost obsolete, giving a smooth booted effect; the wings are plain without any pale bars or edgings; and the rectrices are broad and soft. Fitzpatrick (in conversation) says they share similar feeding habits, walking along the ground and leaping up to pick insects from the under sides of leaves. I place *Corythopis* and *Pseudotriccus* together, and leave them between *Phylloscartes* and the *Todirostrum* group of genera, not because I am convinced that is where they belong, but because I know of no better place.

The genera I include in the term "*Todirostrum* group," as used above, are the remaining genera of Hellmayr's Euscarthminae: *Hemitriccus*, *Perissotriccus*, *Myiornis*, *Atalotriccus*, *Colopteryx*, *Lophotriccus*, *Idioptilon*, *Taeniotriccus*, *Poecilotriccus*, *Snethlagaea*, *Microcochlearius*, *Euscarthmornis*, *Oncostoma*, *Ceratotriccus* and *Todirostrum*. They are a closely related group, characterized by long slender tarsi, greater than 29 per cent of wing length, and long wide bills, greater than 25 per cent of wing length, culminating in the spatulate bill of *Todirostrum*. A generalized plumage pattern is found in at least some species of most genera: olive green or brown above; whitish below on throat and breast with darker streaking, and yellowish or olive on abdomen; remiges edged with olive or yellow. All species have yellow under wing coverts, which usually extend enough around the bend of the wing to make a yellow spot when the wing is folded. All recorded nests are of the pendent, purse-shaped or pyriform type.

Of the genera that Ames (1971: 67) examined all belonged in his *Colopteryx* group except *Todirostrum*. The cranial characters were alike in those genera that Warter (1965: 33) examined, but similar crania were found in *Phylloscartes* and *Pseudocolopteryx*, and in *Rhynchocyclus*, *Tolmomyias* and *Cnipodectes* of Hellmayr's Platyrinchinae. Zimmer (1940a: 13, 22) merged *Euscarthmornis* into *Idioptilon*, and *Perissotriccus* into *Myiornis*, and these changes were accepted by Meyer de Schauensee (1966).

Myiornis (including *Perissotriccus*) is a genus characterized by minute size; wing length in males averages less than 40 mm in all three species, and they are the smallest of the Tyrannids. Tail length is very short in *ecaudatus*, the type of *Perissotriccus*, but it is normal in *auricularis* and intermediate in *albiventris*. Bill and tarsal proportions fall into the normal range of the tody-tyrants.

Lophotriccus, *Colopteryx* and *Atalotriccus* have been placed together in the past, but the evidence for including *Atalotriccus* is equivocal. *Lophotriccus* is distinguished from the remainder of the tody-tyrants by its distinctive crest; the crown feathers are elongated and edged in contrasting gray or rusty. *Colopteryx galeatus* is the same as *Lophotriccus* in plumage, but has the three outer primaries much reduced. *Atalotriccus pilaris* has a normal crown, but has the four outer primaries even more reduced, narrowed and pointed. The plumage patterns and crest of *Lophotriccus* and *Colopteryx* are so much alike that the relationship must be close. I merge them here because I do not consider peculiar primaries a "generic" character in the flycatchers. *Atalotriccus* has been kept with *Colopteryx* because both have shortened outer primaries. If *Atalotriccus* has indeed been derived from *C. galeatus*, then the ornamental crest must have been lost secondarily. But it is just as easy to conceive *Atalotriccus* as an *Idioptilon* that has independently acquired reduced outer pri-

maries and converged on *Colopteryx* in this character. The relatively long *Atalotriccus* tarsus is more like that of *Idioptilon* than that of *Lophotriccus*. Eisenmann (*in litt.*) believes *Atalotriccus* behaves more like *Todirostrum sylvia* than like *Lophotriccus*. Considering the doubts about the origin of *Atalotriccus*, I accept it as a distinct genus. Since this tody-tyrant group is uniform in cranial and syringeal characters, I doubt if further anatomical study will help clarify the relationships.

Fitzpatrick (1976) has just published a valuable paper on *Todirostrum* and related genera. He construed somewhat more strictly the concept of "related genera," and his study omits the following genera listed above: *Hemitriccus*, *Myiornis*, *Atalotriccus*, *Colopteryx* and *Lophotriccus*. Fitzpatrick attempted to trace the lineage and generic relationships of his tody-tyrants, and he made the following taxonomic suggestions:

1. The genus *Ceratotriccus* should be merged with *Idioptilon*.
2. The genera *Taeniotriccus* and *Poecilotriccus* should be moved to positions immediately preceding *Todirostrum*, reflecting their affinities with *Todirostrum capitale*.
3. *Todirostrum* and *Idioptilon* should continue to stand as separate genera.
4. The genera *Snethlagaea* and *Microcochlearius* are best merged with *Idioptilon*, while *Oncostoma* should continue to be generically recognized.

Fitzpatrick's lineage is shown diagrammatically in Figure 5, reprinted from his Figure 4 (p. 443). The genera that he does not consider, *Myiornis*, *Atalotriccus*, *Colopteryx* and *Lophotriccus*, would branch off further down the stem, on the way to the more highly specialized *Todirostrum*. With the exception that I consider *Hemitriccus* to belong to the "green" section of *Idioptilon*, I believe Fitzpatrick's tree accurately depicts the evolution and relationships of the tody-tyrants.

If his diagram is correct, then his taxonomic treatment of the *capitale* group, in-

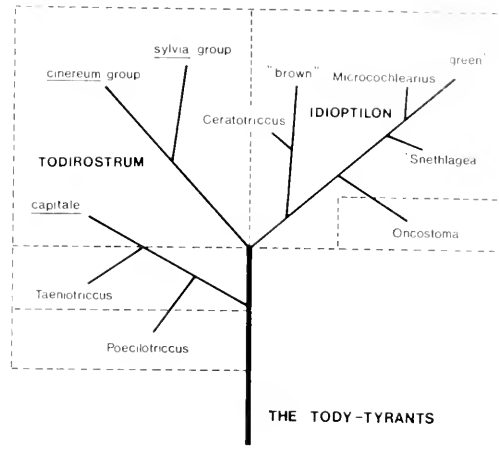

Figure 5. Fitzpatrick's (1976, Fig. 4) tree showing the lineage of the tody-tyrants. The stem to the lower left, leading to *Todirostrum capitale*, is here considered a single genus, *Poecilotriccus*.

cluding *Todirostrum capitale*, *Taeniotriccus andrei* and *Poecilotriccus ruficeps*, must be questioned. These three species are united by a unique plumage pattern with chestnut crown, and by the striking sexual dimorphism in *capitale* and *andrei*. As Fitzpatrick says (p. 441), "Affinities among the three species are closer than those between the lineage as a whole and *Todirostrum* or *Idioptilon*." If this is so, the resemblance between the bill of *capitale* and those of *Todirostrum* species must be due to convergence, and placing *capitale* in *Todirostrum* makes that genus polyphyletic. Fitzpatrick recognized that the three species might possibly belong in a genus of their own, but hesitated to make such a major taxonomic shift without further anatomical and behavioral study. However, I believe that the data require such a move now, and I place *capitale*, *andrei* and *ruficeps* in a separate genus for which *Poecilotriccus* is the oldest name.

Hemitriccus has been kept separate from *Idioptilon* because of the former's allegedly longer tail, and because of the slightly shortened 7th primary in males. While tail length in *H. diops* is proportionately longer than that of any *Idioptilon* species, the

same is not true of *H. flammulatus* whose tail length is well within the normal *Idioptilon* range. In males the 7th primary is slightly shorter than the 6th and 8th, so the edge of the opened wing shows a slight notch rather than a smooth contour; the female wing is normal. Considering the variation in primaries within such genera as *Pseudocolopteryx*, this characteristic hardly rates generic separation. Plumage characters are like those of *Idioptilon*, and female *H. flammulatus* can hardly be told from the sympatric *I. zosterops griseipectus*. Merging *Hemitriccus* with *Idioptilon* will lead to yet another unfortunate change in the name of this beleaguered genus. Known as *Euscarthmus* to Sclater (1888) and Berlepsch (1907), it was *Euscarthmornis* to Hellmayr (1927), *Idioptilon* to Meyer de Schauensee (1966), and *Cerototriccus* to Fitzpatrick (1976); it must now be called *Hemitriccus*, the oldest available name.

To summarize the *Todirostrum* group, the sequence of the genera and their synonymies will be:

Myiornis (syn: *Perissotriccus*)
Lophotriccus (syn: *Colopteryx*)
Atalotriccus
Poecilotriccus (syn: *Taeniotriccus*)
Oncostoma
Hemitriccus (syn: *Idioptilon*, *Euscarthmornis*, *Snethlagaea*, *Microcochlearius*, *Ceratotriccus*)
Todirostrum.

Hellmayr's Platyrinchinae—*Platyrinchus*, *Rhynchocyclus*, *Tolmomyias*, *Ramphotrigon* and *Cnipodectes*—have occupied a position between the "large" flycatchers and the *Todirostrum* group since Berlepsch (1907), although *Platyrinchus* was put with the Todirostrines by Berlepsch, and with *Rhynchocyclus et al.* by Hellmayr. Warter considered that on cranial characters the Platyrinchinae graded into the Euscarthminae via *Todirostrum* and *Oncostoma*, but in general form and appearance, they do not seem closely related to any other genus or group of genera. They have been kept together in part because of their broad, flat bills, moderate to heavy rictal bristles and fairly short, slender tarsi, but in the case of *Platyrinchus*, these are probably convergent characters. The bills of *Rhynchocyclus* and *Tolmomyias* are the extremes of broad and flat but swollen-appearing bills with strongly convex lateral edges; *Cnipodectes* is somewhat narrower at the base, and *Ramphotrigon* even more so, with the lateral edges straight. *Platyrinchus* has the same broad, convex bill, but it is much flattened.

Rhynchocyclus and *Tolmomyias* resemble each other closely externally, the latter seeming a smaller version of the former. However, Ames (1971: 161) found they "differ so strongly in their syringeal structure that one may seriously question the reliability of bill shape as a common character." Also, Skutch (1960: 515) has pointed out well-marked differences in mating behavior, egg coloration and the extent of down on the nestlings. *Cnipodectes* is close to these two, but its brown coloration, uniquely twisted primaries in the male, and extreme sexual dimorphism merit recognition. In plumage pattern, *Ramphotrigon* species, particularly *fuscicauda*, look very much like *Rynchocyclus*, but the bill is slender and straight edged, the mandible is blackish rather than pale horn (in dried skins), and they have two well-marked buffy or chestnut wing-bars, which are not found in *Rhynchocyclus*. Ames (1971 : 161) supported Zimmer's (1939c: 16) transfer of *megacephala* from *Tolmomyias* to *Ramphotrigon*. He found the syrinx of *megacephala* strikingly different from that of *Tolmomyias sulphurescens*. The *Ramphotrigon* nest has not been described; *Rhynchocyclus* and *Tolmomyias* make pendent retort-shaped nests (Smithe, 1966: 322), and *Cnipodectes* makes a pendent nest whose completed shape is not known (Wetmore, 1972: 508).

As noted before, *Platyrinchus* does not fit easily into this assemblage. The species all have short tails, less than 50 per cent of

wing length, a pale patch on the throat, pale instead of blackish feet and tarsi and brightly colored crests; they all build cup-shaped rather than pendent nests. *Platyrinchus* has a type 3 nasal septum, found elsewhere only in *Onychorhynchus* and *Leptopogon*, while *Cnipodectes*, *Tolmomyias* and *Rhynchocyclus* have type 1. However, in the last three, the nasal septum evidently approaches the type 3, so the difference may not be so great as it appears at first glance. The syrinx of *Platyrinchus* most resembles that of Ames' *Colopteryx*, and is not at all like that of *Tolmomyias* or *Rhynchocyclus*. Although the relations of *Platyrinchus* are almost certainly with the Elaeniinae, it does not seem closely related to any of the other genera, and I leave it at the end of the subfamily.

FLUVICOLINAE

The subfamily Fluvicolinae as now constituted, with the addition of the major part of the old Myiarchinae, has a number of genera that in size and plumage pattern resemble the more generalized Elaeniinae. Such genera as *Myiobius* and *Myiophobus* are close in size, proportions and plumage pattern to the Elaeniine *Phyllomyias* and *Phylloscartes*. Externally they are best distinguished by the broad, triangular flattened bill and heavy rictal bristles; internally they all have Warter's type 6 nasal septum, which occurs elsewhere only in *Polystictus* and *Zimmerius*, where it has almost certainly been derived independently. Within the Fluvicolinae there appear to be two lineages. The first starts with *Myiobius*, *Myiophobus* and allies, and leads to *Empidonax*, *Contopus* and *Sayornis*, which have speciated extensively in North and Central America. The second starts with the generalized *Ochthoeca* and runs through the highly successful *Xolmis* and *Muscisaxicola* to a number of truly aberrant genera such as *Muscigralla*; the center of speciation and generation in this lineage has been southern South America. Besides being separable on external morphological and zoogeographical grounds, the members of the North American lineage, except for *Myiophobus*, *Cnemotriccus* and *Nuttallornis*, all have type 3 palatines, while none of the South American lineage have them.

I begin the Fluvicolinae with *Onychorynchus*, a genus that is highly specialized but apparently is an early offshoot of the primitive stock. Both sexes of *Onychorhynchus* have long, elaborate transverse crests, red or yellow tipped with iridescent blue or violet, and long, broad, flattened bills with heavy rictal bristles reaching the tip of the bill. Ames (1971: 160) placed *Onychorhynchus* in the *Myiobius* group with *Terenotriccus* and *Pyrrhomyias*, but Warter (1965: 37) made it a monotypic tribe in his Platyrinchinae, and said it most resembled *Platyrinchus* and *Tolmomyias*. *Onychorhynchus* shares the type 3 nasal septum with *Platyrinchus*, and this type is also suggested in *Tolmomyias*. However, *Onychorhynchus* lacks the type 4 interorbital septum, which characterizes the Elaeniinae in general and is found in *Platyrinchus* and allies. On external morphology, Hellmayr placed *Onychorhynchus* near *Myiobius*, and they certainly share the most extreme development of the rictal bristles, which extend beyond the tips of the broad flat bills. The syringeal evidence supports this association of the two genera. I keep *Onychorhynchus* in the Fluvicolinae, even though it is the only genus in the subfamily, except for the aberrant *Muscigralla*, that does not have a type 6 nasal septum.

Wetmore (1972: 532) notes that the eggs of *Onychorhynchus* and *Lophotriccus* resemble each other in having a "bright to dark reddish gray ground color, thickly marked with carmine in scrawling lines," a type not found elsewhere among the Tyrannidae. This suggested to him that a possible relationship might exist between the genera. Eisenmann (*in litt.*) notes that *Lophotriccus* displays its crest in hostile situations in the same manner as *Onychorhynchus*, by spreading it laterally, opening

its beak, and rotating the head through 180°. Although these shared characters are suggestive, they are not supported by any anatomical or external morphological characters. The two genera do not share any of Warter's cranial characters, and Ames has them in different syringeal groups—*Onychorhynchus* in his *Myiobius* group without intrinsic muscles, and *Lophotriccus* in his *Colopteryx* group with intrinsic muscles. Externally, *Onychorhynchus* is much larger, with wing length about 60 per cent longer than that of *Lophotriccus*, and has a proportionately longer bill, about 32 per cent of wing length compared to about 25 per cent in *Lophotriccus*. The tarsus of *Onychorhynchus* is comparatively much shorter than that of *Lophotriccus*, and the most striking difference in proportions is seen in the ratio culmen tarsus, which is about 155 per cent in *Onychorhynchus* and about 80 per cent in *Lophotriccus*. Although the long crests are used in the same way, they seem to have evolved differently. That of *Onychorhynchus* appears to have developed from a bright orange or yellow crown of the type found in *Tyrannus*, being composed of bright feathers greatly lengthened and tipped with iridescent blue. The crest of *Lophotriccus*, on the other hand, is made up of lengthened ordinary crown feathers, edged with rusty or gray. Both genera make pensile nests, but this is true of all their potential relatives, *Myiobius*, *Rhynchocyclus* and Ames' *Colopteryx* group. Although it is unusual to find simultaneous convergence in two such unrelated characters as egg color and crest display, I do not believe that *Onychorhynchus* is closely related to *Lophotriccus*.

The genera *Myiobius* and *Terenotriccus* form a natural group because they and *Onychorhynchus* are the only genera of Fluvicolines to make a pendent, purse-shaped nest, similar to that found in the *Todirostrum* group of the Elaeniinae. *Myiotriccus* closely resembles *Myiobius* in form and plumage pattern, and I include it here even though its nest is unrecorded. I do not merge the two because *Myiotriccus* is more brightly colored and lacks the heavy rictal bristles, extending beyond the bill tip, that are characteristic of *Myiobius*. This group of genera is related to *Onychorhynchus* on the one hand and to *Pyrrhomyias* on the other by their peculiar syringes, in which there are no intrinsic muscles.

The remaining genera of Warter's "Contopini," formerly in the Myiarchinae of Hellmayr, are an unusually difficult group to order lineally. The majority seem to have characters relating them to two or more of the others, and there are a few about which little is known that must be inserted next to their apparent nearest relatives, thereby interrupting an otherwise orderly progression. Webster (1968), in his review of the genus *Mitrephanes*, suggested the following sequence for the genera that he considered closely related (I invert his sequence to make it comparable with mine): *Empidonax*, *Xenotriccus*, *Pyrrhomyias*, *Mitrephanes*, *Contopus*, *Nuttallornis*. I agree with this sequence, except that I would place *Empidonax* at the other end, next to *Contopus* and *Nuttallornis*. Not only are these genera close in appearance, but an intergeneric hybrid between *Contopus* and *Empidonax* has been recorded by Short and Burleigh (1965). My sequence, including those genera not considered by Webster, is *Myiophobus*, *Aphanotriccus* (including *Praedo*), *Xenotriccus* (including *Aechmolophus*), *Pyrrhomyias*, *Mitrephanes*, *Contopus* (including *Nuttallornis* and *Blacicus*), *Empidonax*, *Nesotriccus*, *Cnemotriccus*, *Sayornis* and *Pyrocephalus*.

Myiophobus is a genus that is superficially like *Myiobius*, but probably not closely related. The two are similar in proportions and general appearance, but *Myiophobus* lacks the bright crest and rump characteristic of *Myiobius*, and makes a cup-shaped rather than a pensile nest. *Myiophobus* is not placed by Ames in any of his syringeal groups, but *Myiobius* is part of the group lacking intrinsic muscles. It is risky to generalize about *Myiophobus*,

because the only species for which the syrinx and cranium were available, and whose nest and habits have been recorded, is *fasciatus*, the least typical ecologically. Of the nine species of *Myiophobus*, all but *fasciatus* are found in the subtropical zone of the Andes, where several have notably restricted and fragmented ranges. On the other hand, *fasciatus*, is found throughout the drier lowlands of South America, even reaching Costa Rica.

Aphanotriccus (including *Praedo*) and *Xenotriccus* (including *Aechmolophus*) are each composed of two relict species with restricted ranges in Central America and adjoining Colombia. Both were included in Ames' *Nuttallornis* group of genera on syringeal characters. The species of *Aphanotriccus* show the same type of color variation, in which cinnamon and olive replace each other, as is found in *Pyrrhomyias* and *Mitrephanes*. One species of *Xenotriccus* is dull colored like *Contopus*. Their relict distribution suggests they may be remnants of an earlier stock from which the currently successful Central and North American genera *Contopus*, *Empidonax* and *Sayornis* were derived.

Pyrrhomyias cinnamomea is a difficult genus and species to place because it combines the peculiar syrinx of Ames' *Myiobius* group, which lacks intrinsic muscles, with the form and coloration of *Mitrephanes*. In the *Myiobius* group it would be the only species that makes a cup-shaped instead of a pendent nest and has a pointed instead of a much rounded wing, with 10th primary equal to the 5th or 6th in length, rather than shorter than the first. In its pointed wing, and even more, in its comparatively very short tarsus, it agrees with *Mitrephanes* and *Contopus*. I can find nothing recorded on the habits of *cinnamomea*, an Andean subtropical species from Venezuela to Bolivia, but *Mitrephanes phaeocercus* is reported by Webster (1968) and Eisenmann (*in litt.*) to be a miniature *Contopus* in habits.

Contopus (including *Nuttallornis* and *Blacicus*), *Empidonax*, *Pyrocephalus* and *Sayornis* comprise what I have been calling the Central and North American genera. All but *Pyrocephalus* were included in Ames' *Nuttallornis* group on the basis of syringeal characters. Warter (1965: 36) also removed *Sayornis* and *Pyrocephalus* from Hellmayr's Fluvicolinae to the vicinity of *Contopus* and *Empidonax* on cranial characters. The removal of *Sayornis* from the restricted Fluvicolinae on zoogeographical grounds was suggested by Ihering in 1904 (p. 320), but his idea was ignored by Berlepsch and Hellmayr. Actually, placing *Sayornis* near *Contopus* and *Empidonax* is a familiar arrangement to North American ornithologists, because the American Ornithologists' Union Checklist (1957) and Mayr and Short (1970) place it there.

Sayornis and *Empidonax* are the most truly North American flycatchers. All three species of *Sayornis* breed in North America, and one of them, *nigricans*, has recently invaded South America along the Andes, where it differs only subspecifically. There are 10 species of *Empidonax* breeding in North America, six in Central America and only two in South America; possibly the latter represent an invasion from the north, but the evidence is not so clear as in the case of *Sayornis nigricans*. The species of *Contopus* are more evenly distributed geographically, but the genus is closely related to *Empidonax*, as witness an intergeneric hybrid reported by Short and Burleigh (1965). Considering present distribution, *Contopus* may well have been the primitive stock from which the others were derived. *Pyrocephalus* has a wide but disjunct range from southern North America through drier tropical South America, and even in the Galapagos; its geographical origins are not clear, but it bears a close resemblance in general form and in cranial characters to *Sayornis*.

Cnemotriccus fuscatus is found throughout the tropical lowlands of South America. In plumage, *fuscatus* is very close to *Empidonax*, but it has a white superciliary in-

stead of the white eye-ring characteristic of that genus, and has also a blackish mandible and a rounded rather than square tail. Hellmayr (1927: 225) included *poecilurus* in *Cnemotriccus* but Zimmer has shown (1937b: 26) that this species is a hen-colored *Knipolegus*. Proportions are so constant within the medium-sized Fluvicolinae that plumage pattern and color and bill form are frequently the best guides to relationships.

Nesotriccus ridgwayi, the endemic genus and species of Cocos Island, seems to fit best in the vicinity of *Cnemotriccus* and *Empidonax*, despite cranial evidence to the contrary. *Nesotriccus* has always been assumed to be an island representative of *Myiarchus*, but the reasons are more inferential than logical. The Geospizinae of the Galapagos have an obvious representative in *Pinaroloxia* of Cocos Island, and when an endemic flycatcher was discovered on Cocos, it was assumed (Townsend, 1895: 124) to be a representative of *Eribates* (= *Myiarchus*) *magnirostris* of the Galapagos. *Magnirostris* is a typical *Myiarchus* in plumage, and differs only in having the proportionately longer bill and tarsi characteristic of island forms. *Nesotriccus*, however, is not at all Myiarchine in plumage, but most nearly resembles *Empidonax euleri* or *Cnemotriccus fuscatus* in both adult and juvenal plumages. The bill and tarsi are even more lengthened proportionately than in *Eribates*. The nest form would give the best evidence of affinities, but unfortunately the nest of *Nesotriccus* is unknown. Swarth (1931: 84), comparing the behavior of *ridgwayi* and *magnirostris* writes, "The supposed resemblance between these two species is non-existent to me," and Slud (1967: 286) says *Nesotriccus* suggested to him a long-billed, slim *Empidonax*; it moved about in the foliage in finch-like hops and spurts, and proved itself adept at aerial feeding, making flickering short sallies. *Nesotriccus* lacks the type 6 nasal septum characteristic of the Fluvicolinae, but its other cranial characters are sufficiently mixed that Warter (1965: 37) considered it intermediate between *Myiarchus* and *Todirostrum*. I shall leave *Nesotriccus* between *Cnemotriccus* and *Empidonax*.

The mergings of genera indicated above have all been previously suggested. *Nuttallornis* has been merged with *Contopus* by Phillips, Marshall and Monson (1964: 90) and *Blacicus* was placed in *Contopus* by Bond (1943: 117). *Aechmolophus* was made a synonym of *Xenotriccus* by Webster (1968: 289). *Praedo* was made a synonym of *Aphanotriccus* by Griscom (1929: 176) although Wetmore (1952: 487) continues to recognize the former.

The remainder of the Fluvicolinae are the South American element that historically made up the restricted subfamily of that name. It is composed of a number of specialized, terrestrial genera with numerous sympatric species, some more generalized, arboreal forms and several distinctive monotypic genera. Despite the great variation in size, proportions, plumage and behavior, the Fluvicolines seem a closely related group. Ames (1971: 158) includes a broad spectrum of genera in his *Fluvicola* group, which is of more significance than the fact that many closely related genera were not part of the group. Warter found that, with the exception of *Muscigralla*, all had a type 6 nasal septum, and types 1 or 2 palatines. Geographically, all belong to the dry country or temperate zones of South America, or are specialized for marshes or riverine habitats. None occur in the humid forests of Amazonia, although *Muscisaxicola fluviatilis* and *Ochthoeca* (*Ochthornis*) *littoralis* are found on beaches and on edges of Amazonian waterways.

Smith and Vuilleumier (1971) reviewed the evolutionary relationships of a number of the ground tyrants; Vuilleumier used evidence from external morphology and ecology and Smith from behavior. They included in their study the following genera of Hellmayr: *Agriornis*, *Xolmis*, *Muscisaxicola*, *Myiotheretes*, *Cnemarchus*,

Neoxolmis, *Ochthodiaeta*, *Ochthoeca* and *Muscigralla*. In their conclusions they merged *Myiothretes*, *Cnemarchus* and *Octhodiaeta* with *Xolmis*; they also kept *Pyrope* in *Xolmis* as Hellmayr had it, although Zimmer (*Ms.*) and Meyer de Schauensee (1966: 335) recognized it as a distinct genus. *Muscigralla* was made a subgenus of *Muscisaxicola*, and the species *murina* was transferred from *Xolmis* to *Agriornis*. Their sequence of genera was *Ochthoeca*, *Xolmis*, *Neoxolmis*, *Agriornis* and *Muscisaxicola*, since they considered the arboreal or bush haunting genera more primitive or generalized than the puna or steppe inhabiting terrestrial forms.

I agree with Smith and Vuilleumier's exposition of the relationships among these "ground tyrants," but I feel they have gone too far in lumping some of the genera. All the species included in Hellmayr's *Myiotheretes*, *Cnemarchus* and *Ochthodiaeta* are characterized by brown, buff or rusty plumage, and are found only in brush or the edge of forest in the high Andes, from Venezuela to northwestern Argentina. The species of Hellmayr's *Xolmis*, on the other hand, are with one exception patterned in black, gray or white and are found in tropical to temperate lowlands from eastern Brazil and Bolivia south to Patagonia. I feel that the dichotomy between these two groups is so marked that, even though they may have had a common ancestor, their present relationship is best shown by the recognition of two genera—*Myiotheretes* (including *Cnemarchus* and *Ochthodiaeta*) and *Xolmis*.

The one exception to the black, gray and white plumage pattern in *Xolmis* is *rubetra*, which is brown above with a russet crown, and whitish below, streaked dark brown on throat and breast, and with a russet wash on the flanks. Vuilleumier (in Smith and Vuilleumier 1971: 197) says, "In color, pattern and habits, *X. rubetra* is intermediate between the other species of *Xolmis* and *Neoxolmis rufiventer*, and may represent an evolutionary transitional "stage" between arboreal and terrestrial tyrants." *Neoxolmis* is almost wholly terrestrial in habits, only occasionally perching on low bushes, and it was for this reason, along with the proportionately longer tarsus associated with terrestrial habits, that Vuilleumier recognized it. *Rubetra* is the most terrestrial of the *Xolmis* species, with a tarsus proportionately as long as in *rufiventris*, and its plumage is not far from the female plumage of *rufiventris*. *Rubetra* and *rufiventris* have allopatric breeding ranges, the former in northern Patagonia from Mendoza to Chubut, the latter in southern Patagonia and Tierra del Fuego. I believe that transferring *rubetra* from *Xolmis* to *Neoxolmis* best shows the relationships of these forms.

In the remainder of the genera treated, I accept Smith and Vuilleumier's revision with a single exception, the inclusion of *Muscigralla* in *Muscisaxicola*. As discussed in more detail below, I find the former so distinct morphologically that I cannot consider it closely related to any other genus. I have also accepted Vuilleumier's (p. 192) tentative suggestions that the monotypic genera *Ochthornis* and *Colorhamphus* be merged in *Ochthoeca*. *Ochthornis littoralis* is a riverine species found throughout Amazonia, while the species of *Ochthoeca* are found in temperate Andean forest or scrub. *Littoralis* is dull brown throughout, but with the white superciliaries of *Ochthoeca*; in proportions it has a longer bill and shorter tarsus than the Andean forms. In plumage and proportions it bears the same relation to *Ochthoeca* that *Muscisaxicola fluviatilis* (also a riverine form of Amazonia) bears to the remaining Andean species of its genus, and I place *Ochthornis* in *Ochthoeca*. *Colorhamphus parvirostris* has been kept in the Serpophaginae (now Elaeniinae), but it also appears to be a dulled *Ochthoeca*. Cranial characters, which might give more positive evidence, are lacking. In size and proportions *parvirostris* is identical with *Ochthoeca rufipectoralis*; however, in plumage it is closest to *oenanthoides*, of which it appears to be a

geographical representative. *Oenanthoides* breeds south through the Andes to the mountains of northwestern Argentina, while *parvirostris* replaces it in Patagonia and Fuegia. Vuilleumier (*loc. cit.*) also suggested that *Tumbezia* be included in *Ochthoeca*. The former has a more slender bill and more pointed wing than the *Ochthoecas*, and inhabits the arid coastal zone of Peru along with the peculiar *Muscigralla*. Although these are not trenchant characters, *Tumbezia* does not suggest *Ochthoeca* to me, and I keep it monotypic.

Lessonia appears to be a link, phenotypically at least, between the terrestrial *Muscisaxicola* and the more arboreal *Knipolegus*. In form the *Lessonia* species are similar to *Muscisaxicola*, with long tarsi and pointed wings; they are completely terrestrial, and have a lengthened hind claw like many of the pipits (*Anthus*). On the other hand, they are markedly sexually dimorphic, the males are mostly black and the females brownish like the majority of *Knipolegus*.

In *Knipolegus* I include *Phaeotriccus* and *Entotriccus*, two genera showing the same type of sexual dimorphism, blue-black bill and form as *Knipolegus*, but separated from the latter by the narrow, blade-shaped outer primaries. In *Phaeotriccus* the three outer primaries are narrowed, as are all in *Entotriccus*, but aberrant primaries vary intragenerically so often in the flycatchers, that by themselves they serve only as specific characters. Short (1975: 269) has also suggested merging the three.

Hymenops (*Lichenops* in Hellmayr) is intermediate between *Knipolegus* and the palustrine *Fluvicola* and *Arundinicola*. In plumage it is similar to *Knipolegus*, having a black male and a brown female with heavily streaked white underparts. However, the male has a bright yellow bill and yellow caruncles around the eye, and both sexes have a short, rounded wing, with the 7th secondary almost reaching the wing tip. *Hymenops* is palustrine, as are *Fluvicola* and *Arundinicola*. The latter two, although differing in proportions and wing form, are so alike in their black and white or brown and white plumage, palustrine habitat and nest form, that I feel they must be united under the oldest name, *Fluvicola*.

Following *Fluvicola* is a group of four fancy-tailed tyrants that Warter (1965: 130) thinks should be treated as a distinct tribe, Alectrurini, within the Fluvicolines. At present they are kept in four monotypic genera, *Colonia*, *Gubernetes*, *Alectrurus* and *Yetapa*. *Colonia*, with its black and white plumage, seems to link this group with *Fluvicola*, although Ames said the syrinx of *Colonia* was unlike *Fluvicola* and more nearly like *Ochthoeca*. *Colonia* differs from the other three species in having the central instead of the outer rectrices developed into ornamental plumes, and in being a short-billed, short-legged, arboreal, hole-nester, rather than a long-billed, long-legged, terrestrial, ground-nester. *Gubernetes*, *Alectrurus* and *Yetapa* have always been considered closely related. The last two should be merged as suggested by Short (1975: 269); the only differences are in the shape of the ornamental rectrices, and the fact that the male of *A. tricolor* loses the feathers of the face during the breeding season. *Gubernetes* is much larger, lacks the black and white plumage found in the males of *Alectrurus*, and has a forked tail like *Muscivora tyrannus* rather than ornamental outer rectrices. I keep it as a distinct genus. While I accept the near relationship of *Colonia*, *Gubernetes* and *Alectrurus* as shown by the cranial characters, I do not consider them more distinct than the other groups of Fluvicoline genera.

There remain in the Fluvicolinae six monotypic genera that are kept together not because they are necessarily related to each other, but because none of them seems to have any demonstrable close relative. They are: *Satrapa*, *Tumbezia*, *Muscigralla*, *Hirundinea*, *Machetornis* and *Muscipipra*. The first two may be related. Both have dark, uniform upperparts, olive green in

Satrapa and brown in *Tumbezia*, and both have a yellow forehead, superciliaries and underparts. *Satrapa*, however, is a larger bird with proportionately much shorter tarsus—20.5 per cent of wing length compared to 29 per cent. *Tumbezia* occurs on the arid Peruvian coast and *Satrapa* in the dry country east of the Andes and south of Amazonia. They may, as noted before, turn out to be related to *Ochthoeca*.

Smith and Vuilleumier (1971) made *Muscigralla* a subgenus of *Muscisaxicola*. However, *Muscigralla brevicauda* is unlike any *Muscisaxicola* in proportions and plumage pattern, and has tarsal scutellation unlike any flycatcher. It has rounded wings rather than the very pointed wings of *Muscisaxicola*, a proportionately short tail, and much longer culmen and tarsus. Unlike the species of *Muscisaxicola*, which have uniform dull brownish backs and blackish tails and tail coverts, *brevicauda* has pale buff tipping on the rump feathers, bright chestnut uppertail coverts, and a blackish tail tipped with pale buff. It also has a concealed yellow crest of a type not found in *Muscisaxicola*. The most distinctive differences, however, are found in the tarsi. All *Muscisaxicola* have typically exaspidean tarsi, with at most a few scutes on the proximal half of the plantar surface; there is a deep groove on the inner surface where the scutes meet, but none on the outer surface, and the scutes are smooth. *Muscigralla* has a classic holaspidean tarsus, with a deep groove on both inner and outer surfaces, and the distal edges of the scutes are raised, giving a roughened serrate feel. Furthermore, this scutellation extends for about 10 mm above the tibio-tarsal joint as in the shorebirds, a condition found in no other flycatcher. Ames (1971: 160) believed its syrinx was most nearly related to *Nuttallornis* and not the Fluvicolinae. Warter (1965: 36) found it to be a good Tyrannid, but (p. 31) listed it as the only Fluvicoline without a type 6 nasal septum. Its geographic range, the arid coast from Ecuador to southern Peru, is typical of species in several groups. Despite the fact that Smith and Vuilleumier (1971: 201, 253) and Fitzpatrick (*in litt.*) consider its displays and vocalizations closely related to those of *Muscisaxicola*, I cannot see that *Muscigralla* has any close relatives; morphologically and anatomically it is not typical of the Fluvicolines. On the other hand, it is equally out of place in any other group, and considering its generally brownish color, terrestrial habits and restricted non-forest range, it was probably an early offshoot of the Fluvicoline stock, and I shall keep it at the end of that group with other aberrant genera.

Hirundinea is a monotypic genus placed by Berlepsch (1907) without comment between *Myiobius* and *Onychrorhynchus* at the end of the Myiarchinae. I cannot see any relationship with that group. *Hirundinea ferruginea* is a pointed winged, aerial feeder with proportionately the shortest tarsus of any flycatcher, 12 per cent of wing length; the bill is long but the rictus only moderately bristled. It occurs in woodland and campos north and south of Amazonia, extending to northern Argentina and temperate Bolivia. It nests primarily on cliff faces, but in some areas it is virtually a commensal of man, placing its nest in niches of buildings or old oven bird nests, and it will sometimes wall off its nest with pebbles (Euler, 1900: 48). *Onychrorhynchus* and *Myiobius*, on the other hand, are round winged, forest haunting birds, with the heaviest rictal bristles of any of the flycatchers, and make long, pendent purse-shaped nests. In proportions, *Hirundinea* is more like the Tyrannine flycatchers with its pointed wing and short tarsi, but it is unlike any of that group in plumage and nesting habits. In distribution it is typical of the Fluvicolines, and I place it with the other peculiar monotypic genera of that group. Unfortunately, no one has had anatomical material available for study.

Machetornis rixosus is a rounded winged, long-legged, terrestrial species that in plumage pattern and in temperment is re-

markably like the tropical kingbirds of the genus *Tyrannus*. It would be tempting to consider it a member of the latter group, secondarily adapted for terrestrial life, were it not for the fact that its cranium is typically Fluvicoline, and it does not share a single cranial character with the Tyrannines. Ames (1971: 147) says that the Mm. sternotracheales of *Machetornis* strongly resemble those of *Xolmis*, but that it lacks intrinsic muscles. He considered that if the relationship to the other "ground tyrants" was real, *Machetornis* must have lost its intrinsic muscles. The last of the aberrant Fluvicolines, *Muscipipra vetula*, is again much like the Tyrannine kingbirds, both in plumage and proportions. In absolute size and proportions it is very close to *Tyrannus savana* (*Muscivora tyrannus*), but it is dull gray rather than black and white, lacks any bright crest, and the fork of the tail is less deep. On the other hand, it shares the same proportions with *Colonia* among the Fluvicolines, and on the basis of syringeal characters, Ames (1971: 158) placed it in his *Fluvicola* group. Warter had no specimen and I can find nothing on its habits. Its restricted range in southeastern Brazil and adjoining Paraguay and Misiones, Argentina, tells us little. *Muscipipra* may well prove to be a Tyrannine, but in the absence of more concrete evidence, I leave it in the Fluvicolines.

TYRANNINAE

The remaining subfamily, Tyranninae, consists of Hellmayr's old Tyranninae plus *Myiarchus* and allied genera. While it is difficult to define the subfamily as advanced or specialized, it is certainly successful and is the one that appears to have undergone the most recent radiation. Almost all the genera and many of the species are found throughout Central and South America, and the majority are aggressive and dominant wherever found. The extreme uniformity of the crania is evidence of recent radiation; only two types of nasal septa occur, both without basal plates, and interorbital septa, palatines and cranial types are identical throughout.

Warter recognized Attilinae as a subfamily (1965: 95, 140) because of its peculiar cranial characters; it included *Attila*, and presumably *Pseudattila* and *Casiornis*, which Warter was unable to examine. However, as noted before, external morphology and syringeal characters strongly suggest that *Attila* (including *Pseudattila*), *Casiornis*, *Laniocera* and *Rhytipterna* are a closely related group of genera belonging with *Myiarchus*. *Rhytipterna* and *Myiarchus* in turn are clearly part of the subfamily Tyranninae, as evidenced by cranial characters. Despite the contrary cranial evidence separating *Attila* from the rest of the *Myiarchus* group, I believe the weight of evidence is in favor of keeping them all together.

I begin the Tyranninae with the *Myiarchus* group. *Syristes*, which has previously been placed near *Tyrannus* by Hellmayr (1927: 119), but in the Cotingidae by Ridgway (1907: 815), also belongs here. It has a holaspidean tarsus similar to *Casiornis* or *Rhytipterna*, and the cranial characters of *Syristes* and *Rhytipterna* are identical. Although the plumage is more like that of *Tyrannus*, the rounded wing, holaspidean tarsus and type 2 nasal septum place it with *Rhytipterna* and near *Myiarchus*. This is essentially the sequence of Wetmore (1972: 433), who put it between *Myiarchus* and *Attila*. *Hylonax* and *Eribates* are included in *Myiarchus*. *Deltarhynchus flammulatus*, which is pure *Myiarchus* in plumage, is separated from the latter by its short, triangular bill. Unfortunately nothing has been published on the anatomy or behavior of *flammulatus*. If it is found to be a hole nester, using a few scraps of snake skin for decoration, it should certainly be merged in *Myiarchus*.

The remainder of the genera are those included by Hellmayr in his Tyranninae. Although they are related to the *Myiarchus* group through identical interorbital septa, palatines and crania, they differ, with the

exception of *Legatus*, in having a type 1 instead of a type 2 nasal septum, and the majority belong to the *Tyrannus* syringeal group rather than the *Myiarchus* group.

Meise (1949) reviewed Hellmayr's Tyranninae, and separated the genera into three groups on the basis of nest type. They were: 1) those with open, bowl-shaped nests—*Tyrannus* (including *Tyrannopsis* and *Tolmarchus*), *Muscivora*, *Empidonomus*, *Legatus*, *Conopias* (including *Coryphotriccus*) and *Megarhynchus*; 2) hole nesters—*Myiodynastes*; and 3) those with globular nests—*Myiozetetes* and *Pitangus*. Although Meise's classification is a useful approach, increasing knowledge has made some of his conclusions questionable. *Conopias parva* turns out to nest in holes and nested at least once in an abandoned cacique nest (Haverschmidt 1957: 240; 1973: 207). Within the genus *Pitangus*, *sulphuratus* makes a globular nest and *lictor* usually a cup-shaped nest. The nest described for *Conopias inornata* by Cherrie (1916: 238), a small cup, saddled on a branch and neatly covered with lichens, is totally unlike the loose, stick nests in forks or crotches characteristic of other cup-nest builders in this subfamily. Finally *Legatus* usurps the domed nests of many species from different families, annoying the owners until they abandon the completed nest (Skutch, 1960: 451; Haverschmidt 1968: 305). Although nest type is an important character, it cannot be the primary basis for a classification.

There are five currently recognized genera in which the same distinctive plumage pattern occurs in at least one species. These are *Pitangus*, *Myiozetetes*, *Conopias*, *Myiodynastes* and *Megarhynchus*. The plumage characteristic of this group of genera has the crown blackish with a concealed yellow or orange crest; white forehead and superciliaries, with the latter usually extending around to meet on the nape; broad black band through the eye; upperparts olive to brown, in contrast with the dark crown; wings and tail brown, the feathers edged with the color of the back or with chestnut; throat white or yellow; breast, belly and crissum bright yellow. This pattern is found *inter alia* in *Myiodynastes hemichrysus*, *Megarhynchus pitangua*, *Conopias parvus*, *Myiozetetes cayannensis* and *similis*, and *Pitangus sulphuratus* and *lictor*.

In Table II the species of these genera are listed with some of the character states used to separate them. The table shows the species in each genus are for the most part more closely related to each other than they are to any outside species; what is not clear is how many genera should be recognized. *Myiodynastes* is separated from all others except *Megarhynchus* by large size, long stout bill and short tarsus (except for *bairdii*), and from all except *Conopias parvus* by its hole-nesting habits. In external form *Megarhynchus* is merely an exaggerated *Myiodynastes* with a long, deep, decurved bill, but it does make an exposed, cup-shaped nest high up in trees, a typical *Tyrannus*-type nest, in contrast to the hole nesters. Fitzpatrick (*in litt.*) says *Megarhynchus* is much closer to *Pitangus* in behavior, since it feeds in the open, rather than within the foliage as does *Myiodynastes*. The three typical *Myiozetetes*, *cayannensis*, *granadensis* and *similis*, are well defined by short bill, globular nest and syrinx unlike any other; the nest of *luteiventris* [placed in *Tyrannopsis* by Zimmer (*Ms.*), and Meyer de Schauensee (1966)] is unknown. However, they share the short bill with *Conopias inornatus* (nest cup-shaped), and the globular nest with *Pitangus sulphuratus* (large and long-billed). *Conopias* is the least known genus as far as behavioral or anatomical characters go. *C. parva* is a hole nester; if this holds for the other two "typical" species, then *Conopias* is probably more closely related to *Myiodynastes* than to *Myiozetetes*. *C. inornatus* has the size and proportions of *Myiozetetes*, but lacks a brightly colored crest, as do *Conopias trivirgata* and *chinchoneti* for the most part, and has yellow

TABLE 2.

Species of Tyranninae	Av. wing length	Bill as % of wing	Tarsus as % of wing	Crest: + present 0 absent	Nest type	Syrinx from Ames	Cranium from Warter
Myiodynastes luteiventris	117	22.1	17.0	+	hole in tree	*Tyrannus* group	typical tyrannine
maculatus	112	24.0	17.8	+	hole or niche	not examined	typical tyrannine
bairdii	119	25.7	21.8	+	hole or niche	*Tyrannus* group	not examined
hemichrysus	107	23.8	17.9	+	niche	not examined	not examined
chrysocephalus	112	24.0	17.0	+	niche	not examined	not examined
Conopias trivirgata	75	22.8	23.4	trace	unknown	*Tyrannus* group	not examined
cinchoneti	86	22.4	20.0	trace	unknown	not examined	not examined
parva	82	25.1	21.0	+	hole or old nest	not examined	not examined
inornata	96	18.4	21.6	0	neat, shallow cup	not examined	not examined
Myiozetetes luteiventris	80	17.5	19.4	+	unknown	not examined	not examined
cayannensis	89	18.1	21.4	+	globular	ungrouped	typical tyrannine
granadensis	92	17.3	19.5	+	globular	ungrouped	typical tyrannine
similis	89	18.5	21.2	+	globular	ungrouped	typical tyrannine
Megarhynchus pitangua	121	28.8	16.6	+	shallow cup	*Tyrannus* group	typical tyrannine
Pitangus sulphuratus	110	25.6	22.2	+	globular	*Tyrannus* group	typical tyrannine, but
lictor	91	26.9	21.4	+	cup	ungrouped	*lictor* differs from *sulphuratus* more than any other congeners

rather than buff inner edges to the primaries. Based on one record (Cherrie, 1916: 238), *inornatus* builds a neat shallow cup nest, covered with lichens, and saddled on a large limb. If true, this sets *inornatus* apart from either *Conopias* or *Myiozetetes*. For the moment I leave *inornatus* in *Conopias*, although Zimmer (*Ms.*) and Meyer de Schauensee (1966) place it in *Myiozetetes*. A final problem in this group is the status of the two *Pitangus* species, *sulphuratus* and *lictor*. The two are virtually identical in plumage and proportions, and have more slender bills than other tyrannines. However, *sulphuratus* builds a globular nest, and *lictor* an open cup (Haverschmidt, 1957: 240; Smith, 1962: 111); the eggs of *lictor* are a much broader oval than those of *sulphuratus* (Meise, 1968: 78); *sulphuratus* has a typical tyrannine syrinx, but according to Ames (1971: 159),"*Pitangus lictor* lacks most of the features of the [*Tyrannus*] group and, in view of the structural homogeneity among those listed above, it is difficult to believe *lictor* and *sulphuratus* are more closely related to each other than the latter is to *Tyrannus*"; and Warter (1965: 36) says the crania of *lictor* and *sulphuratus* differ more than any other congeners . If *lictor* and *sulphuratus* are not congeneric, there is no logical genus in which to place the former. With its slender bill, it is the antithesis of the other cup-nest maker *Megarhynchus*, and on syringeal characters it differs as much from *Myiodynastes*, *Megarhynchus* and *Conopias* as it does from *P. sulphuratus*. *Myiozetetes* also differs from the tyrannines on syringeal characters, but not in the same way as *lictor*, and the nest of the latter is unlike the globular nest of *Myiozetetes*. Wetmore (1972: 422) says *lictor* should probably be placed in a separate genus, but considering my imperfect knowledge of this and related groups, I cannot see creating a new genus at this time. I shall leave *lictor* in *Pitangus*, but only for lack of a better place to put it.

I recognize the above five genera, not because I consider them satisfactory, but because at the moment I have nothing better to suggest. A case can be made for uniting *Myiozetetes* with *Conopias*, or *Pitangus* with *Myiozetetes*, but as noted in the discussion above, there are good reasons for not doing so. Until more is known about the behavior and nesting habits of some of the more obscure species, I feel more comfortable leaving them as they are. They are listed in the order *Pitangus*, *Megarhynchus*, *Myiozetetes*, *Conopias* and *Myiodynastes*.

Legatus leucophaius is almost identical in both juvenal and adult plumages with *Empidonomus varius*; the only noticeable difference is the pale buff edge on the inner webs of the primaries in *leucophaius* contrasted with the yellow edge in *varius*. In size, however, *leucophaius* is smaller, with a proportionately shorter, broader bill, shorter tail but longer tarsus. They differ markedly in nesting habits, *leucophaius* usurping the domed nests of other species, while *varius* builds an open cup. Warter (1965: 32) found *Legatus* had a type 2 nasal septum like *Myiarchus*, rather than the type 1 found in the rest of the restricted tyrannines, and Ames (1971: 159) reported the syrinx to be unlike the rest of the *Tyrannus* group. Considering these differences, the similarity in plumage is probably due to convergence.

Empidonomus varius and *aurantioatrocristatus* are closely related to *Tyrannus*. They are an obvious species pair, being almost identical in measurements, and each having a long blackish crest with bright yellow vertex; *varius*, however, is streaked above and below, while *aurantioatrocristatus* is plain brown above and gray below. Meise (1949: 71) considered *Empidonomus* separable from *Tyrannus* by its short bill and long tail. The former does have a short bill compared to the Tropical Kingbird, *T. melancholicus*, but no shorter than the North American Kingbird, *T. tyrannus*, the bill/wing ratios being 17–18 per cent. Similarly, the tails of *Empidonomus* species are proportionately the same as that of *T.*

melancholicus, 81–83 per cent of wing length. Syrinx, cranium, notching of primaries, and nest form are the same in both genera. Further evidence of the close relationship of *Empidonomus* and *Tyrannus* is the fact, demonstrated by Meise (1949: 61) that *Laphyctes apolites* Cabanis and Heine is a hybrid between *E. varius* and *T. melancholicus*. The one character I consider sufficient to maintain their separation is the much more slender build of *Empidonomus*. When specimens of the two genera, prepared by the same collector, are compared, those of *Empidonomus* are invariably more slender and cigar-shaped, while those of *Tyrannus* are broader and more chesty. While such a difference is not precise, it must reflect some anatomical and probably behavioral difference, and for the moment I recognize the two genera. The streaked plumage of *varius* would also be out of place in *Tyrannus*.

Tyrannopsis is a peculiar monotypic genus that is apparently most closely related to *Tyrannus*, although the single species *sulphurea* was for a long time carried in *Myiozetetes*. It differs from *Myiozetetes* in being larger, with a proportionately shorter tail and longer culmen, in having a syrinx belonging to the *Tyrannus* group, while that of *Myiozetetes* is unlike any other, and in building a *Tyrannus*-like cup-shaped nest instead of a globular one. In plumage, *sulphurea* is a saturated version of *Tyrannus melancholicus* with a dark gray head and orange crest, dark olive back, gray throat with a white center, and yellow breast and belly. Where the gray of the sides of the throat bleeds into the yellow breast, there is olive streaking, a character not found in any of the kingbirds. In size and proportions *Tyrannopsis* fits within the overall limits of *Tyrannus*, but is not close to any one species, having the short bill of the North American *tyrannus* and *verticalis*, and the long tarsus of the insular *caudifasciatus*. The male lacks the notched primaries present in all continental *Tyrannus*. The range of *sulphurea* is extensive in the tropical lowlands east of the Andes, south to southern Amazonia and east to Maranhão, Brasil, but its distribution is restricted to areas where the Mauritia palm, in which it nests, is found. Meise (1949: 71) placed *sulphurea* in *Tyrannus*, but Smith (1966) in his review of that genus did not mention it as a possible *Tyrannus*. To further complicate its possible relationships, Zimmer (*Ms.*) followed by Meyer de Schauensee (1966: 346) added to *Tyrannopsis Myiozetetes luteiventris*, a species that by no stretch of the imagination could be considered a *Tyrannus*. *Luteiventris* is a miniature of *sulphurea* in coloration, even smaller than the smallest *Myiozetetes*, and it is identical with the latter in proportions; its nest is not known. I feel, as did Blake (1961), that *luteiventris* should remain in *Myiozetetes*. I also recognize *Tyrannopsis* as a genus, at least until it is better known behaviorally.

The last genus in the family is *Tyrannus*. It is the most widespread geographically, both as a genus and in the individual ranges of some species, and the species are usually aggressive and dominant wherever they occur. Considering the uniformity of the species, both morphologically and behaviorally, they probably represent the most recent radiation in the family.

Smith (1966) comprehensively reviewed communications and relationships within the genus *Tyrannus*. He merged with *Tyrannus* the monotypic *Tolmarchus* of the West Indies, and *Muscivora* with its two fork-tailed species, *tyrannus* and *forficata*. The merging of *Tolmarchus* with *Tyrannus* had been previously recommended by Meise (1949: 73) and Bond (1958); it is supported by syringeal and cranial evidence. Smith's merging of *Muscivora* has had a mixed reception, being followed by Lanyon (1967a: 606) and by Mayr and Short (1970: 59), but opposed by Howell (1972: 325). The union of *Tyrannus* with *Muscivora* requires that *Muscivora tyrannus* be called *Tyrannus savana*, to avoid homonymy with the North American *Ty-*

rannus tyrannus. Smith's decision was based on behavioral considerations, but other evidence is equally strong. Cranial characters, syrinx, nest form and notched primaries are alike in *Muscivora* and *Tyrannus*. Except for the long, forked tail, the *Muscivora* species are almost identical in size and proportions with the North American *Tyrannus tyrannus* and *verticalis*. This is of particular interest, since Meise (1949: 75) believed *savana* and *forficata* evolved independently from *T. tyrannus* and *verticalis* respectively. Further evidence of close relationship is found in the hybrid between *verticalis* and *forficata* described by Davis and Webster (1970). If *savana* and *forficata* did evolve independently, then their long forked tails are convergent, and there is no taxon *Muscivora*. At present I do not know of any characters that could be used to prove or disprove this hypothesis. I do not recognize *Muscivora* even as a subgenus because of its close relation to *Tyrannus*, but I keep *savana* and *forficata* together because of their possible common origin.

PHYLOGENY

Any attempt to derive a phylogeny requires some knowledge of the primitive and derived states of the characters on which the classification is based. Also, it must be possible to determine whether the derived state is monophyletic or whether it evolved independently two or more times, and as a corollary, whether a state is really primitive or just a secondary regression from a derived state. When the characters used to classify the Tyrannidae are viewed in this light, there are few that serve for determining a phylogeny.

There are a number of morphological characters that occur regularly in the family, but the characters are so randomly distributed they must have evolved or been lost independently many times. Bright coronal crests, aberrant primaries, and holaspidean, taxaspidean or pycnaspidean tarsi are found in unrelated groups in all three subfamilies, and merely represent a genetic potential within the family for this type of mutation. Even the pendent, pyriform nest, which is an elaborate structure requiring a special set of behavioral patterns for its construction, must have evolved at least twice—in the *Myiobius* group of the Fluvicolinae and in the tody-tyrants of the Elaeniinae. As Ames (1971: 150) noted, "The application of syringeal morphology increases in reliability toward the generic level," and he made no attempt to rate his groups of genera as primitive or advanced. The only characters that seem amenable to classification as primitive or derived are the cranial characters of Warter.

In classifying the states of the cranial characters, I have used the evidence of their present distribution within the subfamilies, rather than trying to determine which are intrinsically primitive or derived.

1) Nasal septum – types 1 and 2 are found in significant proportions in both Tyranninae and Elaeniinae, while a type 6 septum is found in all the Fluvicolinae except the two aberrant genera *Muscigralla* and *Onychorhynchus*. Types 3 and 5 occur once each in the Fluvicolinae and occasionally in the Elaeniinae. Type 1 or 2 is almost certainly primitive, and the others derived, but only type 6 appears significant phylogenetically.
2) Interorbital septum – type 1 occurs regularly in the Fluvicolinae, exclusively in the Tyranninae and twice in the Elaeniinae. Type 2 is mostly confined to the Fluvicolinae, but occurs twice in the Elaeniinae; type 3 is found occasionally in both, but type 4 is found only in the Elaeniinae, where it occurs in 77 per cent of the studied genera. Evidently type 1 is the primitive type, type 4 is derived and characterizes the Elaeniinae, and types 2 and 3 have evolved

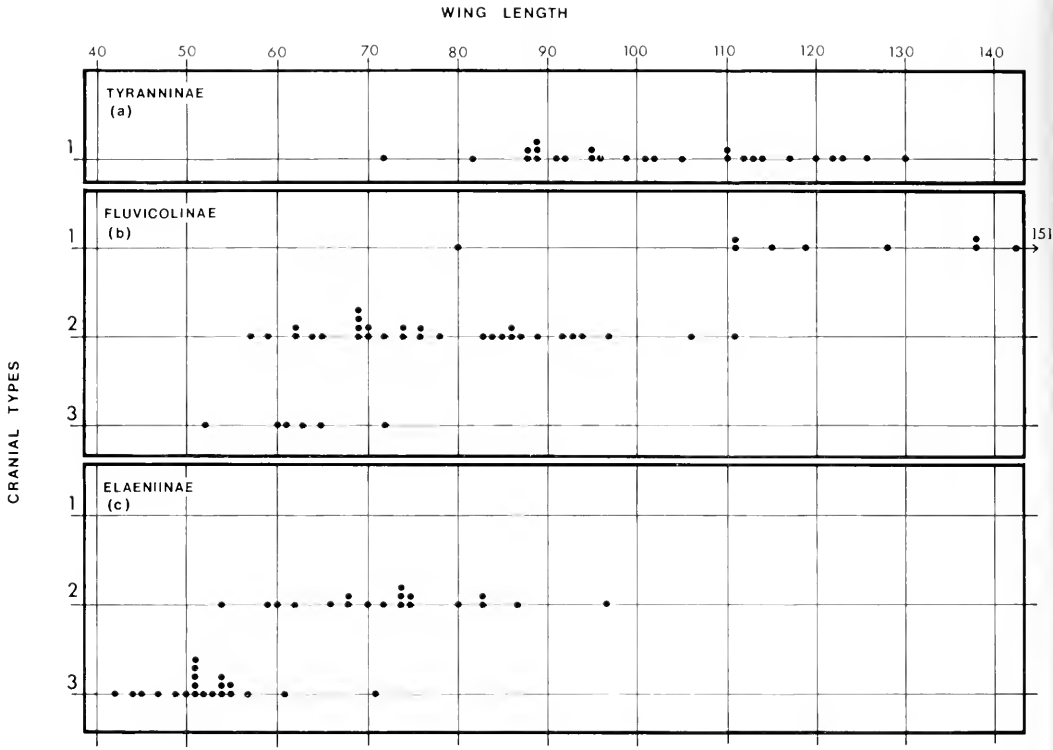

Figure 6. Warter's cranial types plotted as a function of wing length for the three subfamilies of Tyrannidae. In the Tyranninae (a) only type 1 occurs, and it is characteristic of the subfamily. In the Fluvicolinae (b) and Elaeniinae (c), the cranial types show a close correlation with size, as represented by wing length, and are without taxonomic significance.

independently in Fluvicolinae and Elaeniinae.

3) Palatines – type 1 occurs regularly in all three subfamilies, and is the only type found in the Tyranninae; it must be the primitive type. Type 2 is also common in the Fluvicolinae and Elaeniinae, but type 3 is confined with one exception to the "Contopine" lineage of the Fluvicolinae.

4) Cranium – with the exception of the Tyranninae, the cranial types are strongly correlated with size as expressed by wing length—type 1 being found in the largest birds and type 3 in the smallest (Fig. 6). In the Tyranninae only type 1 occurs, regardless of wing length. Assuming the primitive flycatchers were small arboreal forms, nearest the present Elaeniinae, then types 2 and 3 are primitive, and type 1 derived.

Figure 7 is a diagram suggesting the possible origin of the subfamilies of flycatchers, incorporating the primitive and derived states of the cranial characters. The putative proto-flycatcher appears within the circle, with the different subfamilies leading off from it. The derived cranial characters defining the subfamilies are indicated, and in two cases the subfamilies are further subdivided. Finally, Ames' seven syringeal groups are indicated, showing the close correlation between the two

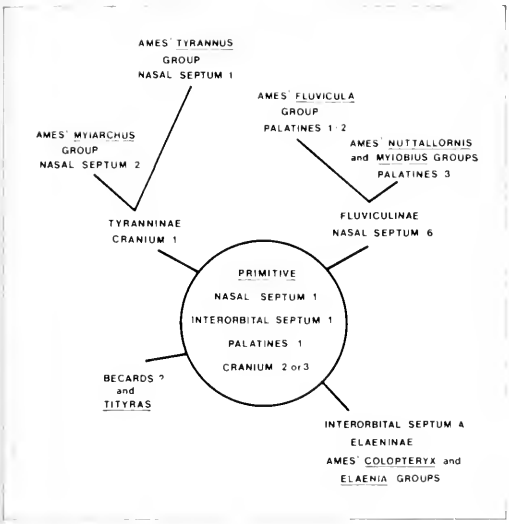

Figure 7. Postulated origin of the subfamilies of Tyrannidae, based on Warter's cranial characters. Ames' groups of genera, based upon syringeal characters, are added to show the close correlation between these character complexes.

types of anatomical characters. It is tempting to try to carry out further subdivisions within the subfamilies, based on cranial or other evidence, but it is unprofitable for two reasons. First, the evidence, even within the cranial characters, becomes conflicting, and second, there are too many unexamined genera whose allocation would be guesswork.

The circular form of diagram in Figure 7 is used because the three subfamilies of flycatchers seem to have arisen independently rather than sequentially, one from another. There are no genera in any given subfamily that seem ancestral to or even closely related to either of the other subfamilies. *Onychorhynchus* was placed in my Elaeniinae by Warter, and in the Fluvicolinae here, but the difficulty is not that *Onychorhynchus* is intermediate between the two, but that its high specialization makes it difficult to place it in either. If my reconstruction of the proto-flycatcher characters is correct, then none of the modern taxa retain the primitive condition.

ELAENIINAE—This subfamily is characterized by the type 4 interorbital septum, which is found in 27 of the 35 genera examined by Warter. The remaining genera have variously types 1, 2 or 3, and the evidence suggests these represent a secondary loss of type 4 rather than the retention of a primitive state. Seven of these genera—*Myiopagis*, *Elaenia*, *Suiriri*, *Sublegatus*, *Phaeomyias*, *Zimmerius* and *Tyrannulus*—belong to the old restricted subfamily Elaeniinae, and all but *Sublegatus* and *Zimmerius* are part of Ames' *Elaenia* syringeal group. However, their relationships are otherwise divided among groups still retaining the type 4 interorbital septum. *Elaenia*, *Suiriri* and *Sublegatus* share a type 5 nasal septum with the nearly related *Anairetes*, *Serpophaga*, *Inezia* and *Mecocerculus*. This type of septum is certainly derived and is found only here, with the exception of the peculiar *Muscigralla* of the Fluvicolinae. *Phaeomyias*, on the other hand, is most closely related to *Camptostoma*, which has a type 4 interorbital septum. The last genus to lack the type 4 interorbital septum is *Polystictus*, which is related to *Pseudocolopteryx*, which has the normal type. A second of Ames' syringeal groups, the *Colopteryx* group, includes most of the tody-tyrants, all of which have the type 4 interorbital septum.

FLUVICOLINAE—The Fluvicolinae are characterized by the type 6 nasal septum, which is found in all genera except the highly specialized *Muscigralla* and *Onychorhynchus*. This type of nasal septum has also evolved independently twice in the Elaeniinae, in *Polystictus* and in *Zimmerius*. The fact that these two genera have the Fluvicoline nasal septum and lack the characteristic type 4 interorbital septum of the Elaeniinae might suggest that one or both are primitive links between the Elaeniinae and Fluvicolinae. However, in general conformation and appearance they are typically Elaeniinae and unlike any Fluvicolinae, so I believe the resemblance in cranial characters is due to convergence. Certainly it would be difficult to conceive of both

representing the same primitive stock, since *Polystictus* is a brown, streaked grassland form, and *Zimmerius* a green, forest group.

The Fluvicolinae are further subdivided by the possession of the derived type 3 palatine in Warter's "Contopine" lineage. This palatine occurs elsewhere only in *Platyrinchus* of the Elaeniinae, where it is almost certainly independently derived. Three of the genera of the "Contopines," *Nuttallornis*, *Cnemotriccus* and *Myiophobus*, have a type 2 palatine, but this almost certainly represents a secondary loss of the type 3. This is most evident for *Nuttallornis*, whose congeners in *Contopus* all have type 3 palatines, and for *Cnemotriccus*, whose closest relative is *Empidonax* with type 3 palatines. *Myiophobus* does not have any single close relative, but the genera closest to it on other characters, *Mitrephanes*, *Pyrrhomyias* and *Myiobius*, all have type 3 palatines.

Ames' syringeal groups support this derivation of the Fluvicolinae. Two of them, the *Myiobius* group and the *Nuttallornis* group, are part of the "Contopine" lineage, while the *Fluvicola* group falls in the restricted Fluvicolines.

Tyranninae—The Tyranninae are remarkable in that all genera, with the exception of *Attila*, have one of two invariant sets of cranial characters. All but *Attila* have type 1 interorbital septa, palatines and crania, and these are associated with either type 1 or 2 nasal septa. The restricted Tyrannines all have type 1 nasal septa, with the exception of *Legatus*, and the Myiarchine group have type 2, with the exception of *Attila*. The latter type is presumably the derived form, since the type 1 is more common among the Elaeniinae. Ames' syringeal groups fit this dichotomy of the Tyranninae. The *Myiarchus* group includes those genera with type 2 nasal septa, plus *Attila*, and the *Tyrannus* group includes only genera with type 1 nasal septa, the restricted Tyranninae.

The most interesting aspect of the Tyrannine cranium is the extreme uniformity, as if all the character states were inherited as a package. This is not implicit in the type 1 characters as such: type 1 interorbital septa occur with all three types of palatines and crania in the Elaeniinae and Fluvicolinae, and type 1 palatines occur with all types of interorbital septa and cranial types. The only correlation that appears structural is that type 1 crania almost always occur with type 1 palatines; the reverse, however, is not true. The uniformity in the Tyrannine cranium suggests a late origin for this subfamily; the fact that they are a highly successful and dominant group with evidence of recent radiation supports this view. On the other hand, three of the character states delineating this uniform cranium are primitive; only the type 1 cranium is a derived state. This leaves us with the anomaly of the most successful subfamily being the most primitive anatomically. Possibly the explanation is that retention of the primitive or generalized characters left the Tyranninae with a greater potential for radiation, which they have only recently exploited.

SUMMARY

A new classification of the Tyrannidae is presented, based on available morphological, anatomical, behavioral and distributional data. The most useful recent studies on the higher classification of the Tyrannidae were those of Warter (1965) on the cranial characters of the Tyrannoidea, and Ames (1971) on the syrinx of the Passeriformes. The family includes all those genera accepted by Hellmayr (1927), five genera formerly included in the Cotingidae —*Attila*, *Pseudattila*, *Casiornis*, *Laniocera* and *Rhytipterna*—and *Corythopis* from the former family Conopophagidae.

The seven subfamilies of Hellmayr, Fluvicolinae, Tyranninae, Myiarchinae, Platyrinchinae, Euscarthminae, Serpophaginae and Elaeniinae, are reduced to three. The Fluvicolinae now include that part of the Myiarchinae including the genera *Nuttallornis* through *Onychorhyn-*

chus, and the remainder of the Myiarchinae plus the former Cotingid genera are placed in the Tyranninae. The other four subfamilies are merged into one, for which Elaeniinae is the oldest name. The subfamilies are listed in the order Elaeniinae, Fluvicolinae, Tyranninae, since this seems to represent the progression from most primitive or generalized to most specialized or successful.

The genera are listed within each subfamily also from generalized to specialized. However, these are such subjective decisions that the order of Hellmayr (in reverse) is not disturbed unless there is positive evidence for making a change. There has been little analysis of the genera of flycatchers over the past century, and for the most part they have been accepted uncritically from checklist to checklist. Thirty-six of Hellmayr's genera are here synonymized, one is resurrected and one new genus is described. The latter is *Zimmerius*, created for five species formerly in the genus *Tyranniscus*. The new classification is summarized in Appendix A.

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APPENDIX A

Sequence of Genera with Synonyms

Elaeniinae

Phyllomyias (syn: *Xanthomyias*, *Oreotriccus*, *Acrochordopus*, and *Tyranniscus nigrocapillus*, *uropygialis* and *cinereiceps*)
Zimmerius (gen. nov. — includes "*Tyranniscus*" *bolivianus*, *vilissimus*, *cinereicapilla*, *gracilipes*, *viridiflavus*)
Ornithion (syn: *Microtriccus*)
Camptostoma
Phacomyias
Sublegatus
Suiriri
Tyrannulus
Myiopagis
Elaenia
Mecocerculus
Serpophaga
Inezia
Stigmatura
Anairetes (syn: *Uromyias*, *Yanacea*)
Tachuris
Culicivora
Polystictus
Pseudocolopteryx
Euscarthmus
Mionectes (syn: *Pipromorpha*)
Leptopogon
Phylloscartes (syn: *Pogonotriccus*, *Leptotriccus*, *Capsiempis*)
Pseudotriccus (syn: *Caenotriccus*)
Corythopis
Myiornis (syn: *Perissotriccus*)
Lophotriccus (syn: *Colopteryx*)
Atalotriccus
Poecilotriccus (syn: *Taeniotriccus*)
Oncostoma
Hemitriccus (syn: *Idioptilon*, *Euscarthmornis*, *Snethlagaea*, *Microcochlearius*, *Ceratotriccus*)
Todirostrum
Cnipodectes
Ramphotrigon
Rhynchocyclus
Tolmomyias
Platyrinchus

Fluvicolinae

Onychorhynchus
Myiotriccus
Terenotriccus
Myiobius
Myiophobus
Aphanotriccus (syn: *Praedo*)
Xenotriccus (syn: *Acchmolophus*)
Pyrrhomyias
Mitrephanes

Contopus (syn: *Nuttallornis*, *Blacicus*)
Empidonax
Nesotriccus
Cnemotriccus
Sayornis
Pyrocephalus
Ochthoeca (syn: *Ochthornis*, *Colorhamphus*)
Myiotheretes (syn: *Cnemarchus*, *Ochthodiaeta*)
Xolmis (syn: *Pyrope*)
Neoxolmis
Agriornis
Muscisaxicola
Lessonia
Knipolegus (syn: *Phacotriccus*, *Entotriccus*, *Eumyiobius*)
Hymenops
Fluvicola (syn: *Arundinicola*)
Colonia
Alectrurus (syn: *Yetapa*)
Gubernetes
Satrapa
Tumbezia
Muscigralla
Hirundinea
Machetornis
Muscipipra

Tyranninae

Attila (syn: *Pseudattila*)
Casiornis
Rhytipterna
Laniocera
Syristes
Myiarchus (syn: *Hylonax*, *Eribates*)
Deltarhynchus
Pitangus
Megarhynchus
Myiozetetes
Conopias (syn: *Coryphotriccus*)
Myiodynastes
Legatus
Empidonomus
Tyrannopsis
Tyrannus (syn: *Muscivora*, *Tolmarchus*)

Sedis Incertae

Xenopsaris

APPENDIX B

Generic Changes Since Hellmayr (1927)

Acrochordopus = *Phyllomyias*, here synonymized
Aechmolophus Zimmer 1938, Auk **55**: 663 = *Xenotriccus*, Webster (1968: 289)
Alectrurus – includes *Yetapa*, Short (1975: 269)
Anairetes 1850, replaces *Spizitornis* 1920; Peters and Griswold (1943: 316); includes *Yanacea* and *Uromyias*, which see
Aphanotriccus – includes *Praedo*, Griscom (1929: 176)
Arundinicola = *Fluvicola*, here synonymized
Attila – transferred from the Cotingidae, Snow (1973: 7); Ames (1971: 155)
Blacicus = *Contopus*, Bond (1943: 117)
Cnenotriccus = *Pseudotriccus*, Zimmer (1940a: 22)
Capsiempis = *Phylloscartes*, here synonymized
Casiornis – transferred from the Cotingidae, Snow (1973: 7); Ames (1971: 155)
Ceratotriccus = *Idioptilon*, Fitzpatrick (1976); here synonymized with *Hemitriccus*
Cnemarchus = *Myiotheretes*, here synonymized; see also Smith and Vuilleumier (1971: 193)
Colopteryx = *Lophotriccus*, here synonymized
Colorhamphus = *Ochthoeca*, here synonymized
Conopias – includes *Coryphotriccus*, Meise (1949: 76)
Contopus 1855, replaces *Myiochanes* 1859, American Ornithologists' Union, Checklist Committee (1947: 449); includes *Nuttallornis* and *Blacicus*, which see
Corythopis – added to the Tyrannidae, Ames, Heimerdinger and Warter (1968)
Coryphotriccus = *Conopias*, Meise (1949: 76)
Elaenia – no longer includes *Myiopagis*, Zimmer (1941a: 20)
Entotriccus = *Knipolegus*, Short (1975: 270)
Eribates = *Myiarchus*, Swarth (1931: 84)
Eumyiobius Brodkorb 1937, Proc. Biol. Soc. Washington, **50**: 1 = *Knipolegus*, Zimmer, 1937b: 27
Euscarthmornis = *Idioptilon*, Zimmer (1940a: 13) = *Hemitriccus*, here synonymized
Fluvicola – includes *Arundinicola*, here united
Habrura 1859 = *Polystictus* 1850, Meyer de Schauensee (1966: 374)
Hemitriccus – includes *Ceratotriccus*, *Microcochlearius*, *Snethlagaea*, *Euscarthmornis* and *Idioptilon*, here united; see also Fitzpatrick (1976)
Hylonax = *Myiarchus*, Lanyon (1967b: 339)
Hymenops, 1828, replaces *Lichenops*, 1835, Meyer de Schauensee (1966: 342)
Idioptilon – includes *Euscarthmornis*, Zimmer (1940a: 13) = *Hemitriccus*, here synonymized
Knipolegus – includes *Phacotriccus* and *Entotriccus*, Short (1975: 270)
Laniocera – transferred from the Cotingidae, Snow (1973: 7); Ames (1971: 155)
Leptotriccus = *Phylloscartes*, here synonymized
Lichenops 1835 = *Hymenops* 1828, Meyer de Schauensee (1966: 342)
Lophotriccus – includes *Colopteryx*, here united
Microcochlearius = *Idioptilon*, Fitzpatrick (1976) = *Hemitriccus*, here synonymized
Microtriccus = *Ornithion*, Zimmer (1941c: 3)
Mionectes – includes *Pipromorpha*, Dickey and van Rossem (1938: 397)
Muscivora = *Tyrannus*, Smith (1966: 167)

Myiarchus – includes *Hylonax* and *Eribates*, which see

Myiochanes 1859 = *Contopus* 1855, American Ornithologists' Union, Checklist Committee (1947: 449)

Myiopagis – synonymized in *Elaenia* by Hellmayr, but now recognized, Zimmer (1941a: 20)

Myiornis – includes *Perissotriccus*, Zimmer (1940a: 220)

Myiotheretes – includes *Cnemarchus* and *Ochthodiaeta*, here united; see also Smith and Vuilleumier (1971: 193)

Nuttallornis = *Contopus*, Phillips, Marshall and Monson (1964: 90)

Ochthodiaeta = *Myiotheretes*, here synonymized; see also Smith and Vuilleumier (1971: 193)

Ochthoeca – includes *Colorhamphus* and *Ochthornis*, here united

Ochthornis = *Ochthoeca*, here synonymized

Oreotriccus = *Phyllomyias*, here synonymized

Ornithion – includes *Microtriccus*, Zimmer (1941c: 3)

Perissotriccus = *Myiornis*, Zimmer (1940a: 22)

Phaeotriccus = *Knipolegus*, Short (1975: 270)

Phyllomyias – includes *Xanthomyias*, *Oreotriccus*, *Acrochordopus* and *Tyranniscus* (pt.), here united

Phylloscartes – includes *Pogonotriccus*, *Leptotriccus* and *Capsiempis*, here united

Pipromorpha = *Mionectes*, Dickey and van Rossem (1938: 397)

Pogonotriccus = *Phylloscartes*, here synonymized

Polystictus 1850, replaces *Habrura* 1859 – Meyer de Schauensee (1966: 374)

Praedo = *Aphanotriccus*, Griscom (1929: 176)

Pseudattila Zimmer 1936, Amer. Mus. Novit. No. 893: 6 = *Attila*, Short (1975: 265); transferred from the Cotingidae, Meyer de Schauensee (1970: 297), Snow (1973: 7)

Pseudotriccus – includes *Caenotriccus*, Zimmer (1940a: 22)

Pyrope = *Xolmis*; synonymized by Hellmayr (1927: 10), resurrected by Meyer de Schauensee (1966: 335), and synonymized again by Smith and Vuilleumier (1971: 193)

Rhytipterna – transferred from the Cotingidae, Snow (1973: 8); Ames (1971: 155)

Snethlagaea = *Idioptilon*, Fitzpatrick (1976) = *Hemitriccus*, here synonymized

Spizitornis 1920 = *Anairetes* 1850, Peters and Griswold (1943: 316)

Tolmarchus = *Tyrannus*, Meise (1949: 73); Bond (1958)

Tyranniscus (*nigrocapillus*, *uropygialis*, *cinereiceps*) = *Phyllomyias*, here synonymized; the remaining species are in the new genus *Zimmerius*.

Tyrannus – includes *Muscivora* and *Tolmarchus*, which see

Uromyias = *Anairetes*, Smith (1971: 275)

Xanthomyias = *Phyllomyias*, here synonymized

Xenopsaris – here placed at end of Tyrannidae, *incertae sedis*

Xenotriccus Dwight and Griscom 1927, Amer. Mus. Novit. No. 254: 1 – includes *Aechmolophus*, Webster (1968: 289)

Xolmis – includes *Pyrope*, Smith and Vuilleumier (1971: 193)

Yanacea – Carriker, 1933, Proc. Acad. Nat. Sci. Philadelphia **85:** 27 = *Anairetes*, here synonymized

Yetapa = *Alectrurus*, Short (1975: 269)

Zimmerius – here described, includes *Tyranniscus bolivianus*, *vilissimus*, *cinereicapilla*, *gracilipes*, and *viridiflavus* of Hellmayr

APPENDIX C

Ames' (1971: 158–162) Groups of Genera

1. *Fluvicola* group. The nucleus of this group is composed of *Xolmis*, *Neoxolmis*, *Agriornis*, *Muscisaxicola*, *Fluvicola*, *Gubernetes*, *Knipolegus*, *Muscipipra* and *Phaeotriccus*. *Hymenops* is probably an offshoot. *Satrapa* and *Entotriccus* probably also belong here. *Lessonia* agrees with them in musculature.
2. *Tyrannus* group. The group includes *Tyrannus*, *Muscivora*, *Tolmarchus*, *Tyrannopsis*, *Empidonomus*, *Myiodynastes*, *Megarhynchus*, *Conopias* and *Pitangus* (*sulphuratus* only).
3. *Nuttallornis* group. Closest to the *Fluvicola* group. Includes *Nuttallornis*, *Sayornis*, *Contopus*, *Blacicus*, *Empidonax*, *Aechmolophus*, *Aphanotriccus* and possibly *Muscigralla*.
4. *Myiobius* group. Includes *Myiobius*, *Terenotriccus*, *Pyrrhomyias* and *Onychorhynchus*. The manakin *Piprites* probably also belongs here.
5. *Myiarchus* group. Includes *Myiarchus*, *Eribates*, *Attila*, *Casiornis*, *Laniocera* and *Rhytipterna*.
6. *Colopteryx* group. Contains *Colopteryx*, *Oncostoma*, *Euscarthmornis*, *Hemitriccus*, *Myiornis* and *Lophotriccus*. *Platyrinchus* might belong near here. *Tolmomyias*, *Rhynchocyclus* and *Platyrinchus* differ greatly among themselves.
7. *Elaenia* group. Included are *Elaenia* (including *Myiopagis*), *Suiriri*, *Camptostoma*, *Tyrannulus* and *Phaeomyias*. *Microtriccus* and *Tyranniscus nigrocapillus* probably belong near here.

APPENDIX D

Figures 2 and 3, and Table II of Warter, 1965: 27–34

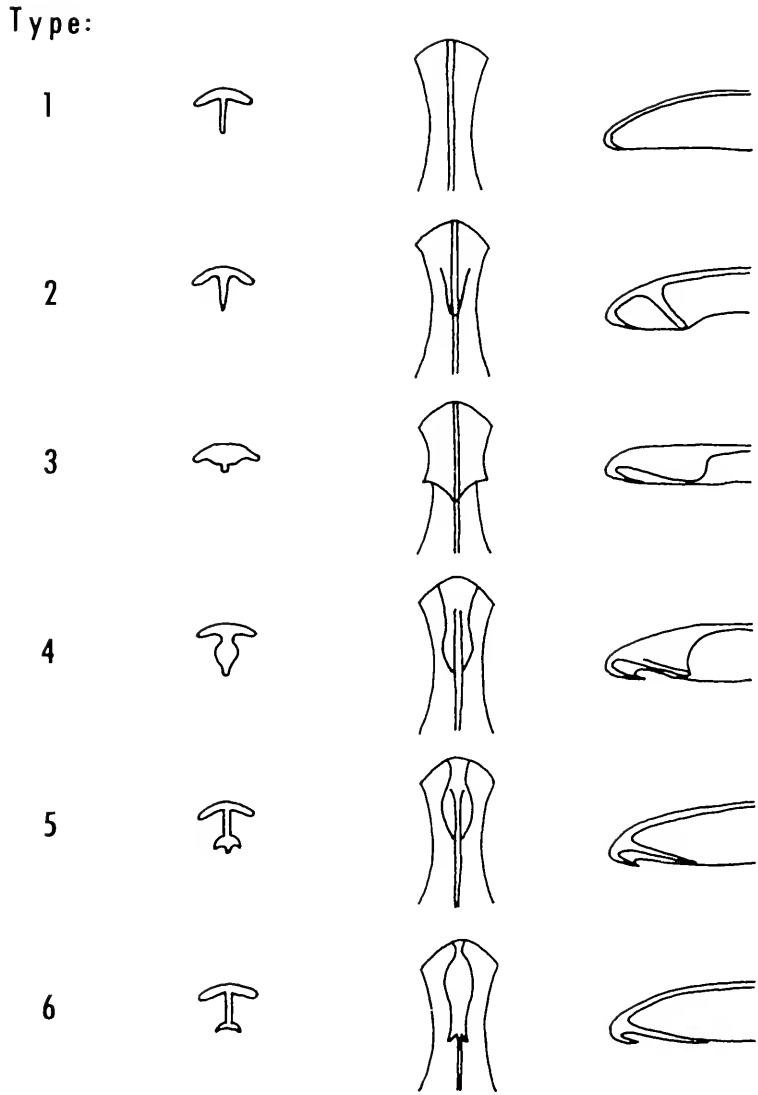

Figure 2. Types of Nasal Septa. Left column, cross section; center column, ventral aspect; right column, lateral aspect (all illustrations diagrammatic).

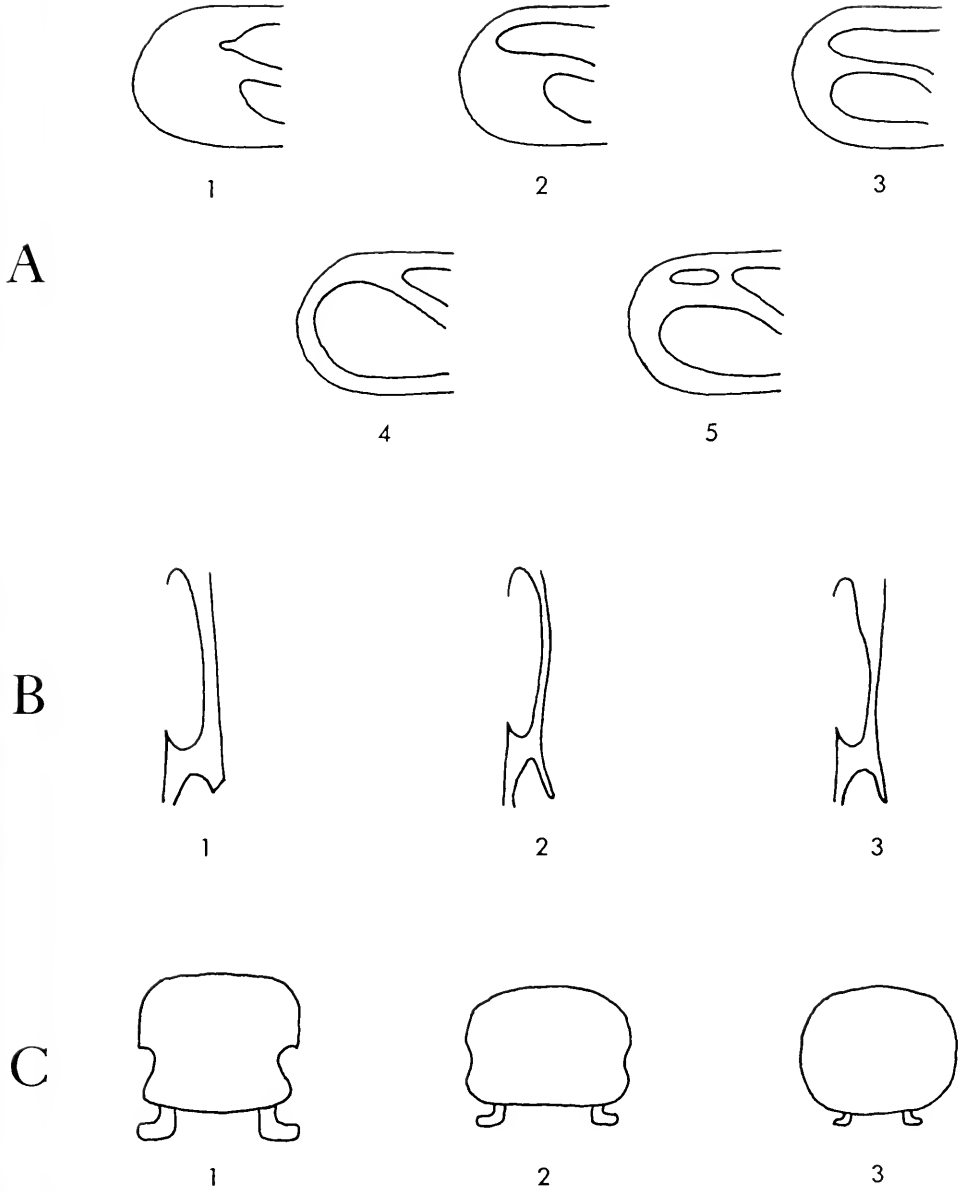

Figure 3. Features of Type I Skulls. A, types of interorbital septa; B, types of palatines; C, types of crania (posterior aspect).

TABLE 2. VARIABLE CHARACTERS OF FLYCATCHER SKULLS. NUMBERS IN COLUMNS REFER TO "TYPES" ILLUSTRATED IN FIGURES 2 AND 3. COLUMN I—NASAL SEPTUM. COLUMN II—INTERORBITAL SEPTUM. COLUMN III—PALATINES. COLUMN IV—CRANIUM. COLUMN V—PALATOMAXILLARIES (+ = PRESENT).

Genus	I	II	III	IV	V
FLUVICOLINAE					
Agriornis	6	2	1	1	+
Xolmis	6	2	1	1	+
Muscisaxicola	6	2	1	2	+
Lessonia	6	3	2	3	+
Myiotheretes	6	?	1	1	+
Neoxolmis	6	2	1	1	+
Ochthoeca	6	2	2	2	
Sayornis	6	2	3	2	+
Colonia	6	1(4)	2	2	
Gubernetes	6	1	1	1	
Yetapa	6	1(4)	1	2	+
Knipolegus	6	2	1	2	
Entotriccus	6	2	2	2	
Lichenops	6	3	2	2	+
Fluvicola	6	3	2	2	
Arundinicola	6	3	1	2	
Pyrocephalus	6	2	2(3?)	2	+
Ochthornis	6	2	1	2	
Muscigralla	5	2	1	2	
Satrapa	6	3	2	2	
Machetornis	6	2	2	2	
TYRANNINAE					
Muscivora	1	1	1	1	+
Tyrannus	1	1	1	1	+
Empidonomus	1	1	1	1	+
Legatus	2	1	1	1	
Sirystes	2	1	1	1	+
Myiodynastes	1	1	1	1	
Megarynchus	1	1	1	1	+
Coryphotriccus	1	1	1	1	+
Myiozetetes	1	1	1	1	+
Tyrannopsis	1	1	1	1	+
Pitangus	1	1	1	1	+
Tolmarchus	1	1	1	1	+
MYIARCHINAE					
Myiarchus	2	1	1	1	+
Rhytipterna	2	1	1	1	+
Eribates	2	1	1	1	+
Nesotriccus	2	4?	1	3	
Nuttallornis	6	1	2	1	
Contopus	6	1	3	2	+
Blacicus	6	1	3	2	
Empidonax	6	2	3	3	+

TABLE 2. (CONTINUED)

Genus	I	II	III	IV	V
Aechmolophus	6	2	3(2)	2	
Cnemotriccus	6	2	2	2	
Mitrephanes	6	2	3	2	
Terenotriccus	6?	2	3	3	
Myiobius	6	1	3	2	
Pyrrhomyias	6	4?(1)	3	2	
Myiophobus	6	4?(1)	2	2	
Onychorhynchus	3	1	3	1	+
PLATYRINCHINAE					
Platyrinchus	3	4	3	3	
Cnipodectes	1(3)	4	1(2)	2	+
Tolmomyias	1(3)	4	1	2	
Rhynchocyclus	1(3)	4	2(3)	2	
EUSCARTHMINAE					
Todirostrum	2	4	2	3	
Oncostoma	1	4	1	3	
Euscarthmornis	1?	4	1(2)	3	
Snethlagaea	1	4	2	3	
Lophotriccus	2	4	2	3	+
Colopteryx	?	4	2	3	+
Myiornis	1	4	2	3	+
Pogonotriccus	3?	4	2	3	
Leptotriccus	?	4	2	3	
Phylloscartes	1	4	2	3	
Capsiempis	2?	4	2	?	+
Pseudocolopteryx	2?	4	1(2)	3	
Habrura	6	3	2(1)	3	
SERPOPHAGINAE					
Tachuris	?	4	2	3	
Spizitornis	5	4	2	3	
Stigmatura	2	4	2	3	
Serpophaga	5	4	2	3	
Inezia	5	4(3)	2(1)	2	+
Mecocerculus	5	4	1(2)	3	
ELAENIINAE					
Myiopagis	1?	3	1	3(2)	
Elaenia	5	1	1	2	+
Sniriri	5	2	2	2	
Sublegatus	5	1	2	3	
Phaeomyias	2	2	2	3	
Camptostoma	2	4	2	3	
Xanthomyias	1	4	?	3(2)	
Tyranniscus	6	3	2	3	+
Tyrannulus	2	3	?	3	
Microtriccus	2–3	4	1	3	
Leptopogon	3	4	1	2	+
Mionectes	5?	4	1	2	+
Pipromorpha	5?	4	?	2	+

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Bulletin of the
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The Orb-Weaver Genera *Metepeira*, *Kaira* and *Aculepeira* in America North of Mexico (Araneae: Araneidae)

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VOLUME 145, NUMBER 5
[illegible] NUMBER [illegible] 1977

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
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HARVARD UNIVERSITY

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BULLETIN 1863–
MEMOIRS 1864–1938
JOHNSONIA, Department of Mollusks, 1941–
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THE ORB-WEAVER GENERA *METEPEIRA*, *KAIRA* AND *ACULEPEIRA* IN AMERICA NORTH OF MEXICO (ARANEAE: ARANEIDAE)

HERBERT W. LEVI[1]

ABSTRACT. *Metepeira* and *Kaira* are known only in the Americas. Eleven species of *Metepeira* live north of Mexico, frequently in semiarid regions. A number of species are sympatric in the southwestern United States and are often collected together. Only four species of *Kaira* have been found north of Mexico; in one of these only females are known, in another, only males. The habits of *Kaira* species remain a mystery. *Aculepeira* is mainly an Eurasian genus, but two species live in North America; both North American species also occur in Siberia. One, *A. packardi*, is found in the Arctic, in western mountains, in meadows and in sagebrush. The other, *A. carbonarioides*, has been discovered only between boulders in talus slides of the Arctic, the Rocky Mountains, the Gaspé Peninsula and the White Mountains of New Hampshire. Identification of Eurasian species was difficult because few specimens were available.

INTRODUCTION

The genera sequence of these revisions is unfortunately not phylogenetic; instead their arrangement develops from the order in which specimens could be sorted out most easily from the available collections. I started with *Argiope* and the large species of *Araneus*. This paper includes species that have at times been confused with those in *Araneus* and other genera. When I started this revision of the three genera, I thought *Aculepeira* was close to *Metepeira*. Species of both genera have a median white streak on the venter of the abdomen, the median apophysis of the male palpus has two flagella and species of both inhabit extreme climates. The *Metepeira* species are most abundant in semidesert, an unusual habitat for orb-weavers. The two *Aculepeira* species are found in mountain meadows and talus slopes where it is very hot during the day, but becomes freezing at night, even in midsummer. But here the similarity ends. After careful study I found *Metepeira* and *Kaira* are not closely related to *Araneus* and are limited to the Americas, but *Aculepeira* is an Old World genus close to *Araneus*. Two Siberian species of *Aculepeira* are believed to have spread over the North American continent into various "vacant" niches. At least four other species are known from Eurasia (Figs. 187–231), but no others are known from America.

For this study the collections of the Museum of Comparative Zoology (MCZ) were used. I would like to thank the following for specimens: J. A. Beatty; D. E. Bixler; J. E. Carico; R. Crabill (National Museum of Natural History); C. D. Dondale (Canadian National Collections, CNC); S. I. Frommer (University of California, Riverside Collections); M. Grasshoff (Senckenberg Museum, Frankfurt, SMF); J. Gruber (Naturhistorisches Museum, Wien); N. Horner; M. Hubert (Muséum National d'Histoire Naturelle, Paris); W. R. Icenogle; B. J. Kaston; J. B. Kethley (Field Museum); T. Kronestedt (Natural History Museum, Stockholm, NRS); R. Leech; W. B. Peck (Exline-Peck Collection); W. J. Gertsch and N. I. Platnick (American Museum of Natural History, AMNH and Cornell Uni-

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versity Collections, CUC); G. Levy (Hebrew University Collections, Jerusalem, HUCJ); S. Riechert; V. D. Roth; R. X. Schick and P. H. Arnaud (California Academy of Science); W. A. Shear; W. T. Sedgwick; K. Thaler (KT); M. E. Thompson; E. S. Sutter (Naturhistorisches Museum, Basel; NMB); B. Vogel; H. K. Wallace; F. R. Wanless (British Museum, Natural History, BMNH); W. Staręga (Polish Academy of Sciences); and H. V. Weems (Florida State Collection of Arthropods). In addition, V. D. Roth and W. R. Icenogle supplied living specimens from Arizona and California, and W. R. Icenogle provided careful habitat notes on sympatric California *Metepeira* species. P. Brignoli (PBC), besides loaning specimens, made a gift of a specimen and provided helpful information. M. Troeger mapped the species and reworded awkward sentences, D. Randolph typed the various stages of the manuscript. The observations on the American *Aculepeira* species were made while at the Rocky Mountain Biological Laboratory, Crested Butte, Colorado; supported in part by National Science Foundation Grant No. G-2335 in 1956 and 1958. The research and publication was supported in part by National Science Foundation grant number DEB 76-115568.

METHODS

The method used to obtain the results presented here is the usual one: comparing specimens or those morphological features of specimens that have proven most useful in the past in taxonomy of spiders (Levi, 1977). The useful morphological characters, in all spiders, are the genitalia (the female epigynum, the male palpus); in araneids, the color patterns of the carapace and abdomen and the proportions and setation of the legs. Differences of several characters between groups of specimens are important because they indicate populations that do not interbreed. Often numerous outline drawings were made to find such differential characters.

Species differences proved subtle in *Metepeira*; these species are difficult to separate. Not only are several species sympatric, but no differences in their habits are even known at present. Unlike *Metepeira* species, the two American species of *Aculepeira* are quite variable, with no two specimens exactly alike and some specimens more than twice the size of others. Despite this variability, no populations could be segregated as having several distinct features. There is the possibility, though, that the eastern population of *A. carbonarioides* is distinct. A larger series of specimens is needed to ascertain the differences. But even if they are not distinct morphologically, can we be certain that the four isolated populations of *A. carbonarioides* are potentially interbreeding? In an attempt to answer this, I tried to raise Colorado specimens, but could not keep them alive in the laboratory.

Some of the problems of taxonomy are illustrated by the Eurasian species. Can I be sure that the three Siberian species described in the past (but with no specimens now available except for a female from Kamchatka) are the same species as those I did examine that were found in the American Arctic? While the study of specimens of the three Mediterranean species (Figs. 187–217) indicated they were far apart morphologically and easy to separate, the few specimens close to *A. armida* available from Asia were puzzling. Some that were labeled *A. karabagi* (Karol) seemed very distinct. But further specimens from Israel (one from Galilee and others from the Negev Desert) were intermediate with *A. armida*, having the characteristic lamellae posterior of the epigynum bent at right angles (Fig. 211) but much wider than the illustrated specimens from Europe. Despite this I believe *A. karabagi* to be a distinct species with the oldest name *A. noseki*. Drensky (1943) synonymized *A. victoria* Thorell with *A. armida*. Can I be sure by examining two specimens labeled *Araneus victoria* in the available collections that

Drensky was correct? I suspect Drensky was wrong, but it is impossible to obtain large series of these populations. Perhaps *A. armida* is a highly variable species and all doubtful specimens belong to it. I decided then to leave the Old World problems to a colleague closer to the critical areas (the Balkans and Asia Minor) who can resolve the question by further collecting and field observations.

Metepeira F.P.-Cambridge

Metepeira F.P.-Cambridge, 1903, Biologia Centrali-Americana, Araneidea, 2: 457. Type species by original designation *M. spinipes* F.P.-Cambridge, 1903. The name is feminine.

Note. In 1942 Chamberlin and Ivie named 14 species of *Metepeira* and mentioned 16 others in a paper on diverse new species from the Americas. It is difficult to see this as a revisionary study since the majority of the University of Utah collections then available had not been determined (except for some immatures!). Apparently, individual specimens that looked different were picked out of the collection and named. No distinguishing features were given by Chamberlin and Ivie for the new species and only a few of the illustrations feature diagnostic characters. The usual wording in the description regarding diagnosis is "showing minor differences in the palpus," or "the palpus and epigynum are distinct as shown by the figures." Nevertheless, most of the names of Chamberlin and Ivie actually do apply to different species and only a few names are synonymized.

Diagnosis. Metepeira differs from other araneid genera in having the eye region lighter than the remainder of the carapace (when in alcohol). The posterior head region is often darkest (Figs. 3, 37, 39). Unlike most other araneid genera, *Metepeira* has a median, longitudinal white line contrasting with the black background on the venter of the abdomen (Plates 1, 2, 3; Figs. 4, 38, 40). This line is absent, however, in the light-colored *M. gosoga*, in which only two black streaks remain (Fig. 36). There are usually white spots on black background on each side of the spinnerets (Plates 1, 2; Figs. 4, 38, 40). Unlike all other genera, the white line continues on the sternum (Plates 1, 2; Figs. 4, 38, 40). The few exceptions to this are *M. foxi*, *M. grandiosa* and *M. datona* (Figs. 86, 95, 98, 100). In still another difference between *Metepeira* and most other araneid genera related to *Araneus*, the combined length of metatarsus and tarsus is longer than that of the patella and tibia of the same leg (Fig. 3). (An unusual exception is *M. datona*; Plate 4.) An additional diagnostic trait is the very small, weakly sclerotized epigynum (Fig. 14) and the small palpus that has a median apophysis bearing two filiform appendages (flagella) (Figs. 10, 19, 20, 26, 27). The palpal tibia has two strong macrosetae (Figs. 8, 10, 19), as does the palpal patella (Fig. 8) in most species. The web, too, is diagnostic (see below), differing distinctly from that of species in related genera.

Metepeira, like *Aculepeira*, has a ventral median white mark on the abdomen, and the median apophysis of the male palpus has two flagella. *Metepeira* differs from *Aculepeira* by having a more spherical abdomen (Figs. 3, 4) and by the relatively smaller genitalia with a different structure. *Metepeira* is close to *Kaira* but the *Metepeira* abdomen is spherical (Figs. 3, 4); the *Kaira* abdomen is higher than long with tuberculate dorsal humps (Figs. 122–126) and the ventral abdominal mark is indistinct.

Description. The carapace has the anterior of the head lighter and, in all species, it is covered by white down (Plates 1, 2, 3). The thoracic depression is an indistinct longitudinal shallow groove. In all species the anterior median eyes are slightly larger or subequal in size with the others (Figs. 1, 5). Also in all species, the anterior median eyes are separated from each other by their diameter or slightly more, and from the laterals by one to one and one-half diameters (Figs. 1, 5). The posterior median eyes are

Plate 1. *Metepeira labyrinthea.* Upper left, female (Florida). Right, retreat, in barrier-web, and orb (Indiana); photo B. Opell. Bottom, orb with barrier-web and retreat, cornstarch dusted (Tavernier, Florida). Horizontal diameter of viscid area of web, 23 cm.

slightly less than their diameter apart in females, and two to three diameters from the laterals (Fig. 1). In males the posterior median eyes are their radius to slightly less than their diameter apart, and one and one-half to slightly more than two diameters from the laterals (Fig. 5). The height of the clypeus is less than the diameter of the anterior median eyes. The endites are longer than in many other araneid genera (Fig. 2). The legs are banded (Plates 1, 2; Fig. 3). The abdomen is usually oval, but spherical in *M. foxi* and *M. grandiosa* (Figs. 94–100) and is wider than long in *M. datona* (Plate 3; Fig. 85). The abdomen always has a dorsal folium pattern, which is more distinct posteriorly, and there may be black shoulder patches anterior-laterally (Plates 1, 2; Figs. 3, 68, 85). The black venter, with its characteristic white streak (Plate 1), contrasts with the light dorsum.

Living *Metepeira labyrinthea*, *M. grinnelli* and *M. crassipes*, as well as *M. foxi* and *M. datona* that I have seen and photographed, have on the abdomen, especially to the sides of the folium, some red pigment that washes out in alcohol. *Metepeira grinnelli* has reddish areas on the borders of the white line on each side of the folium, and anteriorly the folium has black pigment grading into brown. There is also a reddish brown area on the venter on each side of the black mark.

Males have no hook on the first coxa and no groove on the second femur. The male's first femur has strong macrosetae anteriorly, with the largest medially in the *M. foxi* group (Fig. 96), and distally in other groups (Figs. 12, 13). The fourth coxae are not modified. While males are smaller than females, in most species they do come in various sizes—some small, some larger, the larger ones presumably having gone through more instars and a longer period of growth.

The proportions of most species are about the same and the sizes overlap, but members of the *M. foxi* group are, in general,

Plate 2. *Metepeira grinnelli*, female (Arizona).

slightly smaller. Measurements of a female *M. labyrinthea* from Virginia are: total length 7.0 mm; carapace 2.8 mm long, 2.2 mm wide. First femur, 3.8 mm; patella and tibia, 3.9 mm; metatarsus, 3.6 mm; tarsus, 1.2 mm. Second patella and tibia, 3.1 mm; third, 1.9 mm; fourth, 2.9 mm. Measurements of a male from Virginia are: total length 4.2 mm; carapace 1.9 mm long, 1.6 mm wide. First femur, 3.3 mm; patella and tibia, 3.2 mm; metatarsus, 3.4 mm; tarsus, 1.1 mm. Second patella and tibia, 2.6 mm; third, 1.3 mm; fourth, 1.8 mm.

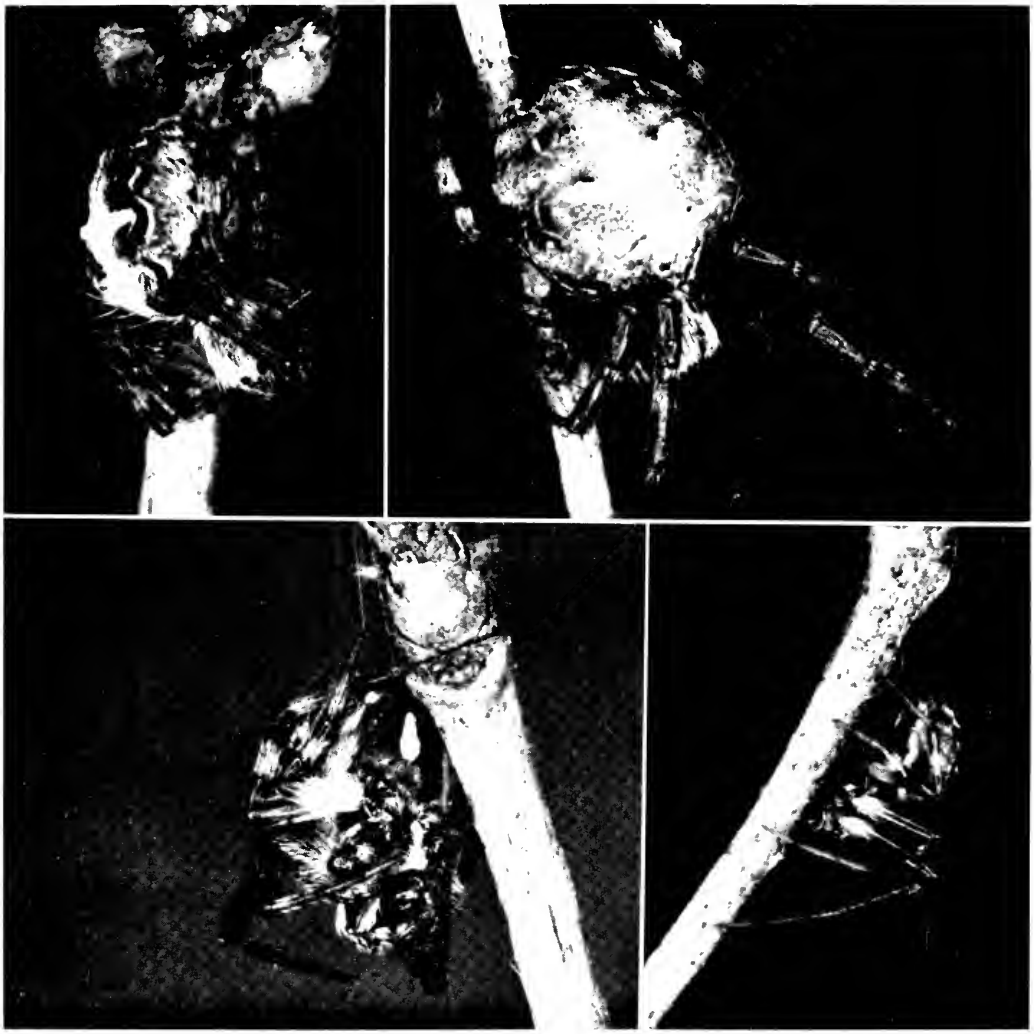


Plate 3. *Metepeira crassipes* (Riverside Co., California). Upper photographs, females, dorsal. Lower left, female venter; right, male. Laboratory photographs.

Genitalia. The epigynum is very small and lightly sclerotized, making it difficult to study (Fig. 14). The openings are in a species-characteristic depression (Fig. 18). Because of the small size of the soft structure, it is necessary, when the species is uncertain, to examine it as a temporarily cleared microscope mount. Below the opening is a sclerotized spherical structure from which ducts lead to the seminal receptacles (Figs. 18, 25, 32).

The femur of the male palpus lacks the pointed tooth usually present on the proximal end in all related genera and also lacks the tooth of the endite that is usually facing that of the femur. The median apophysis of the palpus bears two flagella (Figs. 10, 20) and often has a keel distally (ventrally on the palpus) (Figs. 10, 26, 27, 91, 93, 109, 111). Even though the median apophysis is the most prominent part of the palpus, its shape varies and, therefore, it

is only occasionally of diagnostic value. The shape of the triangular conductor (Figs. 10, 11) is similar in many species, but is wider than long in *M. foxi* (Fig. 92). Of greatest importance for diagnosis is the embolus, which is hidden partly behind the flagella of the median apophysis and partly by the overhanging terminal apophysis (Figs. 9, 10, 19, 26). The portion of the embolus containing the duct has a soft lobe hanging above it in some species (Figs. 9, 10, 20, 27, 34). Because of its diagnostic importance, it is unfortunate that this lobe is partly hidden. In virgin males the embolus is capped (Figs. 34, 52). The cap has been lost in presumably mated males (Figs. 33, 51). The cap, which has a minute barb at its tip, is found in the opening of the epigynum, plugging it (Figs. 25, 73), and apparently preventing a second mating of the female. There is never more than one cap found on each side in the epigynum. This cap contains an open duct in *Metepeira*. Some palpi (when handled through different solutions) emit tube-shaped material from their tips, probably propelled outward by osmotic pressures. Below the section of the embolus carrying the duct is a larger lobe in all species that projects on the outside of the conductor (right in the left palpus) in ventral view (Figs. 9–11) in the contracted palpus. Large and small males of the same species may have slightly different proportions in the softer parts of the palpus, but not in the embolus.

Natural History. *Metepeira* has an orb and a barrier-web—an irregular web to the side and slightly above. Lubin (1975) recently suggested that the barrier web may be a moisture gathering device. The orb may be incomplete on top (Plate 1). The hub has a mesh and several trap lines travel from the hub to the retreat in the center of the barrier-web (Plates 1, 5). The retreat is a small cap of silk covered by insect remains or leaves (Plates 1, 5). The web of *M. labyrinthea* is often in dead branches. Egg-sacs are brown, lenticular and hung in a string below the retreat with the most recent on the bottom (Comstock, 1940; Kaston, 1948). According to Kaston (1948), *M. labyrinthea* has about 35 radii and there are 5 to 6 egg-sacs with up to 63 eggs. The cocoon lasts until spring. *Metepeira* in Riverside County, California observed by Icenogle (personal correspondence) feed, to a great extent, on crane flies. Comstock claims that *M. labyrinthea* matures in fall, but in the collections there are mature males and females gathered from early summer to fall. Judging by *Metepeira*'s abundance in semidesert areas, the dense retreat and barrier-web must provide sufficient protection against desiccation. In many habitats it is the only orb-weaver found. One Mexican and Central American species, *M. spinipes* F.P.-Cambridge, is colonial, the others are not.

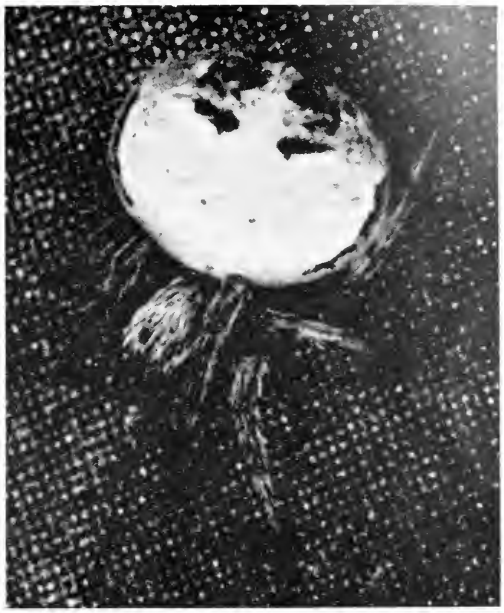


Plate 4. *Metepeira datona*, female (Florida).

The *Metepeira* species of the eastern states are known to have very different habitat preferences: *M. labyrinthea* usually places its webs in shrubs of deciduous forests; *M. grandiosa palustris* selects north-

Plate 5. Orb-web, barrier-webs and retreats of *Metepeira grandiosa alpina* from Colorado. Upper left, side view, sprayed with Krylon® white paint. Upper right, side view, dusted with cornstarch. Bottom, frontal view from slightly below, dusted with cornstarch. Diameter of viscid area of lower web about 25–30 cm.

ern bogs; and *M. datona* uses shaded shrubs on ocean shores. One might thus expect the numerous western species to each have different habitats. But four species (*M. crassipes*, *M. ventura*, *M. foxi* and *M. g. grandiosa*) have all been found side by side in California buckwheat (*Eriogonum fasciculatum*) and sage (*Artemisia californica*) in Riverside County, California. The first two species are commonly found in this environment, according to the best documented collections by W. Icenogle.

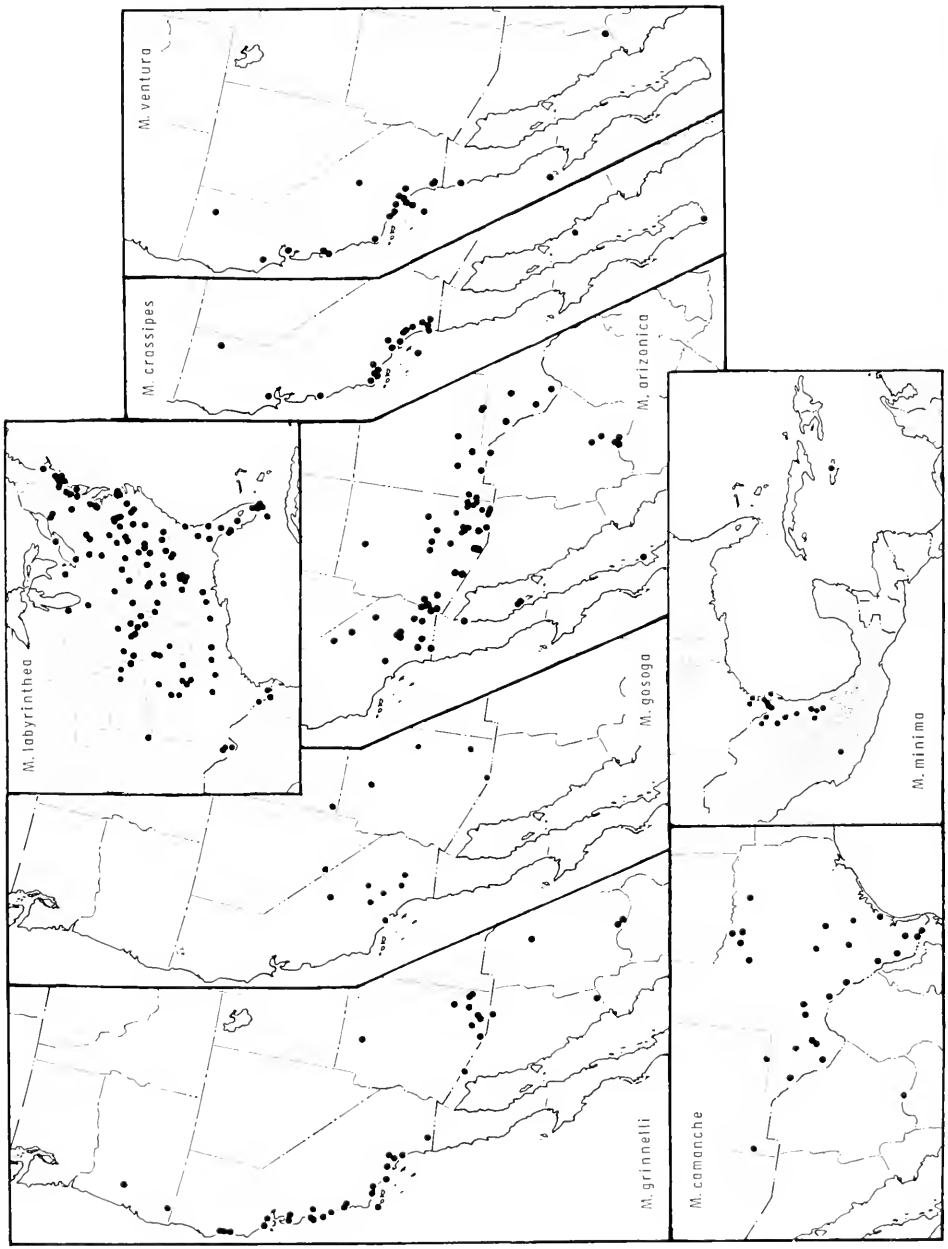
All species are commonly preyed upon by mud-dauber wasps of the genera *Trypoxylon* and *Trypargilum* (Sphecidae).

Species. No *Metepeira* species are known from other continents, all are American, and they range from Alaska to Tierra del Fuego. All, at one time or another, have been referred to as *M. labyrinthea* because of their similar size and coloration. (*Metepeira foxi* and *M. datona* are smaller than most species.) Roewer (1942) gives the distribution of *M. labyrinthea* from Patagonia to Labrador; Bonnet (1957) claims it extends from Canada to Patagonia, Chile, as well as appearing in east Africa. Actually it has a very limited distribution, occurring only in the eastern United States (Map 1).

Systematic characters. Numerous characters were checked and illustrated in the hope of finding discontinuities or of finding characters that would go together, thus indicating species. I studied absolute sizes, proportions, coloration and color pattern, and the ventral and anterior macrosetae of the male femora. Color pattern is useful to segregate the *M. gosoga* and the *M. foxi* group of species. More macrosetae are present in large specimens of each species than in small ones, so I did not find these setae very useful (Figs. 12, 13); however, males of the *M. foxi* group (*M. datona*, *M. foxi*, *M. grandiosa*) have the longest macrosetae in the middle of the femur (Fig. 96), while the *M. labyrinthea* has them distally (Fig. 6). Various aspects of the epigynum, different ones in different species, are useful. The shape of the terminal apophysis of the palpus segregates the *M. labyrinthea* and *M. foxi* species groups (Figs. 19, 91). The conductor, because it is too similar and variable, is not of much use. The median apophysis, which is sometimes very distinct, is variable and therefore of doubtful use alone, but when used with the shape of the embolus it proves a satisfactory character. Matching males with females of the same species can be a problem. It is helpful to collect males with females because this facilitates identifications, in some species the male, in others the female, is easiest to determine.

Species groups. The species north of Mexico belong to two species groups: *M. labyrinthea* and *M. foxi*. The *M. labyrinthea* group has a longitudinal white line across the sternum (Fig. 4); the median apophysis of the male palpus has only a short distal keel beyond the flagella-bearing proximal part (Figs. 10, 19, 20, 26, 27). All species within this group are about the same size. Species in the *M. foxi* group have a black sternum (Fig. 95) and the median apophysis of the palpus has a distal (ventral on the palpus) tuberculate keel (Figs. 91, 93, 104, 105, 115, 116). The species in this group are smaller in size. Two of the three species of the *M. foxi* group are common and come in large numbers in collections. It is interesting that of the species of the *M. labyrinthea* group, whose sternal white line is often broken and partly missing (Fig. 38), *M. grinnelli* also has an extension (though relatively small) on the median apophysis beyond the flagella (Figs. 26, 27). It is difficult at present to decide which of these species groups is the derived and which the more primitive. I consider *M. datona* most primitive because of the shorter metatarsus and the less specialized coloration.

Metepeira grandiosa is puzzling and I consider all specimens to be *M. grandiosa* with three subspecies for the three distinct allopatric forms. I have a suspicion, however, that with more data, some will turn out to be distinct.



Map 1. Distribution of *Metepeira labyrinthea*, *M. grinnelli*, *M. gosoga*, *M. arizonica*, *M. crassipes*, *M. ventura*, *M. comanche* and *M. minima*.

Key to female *Metepeira* north of Mexico

1. Sternum black (Figs. 95, 98, 100), sometimes in Florida specimens with a lighter brown anterior and posterior patch (Fig. 86) 2
– Sternum with a white longitudinal band (Figs. 4, 36, 40), rarely broken and partly missing (Fig. 38) 6
2(1) Abdomen wider than long, anterior half of dorsum light (Plate 4; Fig. 85); openings of epigynum on each side in depression (Fig. 78); Florida coast ..... *datona*
– Abdomen spherical to slightly longer than wide, usually with a dorsal folium (Figs. 94–100); opening of epigynum hidden (Figs. 87, 101–112); most of area but not in southeastern United States 3
3(2) Coxae black like sternum (Fig. 98); Canada, south to Maine and South Dakota (Map 2) ..... *grandiosa palustris*
– Coxae light yellowish to orange 4
4(3) Epigynum with a bordered, longitudinal depression on each side of narrow scape (Fig. 87); western United States (Map 2) ..... *foxi*
– Epigynum with transverse depression (Figs. 101, 106, 112); North Dakota, Colorado, western United States 5
5(4) Epigynum scape wide at base (Fig. 106); in posterior view middle piece shorter ventrally than lateral ones (Fig. 107); western Canada to Oklahoma; Chihuahua west to eastern Oregon (Map 2) ..... *grandiosa alpina*
– Epigynum scape usually narrow, sometimes with a slight median ridge (Fig. 112); in posterior view middle piece about same length ventrally as lateral ones (Fig. 113); British Columbia to California (Map 2) ..... *grandiosa grandiosa*
6(1) Epigynal scape fleshy triangular, greatest width as wide or wider than visible base on either side (Figs. 41–43); depressions on each side of scape small, visible diameter less than diameter of their rim (Fig. 41); western Texas, Chihuahua, to California and Gulf of California (Map 1) ..... *arizonica*
– Scape otherwise an equal to or narrower than base visible to side of it (Figs. 14, 21, 47); depressions small or larger (Figs. 47, 53, 61) 7
7(6) Visible depression on each side of scape appearing as anterior-posterior slits with their lateral borders parallel (Fig. 70); southern Texas to central Mexico, West Indies (Map 1) ..... *minima*
– Depression otherwise (Figs. 14, 28, 47) 8
8(7) Posterior rim of depression narrow (Fig. 61) and a round opening visible on each side in posteroventral view (Fig. 62); Texas, New Mexico to Chihuahua (Map 1) ..... *comanche*
– Epigynum otherwise (Figs. 14, 53) 9
9(8) Eastern North America to western Oklahoma, western Texas (Map 1); epigynum as in Figs. 14–18 ..... *labyrinthea*
– Western United States, New Mexico to Pacific coast 10
10(9) Carapace light brown, with posterior head dark (Fig. 35) and whitish abdomen with two ventral black streaks (Fig. 36); epigynum as in Fig. 28; Utah, Nevada, Arizona to California (Map 1) ..... *gosoga*
– Carapace, except for eye area, dark brown (Figs. 39, 59) and venter of abdomen black with median white longitudinal line (Figs. 40, 60); epigynum otherwise 11
11(10) Width of scape less than one-fourth width of epigynal base (Fig. 53); posterior rim of depression narrow (Fig. 53); California, Sonora and Baja California (Map 1) ..... *ventura*
– Width of scape about one-third width of epigynal base (Figs. 21, 47); posterior rim of depression wider (Figs. 21, 47); Arizona, Oregon to California 12
12(11) Depressions round and small with width of posterior border wider than visible diameter of depression (Fig. 47); California to Baja California (Map 1) ..... *crassipes*
– Depression flaring and width of its posterior border narrower than visible diameter of depression (Fig. 21); Arizona to Oregon and California, Chihuahua and Sonora (Map 1) ..... *grinnelli*

Key to male *Metepeira* north of Mexico

1. Sternum black, without longitudinal light line (Figs. 86, 95, 98, 100); base of palpal embolus at the distal tip of bulb (Figs. 82, 91, 109); median apophysis with a prominent ventrally directed tubercular keel beyond base of two flagella (Figs. 84, 93, 111) 2
– Sternum with a median longitudinal light band (Figs. 4, 36, 38); terminal apophysis overhanging palpal embolus (Figs. 10, 11, 19, 26); median apophysis without such a keel or with only a small smooth extension (Figs. 21, 27, 34, 46) 6

2(1) Embolus thick as in Figs. 82, 84; terminal apophysis a narrow, curved, soft prong (Fig. 83); Florida coast ... *datona*

– Embolus thin (Figs. 91, 104, 105, 109, 111, 115, 116); terminal apophysis otherwise (Figs. 92, 104, 109, 110, 115); whole region except southeastern United States ... 3

3(2) Coxae black like sternum (Fig. 98); Canada, south to Maine and South Dakota (Map 2) ... *grandiosa palustris*

– Coxae light yellowish to orange; western North America ... 4

4(3) Embolus of palpus with thin terminal part pointed at 45° angle to wider basal portion (Figs. 91, 93); tubercular keel of median apophysis larger than proximal flagella bearing part (Figs. 91, 93); western United States (Map 2) ... *foxi*

– Embolus of palpus with terminal part curved at right angle to wider basal portion (Figs. 104, 105, 109, 111, 115, 116); tubercular keel of median apophysis equal to or smaller than proximal flagella bearing part (Figs. 105, 111, 116); North Dakota, Colorado and western United States ... 5

5(4) Terminal part of embolus narrower (Fig. 111); western Canada to Oklahoma, Chihuahua, west to eastern Oregon, eastern California (Map 2) ... *grandiosa alpina*

– Terminal part of embolus wider (Fig. 116); British Columbia to California (Map 2) ... *grandiosa grandiosa*

6(1) Embolus of palpus with a parallel lobe above terminal portion containing duct (Figs. 20, 27, 34); lobe partly hidden by terminal apophysis (Figs. 19, 26, 33) ... 7

– Embolus of palpus without such a lobe (Figs. 46, 52, 58, 67) ... 9

7(6) Embolus tip strongly curved, the lower edge of its base concave (Fig. 20) and median apophysis with an indistinct small keel beyond flagella (Figs. 19, 20); eastern United States to western Oklahoma and western Texas (Map 1) ... *labyrinthea*

– Embolus tip less curved (Figs. 27, 34) and median apophysis with larger keel (Fig. 27) or no keel; western United States ... 8

8(7) Embolus curved and lobe overhanging tip (Fig. 27); median apophysis with a keel beyond flagella (Figs. 26, 27); Arizona to Oregon and California, Chihuahua and Sonora (Map 1) ... *grimmelli*

– Embolus tip with upper edge straight and lobe less than half length of tip (Fig. 34); median apophysis without keel (Fig. 34); Utah, Nevada, Arizona to California (Map 1) ... *gosoga*

9(6) Proximal flagellum of median apophysis (left one of left palpus) more than four times length of distal one (Figs. 74, 75); southern Texas to central Mexico, West Indies (Map 1) ... *minima*

– Proximal flagellum of median apophysis less than three times length of distal one (Figs. 46, 58); Texas, California and southwestern United States ... 10

10(9) Base of embolus with a distinct lobe at base of tip (Figs. 66, 67); Texas, New Mexico to Chihuahua (Map 1) ... *comanche*

– Embolus otherwise or if with lobe; not from Texas or New Mexico ... 11

11(10) Embolus gracefully curved, fairly long (Figs. 45, 46); base of median apophysis wide and both flagella recurved (Figs. 45, 46); western Texas, Chihuahua to California and Gulf of California (Map 1) ... *arizonica*

– Embolus curved but shorter (Figs. 52, 58); base of median apophysis narrow, distal flagellum not recurved (Figs. 52, 58); Oregon to Baja California, Sonora ... 12

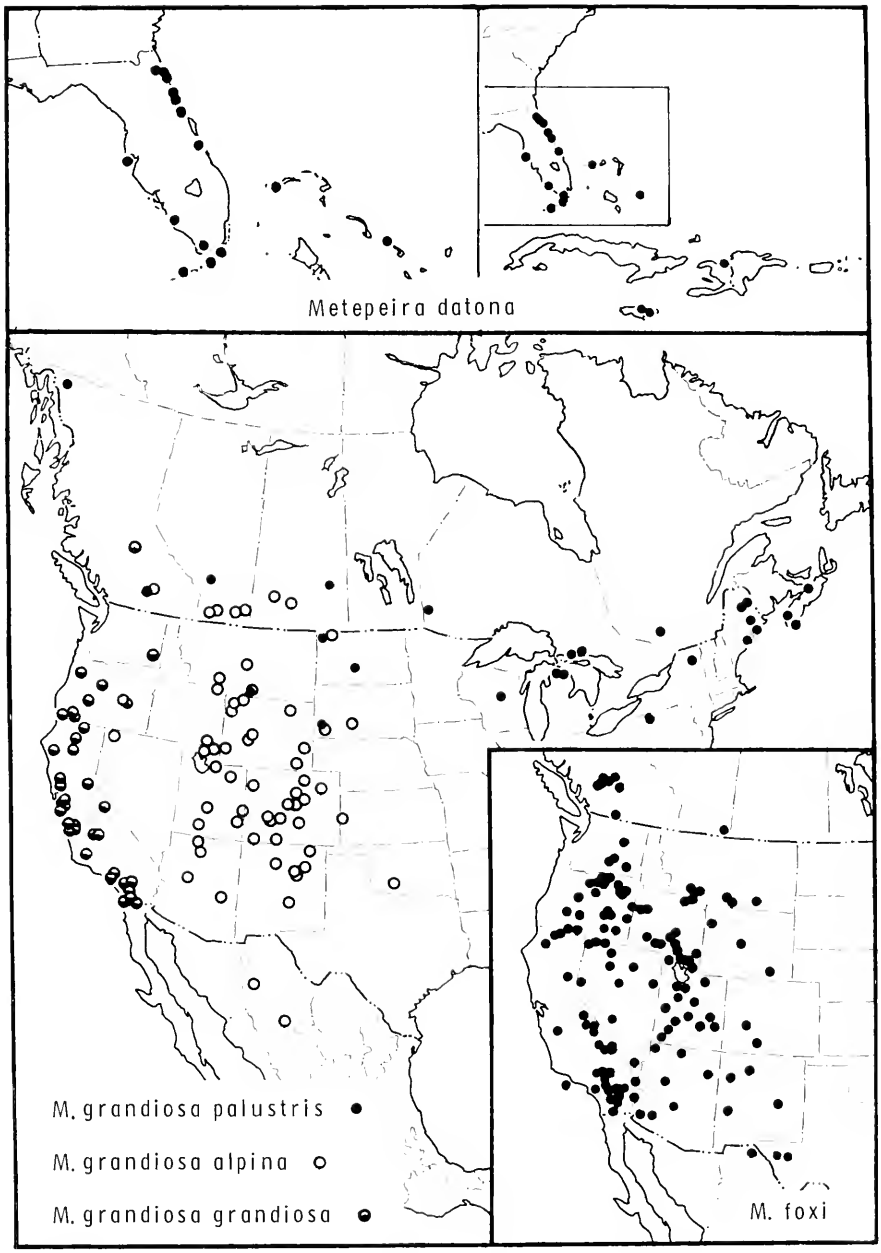
12(11) Proximal flagellum of median apophysis, noticeably longer and much wider than transparent distal one (Figs. 57, 58); median apophysis higher (Figs. 57, 58); California, Sonora and Baja California (Map 1) ... *ventura*

– Proximal flagellum of median apophysis almost subequal in length and width to distal one (Figs. 51, 52); median apophysis narrower (Figs. 51, 52); California to Baja California (Map 1) ... *crassipes*

Metepeira labyrinthea (Hentz)
Plate 1; Figures 1–11, 14–20; Map 1

Epeira labyrinthea Hentz, 1847, J. Boston Soc. Natur. Hist., 5: 471, pl. 31, fig. 3, ♀. Type specimens from North Carolina and Alabama, destroyed. Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 314, pl. 34, fig. 8, pl. 36, fig. 11, ♀, ♂. Keyserling, 1893, Spinnen Amerikas, 4: 215, pl. 10, fig. 160, ♀, ♂. Emerton, 1902, Common Spiders, p. 174, figs. 408–410, ♀, web.

Epeira crucifera Keyserling, 1864, Sitzungsber. Naturwiss. Gesell. Isis, Dresden, p. 132, pl. 6, figs. 11, 12, ♀. Female holotype from Baltimore in the British Museum, Natural History, examined. (The locality of Baltimore is not pub-



Map 2. Distribution of *Metepeira datona*, *M. grandiosa* and *M. foxi*.

lished but is on the label in the vial. Name preoccupied by Lucas, 1835.)

Metepeira labyrinthea:—F.P.-Cambridge, 1903, Biologia Centrali-Americana, Araneidae, 2: 458, pl. 43, figs. 6, 7, ♀, ♂. Comstock, 1940, The Spider Book, rev. ed., p. 476, figs. 187, 476–479, ♀, ♂, web. Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., 7(1): 63, figs. 161–164,

♀, ♂. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 226, figs. 704, 724, 2036, ♀, ♂, web.

Aranea keyserlingi Roewer, 1942, Katalog der Araneae, 2: 861. New name for *Epeira crucifera* thought preoccupied. NEW SYNONYMY.

Variation. Females are from 4.0 to 8.6 mm total length, carapace 1.7 to 3.5 mm long, 1.1 to 3.0 mm wide. Males are 3.0 to 6.8 mm total length, carapace from 1.6 to 3.0 mm long, 1.2 to 2.2 mm wide. The length of the first patella and tibia is 1.2 to 1.3 times carapace length in females, 1.6 times in males.

Diagnosis. Over most of its range, *M. labyrinthea* is the only *Metepeira*. In the north its range overlaps with *M. grandiosa palustris* and in Florida with *M. datona*; both, unlike *M. labyrinthea* (Fig. 4), lack the longitudinal light line on the sternum. Only in Texas does *M. labyrinthea* overlap the range of other species, and females can be separated by the scape of the epigynum, which has a narrow neck at its base. The scape is wider (Figs. 14, 15) than that of *M. minima* and *M. comanche* and narrower than that of *M. arizonica*, and the epigynal depression on each side of the scape (Fig. 18) is a different shape from those of the three other species. The embolus, unlike these three other species, is strongly curved with a lobe overhanging it (Figs. 19, 20).

Natural History. This is a forest species and is found on shrubs. It has been collected in floodplain forest in Tennessee, in thick forest on trees and bushes in Virginia, on the edge of oak woods and fields in Wisconsin, in oak, hickory and birch woods in Missouri, in a deciduous forest in Kansas, in woods in Texas and in the shade below trees growing among cacti in the Florida Keys. Adult males are found during July and August, females from spring to late fall, and, in southern Florida, females are found all year.

Distribution. Massachusetts, southern Ontario, southern Wisconsin, to western Oklahoma and western Texas, south to the Florida Keys and Tamaulipas (Map 1).

Metepeira grinnelli (Coolidge)
Plate 2; Figures 21–27, 37, 38; Map 1

Epeira labyrinthea grinnelli Coolidge, 1910, J. Entomol. Zool., Claremont, 2: 281. There are no type specimens in the Los Angeles County Museum, Pomona College or in the major arachnid collections.

Metepeira douglasi Chamberlin and Ivie, 1941, Bull. Univ. Utah, biol. ser., 6(3): 18, figs. 21–23, ♀. Female holotype from Santa Ana, California in the American Museum of Natural History, examined. Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., 7(1): 66, figs. 169–170, ♂. NEW SYNONYMY.

Note. Females of this species are often larger than those of *M. labyrinthea*, the coloration is more pronounced and the banding of the legs is more distinct as described by Coolidge. Also it is the most common species of the three localities cited by Coolidge: Palo Alto, Pasadena and Lompoc.

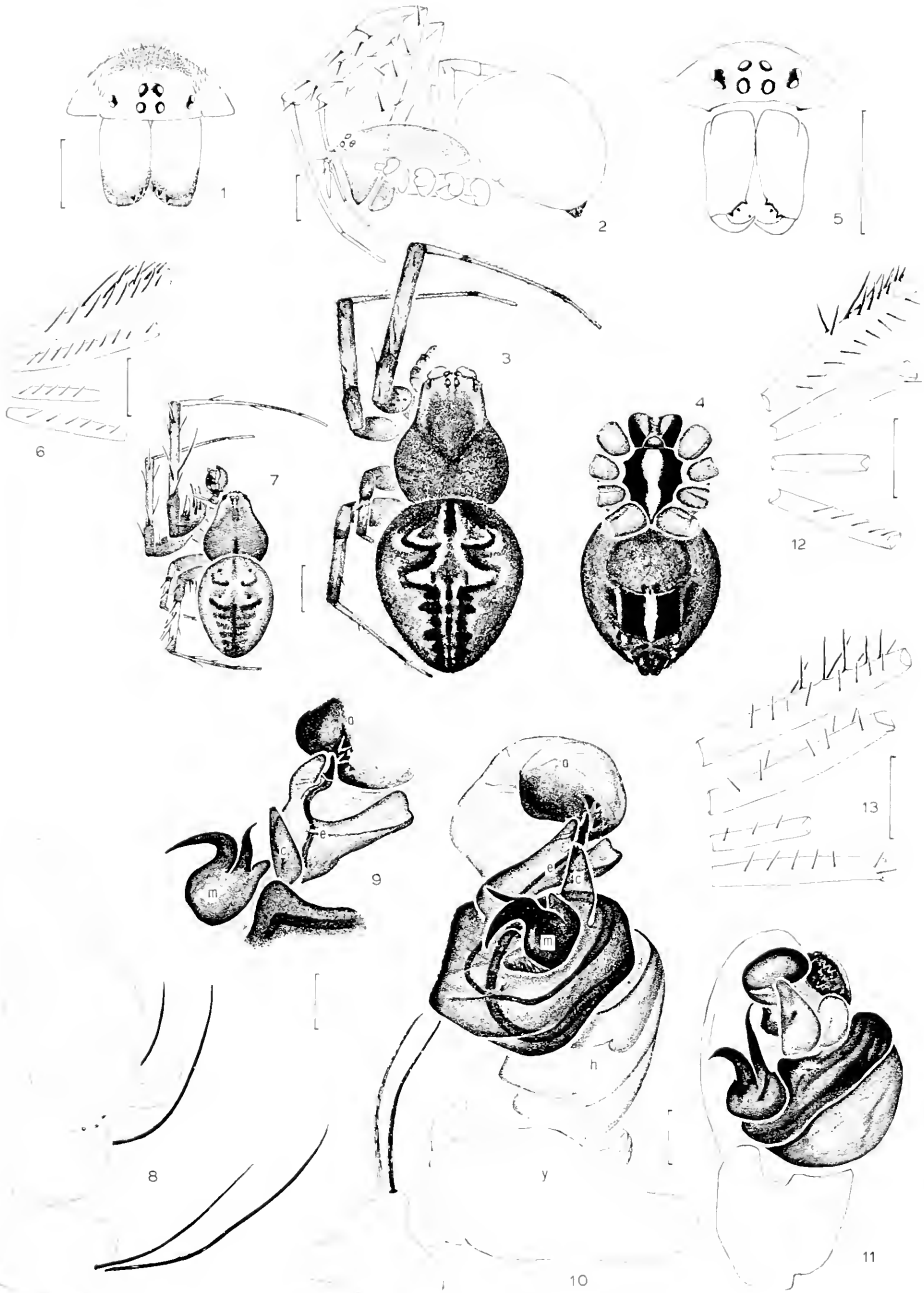
Variation. Most specimens have the ventral white line of the sternum broken by black pigment (Fig. 38); sometimes the anterior or posterior part of the line is missing. Total length of females 5.0 to 9.4 mm, carapace 2.3 to 4.1 mm long, 1.7 to 3.4 mm wide. Total length of males 3.6 to 6.7 mm, carapace 1.9 to 3.3 mm long, 1.4 to 2.6 mm wide. The first patella and tibia is 1.2 to 1.4 times the carapace length in the female, 1.5 to 1.7 in the male.

Diagnosis. This species tends to be larger in size and darker in coloration than sympatric species. It is very close to *M. labyrinthea*. Females differ by the longer scape,

→

Figures 1–11. *Metepeira labyrinthea* (Hentz). 1–4. Female: 1. Eye region and chelicerae. 2. Lateral. 3. Dorsal. 4. Ventral. 5–11. Male: 5. Eye region and chelicerae. 6. Left femora, ventral. 7. Dorsal. 8. Left cymbium, tibia and patella; bulb removed. 9. Left median apophysis, conductor and embolus, pulled apart. 10. Left palpus, expanded. 11. Left palpus, ventral view.

Figures 12, 13. *M. arizonica* Chamberlin and Ivie, left male femora, ventral view: 12. (Chiricahua Mountains, Arizona.) 13. (Canyon Lake, Maricopa County, Arizona.)



Abbreviations. a, terminal apophysis; c, conductor; e, embolus; h, hematodocha; m, median apophysis; y, cymbium.

Scale lines. Figs. 1–7, 12–13, 1.0 mm; Figs. 8–11, 0.1 mm.

which does not have the neck of that of *M. labyrinthea*. Also, in a posteroventral view of the epigynum, the openings appear in two circular dark areas (Fig. 22), those of *M. labyrinthea* in a dark streak (Fig. 15). *M. grinnelli* differs from *M. arizonica* in having the posterior head region darker usually than the thorax to the sides (Fig. 37). While most females can readily be separated from *M. arizonica* by the much narrower scape and rims (Fig. 21), and from *M. ventura* by the wider scape and wider rims, they can be distinguished as well by the pockets of the median depression (Fig. 25) that are visible ventrally using a cleared posterior view. The epigynum differs from that of *M. crassipes* by the longer scape and larger depression on each side (Fig. 21). The embolus of the male is not as strongly curved as that of *M. labyrinthea* (Figs. 26, 27) and its overhanging lobe is larger (Fig. 27). Most distinct is the ventral extension, or keel, of the median apophysis that extends beyond the two flagella (on the right of the left palpus, Figs. 26, 27) and is less distinct in *M. labyrinthea*. This keel is variable in shape.

Natural History. Adult males are found from July to September, females from July to October; in Sonora females are found in April. None of the specimens in collections come with ecological data.

Distribution. Arizona, Oregon, California to Chihuahua and Sonora (Map 1).

Metepeira gosoga Chamberlin and Ivie
Figures 28–36; Map 1

Metepeira gosoga Chamberlin and Ivie, 1935, Bull. Univ. Utah, biol. ser., 2(8): 21, figs 82–83, ♀. Female holotype from Pilot Knob Valley, Mohave Desert [34 km west of Johannesburg, San Bernardino County], California in the American Museum of Natural History, examined.

Variation. Total length of females 7.5 to 9.4 mm, carapace 3.2 to 4.1 mm long, 2.4 to 3.2 mm wide. Total length of males 4.4 to 5.8 mm, carapace 2.3 to 2.9 mm long, 1.7 to 2.4 mm wide. The first patella and tibia of females is 1.1 to 1.2 times the carapace length, that of the male 1.4 times.

Diagnosis. Metepeira gosoga can readily be recognized by the light colored carapace having only the posterior head region dark, by the white abdomen, which only posteriorly shows a folium (Fig. 35), and by the two adjacent ventral black marks surrounded by white pigment (Fig. 36). The middle piece of the epigynum in posterior view is sclerotized at its dorsal end (toward the abdomen) but not ventrally toward the short stubby scape. In cleared posterior view the ventrolateral pockets each have a median extension (Fig. 32) that is not present in the related species of *M. grinnelli*, *M. arizonica* and *M. labyrinthea*. The embolus of the male has a lobe above (Fig. 34), but unlike that of *M. grinnelli* and *M. labyrinthea*, the lobe is shorter than the sclerotized part bearing the duct (Fig. 34).

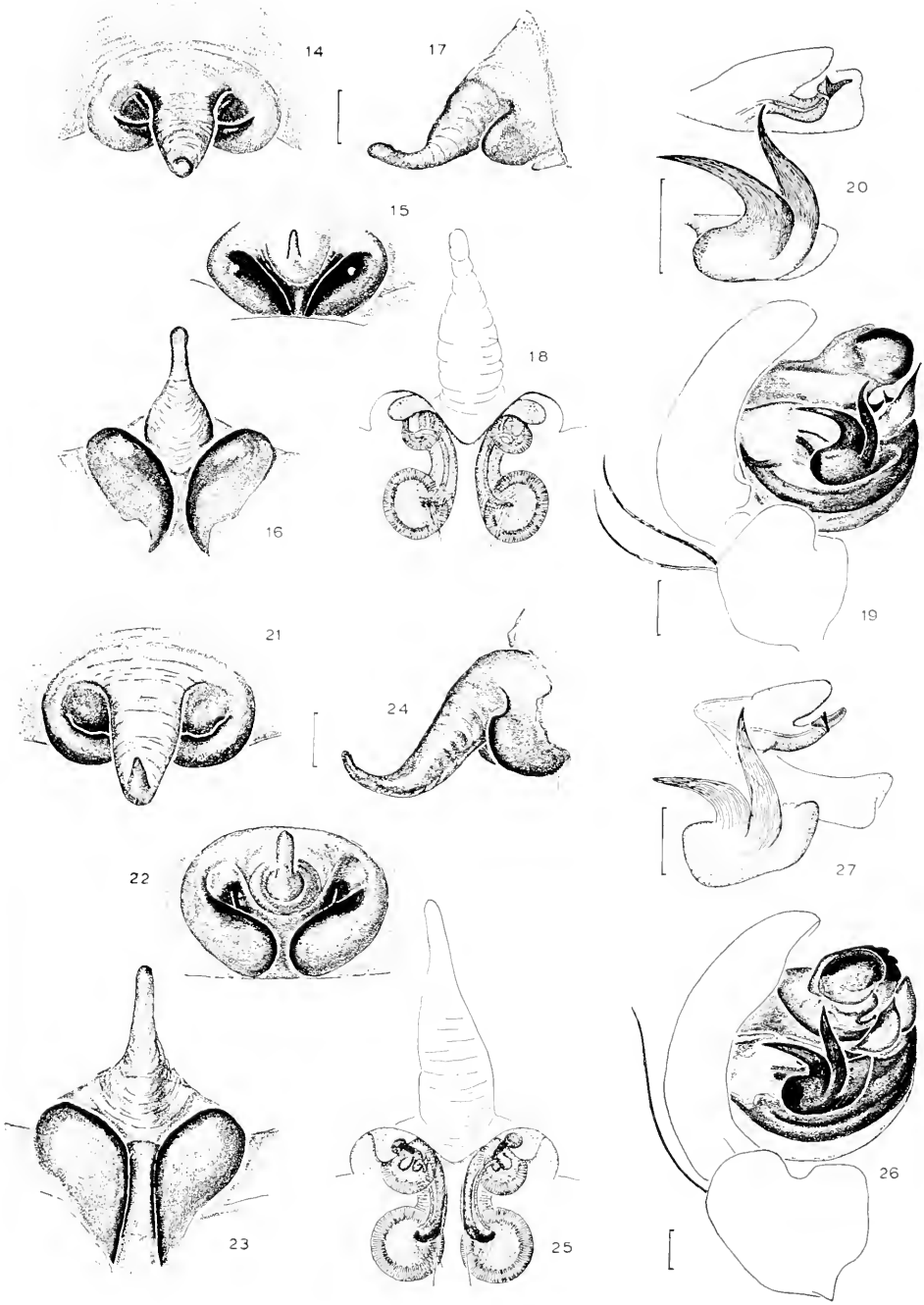
Natural History. Adult males and females have been collected from June to August. The only specimen with notes was collected on a cholla cactus (*Opuntia* sp.). It is likely that this species is often found on desert vegetation.

Distribution. Southern Utah to southern Arizona west to California (Map 1). One specimen from Mount Tamalpais State Park, near Bootjack, Marin County, California, 28 Nov. 1968 (M. Bentzien) was considered doubtful and is not mapped.

Metepeira arizonica Chamberlin and Ivie
Figures 12, 13, 39–46; Map 1

Metepeira arizonica Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., 7(1): 69, figs. 182–187, ♀, ♂. Female holotype, paratypes from Canyon Lake, W 111° 30′ : N 33° 30′, Arizona [Tonto National Forest, 25 mi. east of Phoenix, Maricopa Co.], in the American Museum of Natural History, examined.

Variation. Rare specimens are light in color on the carapace and dorsum. Total length of females 4.7 to 8.4 mm, carapace 2.0 to 3.5 mm long, 1.5 to 2.3 mm wide. Total length of males 2.7 to 3.8 mm, carapace 1.5 to 1.9 mm long, 1.2 to 1.6 mm wide. The first patella and tibia of the female is 1.1 to 1.2 times the carapace length, that of the male 1.3 to 1.4.



Figures 14–20. *Metepeira labyrinthea* (Hentz). 14–18. Epigynum: 14. Ventral. 15. Posteroventral. 16. Posterior. 17. Lateral. 18. Posterior, cleared. 19. Left male palpus, mesal. 20. Median apophysis and embolus.

Figures 21–27. *M. grinnelli* (Coolidge). 21–25. Epigynum. 21. Ventral. 22. Posteroventral. 23. Posterior. 24. Lateral. 25. Posterior, cleared. 26. Male palpus, mesal. 27. Median apophysis and embolus.

Scale lines. 0.1 mm.

Diagnosis. Unlike *M. grinnelli* and *M. gosoga*, but like *M. crassipes*, the carapace is very dark brownish black except for the contrasting light transverse anterior head region (Fig. 39). The epigynum of *M. arizonica* has a swollen-looking appearance, and unlike all related species, the diameter of the scape is wider than the width of the base on each side of the scape (Figs. 41–44). *Metepeira crassipes* is very similar, though slightly smaller. The epigynum has a similar small depression with seemingly swollen lips; the scape, however, is much narrower and has a proximal constriction. The gracefully curved embolus of the male (convex below and lacking a lobe above (Figs. 45, 46) is longer than that of *M. ventura*. The two flagella of the median apophysis (Figs. 45, 46) are about the same width, unlike those of *M. ventura*, and are directed more posteriorly than those of *M. crassipes*. In addition, the median apophysis (Fig. 46) lacks the ventral keel beyond the flagella that is present in *M. grinnelli*. The sternal light band is never broken (Fig. 40), while in *M. ventura* it often is broken.

Natural History. Adult males have been collected from March to November, females from March to December. Several specimens from Yuma County, Arizona came from alfalfa fields, one came from a cactus in Organ Pipe National Monument; others were from oak-pine-juniper woodland in Cave Creek Canyon, Chihuahua Mountains, Arizona.

Distribution. Western Texas, northern Arizona to California to Chihuahua and Baja California (Map 1).

Metepeira crassipes Chamberlin and Ivie
Plate 3; Figures 47–52; Map 1

Metepeira josepha Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., 7(1): 64, fig. 165, ♀. Female holotype from Kings Mtn. near Palo Alto, California in the American Museum of Natural History, examined. NEW SYNONYMY.

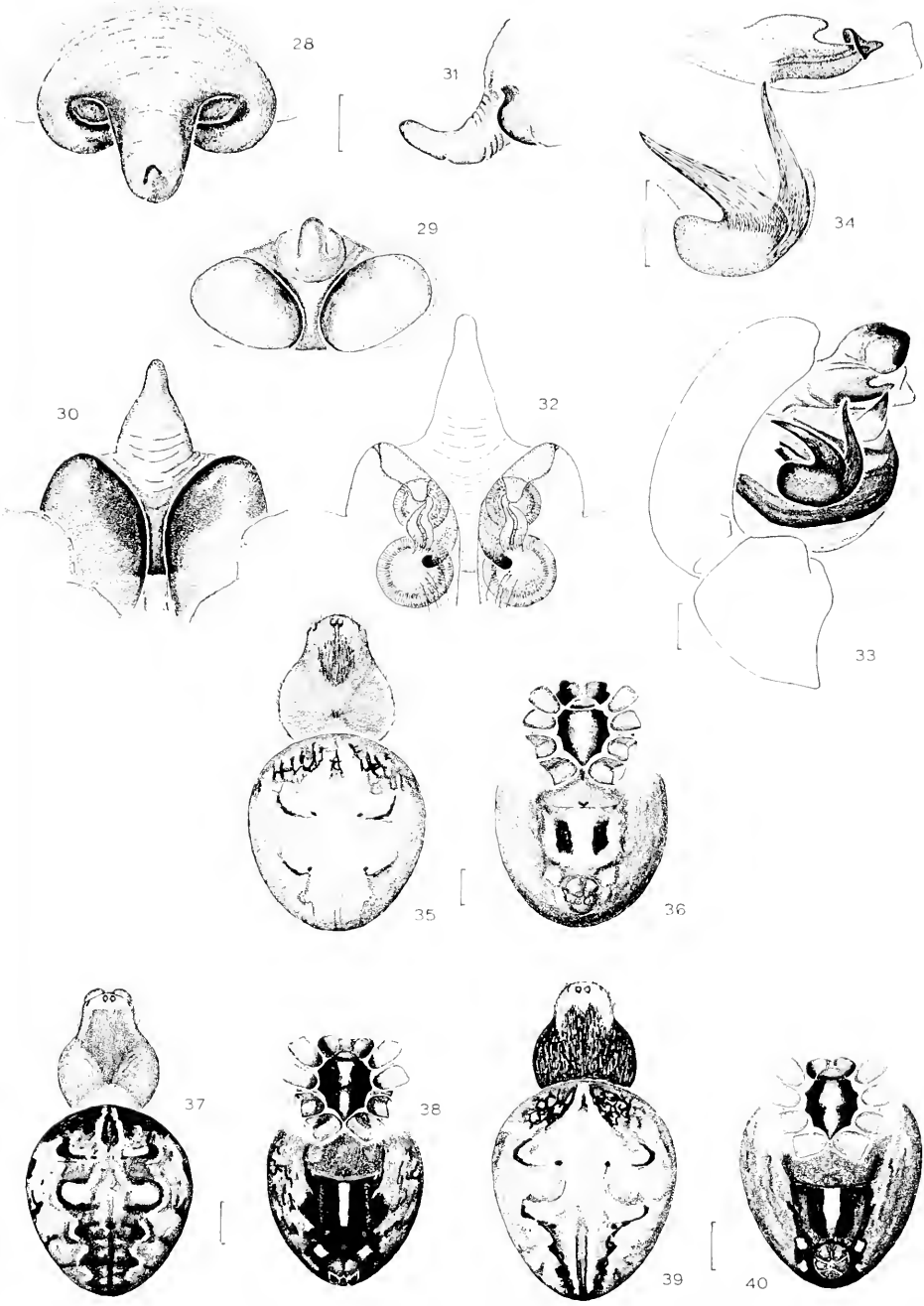
Metepeira crassipes Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., 7(1): 66, figs. 171–173, ♀, ♂. Male holotype, female, male paratypes from Laguna Beach, California in the American Museum of Natural History, examined.

Note. Although *M. josepha* has a page priority, as first revisor I prefer to use *M. crassipes* since the male is the type and several specimens are available from the type locality.

Variation. The white sternal band may be broken as in *M. grinnelli*. The height of the base of the median apophysis is variable. Total length of females 4.9 to 7.2 mm, carapace 2.2 to 3.2 mm long, 1.7 to 2.3 mm wide. Total length of males 2.9 to 4.7 mm, carapace 1.6 to 2.3 mm long, 1.2 to 1.7 mm wide. The first patella and tibia is 1.0 to 1.2 times the carapace length in females, 1.1 to 1.3 times in males.

Diagnosis. Although sizes overlap, this species is noticeably smaller than *M. grinnelli* when collected with it. Females can be separated from *M. grinnelli* by the shorter scape having a slight constriction (Figs. 47, 49) and from both *M. grinnelli* and *M. ventura* by the smaller depression on each side of the scape (Fig. 47). The females differ from *M. arizonica* in that the side of the base of the epigynum, which is visible on each side of the scape, is wider than the scape itself (Fig. 47). While females can be confused with *M. arizonica*, males are more likely to be mistaken for *M. ventura*. Differences, however, can be detected. Males of this species have both flagella of the median apophysis subequal in length (Figs. 51, 52), while those of *M. ventura* are quite unequal. The space surrounded by the proximal, posteriorly directed flagellum and by the base of the median apophysis is equal or larger than the area of the median apophysis (below it in Figs. 51, 52), while it is smaller in *M. ventura*. The embolus has a much shorter distal duct-bearing portion (Figs. 51, 52) than that of *M. arizonica*, and the terminal apophysis (Fig. 51) appears to be smaller than that of *M. ventura*.

Natural History. Males have been collected from April to October. A large number of specimens were collected from Cali-



Figures 28–36. *Metepeira gosoga* Chamberlin and Ivie. 28–32. Epigynum: 28. Ventral. 29. Posteroventral. 30. Posterior. 31. Lateral. 32. Posterior, cleared. 33. Left male palpus, mesal. 34. Median apophysis and embolus. 35. Female, dorsal. 36. Female, ventral.

Figures 37, 38. *M. grinnelli* (Coolidge). 37. Female, dorsal. 38. Female, ventral.

Figures 39, 40. *M. arizonica* Chamberlin and Ivie. 39. Female, dorsal. 40. Female, ventral.

Scale lines. 0.1 mm except Figs. 35–40, 1.0 mm.

fornia buckwheat (*Eriogonum fasciculatum*) and sage (*Artemisia californica*) in Riverside County, California.

Distribution. California and Baja California (Map 1).

Metepeira ventura Chamberlin and Ivie
Figures 53–60; Map 1

Metepeira ensenada Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., 7(1): 65, figs. 166–168, ♂. Male holotype from beach near Ensenada [Baja California], Mexico in the American Museum of Natural History, examined. NEW SYNONYMY.

Metepeira ventura Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., 7(1): 67, figs. 175–179, ♀. Female holotype, 1 male and 3 female paratypes from between Oxnard and Santa Monica, California, in the American Museum of Natural History, examined.

Note. Although *M. ensenada* has page priority, I prefer to use the name *M. ventura* for this species. since numerous specimens were available from the type locality of *M. ventura* that are more characteristic of this species.

Variation. A median light streak may be present on the carapace (Fig. 59) and the light sternal band is sometimes broken. Females are from 4.7 to 7.4 mm total length, carapace 2.4 to 2.9 mm long, 1.6 to 2.4 mm wide. Males are 2.6 to 6.0 mm total length, carapace from 1.5 to 3.0 mm long, 1.0 to 2.3 mm wide. The length of the first patella and tibia is 1.0 to 1.3 times carapace length in females, 1.4 to 1.6 in males. There is some variation in the width of the epigynal scape.

Diagnosis. The middle of the posterior head region often has a light streak not found in *M. grinnelli*, *M. crassipes* or *M. arizonica*, but this is not always present. The light sternal band may be broken, unlike that of *M. arizonica*. The epigynum of *M. ventura* usually has a much narrower scape (Figs. 53–56) than the sympatric *M. crassipes*, *M. grinnelli*, *M. arizonica* and *M. gosoga*, and the depression to the sides of the scape are wider with the posterior rim narrower (Fig. 53) than that of the other species. The median depression of the epigynum faces the scape but there are pockets on each side as seen in a cleared epigynum from the posterior view (Fig. 56). The embolus of the palpus lacks the lobe above the part containing the duct (Fig. 58), just like that of *M. arizonica* and unlike that of *M. grinnelli*. The embolus is less gracefully curved and shorter than that of *M. arizonica*. The two branches of the median apophysis are more slender than those of *M. arizonica*. In addition, the proximal one is large, the distal one small (Figs. 57, 58), unlike those of *M. crassipes*. The space surrounded by the proximal, posteriorly directed flagellum and median apophysis is less than the area of the median apophysis (below it in Fig. 57), while it is equal or larger in *M. crassipes*.

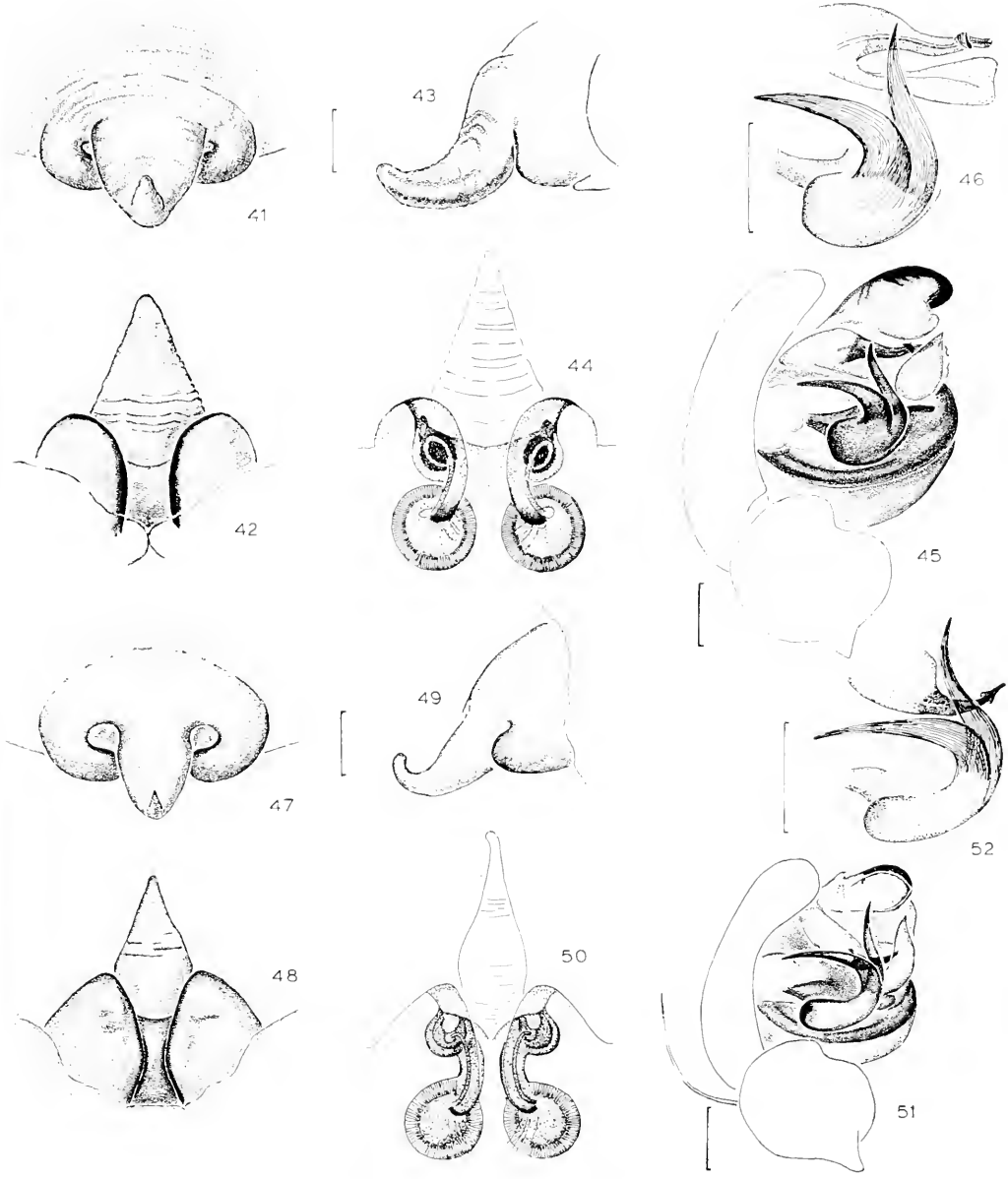
Natural History. Adult males have been collected from May to July, females from May to September. One collection of this species from Lompoc, California came from a mustard (Brassicaceae) field, another from manzanita (*Arctostaphylos*) chaparral, and a larger collection from California buckwheat (*Eriogonum fasciculatum*) and California sage (*Artemisia californica*).

Distribution. California, Sonora, Baja California (Map 1).

Metepeira comanche new species
Figures 61–69; Map 1

Type. Male holotype from 9.7 km west of O'Brien, Haskell Co., Texas, 3.II.1971, from the annual legume guar (*Cyamopsis tetragonolopa*), C. E. Rogers, in the Museum of Comparative Zoology. The name is a noun in apposition after the Indian tribe of the Texas plains.

Description. Female from Webb Co., Texas. Anterior light area of head grades gradually into dark area posteriorly (Fig. 68). A median light streak in many specimens just anterior to thoracic depression. Legs banded. Dorsum of abdomen with usual folium; posteriorly, venter often with white transverse bar connecting with longi-



Figures 41–46. *Metepeira arizonica* Chamberlin and Ivie. 41–44. Epigynum: 41. Ventral. 42. Posterior. 43. Lateral. 44. Posterior, cleared. 45. Left male palpus, mesal. 46. Median apophysis and embolus.

Figures 47–52. *M. crassipes* Chamberlin and Ivie. 47–50. Epigynum: 47. Ventral. 48. Posterior. 49. Lateral. 50. Posterior, cleared. 51. Male palpus, mesal. 52. Median apophysis and embolus.

Scale lines. 0.1 mm.

tudinal mark (Fig. 69). There is one spot on each side, anterior to the spinnerets. Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.7, posterior laterals 0.8 diameter of anterior median eyes. Anterior median eyes slightly less than their diameter apart, 1.3 from laterals. Posterior median eyes their diameter apart. Total length 6.5 mm. Carapace 2.6 mm long, 2.2 mm wide. First femur, 2.9 mm; patella and tibia, 3.2 mm; metatarsus, 2.9 mm; tarsus, 0.5 mm. Second patella and tibia, 2.7 mm; third, 1.6 mm; fourth, 2.2 mm.

Male from Wells Co., Texas. Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.6 diameter of anterior medians. Anterior median eyes 0.6 diameter apart, slightly less than their diameter from laterals. Posterior median eyes 0.5 diameter apart, two diameters from laterals. Anterior margin of chelicerae with four teeth, first one and then three, spaced close together; posterior margin with three teeth. Total length 4.7 mm. Carapace 2.3 mm long, 1.7 mm wide. First femur, 3.2 mm; patella and tibia, 3.4 mm; metatarsus, 3.2 mm; tarsus, 1.1 mm. Second patella and tibia, 2.8 mm; third, 1.6 mm; fourth, 2.2 mm. The male holotype from Haskell Co., Texas: total length 3.0 mm. Carapace 1.6 mm long, 1.2 mm wide. First femur, 2.5 mm; patella and tibia, 2.3 mm; metatarsus, 2.1 mm; tarsus, 0.8 mm. Second patella and tibia, 1.9 mm; third, 1.0 mm; fourth, 1.4 mm.

Variation. No two males are the same size and even males collected together seemed to vary tremendously in size. With this variation in size come differences in the macrosetae: the smaller males have fewer. There are also differences in the palpus of small and large specimens but not in the shape of the sclerotized median apophysis and embolus. The white sternal line may be broken. Females are from 4.5 to 7.2 mm total length, carapace 2.2 to 3.2 mm long, 1.8 to 2.4 mm wide. Males are 3.2 to 5.2 mm total length, carapace 1.8 to 2.4 mm long, 1.5 to 1.9 mm wide. The length of the first patella and tibia is 1.1 times the carapace length of females, 1.3 to 1.6 times that of males.

Diagnosis. Female *M. comanche* differ from the sympatric *M. labyrinthea* by having a much wider depression on each side of the scape with a narrower rim to the sides and posteriorly (Fig. 61). The area adjacent to the scape and part of its base is wide, extending posteriorly in the depression (Figs. 61, 62). The embolus of the male (Figs. 66, 67) lacks the overhanging lobe present in *M. labyrinthea* and differs from that of *M. arizonica* by being more evenly curved and by having a short upper lobe, which is not overhanging (Figs. 66, 67). The color of the venter of the abdomen is often light, showing a transverse light mark anterior to the spinnerets (Fig. 69).

Natural History. Adult males and females have been collected from May to November. None of the collections come with habitat data.

Distribution. Texas, New Mexico, Chihuahua (Map 1).

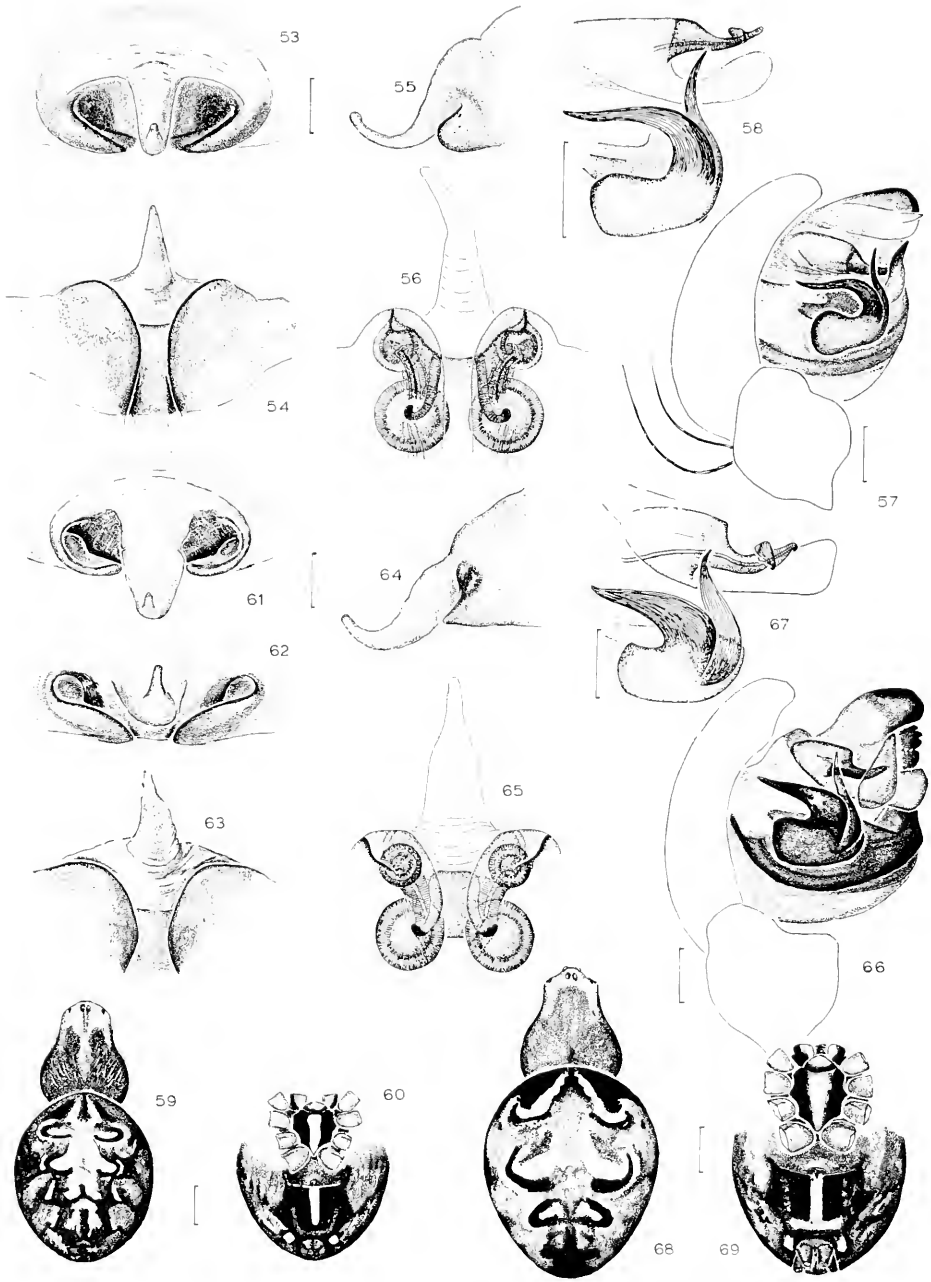
Metepeira minima Gertsch
Figures 70–77; Map 1

Metepeira minima Gertsch, 1936, Amer. Mus. Novitates, no. 852: 10, fig. 31, ♂. Male holotype from Edinburg, Texas in the American Museum of Natural History, examined. Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., 7(1): 67, fig. 174, ♀.

Metepeira jamaicensis Archer, 1958, Amer. Mus. Novitates, no. 1922: 16, fig. 33, ♀. Female holotype from Port Henderson, St. Catherine Parish, Jamaica, in the American Museum of Natural History, examined. NEW SYNONYMY.

Variation. Females are from 4.5 to 6.5 mm total length, carapace 1.9 to 2.6 mm long, 1.4 to 2.2 mm wide. Males are 2.6 to 4.2 mm total length, carapace from 1.3 to 2.7 mm long, 0.9 to 1.6 mm wide. The length of the first patella and tibia is 1.1 times carapace length in females, 1.4 times in males.

Diagnosis. The female *M. minima* epigy-



Figures 53–60. *Metepeira ventura* Chamberlin and Ivie. 53–56. Epigynum: 53. Ventral. 54. Posterior. 55. Lateral. 56. Posterior, cleared. 57. Left male palpus, mesal. 58. Median apophysis and embolus. 59. Female, dorsal. 60. Female, ventral.

Figures 61–69. *M. comanche* n. sp. 61–65. Epigynum: 61. Ventral. 62. Posteroventral. 63. Posterior. 64. Lateral. 65. Posterior, cleared. 66. Male palpus, mesal view. 67. Median apophysis and embolus. 68. Female, dorsal. 69. Female, ventral.

Scale lines. 0.1 mm except Figs. 59, 60, 68. 69, 1.0 mm.

num has a narrow scape with a parallel slit-like depression on each side (Fig. 70) that is quite different from that of other North American species. Males, too, can be readily separated from other species because the proximal flagellum of the median apophysis is several times as long as the distal one (Figs. 74, 75); in all other species north of Mexico the two flagella are of about equal length.

Natural History. Adults can be found in all seasons. No observations of this species are available from the United States or Mexico. In Jamaica I have observed adults in webs along a road in a shady situation and away from the shore.

Distribution. Southern Texas, to central Mexico and Jamaica (Map 1).

Metepeira datona Chamberlin and Ivie
Plate 4; Figures 78–86; Map 2

Metepeira datona Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., 7(1): 68, fig. 196, ♀. Female holotype from Daytona Beach, Florida in the American Museum of Natural History, examined.

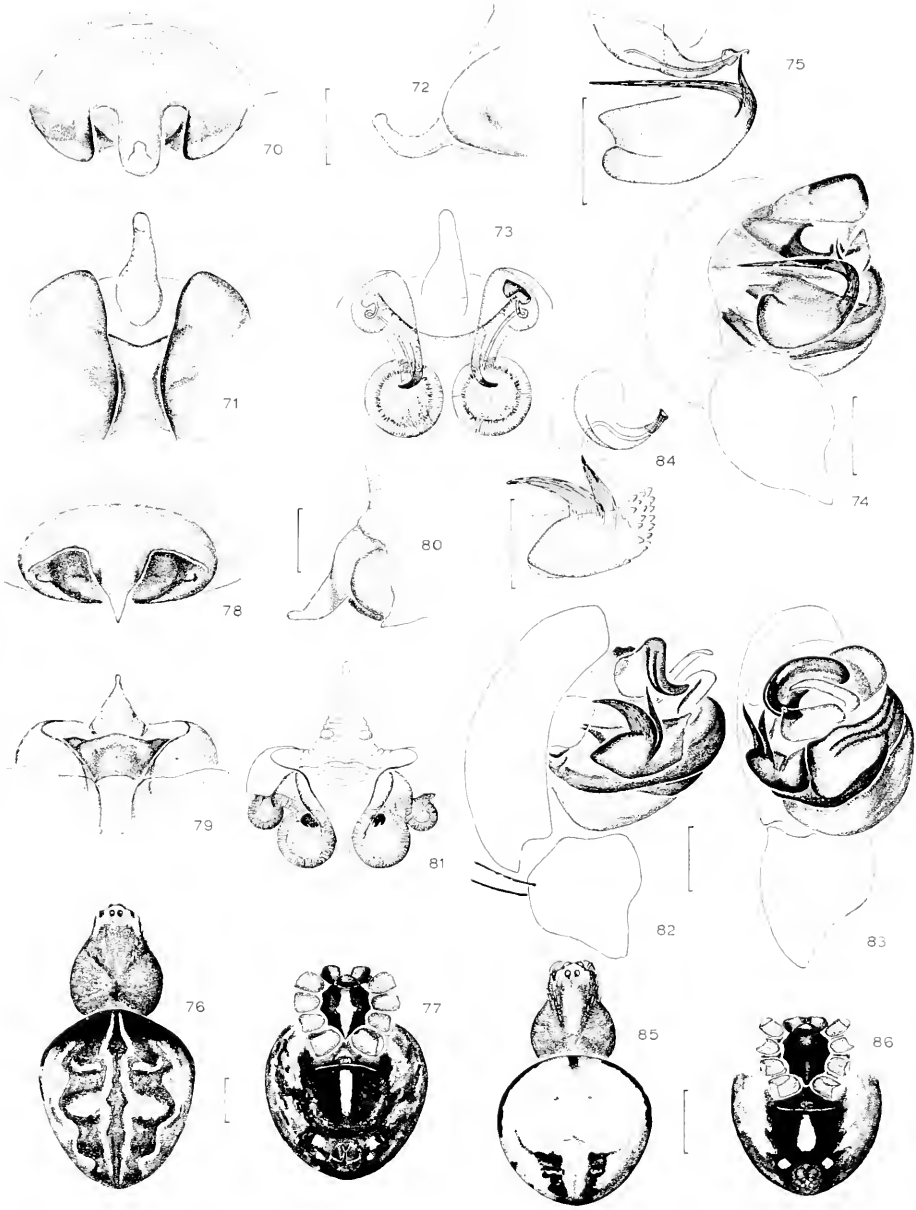
Metepeira inerma Bryant, 1945, Bull. Mus. Comp. Zool., 95: 378, fig. 20, ♀. Female holotype from Cap Haitien, Haiti in poor physical condition in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Description. Female from Flagler Co., Florida. Eye region of carapace orange; and orange longitudinal median line (Fig. 85). Lateral eyes in dark brown area. Sternum black-brown, sometimes with lighter brown area anteriorly and another posteriorly (Fig. 86). Legs are yellow-white with narrow, dark broken bands on dorsum. Dorsum of abdomen light anteriorly with a black posterior folium. Sides black distinctly delineated towards dorsum, but not towards venter. Venter with a median white spot on black. Posterior median eyes subequal to anterior medians. Anterior and posterior laterals 0.8 diameter of anterior median eyes. Anterior median eyes 1.2 diameters apart, 1 diameter from laterals. Posterior median eyes slightly less than their diameter apart, 2.5 from laterals. Abdomen is wider than long (Plate 4; Fig. 85). Total length 3.9 mm. Carapace 1.8 mm long, 1.5 mm wide. First femur, 2.2 mm; patella and tibia, 2.3 mm; metatarsus, 1.5 mm; tarsus, 0.6 mm. Second patella and tibia, 1.9 mm; third, 1.0 mm; fourth, 1.7 mm.

Male from the Bahama Islands. Coloration as in female. Abdomen, dorsum, however, more conservatively colored with a median dorsal line from anterior to posterior. Anterior light patches surrounded by black with a posterior dark patch extending more anteriorly (Plate 4; Fig. 85). Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes slightly more than their diameter apart, the same distance from laterals. Posterior median eyes 0.6 diameter apart, 1.5 from laterals. No tooth on base of palpal femur or on endite. Two femoral macrosetae and two on tibia. Abdomen longer than wide. Total length 3.2 mm. Carapace 1.8 mm long, 1.5 mm wide. First femur, 3.2 mm; patella and tibia, 3.5 mm; metatarsus, 2.4 mm; tarsus, 0.9 mm. Second patella and tibia, 2.7 mm; third, 1.3 mm; fourth, 1.8 mm.

Variation. A male from southern Florida had the eye region the same color as the thoracic area. Females are from 2.6 to 4.6 mm total length, carapace 1.2 to 1.8 mm long, 1.0 to 1.6 mm wide. Males are 2.0 to 3.2 mm total length, carapace 1.0 to 1.8 mm long, 0.9 to 1.5 mm wide. The length of the first patella and tibia is 1.1 to 1.3 times the carapace length in females, 1.9 times in males. The sternum is brownish black and sometimes has a lighter area in the anterior and posterior sections.

Diagnosis. Unlike other North American species, *M. datona* has an abdomen that is wider and more spherical than it is long; the anterior of the dorsum has a light patch framed by black (Figs. 85, 86). It differs, of course, from small *Araneus* species of a similar color, by the ventral median longitudinal white stripe on the abdomen (Fig.



Figures 70–77. *Metepeira minima* Gertsch. 70–73. Epigynum: 70. Ventral. 71. Posterior. 72. Lateral. 73. Posterior, cleared. 74. Left male palpus, mesal. 75. Median apophysis and embolus. 76. Female, dorsal. 77. Female, ventral.

Figures 78–86. *M. datona* Chamberlin and Ivie. 78–81. Epigynum: 78. Ventral. 79. Posterior. 80. Lateral. 81. Posterior, cleared. 82–84. Male palpus: 82. Mesal. 83. Ventral. 84. Median apophysis and embolus. 85. Female, dorsal. 86. Female, ventral.

Scale lines. 0.1 mm except Figs. 76, 77, 85, 86, 1.0 mm.

86). The epigynum is very different from that of other species because the openings appear as small slits on each side of the wide depression (Fig. 78). The palpus differs from that of *M. foxi* by having the embolus heavier and wider (Fig. 82) and by having the terminal apophysis a soft projecting arm (Figs. 82, 83).

Natural History. In Florida adult females have been collected only from November to March. *Metepeira datona* has been collected from vegetation on the beach, from shore shrubs and from beach grape (*Coccoloba uvifera*) in Florida and Jamaica. An adult male was collected in mangroves on Saddle Bunch Keys, in June.

Distribution. Florida coast and Greater Antilles (Map 2).

Metepeira foxi Gertsch and Ivie
Figures 87–96; Map 2

Metepeira foxi Gertsch and Ivie, 1936, Amer. Mus. Novitates, no. 858, p. 20, figs. 42–44, ♀, ♂. Male holotype and female paratype from Richfield, Utah, in the American Museum of Natural History, examined. Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., 7(1): 71, figs. 197, 198, ♀, ♂. Roewer, 1942, Katalog der Araneae, 1: 869. Bonnet, 1957, Bibliographia Araneorum, 2: 2820.

Metepeira nanella Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., 7(1): 71, fig. 199, ♀. Female holotype and paratype from Fillmore, Utah, in the American Museum of Natural History, examined. NEW SYNONYMY.

Variation. Females are from 3.6 to 6.1 mm total length, carapace 1.7 to 2.2 mm long, 1.2 to 1.6 mm wide. Males are from 2.7 to 4.5 mm total length, carapace 1.6 to 4.2 mm long, 1.3 to 1.7 mm wide. The length of the first patella and tibia is 1.2 to 1.4 times carapace length in females, 1.5 to 1.7 times in males.

Diagnosis. Metepeira foxi differs from all other species north of Mexico, except *M. grandiosa* and *M. datona*, in lacking a white longitudinal line on the sternum. It does not occur in Florida, as does *M. datona*, and females can be distinguished from *M. grandiosa* by the narrow scape of the epigynum, which has a bordered longitudinal depression visible on each side (Fig. 87). Male *M. foxi* differ from those of *M. grandiosa* by the 45° angle of the embolus (Figs. 91, 93); in *M. grandiosa* the bend of the embolus is about 90°. *Metepeira foxi* males, in addition, have a conductor that is higher (Fig. 92) than that of *M. grandiosa*.

Natural History. Males have been collected from March to July, most commonly in April and June. *Metepeira foxi* has been collected by sweeping at the edge of ponderosa pine (*Pinus ponderosa*) woods and in meadows in Colorado, from meadows in Wyoming, on sagebrush (*Artemisia* sp.) in California and Oregon, from alkali marsh vegetation in California and on saltbush (*Atriplex* sp.) and hilaria (*Hilaria* sp.) in Utah. Specimens are commonly collected together with *M. grandiosa*; their habitats must be similar.

Distribution. Alberta to New Mexico and west to British Columbia and California (Map 2).

Metepeira grandiosa Chamberlin and Ivie
Plate 5; Figures 97–116; Map 2

Epeira labyrinthea—"bog variety":—Emerton, 1915, Trans. Connecticut Acad. Sci., 20: 138, fig. 6, ♀, ♂.

Metepeira grandiosa Chamberlin and Ivie, 1941, Bull. Univ. Utah, biol. ser., 6(3): 17, figs. 24–26. Female holotype from Ben Lomond, California, in the American Museum of Natural History, examined.

Metepeira palomara Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., 7(1): 72, figs. 200–204, ♀, ♂. Female holotype and paratypes from Mt. Palomar, California, in the American Museum of Natural History, examined. NEW SYNONYMY.

Metepeira dakota Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., 7(1): 73, figs. 205–207, ♀, ♂. Male holotype and female paratype from Noonan, North Dakota, in the American Museum of Natural History, examined. NEW SYNONYMY.

Metepeira palustris Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., 7(1): 73, figs. 208–210, ♀, ♂. Female holotype from Divide County, North Dakota, in the American Museum of Natural History, examined. NEW SYNONYMY.

Metepeira alpina Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., 7(1): 74. Female holo-

Figures 87–96. *Metepeira foxi* Gertsch and Ivie. 87–90. Epigynum: 87. Ventral. 88. Posterior. 89. Lateral. 90. Posterior, cleared. 91–93. Left male palpus: 91. Mesal. 92. Ventral. 93. Median apophysis and embolus. 94. Female, dorsal. 95. Female, ventral. 96. Left male femora, ventral.

Figures 97, 98. *M. grandiosa palustris* Chamberlin and Ivie, juvenile (Nova Scotia). 97. Dorsal. 98. Ventral.

Figures 99, 100. *M. grandiosa alpina* Chamberlin and Ivie, female (northern Arizona). 99. Dorsal. 100. Ventral.

Scale lines. 0.1 mm except Figs. 94–100, 1.0 mm.

type and numerous female paratypes from Fish Lake, Utah, in American Museum of Natural History, examined. NEW SYNONYMY.

Subspecies. The variation of this species is so distinct that I use subspecific names; *palustris* for the eastern and northern, *alpina* for the Rocky Mountain and *grandiosa* for the Pacific subspecies. Evidence for

all belonging to one species is the following. No consistent differences could be found in the genitalia, although many drawings of the epigyna, the internal female genitalia, the embolus and the conductor of the palpus were made. Most distinct is *M. grandiosa palustris*, which has black coxae (Fig. 98). A collection from Medicine Hat, Alberta includes a female with black coxae, a male with yellow coxae; from Stockade Lake, Custer County, South Dakota one female has black coxae, another yellow; from Greeley County, Kansas a female has yellow coxae with some dark; from Medicine Hat, Alberta one female has black coxae with orange distal rings; all are border localities. Several collections from East Rosebud Canyon, Carbon County, Montana, 1963 to 1967 (Vogel collection) are also intermediate: large females, small males, variously marked coxae, some all black, some with two coxae black, two yellow on each side and some with coxae having yellow and black marks.

Diagnosis. Unlike most *Metepeira*, but like *M. foxi*, the median longitudinal band of the sternum is missing, the sternum is entirely black (Figs. 98, 100). But unlike *M. foxi*, the epigynum has a transverse depression on each side posteriorly (Figs. 101, 106, 112) in which the openings are located laterally (Figs. 103, 108, 114). The palpal embolus is evenly curved, the narrower part at about a right angle to the wider base (Figs. 104, 105, 109, 111, 115, 116), while that of *M. foxi* is at about a 45° angle.

Metepeira grandiosa palustris Chamberlin and Ivie
Figures 97, 98, 101–105; Map 2

Note. Emerton's bog variety of *M. labyrinthea* was this subspecies, although some specimens in the collections from Mount Lincoln, Colorado, considered here to be *grandiosa alpina*, were also labeled bog variety. The only name available is *palustris*.

Diagnosis and Variation. Metepeira grandiosa palustris is readily recognized by its black coxae (Fig. 98). It is slightly larger than *M. grandiosa alpina*. Total length of females varies 4.7 to 7.6 mm, carapace 1.9 to 2.9 mm long, 1.6 to 2.2 mm wide. Total length of males 3.1 to 3.8 mm, carapace 1.7 to 1.9 mm long, 1.4 to 1.5 mm wide. First patella and tibia of female is the same length as carapace to 1.2 times its length; that of males, 1.5 its length.

Natural History. Emerton collected specimens in bogs in Maine; they also have been collected in a marsh in the Adirondacks, in low spruce (*Picea* sp.) in Quebec and in a field in Wisconsin.

Distribution. Canada from Nova Scotia to British Columbia, south to Maine, New York, South Dakota (Map 2).

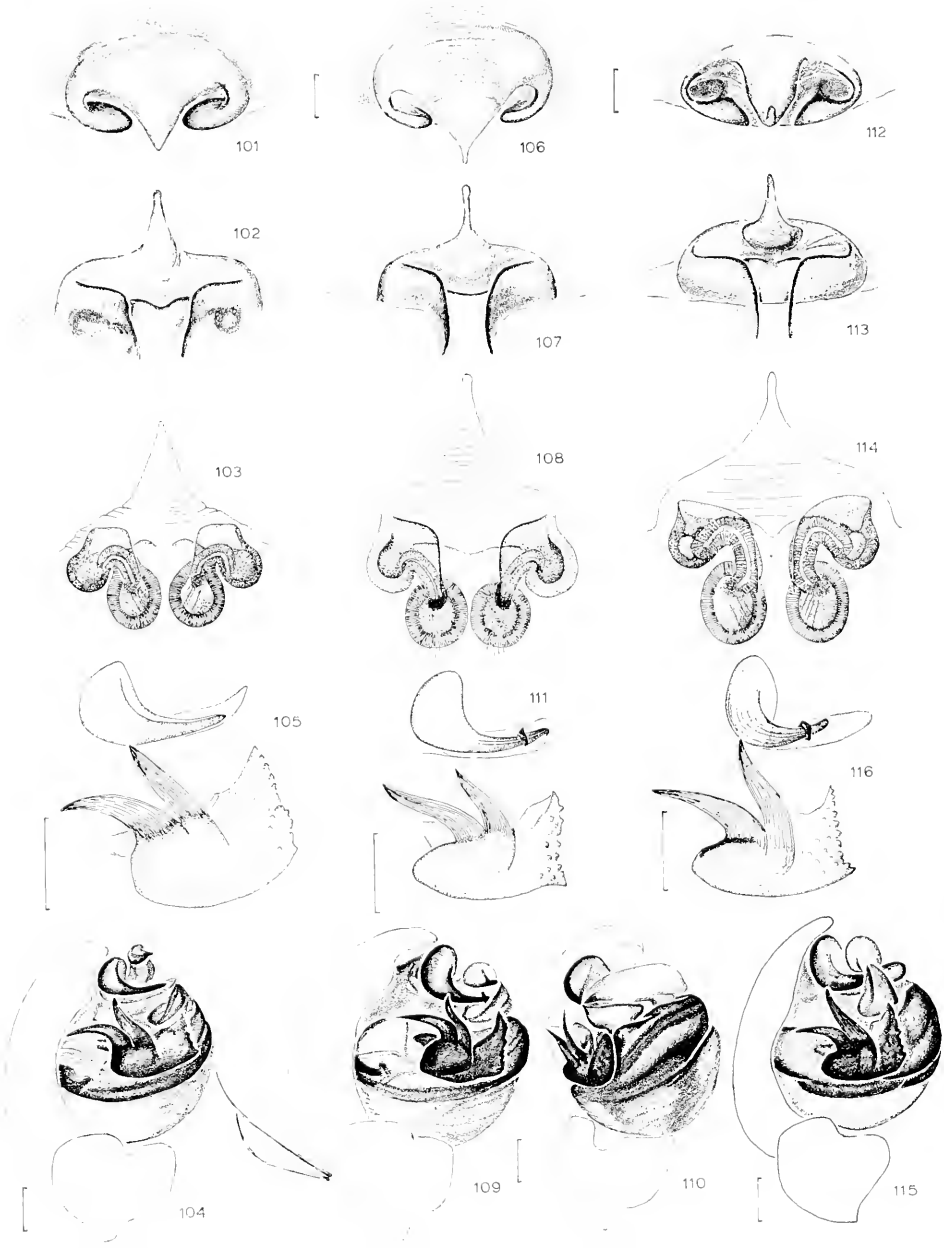
Metepeira grandiosa alpina Chamberlin and Ivie
Figures 99, 100, 106–111; Map 2

Note. The types of names *M. dakota* and *M. alpina* belong to this subspecies. Although the name *M. dakota* has page priority, as first revisor I chose *M. alpina* since the type locality is in the middle of the range of the subspecies and is a place where it is common, while Noonan, North Dakota, the type locality of *M. dakota*, is at the border of the range.

Diagnosis and Variation. This includes the smallest sizes and the most abundant populations. The scape of the epigynum is wide at the base (Fig. 106) and the palpal embolus is intermediate in length (Fig. 111). The coxae are never black, but intermediates are found among the eastern-most specimens (see *M. grandiosa palustris*). Total length of females is from 4.0 to 6.8

→

Figures 101–105. *Metepeira grandiosa palustris* Chamberlin and Ivie (Nova Scotia). 101–103. Epigynum: 101. Ventral. 102. Posterior. 103. Posterior, cleared. 104. Left male palpus, mesal. 105. Median apophysis and embolus.



Figures 106–111. *M. grandiosa alpina* Chamberlin and Ivie (northern Arizona). 106–108. Epigynum: 106. Ventral. 107. Posterior. 108. Posterior, cleared. 109. Male palpus, mesal. 110. Palpus, ventral. 111. Median apophysis and embolus.

Figures 112–116. *M. grandiosa grandiosa* Chamberlin and Ivie (Riverside Co., California). 112–114. Epigynum: 112. Ventral. 113. Posterior. 114. Posterior, cleared. 115. Male palpus, mesal. 116. Median apophysis and embolus.

Scale lines. 0.1 mm.

mm, carapace 1.9 to 2.9 mm long, 1.5 to 2.2 mm wide. Total length of males ranges from 3.1 to 5.3 mm, carapace 1.8 to 2.4 mm long, 1.4 to 1.8 mm wide. The first patella and tibia is 1.0 to 1.5 times the length of the carapace in females, 1.5 to 1.7 times the length in males.

Natural History. Adult males have been collected in June and July, females from June to August. *Metepeira grandiosa alpina* has been collected by sweeping a meadow in South Dakota, from a meadow, browsed aspen, bunchgrass (?*Sporobolus airoides*) and with sage (*Artemisia*) in Wyoming. Additional specimens have been found in a meadow, in oak juniper (two collections), on sagebrush (*Artemisia*) from a dry hillside in Colorado (two collections) and from sagebrush in Oregon. Specimens are commonly collected with *M. foxi.* Their habitats must be similar.

Distribution. Rocky Mountain area of Saskatchewan, North Dakota, Oklahoma, to British Columbia, Oregon and south to Chihuahua (Map 2).

Metepeira grandiosa grandiosa Chamberlin and Ivie
Figures 112–116; Map 2

Note. Types with the names *M. grandiosa* and *M. palomara* belong to this subspecies.

Diagnosis and Variation. Specimens of this subspecies are more variable than those of *M. g. alpina* but tend to be larger in size. Often the scape of the female epigynum is narrower than that of the other subspecies; it has a median ridge (Fig. 112) and the distal part of the embolus is heavier (Figs. 115–116). Total length of females varies from 5.4 to 8.5 mm, carapace 2.3 to 3.5 mm long, 1.9 to 3.0 mm wide. Total length of males is 3.5 to 5.1 mm, carapace 1.9 to 2.7 mm long, 1.4 to 1.9 mm wide. First patella and tibia of female is 1.3 times the length of the carapace, that of the male, 1.3 to 1.8 times.

Natural History. Males have been collected from March to October, females from April to September. They have been collected in the same area as *M. crassipes*, in Riverside County, California. The species was abundant only in spring, not in fall.

Distribution. British Columbia to California (Map 2).

Kaira O.P.-Cambridge

Kaira O.P.-Cambridge, 1889, Biologia Centrali-Americana, Araneidea, 1: 56. Type species *K. gibberosa* O.P.-Cambridge, 1889 designated by F.P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 522. The name *Kaira* is of feminine gender.

Caira Simon, 1895, Histoire Naturelle des Araignées, 2nd ed., 1: 894. New name for *Kaira* (presumably because the Latin alphabet lacks a K), an invalid emendation.

Pronarachne Mello-Leitão, 1937, An. Acad. Brasileira Sci., 11: 9. Type species by monotypy, *P. aries* Mello-Leitão, 1937 (? = *Kaira alba*). NEW SYNONYMY.

Macpos Mello-Leitão, 1969, Rev. Chilena Hist. Natur. 43: 59. Type species by monotypy, *M. monstrosus* Mello-Leitão. NEW SYNONYMY.

Diagnosis. Kaira differs from *Metepeira* and *Aculepeira* by the shape of the abdomen, which is attached in the center of its anterior side and has the longest axis almost at a right angle to that of the cephalothorax (Figs. 123, 125); by the tuberculate dorsal humps on the abdomen of females (Figs. 122, 134, 144, 146); by the heavily armed distal portion of the legs of females that have short metatarsi and tarsi (Figs. 122, 144, 146); and by lacking the black pigmentation around the median white mark on the venter of the abdomen (Fig. 123).

Coloration. The color of all species appears yellowish white, with only scattered black pigment (Figs. 122, 126, 144–146); there is a central white mark on the venter of the abdomen. The males are darker than the females (Fig. 126). It is possible that living specimens are green.

Description. Carapace noticeably narrow in the head region (Figs. 121, 122, 126). Chelicerae armed with three long teeth on the anterior margin (one of the three slightly shorter than the others) and with two denticles on the posterior margin (Fig. 121). Endites short, unlike those of *Mete-*

peira. Height of the clypeus equals that of the anterior median eyes or slightly higher (Fig. 121). Abdomen higher than long, has tuberculate dorsal humps and covered with short setae (Figs. 122, 123). Tibiae slightly sinuous; the metatarsi and tarsi noticeably short and curved (Fig. 123). Distal part of the legs heavily armed, in *K. alba* with short macrosetae (Fig. 121) and in *K. sabino* with both short and long macrosetae (Figs. 144, 146).

Males are smaller than females. Palpal femur lacks the proximal tooth; palpal patella lacks macrosetae. Neither coxae nor legs of males modified; and they lack macrosetae present in the female. Male's abdominal humps much smaller than female's and may not be tuberculate (Figs. 126, 135, 138).

Genitalia. The genitalia are surprisingly similar to those of *Metepeira.* The epigynum is small and as weakly sclerotized as that of *Metepeira* (Figs. 117, 130, 141); the openings are on each side of the posterior face leading into pockets that funnel into the large spherical seminal receptacles (Figs. 120, 123, 143). The palpus has a strongly sclerotized median apophysis with a distal row of teeth and two flagella (Figs. 127–129, 136, 137, 139, 140) similar to that of some species of *Metepeira.* The embolus (e in Fig. 129), as in *Metepeira,* has a lobe below the duct-bearing portion. A long terminal apophysis (a) is separated from the embolus by a distal hematodocha (dh in Fig. 129). It is not known if the virgin embolus has a cap that is transferred to the female when mating.

Natural History. Nothing is known of habits; the species are so rare that one can only speculate what the habits might be. Do the armed distal articles of the legs (Figs. 122, 123) indicate that the spider does not make a web, but instead catches insects with the legs in a crabspider fashion, as do some other Araneidae?

Species. There are so few specimens in collections that it is difficult to decide the limits of species and to match males and females. Species appear to differ by the shape of the abdomen (Figs. 124, 134, 145), by the proportions of the scape of the epigynum (Figs. 118, 131, 141) and by the shape of the conductor of the palpus (c in Fig. 129, Figs. 128, 137, 140) (in contrast to many species of *Metepeira* where the conductors resemble each other). It is probably not safe to identify specimens by abdominal humps alone. The humps of two females of *K. sabino* are very different. The reason for this is that one has probably just molted (Figs. 146, 147), while the other has very recently produced eggs (Figs. 144, 145).

Relationships. The genitalia of *Kaira* resemble *Metepeira* to such an extent that a common ancestor should be assumed. Another similarity is the white spot on the venter of the abdomen. *Kaira* shares the closest relationship with the *M. foxi* group, which also has teeth on the distal keel of the median apophysis (m in Fig. 129). I considered the *M. foxi* group the least specialized of *Metepeira.*

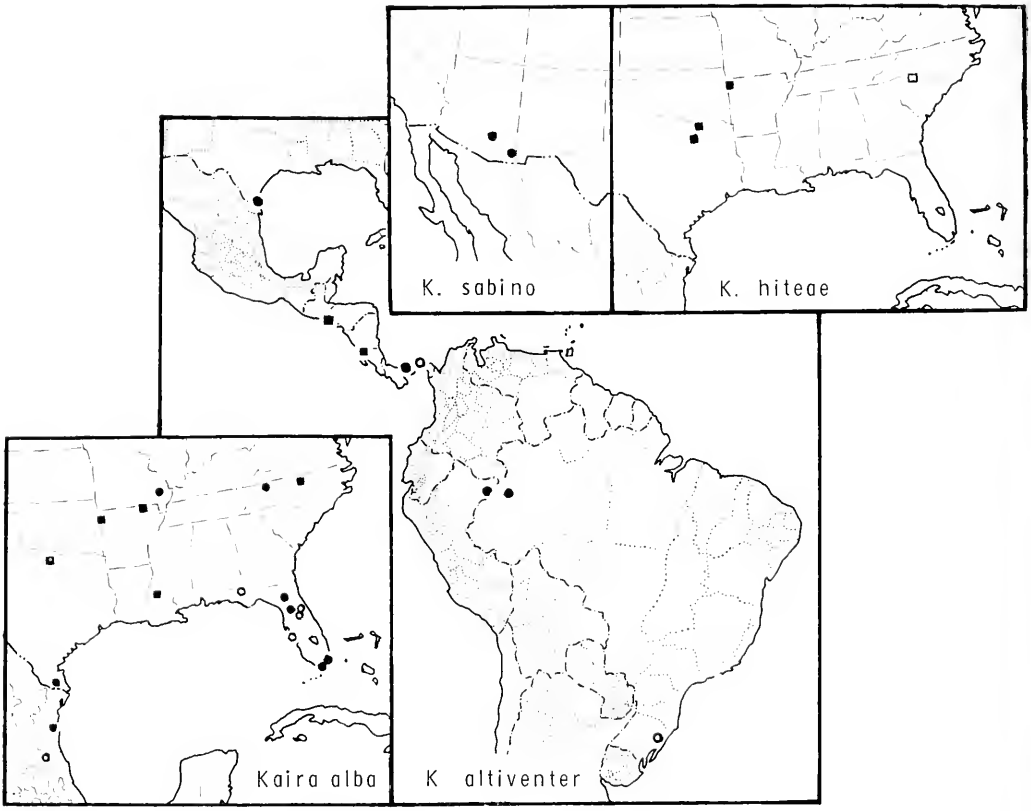
Distribution. *Kaira* species are known only from the warmer and tropical parts of the Americas.

Key to female *Kaira* north of Mexico

1. Epigynum with a longitudinal, longer than wide, transparent keel or hook (Figs. 117, 130) 2
– Epigynum with a transverse, wider than long, transparent scape (Fig. 141); Arizona (Map 3) ..... *sabino*
2(1) Epigynum having a hook-shaped scape (Fig. 132); southern Texas to South America (Map 3) ..... *altiventer*
– Epigynum having a keel-shaped scape, of variable profile (Fig. 119); North Carolina and Missouri to northeastern Mexico (Map 3) ..... *alba*

Key to male *Kaira* north of Mexico

1. Palpus with a light swelling on distal end of conductor, conductor without proximal pocket (Figs. 128, 129, 137); terminal apophysis sharply pointed (Figs. 127, 129, 136) 2
– Conductor with a dark distal swelling overhanging subdivided lateral pockets (Fig. 140); terminal apophysis bluntly pointed



Map 3. Distribution of *Kaira* species found north of Mexico. Circles, females; open circles, juvenile specimens; squares, males; open squares, juvenile males.

(Fig. 139); ? South Carolina, Arkansas, northern Texas (Map 3) ..... *hiteae*

2(1) Proximal flagellum of median apophysis longer than distal one (Figs. 127, 128); tip of conductor pointed mesally, toward median apophysis (Fig. 128); North Carolina and Missouri to northeastern Mexico (Map 3) ..... *alba*

– Flagella of median apophysis equal in length (Figs. 136, 137); tip of conductor pointed laterally, away from median apophysis (Fig. 137); Texas to South America (Map 3) ..... *altiventer*

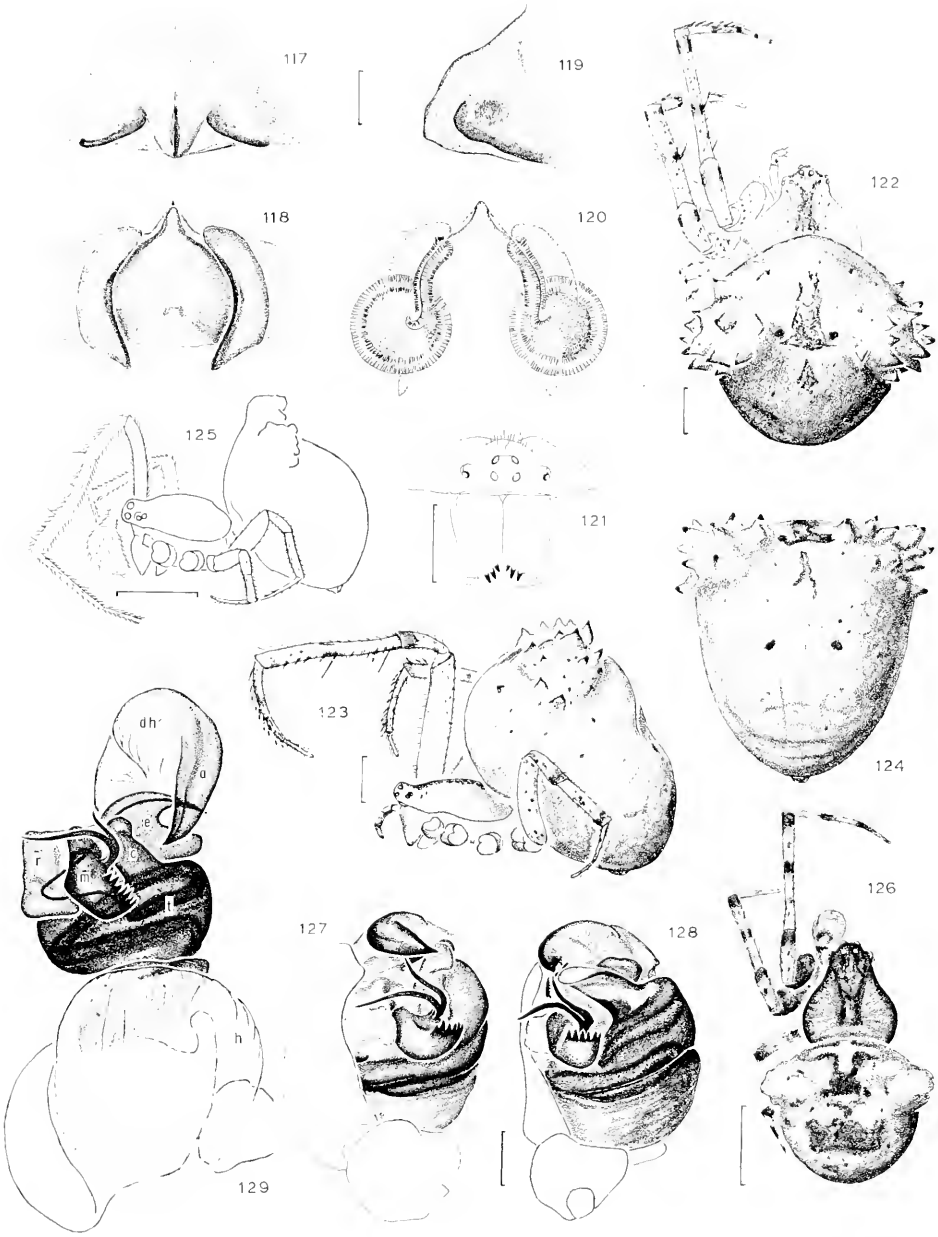
Kaira alba (Hentz)
Figures 117–129; Map 3

Epeira alba Hentz, 1850, J. Boston Soc. Natur. Hist., 6: 20, pl. 3, fig. 7. Female from North Carolina in the Boston Natural History Society, destroyed.

Kaira alba:—Keyserling, 1892, Spinnen Amerikas, 4: 64, pl. 3, fig. 50, ♀. McCook, 1893, American Spiders, 3: 202, pl. 13, fig. 3, ♀. Comstock, 1912, Spider Book, p. 450, fig. 461, ♀; 1940, Spider Book, rev. ed., p. 464, fig. 461, ♀. Roewer, 1942, Katalog der Araneae, 1: 904.

Caira alba:—Bonnet, 1956, Bibliographia Araneorum, 2: 924.

Description. Female from Florida. Carapace yellow-white with a median darker line of black spots and some straggly white setae (Fig. 122). Sternum with tiny black spots. Legs yellowish white with tiny black spots and narrow broken black bands on venter (Fig. 123). Dorsum of abdomen with a black mark between humps, sides with tiny black spots (Figs. 122, 124, 126). Venter spotted black. Posterior median eyes subequal to anterior medians; laterals 0.8 diameter of anterior median eyes. An-



Figures 117–129. *Kaira alba* (Hentz). 117–124. Female: 117–120. Epigynum: 117. Ventral. 118. Posterior. 119. Lateral. 120. Posterior, cleared. 121. Eye region and chelicerae. 122. Female, dorsal. 123. Female, lateral. 124. Abdomen, posterior. 125–129. Male: 125. Lateral. 126. Dorsal. 127–129. Left palpus: 127. Mesal. 128. Ventral. 129. Expanded. subventral.

Abbreviations. a, terminal apophysis; c, conductor; dh, distal hematodocha; e, embolus; h, hematodocha; m, median apophysis; r, radix; t, tegulum.

Scale lines. 0.1 mm except Figs. 122–126, 1.0 mm.

terior median eyes 1.5 diameters apart, 2.5 from laterals. Posterior median eyes 1.4 diameters apart. Height of clypeus equals diameter of anterior median eyes. Anterior margin of chelicerae has two long teeth distally and two smaller ones proximally. On the posterior margin are two distal teeth and two small proximal denticles. Abdomen much higher than long with tuberculate humps (Figs. 123, 124). Total length 6.5 mm. Carapace 2.9 mm long, 2.7 mm wide. First femur, 3.6 mm; patella and tibia, 4.4 mm; metatarsus, 2.3 mm; tarsus, 1.1 mm. Second patella and tibia, 3.6 mm; third, 2.2 mm; fourth, 2.8 mm.

Male coloration darker than that of female (Fig. 126). Anterior median eyes slightly more than their diameter apart, slightly less than one from laterals. Posterior median eyes slightly more than their diameter apart, 1.5 from laterals. Abdomen vertical with large humps that are slightly irregular, only faintly indicating tubercles (Fig. 126). Total length 3.0 mm. Carapace 1.4 mm long, 1.1 mm wide. First femur, 1.7 mm; patella and tibia, 2.1 mm; metatarsus, 1.1 mm; tarsus, 0.7 mm. Second patella and tibia, 1.6 mm; third, 0.9 mm; fourth, 1.2 mm.

Variation. The shape of the two humps of the abdomen is variable. Females vary in total length from 6.5 to 7.3 mm, carapace 2.9 to 3.1 mm long; males from 2.6 to 3.0 mm in total length.

Diagnosis. The median longitudinal keel of the lightly sclerotized epigynum (Figs. 117, 119) separates the species from *K. altiventer.* The shape of the conductor of the palpus (Figs. 128, 129) and the pointed terminal apophysis (Figs. 127, 129) separates the species from *K. hiteae.*

Natural History. Females have been collected in all seasons, males only in early summer. In Florida females have been collected on grass stems; in mangrove hammocks, and in shrubs bordering a red and white mangrove hammock; a male from Arkansas came from oak-hickory brush. We do not know the web of this uncommon species. Males are collected by sweeping vegetation.

Distribution. From North Carolina, Tennessee, Arkansas to northeastern Mexico (Map 3). Juvenile specimens have been mapped with open circles.

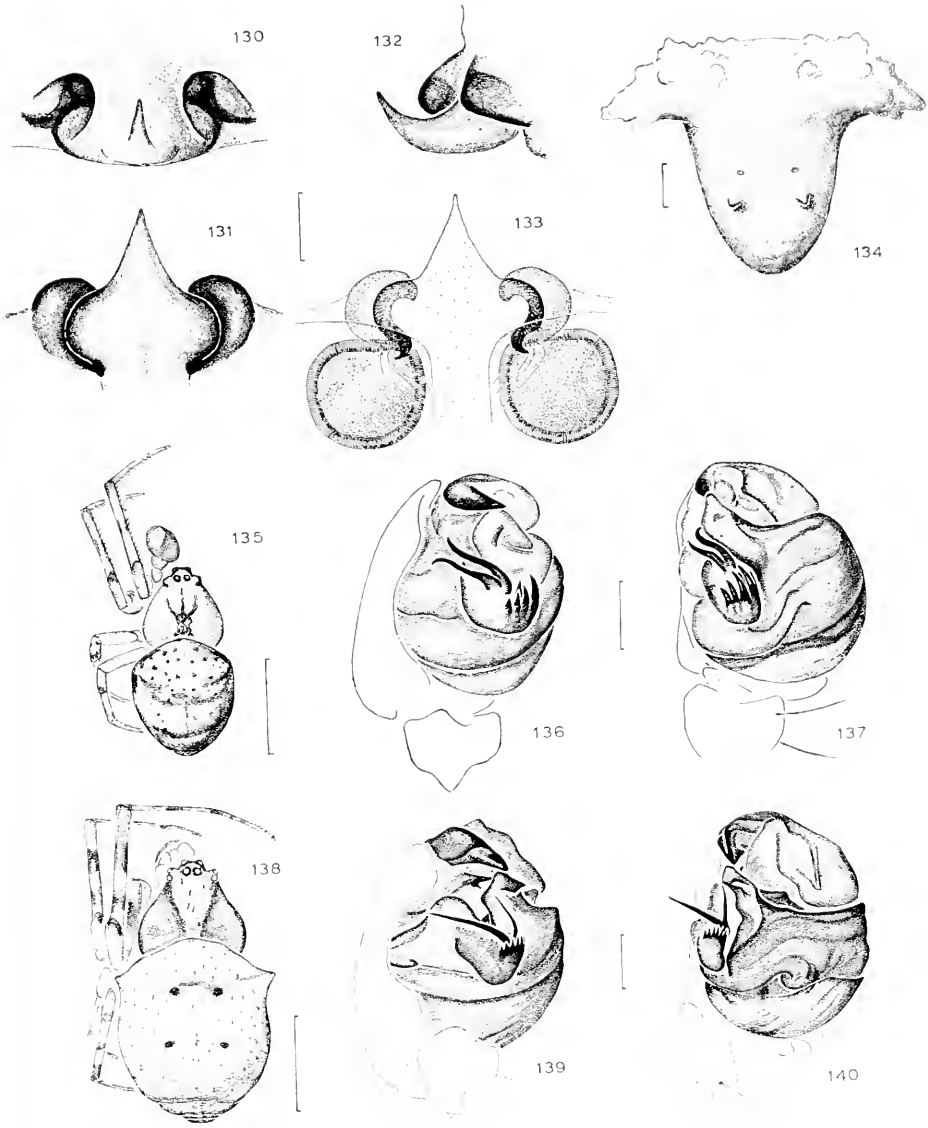
Records. North Carolina. Guilford Co.: 5.2 mi. north of Greensboro, 10 June 1953, ♂ (R.D. Barnes). *Tennessee.* Washington Co.: Johnson City, 12 June 1951, ♀ (O. Bryant). *Florida.* Jackson Co.: 12 May 1935, juv. (H.K. Wallace). Alachua Co.: Gainesville, 10 Oct. 1963, ♀ (L.A. Hetrick). Lake Co.: Leesburg, March 1954, ♀ (M. Statham). Seminole Co.: Sanford, Sept. 1927, juv. (Stone). Osceola Co.: Kissimmee, juv. (N. Banks). Sarasota Co.: Englewood, 1 Apr. 1938, juv. (W.J. Gertsch). Dade Co.: Matheson Hammock, 20 June 1964, ♀ (K. Stone). Monroe Co.: 2 mi. north of Flamingo, 21 June 1964, ♀ (K. Stone). *Mississippi.* Wilkinson Co.: Centreville, 1944, ♂ (A.F. Archer). *Missouri.* Stoddard Co.: Ardeola, 22 July 1950, ♀ (H. Exline). *Arkansas.* Washington Co.: 15 mi. west of Prairie Grove, ♂ (M. Hite). Randolph Co.: 16 June 1963, ♂ (Exline Coll.). *Texas.* Denton Co.?: Decator, 1945, ♂ (H. Exline). Hidalgo Co.: Edinburg, Sept.–Dec. 1933, ♀ (S. Mulaik). *Mexico. Tamaulipas.* Soto La Marina, 16 May 1952, ♀ (W.J. Gertsch). *San Luis Potosí.* Valles, July 1959, juv. (L. Steude).

Kaira altiventer O.P.-Cambridge
Figures 130–137; Map 3

Kaira altiventer O.P.-Cambridge, 1889, Biologia Centrali-Americana, Araneidea, 1: 56, pl. 3, fig. 13, ♀. Female holotype from Veragua, Panama, in the British Museum, Natural History, examined. Keyserling, 1892, Spinnen Amerikas, 4: 62, pl. 3, fig. 48, ♀. F.O.P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 522, pl. 51, fig. 10, ♀. NEW SYNONYMY.

? *Kaira obtusa* Keyserling, 1892, Spinnen Amerikas, 4: 66, pl. 3, fig. 51, juvenile holotype from Taguara, Rio Grande do Sul, examined.

Caira spinosa Simon, 1896, Ann. Soc. Entomol. France, 65: 478. Female lectotype here designated and juvenile paralectotype from São Paulo de Olivença, Amazonica, Brazil and Pebas, Peru



Figures 130–137. *Kaira altiventer* O.P.-Cambridge. 130–134. Female: 130–133. Epigynum: 130. Ventral. 131. Posterior. 132. Lateral. 133. Posterior, cleared. 134. Abdomen, posterior. 135–137. Male: 135. Dorsal. 136, 137. Left palpus: 136. Mesal. 137. Ventral.

Figures 138–140. *K. hiteae*, male. 138. Dorsal. 139, 140. Palpus: 139. 140. Palpus: 139. Mesal. 140. Ventral.

Scale lines. 0.1 mm except Figs. 134, 135, 138, 1.0 mm.

in the Muséum National d'Histoire Naturelle, Paris, examined. NEW SYNONYMY.

Pronarachne aries Mello-Leitão, 1937, An. Acad. Brasileira Sci., 9: 9, fig. 10, ♀. Female holotype from Itatiaia, Rio Grande do Sul in the Museu Nacional, Rio de Janeiro, examined. NEW SYNONYMY.

Description. Female from Texas. Carapace yellow-white with some tiny orange

dots and some white pigment streaks. Dorsum of abdomen with some tiny black and orange spots. Venter with spots. Legs yellow-white with tiny orange spots. Eyes subequal in size. Anterior median eyes 1.2 diameters apart, 2.5 from laterals. Posterior median eyes one diameter apart. Height of the clypeus equals about the diameter of the anterior median eyes. Total length 6.0 mm. Carapace 2.9 mm long, 2.3 mm wide. First femur, 3.0 mm; patella and tibia, 3.9 mm; metatarsus, 2.0 mm; tarsus, 0.9 mm. Second patella and tibia, 3.1 mm; third, 1.6 mm; fourth, 2.3 mm.

Male. Abdomen shield-shaped, humps dorsally directed (Fig. 135). Total length 2.0 mm. Carapace 1.2 mm long, 1.0 mm wide. First femur, 1.1 mm; patella and tibia, 1.3 mm; metatarsus, 0.8 mm; tarsus, 0.4 mm. Second patella and tibia, 1.0 mm; third, 0.6 mm; fourth, 0.8 mm.

Note. It is not certain that the males and females described and illustrated belong together.

Variation. The palpi of the two males differ slightly; the illustrations were made of the male from El Salvador (Figs. 136, 137). The specimen from Costa Rica differs in that the two flagella of the median apophysis are more straight and the conductor seems slightly turned on its longitudinal axis facing the median apophysis, appearing less pointed.

Diagnosis. Females can be separated from *Kaira alba* by the hook-shaped scape of the epigynum (Fig. 132). Males can be separated from those of *K. alba* by the direction of the distal swelling of the conductor (Fig. 137), and by the absence of a lateral fold (Fig. 137) from *K. hiteae.*

Distribution. Texas to South America (Map 3).

Records. Texas. Hidalgo Co.: Edinburg, 6 Dec. 1935, ♀ (S. Mulaik). *El Salvador.* San Salvador, Jan.–March, 1954, ♂ (J.B. Boursot). *Costa Rica.* Guanacaste Prov.: 4 km NW Cañas La Pacifica, 7 Feb.–2 March 1975, ♂ (R. Coville from *Trypargilum nitidum* muddauber nest). *Canal Zone.* Ft. Sherman, Aug. 1939, juv. (A.M. Chickering).

Kaira hiteae new species
Figures 138–140; Map 3

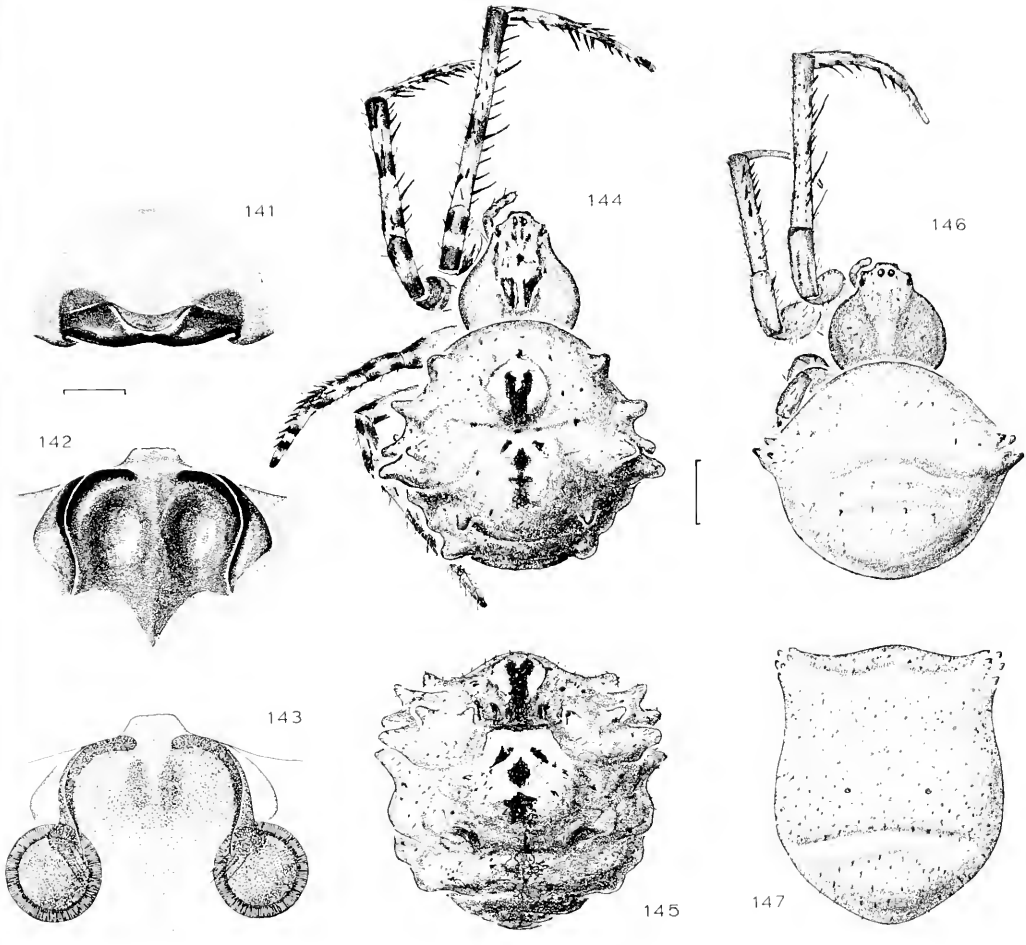
Holotype. Male from Cove Creek Valley, 9.3 km west of Prairie Grove, Boston Mountains, 300 m elevation, Washington County, Arkansas, 26 July to 7 August 1956 (Maxine Hite) in the Museum of Comparative Zoology. The species is named after M. Hite, the collector of several specimens of these rare species.

Description. Male. Carapace yellowish, lighter in center. Legs yellowish, very indistinctly banded. Abdomen with indistinct transverse bands, venter white. Eyes subequal in size, except anterior laterals 0.8 diameter of anterior median eyes. Anterior median eyes 1.3 diameter apart, 1.3 from laterals. Posterior median eyes slightly less than their diameter apart, slightly more than two diameters from laterals. Height of the clypeus equals diameter of the anterior median eyes. Endites are short and square. None of the legs have strong macrosetae. Abdomen is shield-shaped (Fig. 138). Total length 2.6 mm. Carapace 1.3 mm long, 1.2 mm wide. First femur, 1.5 mm; patella and tibia, 1.9 mm; metatarsus, 1.2 mm; tarsus, 0.7 mm. Second patella and tibia, 1.4 mm; third, 0.8 mm; fourth, 1.1 mm.

Note. At first it appeared that these males belonged with the females of *K. sabino*, but I now doubt this.

Diagnosis. Kaira hiteae differ from *K. alba* by lacking black pigment in the center of the carapace and between the humps (Fig. 138); in *K. hiteae* this area is lightest. They differ too by having transverse bands on the abdomen and on the single point of the humps (Fig. 138). The males have a more blunt terminal apophysis (Fig. 139), the conductor has an edge laterally (Fig. 140) and a slightly more distal attachment of the flagellae to the median apophysis (Figs. 139, 140).

Natural History. One male from Dallas



Figures 141–147. *Kaira sabino* n. sp., female. 141–143. Epigynum: 141. Ventral. 142. Posterior. 143. Posterior, cleared. 144–147. Female: 144, 146. Dorsal. 145, 147. Abdomen, posterior. 144, 145. Paratype (Portal, Arizona). 146, 147. Holotype (Sabino, Arizona).

Scale lines. 0.1 mm except Figs. 141–144, 1.0 mm.

County, Texas had a label stating it had been collected with spiders from "road, woods, herbs and shrubs."

Distribution. South Carolina, Arkansas, Texas (Map 3).

Records. South Carolina. York Co.: 3.4 mi. west of Sharon, 4 Aug. 1953, juv. ♂ (R. Barnes). *Arkansas.* Washington County: Cove Creek Valley, Boston Mts., 1000 ft., 26 July, 7 Aug. 1956, 2 ♂ (M. Hite), one deposited in Canadian National Collection. *Texas.* Dallas Co.: Coit, 2 Aug. 1940, ♂ (S. Jones). Grayson Co.: Sherman, 25 July 1963, 2 ♂ (K.W. Haller). (All but first listed specimen have been marked as paratypes.)

Kaira sabino new species
Figures 141–147; Map 3

Holotype. Female from Sabino [? Canyon, Pima County], Arizona, 2 September

1932 (R. Flock) in the Museum of Comparative Zoology. The specific name is a noun in apposition after the type locality.

Note. According to J. Beatty (personal communication), there may be numerous localities with the name of Sabino, Arizona. W.C. Barnes, 1960, *Arizona Place Names* has listed only two, both in Pima County, one of which, Sabino Canyon, is a common collecting site.

Description. Female holotype. Carapace light brown, darker brown on sides. Sternum darker on sides. Legs with indistinct narrow bands. Dorsum of abdomen with transverse bands (Figs. 145, 147). Sides light, venter with white pigment. Posterior median eyes 1.5 diameters of anterior medians, anterior laterals 1.2; posterior laterals 1.5 diameters of anterior medians. Anterior median eyes 2 diameters apart, 2.5 diameters from laterals. Posterior median eyes their diameter apart. Height of the clypeus equals 1.5 diameters of the anterior median eyes. First metatarsus curved and armed with strong and weak setae (Figs. 144, 146). Abdomen appears shield-shaped, having small tubercles on the humps (the abdomen, however, is in very poor condition). Total length 5.8 mm. Carapace 2.4 mm long, 1.9 mm wide. First femur, 3.2 mm; patella and tibia, 4.0 mm; metatarsus, 2.3 mm; tarsus, 1.0 mm. Second patella and tibia, 3.1 mm; third, 1.7 mm; fourth, 2.2 mm.

Note. It appeared at first that these females belonged with the males of *K. hiteae*, but I now doubt this.

Variation. The second specimen, although having a similar epigynum to the first and doubtlessly of the same species, is quite different in appearance: it has scattered black pigment and many more abdominal tubercles (Figs. 144, 145). Since a fluffy egg-sac is in the vial, it must have oviposited and the abdomen shriveled.

Diagnosis. The wide short scape of the epigynum, which appears to be a transverse lip (Fig. 141), is very distinct from the narrow keel or hook of the two other species.

Paratype. Arizona. Cochise Co.: 1 mi. east, 7 mi. north of Portal on San Simon Road, 17 July 1973, ♀ (A. Jung).

Aculepeira Chamberlin and Ivie

Aculepeira Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., 7(1): 75. Type species designated by original authors as *Epeira aculeata* Emerton, which these authors thought to be the name of *A. carbonarioides*; actually *E. aculeata* is a synonym of *A. packardi* (Thorell). The name *Aculepeira* is feminine.

Diagnosis. Aculepeira, like *Metepeira,* has a median, ventral white streak on the abdomen but differs in both sexes by the elongate, egg-shaped abdomen, in the female by the large, sclerotized epigynum with a large scape (Figs. 148, 162), and in the male by the large palpus with long, prominent, median apophysis with two flagella (Fis. 159, 161) and a large boat-shaped to disk-shaped conductor (Figs. 158, 160, 170, 172). *Aculepeira* differs from the related *Araneus* by having an elongate, egg-shaped abdomen that is widest anteriorly (Figs. 154, 166); the abdomen of the large *Araneus* usually ranges in shape from spherical to longer than wide and may have humps. Unlike any of the large *Araneus* species, *Aculepeira* species have a median, ventral white mark on the abdomen (Figs. 155, 168).

Description. Carapace with eye area and thoracic rim light and thorax dark covered by white down; sternum, brownish black. Legs banded; abdomen with a dorsal longitudinal lobed band (Figs. 154, 166) and a ventral white mark on black (Figs. 155, 168). Eyes subequal in size, laterals sometimes smaller. Anterior median eyes slightly more than their diameter apart, posterior median eyes their diameter apart; in female, slightly closer spaced than in male. Height of the clypeus, about 1.5 to almost 2 diameters of the anterior median eyes (Fig. 174). The thorax with a shallow depression (Figs. 154, 166, 174). Abdomen, chicken-egg-shaped, longer than wide, widest anteriorly (Figs. 154, 166) and covered with setae; very hairy in *A. carbonaria* and *A. carbonarioides.*

Plate 6. *Aculepeira packardi*. Above, spider in web; below, spider in a disc-shaped retreat in vegetation.

Male smaller than female (Fig. 157), chelicerae small and anteriorly concave. Endites with a tooth laterally facing another tooth at the proximal end of palpal femur. First coxae with a hook fitting into a groove of second femur. The second coxae with a median ventral pointed hump in most species and the fourth trochanter with a posterior macroseta in most species (Fig. 175). Second tibia distally wider with short macrosetae, one of which is on a projecting hump (Figs. 156, 159).

Genitalia similar to those of *Araneus*, especially to *A. washingtoni* Levi. Epigynum, an annulate scape on a base (Figs. 148–152, 162–163) and lamellae on each side posterodorsally (Figs. 150, 164). Palpal patella with two macrosetae (Fig. 172); palpal parts like those of *A. washingtoni*, except for a long median apophysis with

Plate 7. *Aculepeira carbonarioides*. Top, female; middle and bottom, orb-web in talus in Colorado. Webs dusted with cornstarch. Viscid area of web approximately 15–20 cm diameter.

two proximal flagella (m in Figs. 161, 173). Conductor a deep sclerotized boat-shaped to disk-shaped structure (Figs. 158, 160, 170, 172); embolus (e in Figs. 161, 173) hidden in contracted palpus by the terminal apophysis (a in Figs. 161, 173) and lacking a cap in virgin males. Terminal apophysis a long sclerotized prong with a hook at its base (a in Figs. 161, 173). Subterminal apophysis acutely pointed in *A. packardi*, more blunt in *A. carbonarioides* but hidden underneath the terminal apophysis (Figs. 158, 170 and sa in Figs. 161, 173).

Eurasian Species. The three common European species, frequently confused with the North American ones, have been illustrated (Figs. 187–217). I had first planned to revise *Aculepeira* worldwide, but lack of specimens, especially males from the Near East, made this impossible. There were nomenclatural and biological problems that I could not resolve (see Methods above).

Thorell (1870) gave the name *Epeira victoria* to illustrations by C. L. Koch of a spider from Germany and France on low plants in meadows and the border of forests (C. L. Koch, 1834, 1839). Drensky (1943) thought *A. victoria* to be the same as *A. armida*, although the latter species is not known to occur in Germany.

The specimens from Switzerland labeled *A. victoria* in the British Museum and the Naturhistorisches Museum, Basel are probably *A. armida*. But there are female specimens from Dalmatia and Samarkand, USSR, in the Natural History Museum, Stockholm that may be distinct (Figs. 226–231). These have a shorter scape and wide lamellae posterodorsal to the epigynum.

Epeira armida was described from southern France and northern Israel. Are the populations found in these two areas the same species? I examined several collections from Turkey and all but two were females. None looked quite alike. Karol (1964, 1966) recently described two species (*A. vachoni*, *A. karapagi*) from females from Turkey without making comparative reference to the other species reported from the area.

The type of *A. vachoni* was examined and it appeared to be a female *A. ceropegia* having the scape of the epigynum torn off. *Aculepeira karapagi* appears to be a distinct species previously described as *Epeira similis* Nosek, 1905 (a name preoccupied) and subsequently renamed *E. noseki* Strand, 1907.

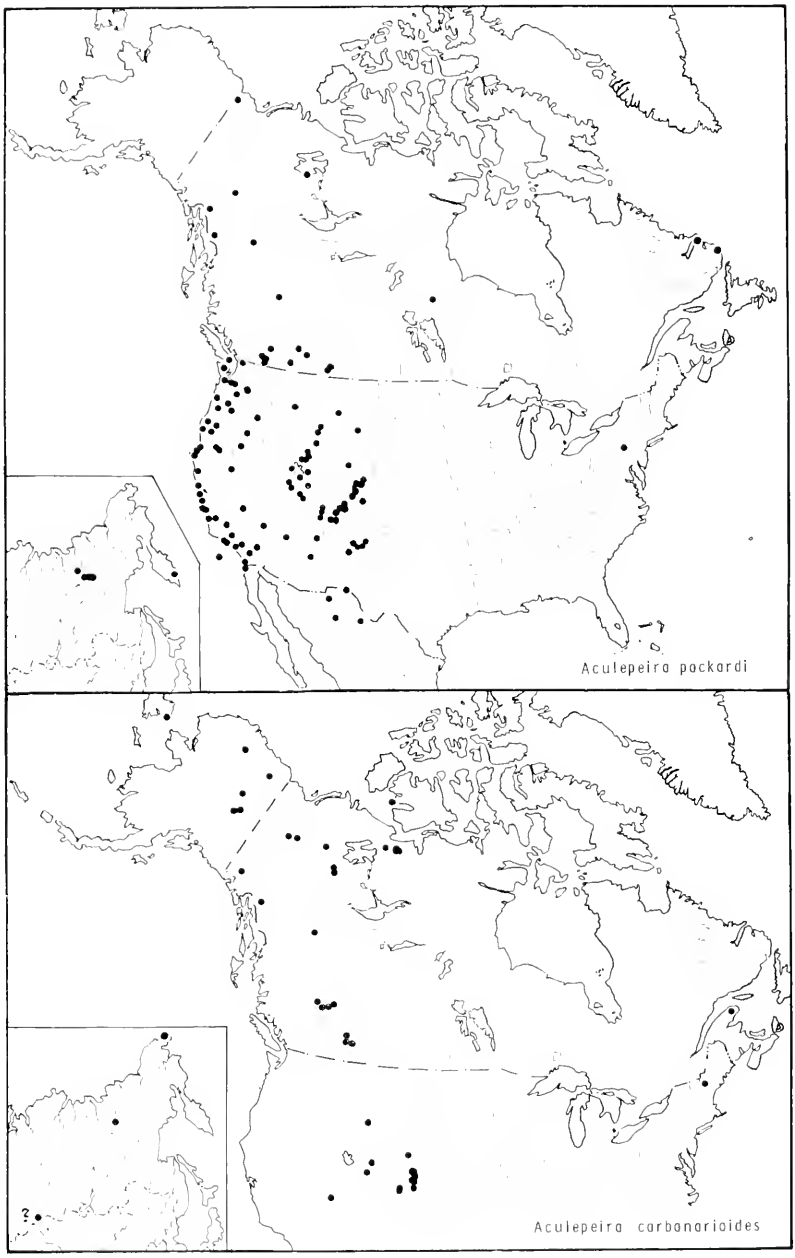
Natural History. Both American species make fairly large orbs and one is found in extreme habitats not otherwise frequented by large orb-weavers. *Aculepeira packardi* has a retreat (Plate 6), *A. carbonarioides* does not (Plate 7). *Aculepeira packardi* males are more commonly collected than females, usually by sweeping, but *A. carbonarioides* males are rare in collections, presumably because it is difficult to collect among boulders.

Note on Names. Both Keyserling and Emerton realized there are two species in North America, but each called a different one *Epeira carbonaria* and gave the second a new name. Neither American species is *A. carbonaria*.

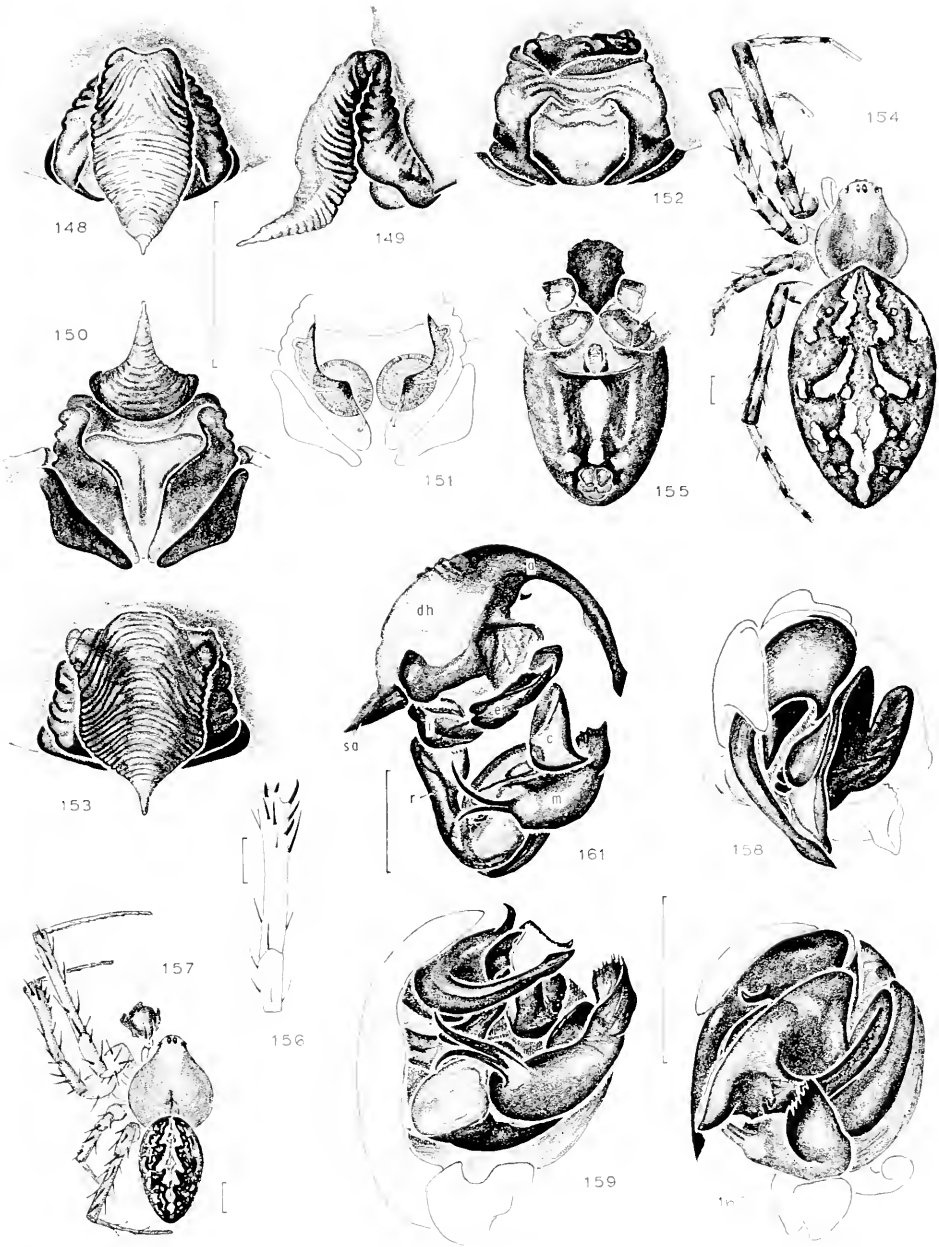
KEY TO AMERICAN *ACULEPEIRA* SPECIES

1. Dorsum of abdomen in both sexes with median, paired, upside-down, comma-shaped marks or posteriorly directed lobes (Figs. 154, 157); width of scape of epigynum more than half the width of base (Fig. 148) or scape torn off (Fig. 152); epigynum in posterior view with median area framed by convexly lobed lateral pieces (Figs. 150, 151); conductor of palpus relatively wide with ventral lip (Figs. 160, 176–181) ..... *packardi*

– Dorsum of abdomen with paired white pigment patches, but no lateral, posteriorly directed lobes (Fig. 166), or with indistinct dark pattern of paired spots (Fig. 167); width of scape of epigynum less than a third the width of base (Figs. 162, 182, 185); scape rarely torn off; epigynum in posterior view with median area framed by concavely curved lateral pieces (Figs. 164, 165, 183, 186); conductor of palpus narrow without a lip around ventral margin (Figs. 170, 172) ..... *carbonarioides*



Map. 4. Distribution of North American *Aculepeira* species.



Figures 148–161. *Aculepeira packardi* (Thorell). 148–153. Epigynum: 148, 152, 153. Ventral. 149. Lateral. 150. Posterior. 151. Posterior, cleared. 152. Scape torn off. 148–151. (California). 152. (Nevada). 153. (Colorado). 154. Female, dorsal. 155. Female abdomen and sternum, ventral. 156. Left male second patella and tibia, dorsal. 157. Male, dorsal. 158–161. Left male palpus: 158. Apical. 159. Mesal. 160. Ventral. 161. Expanded, mesal view.

Abbreviations. a, terminal apophysis; c, conductor; dh, distal hematodocha; e, embolus; i, stipes; m, median apophysis; r, radix; sa, subterminal apophysis.

Scale lines. 1.0 mm.

Aculepeira packardi (Thorell)
Plate 6; Figures 148–161, 174, 176–181; Map 4

Epeira packardii Thorell, 1875, Proc. Boston Soc. Natur. Hist., 17: 490. Left palpus of holotype from Square Island, Labrador in the Natural History Museum, Stockholm, examined; the remaining parts of specimen probably destroyed.

Epeira aculeata Emerton, 1877, Bull. U.S. Geol. Surv. Territ., 3: 528, fig. 18, ♀. Female holotype from Gray's Peak [Front Range, Summit Co.], Colorado, lost. Emerton, 1894, Trans. Connecticut Acad. Sci., 9: 405, pl. 1, fig. 4 a, c, e, ♀, ♂. NEW SYNONYMY.

Epeira carbonaria:—Keyserling, 1892, Spinnen Amerikas, 4: 204, fig. 151, ♀, ♂. McCook, 1894, American Spiders, 3: 157, pl. 5, figs. 1, 2, ♀, ♂. Misidentification, not *A. carbonaria* (L. Koch).

Aranens septentrionalis Kulczynski, 1908, Zap. Imp. Akad. Naouk, (8) 18: 47, fig. 57, ♀. Female holotype from Sataghai, Adytscha River, in central Siberia, in Polish Academy of Sciences, Warsaw, examined. NEW SYNONYMY.

Aculepeira verae Chamberlin and Ivie, 1942, Bull. Univ. Utah, biol. ser., 7(1): 75, figs. 215, 216, ♂. Male holotype from Bear Valley, Idaho in the American Museum of Natural History, examined. NEW SYNONYMY.

Note. This species has been called *carbonarius* by Gertsch and Ivie in collections and *verae* by Chamberlin and Ivie.

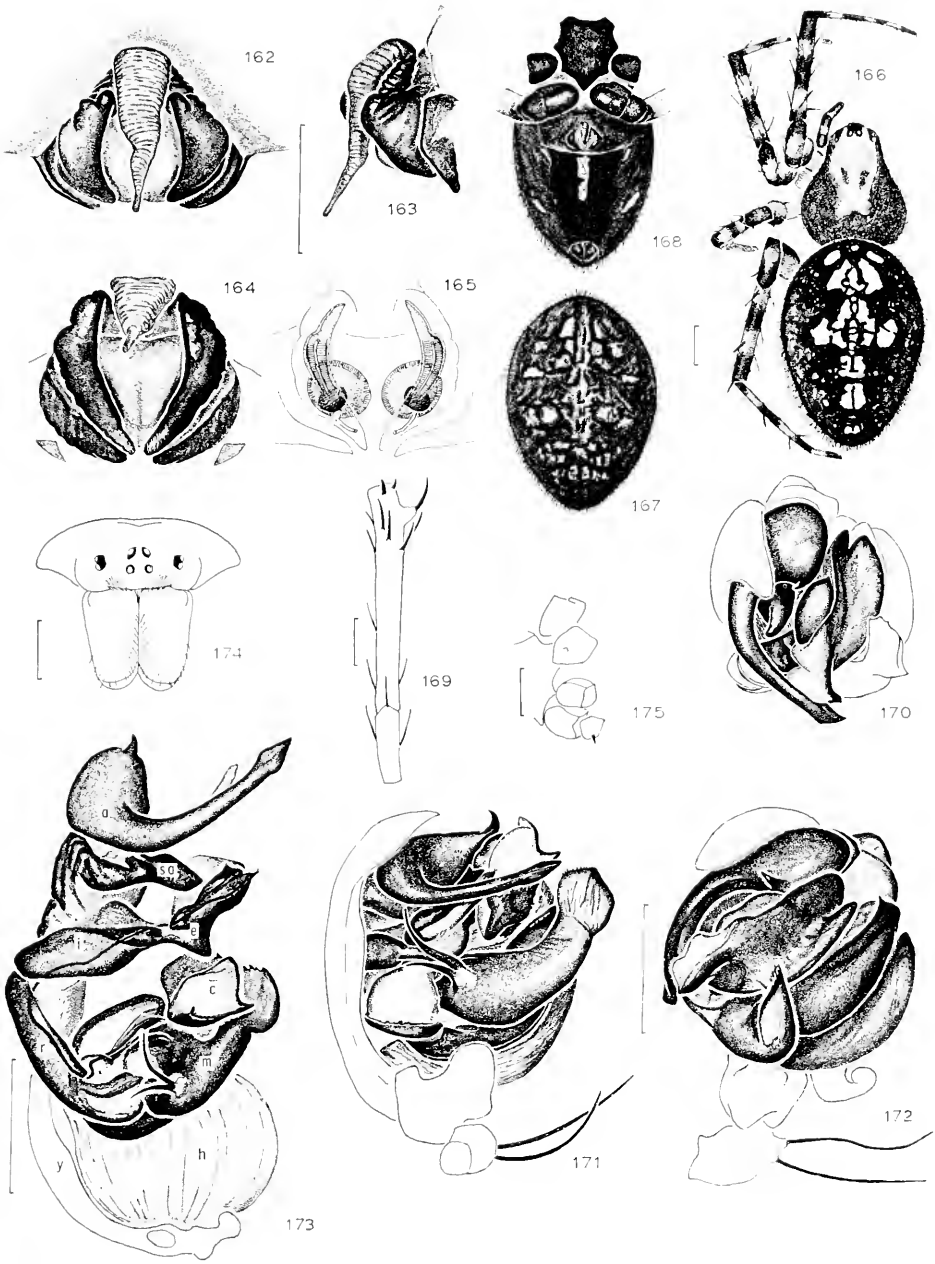
Description. Female from California: carapace brown, head region lighter and covered with white down. Sides of thorax lighter. Dorsum of abdomen with characteristic pattern (Fig. 154). Total length 11.5 mm. Carapace 4.7 mm long, 3.7 mm wide. First femur, 4.7 mm; patella and tibia, 5.8 mm; metatarsus, 4.1 mm; tarsus, 1.4 mm. Second patella and tibia, 5.2 mm; third, 3.1 mm; fourth, 5.0 mm.

Male from California: coloration like female, but legs less distinctly banded (Fig. 157). Chelicerae with three teeth on anterior margin and a small denticle most distant from base of fang, posterior margin with three teeth. Total length 9.4 mm. Carapace 4.4 mm long, 3.6 mm wide. First femur, 5.5 mm; patella and tibia, 6.8 mm; metatarsus, 4.6 mm; tarsus, 1.4 mm. Second patella and tibia, 5.3 mm; third, 3.2 mm; fourth, 5.1 mm.

Variation. The only specimens having a similar shaped scape on the epigynum or similarly shaped conductor on the palpus are those collected together. There is surprising variation in these structures. Specimens with the widest palpal conductor are sympatric with *A. carbonarioides*; those with a narrower conductor are found outside the latter species range, providing an example of character displacement (Figs. 176–181). Total length of females, 5.6 mm (Yukon) to 16.5 mm (Utah), carapace 2.7 to 6.3 mm long, 2.0 to 5.2 mm wide. Total length of males 5.0 (Labrador) to 8.9 mm (Wyoming), carapace 2.6 to 4.4 mm long, 2.1 to 3.7 mm wide.

Diagnosis. This species can be confused with *Neoscona oaxacensis* (Keyserling) because of similar abdomen shape and dorsal pattern. *Neoscona*, however, has two pairs of ventral white patches, while *Aculepeira* has a median, ventral white streak on black (Fig. 155). The dorsal abdominal band, with posteriorly directed lobes (Figs. 154, 157), separates specimens from *A. carbonarioides*. The scape of the epigynum, which is usually torn off after mating, is wider than half the width of the base (Figs. 148, 152) and the conductor is about twice as long as wide with a ventral lip (Figs. 158, 160, 176–181). The scape of *A. carbonarioides* is less than a third of the width of the base and the conductor is almost three times as long as wide and lacks the ventral lip. The species is close to the European *A. ceropegia*; but *A. ceropegia* differs by the triangular scape, by the median sclerotized lobe of the base of the epigynum (Figs. 188–192) and by the enormous, almost circular, conductor (Fig. 197).

Natural History. I have collected and observed this species a number of times in western Colorado where its webs are found among the vegetation of lush meadows at 2500 to 3000 m elevation. It is never abundant. Even an entire summer of collecting may yield only a few specimens. The females are mature in August in Colorado. The adult females make a new web every



Figures 162–173. *Aculepeira carbonarioides* (Keyserling). 162–165. Epigynum: 162. Ventral. 163. Lateral. 164. Posterior. 165. Posterior, cleared. 166–168. Female: 166. Dorsal. 167. Abdomen, dorsal. 168. Abdomen and sternum, ventral. 169–173. Male: 169. Left second patella and tibia, dorsal. 170–173. Left palpus: 170. Apical. 171. Mesal. 172. Ventral. 173. Submesal, expanded.

Figure 174. *A. packardi* (Thorell). Female eye region and chelicerae.

Figure 175. *A. ceropegia* (Walckenaer). Left coxae of male, ventral.

Abbreviations. a, terminal apophysis; c, conductor; e, embolus; h, hematodocha; i, stipes; m, median apophysis; r, radix; sa, subterminal apophysis; y, cymbium.

Scale lines. 0.1 mm.

night, placing the viscid threads as late as 23:00 h. Once, four spokes from the previous web were kept. At daytime the female is found at the side of the web in a shallow retreat (Plate 6) fashioned from several inclined leaves tied together and covered with silk threads. She will actively remove insects caught during the daytime. A large bumblebee, however, was left alone. On 12 August 1957 a female was observed eating a male of the species. Besides lush meadows in the mountains, the species is occasionally collected by sweeping grasses between sagebrush plants (*Artemisia*). The temperatures on clear days fluctuated between 2° C in the morning to 28° C at noon at one collecting site in Gothic, Colorado (near Crested Butte). A web had 19 radii, with about 25 viscid threads below the hub and 24 above. The species has been collected under white spruce (*Picea glauca*) in British Columbia, in sagebrush (*Artemisia*) in New Mexico, and in chaparral in California. It is found at 1400 to 2700 m elevations in Utah. During spring in the southern part of the range, adults of both sexes may be found. Males are as abundant in collections as females. They are probably collected by sweeping.

Distribution. Siberia, Alaska to Labrador and Chihuahua (Map 4). The easternmost record is Cartwright, Labrador, 7 July 1955, ♂ (E.E. Sterns, CNC). Another record is from Pennsylvania, Luzerne Co., Coyningham, ♂, 17 May 1923 (W.G. Dietz in the Academy of Natural Sciences, Philadelphia). The specimen was examined in 1968 but could not be located in 1977.

Aculepeira carbonarioides (Keyserling) Plate 7; Figures 162–173, 182–186; Map 4

Epeira carbonaria:—Emerton, 1884, Trans. Connecticut Acad. Sci., 315: pl. 33, fig. 18, pl. 36, figs. 18, 19, ♀, ♂. Emerton, 1894, Trans. Conn. Acad. Sci., 9: 405, pl. 1, fig. 4b, ♀, 4d, ♂. Misidentification, not *A. carbonaria* (L. Koch).

Epeira carbonarioides Keyserling, 1892, Spinnen Amerikas, 4: 206, pl. 10, fig. 152, ♀. Female holotype from Clear Creek, Colorado (Marx collection) in the National Museum of Natural History, Washington, examined. McCook, 1903, American Spiders, 3: 158, pl. 5, fig. 9, ♀, ♂.

? *Araneus hyperboreus* Kulczynski, 1908, Zap. imp. Akad. Naouk, (8) 18: 45, fig. 58, ♀. Female holotype from Dolgulach River, central Siberia, probably in Polish Academy of Sciences, Warsaw, lost. PROBABLE NEW SYNONYMY.

? *Aranea* (*Epeira*) *charitonovi* Ermolajew, 1928, Zool. Anz., 77: 209. Specimens from Karagai, 1000 m elev. and Chasinicha River, 3000 m elev., Altai Mountains, USSR, deposition unknown.

Araneus vegae Holm, 1970, Entomol. Scandinavica, 1: 198. Male holotype and female allotype from Nun'amo, St. Lawence Bay [Nunyamo], Siberia in the Natural History Museum, Stockholm, examined. NEW SYNONYMY.

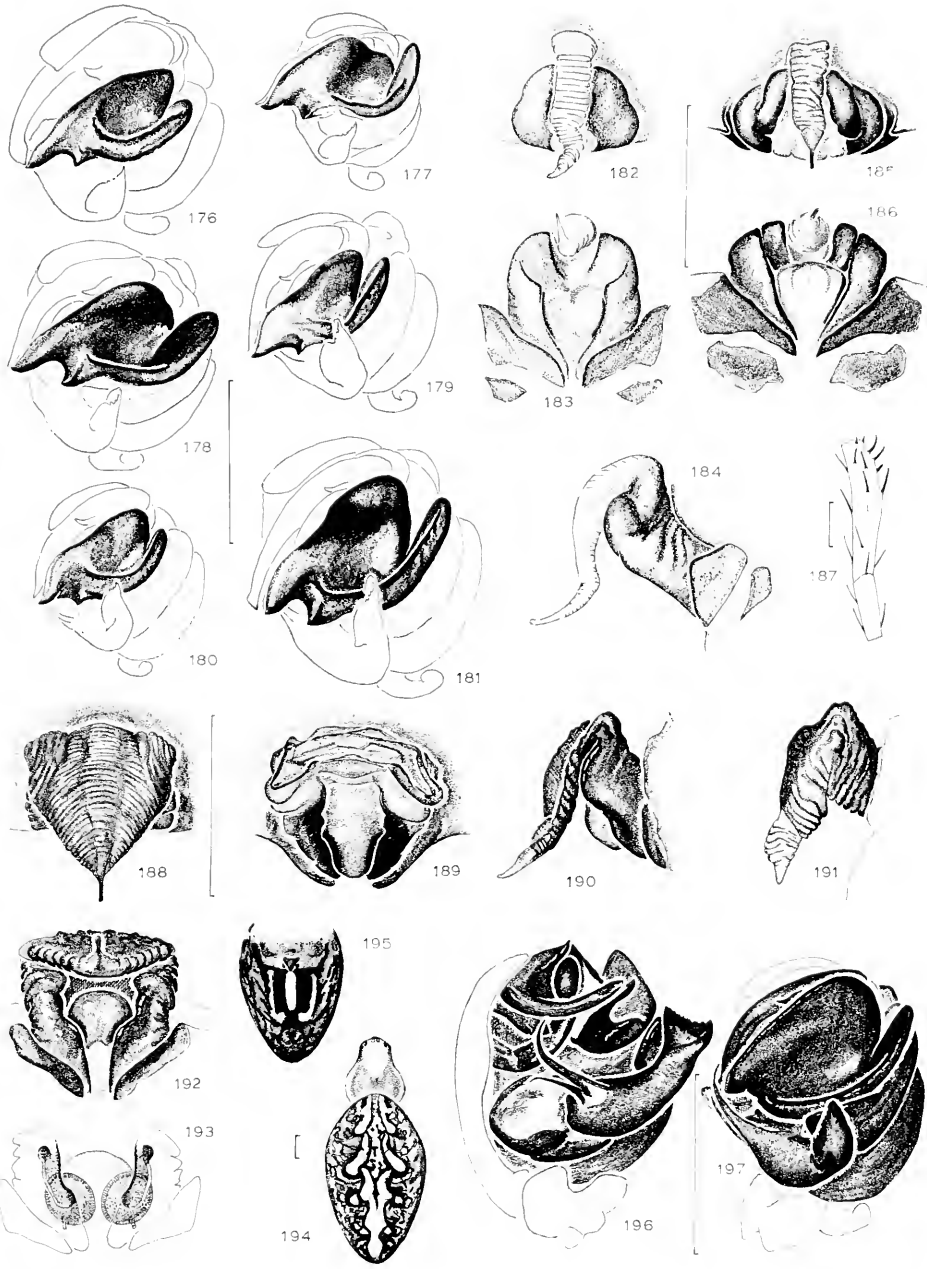
Note. There is little doubt that Clear Creek [County], Colorado (unlike other Marx localities) is correct. The illustration Figures 182–184 are made from the types of *A. carbonarioides*. Specimens of this species from some collections had been labeled *Aranea aculeata*. Kulczynski's illustration of *A. hyperboreus* fits this species. *A. charitonovi* differs from *A. carbonaria*, according to the author, by having a narrower scape; in addition, the illustration fits *A. carbonarioides*. Ermolajew considered the species distinct from *A. hyperboreus* because of larger size; but the size varies widely in this species.

Description. Female from Colorado: head region light yellow-brown. Sides of thorax dark blackish brown with light border. Dorsum of abdomen very dark, covered by patches of light pigment and by tiny white pigment spots, also covered with lots of setae (Fig. 166). Anterior margin of chelicerae with four teeth, the second one from the fang base small; posterior margin

→

Figures 176–181. *Aculepeira packardi* (Thorell), variation of conductor of left male palpus, ventral view. 176. (Kamchatka). 177. (Labrador). 178. (northern British Columbia). 179. (Mohave Desert, California). 180. (Washington). 181. (Arizona).

Figures 182–186. *A. carbonarioides* (Keyserling), variation of epigynum. 182, 185. Ventral. 183, 186. Posterior. 184. Lateral. 182–184. (Clear Creek, Colorado). 185–186. (Grand Teton Mountains, Wyoming).



Figures 187–197. *A. ceropegia* (Walckenaer) (France, Fig. 191 Switzerland). 187. Left male second patella and tibia, dorsal. 188–193. Epigynum: 188. Ventral. 189. Ventral, scape torn off. 190–191. Lateral. 192. Posterior. 193. Posterior, cleared. 194. Female, appendages removed. 195. Female abdomen, ventral. 196, 197. Left male palpus: 196. Mesal. 197. Ventral.

Scale lines. 1.0 mm.

also with four teeth. Total length 12.8 mm. Carapace 4.8 mm long, 3.9 mm wide. First femur, 5.3 mm; patella and tibia, 6.3 mm; metatarsus, 4.7 mm; tarsus, 1.6 mm. Second patella and tibia, 5.8 mm; third, 3.6 mm; fourth, 5.3 mm.

Male from Colorado colored like female. Anterior margin of chelicerae with four teeth, posterior with three on one side, four on other. Total length 8.6 mm. Carapace 4.9 mm long, 4.1 mm wide. First femur, 6.3 mm; patella and tibia, 8.4 mm; metatarsus, 6.1 mm; tarsus, 1.5 mm. Second patella and tibia, 6.6 mm; third, 3.6 mm; fourth, 5.8 mm.

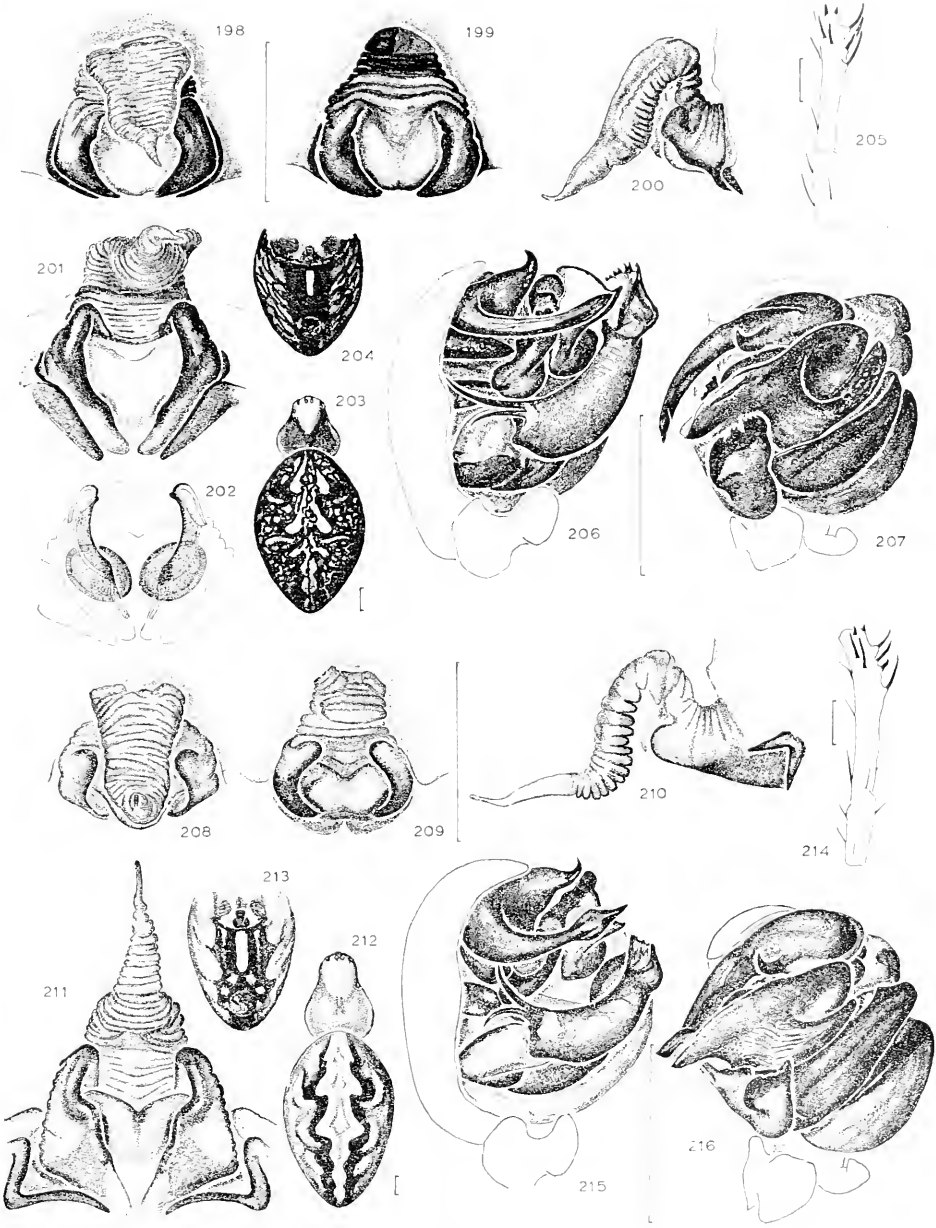
Variation. The coxae may be light or dark or partly dark. The abdominal color pattern is variable (Figs. 166, 167). Total length of females 6.2 (New Hampshire) to 15.0 mm (Colorado), carapace 2.6 to 5.4 mm long, 2.0 to 4.5 mm wide. Total length of males 6.0 (New Hampshire) to 9.1 mm (Colorado), carapace 3.0 to 4.7 mm long, 2.6 to 3.8 mm wide. Alaska and New Hampshire specimens are smallest. New Hampshire males have an embolus that is shorter and wider, with a base more swollen and a tip slightly different from specimens in other localities. On the New Hampshire specimen's embolus tip, the distal teeth seem reduced to denticles and there is an opening of a short filiform portion. In contrast, the opening of Rocky Mountain males is on the top of a short flat portion (e in Fig. 173). Unfortunately there are no males from the northern Rocky Mountains, Alaska or the Arctic in the collections. Perhaps there are several species. But no consistent differences were found in epigyna; differences found (Figs. 182–186) did not vary with the abdominal color pattern, or other characters.

Diagnosis. Like *A. packardi*, this species can be confused with *Neoscona oaxacensis* (Keyserling), again because of the similar abdomen shape and dorsal pattern (Figs. 166, 167). The differences in the white ventral streak (Fig. 168) separate the two. However, the abdomen, unlike that of *A. packardi*, does not have the lobes of the median band posteriorly directed (Figs. 166, 167). The scape of the epigynum is not torn off and is variable in shape but less than a third the width of the base (Figs. 162, 182, 185), and the conductor of the palpus is about three times as long as wide and lacks a ventral lip (Figs. 170, 172). The similar European *A. carbonaria* differs by having a wider scape (Figs. 198, 201) and differently shaped conductor of the palpus (Fig. 207).

Natural History. This species is fairly common in western Colorado where it makes its web between boulders of talus slopes, below and at the timber line (Plate 7). The web forms an angle with the vertical and the spider rests in the center, dropping out of the web at the slightest disturbance. It is then difficult to retrieve since the creature escapes down among rocks. After a few minutes, if undisturbed, it will climb back to the web by means of a thread it pulled out while falling. I have not seen the spider sit on stones on the side of the web. The web sites, 3000 to 3600 m elevation, probably have extremes of temperature in July from below freezing at night to up to 30° C during the day.

The species has been collected in Alaska "between rocks in pika [*Ochotona* sp.] area"; "among rocks at 1900 m" in the Yukon. The lowest elevation at which it has been collected in the American Rocky Mountains was in the Grand Tetons at 2800 m elevation. There are few males in collections, reflecting the difficulties of collecting spiders among the boulders.

Distribution. Central Siberia, Alaska to southern Rocky Mountains (Map 4) (apparently absent from the coast range) in the east on the Gaspé Peninsula and on Mount Washington, New Hampshire; both are areas that escaped glaciation and share many plant relicts. The easternmost record is from Mt. Cartier, Gaspé Peninsula, Quebec, 5 July 1959, ♀ (G. Argus, MCZ) at 1220 m in spruce-fir. Numerous records



Figures 198–207. *Aculepeira carbonaria* (L. Koch) (Switzerland. Fig. 200, Tyrol). 198–202. Epigynum: 198. Ventral. 199. Ventral, scape torn off. 200. Lateral. 201. Posterior. 202. Posterior, cleared. 203. Female dorsal, appendages removed. 204. Female abdomen, ventral. 205. Left second patella and tibia of male, dorsal. 206, 207. Left male palpus: 206. Mesal. 207. Ventral.

Figures 208–216. *A. armida* (Audouin) (Spain). 208–211. Epigynum: 208. Ventral. 209. Ventral, scape torn off. 210. Lateral. 211. Posterior. 212. Female, appendages removed. 213. Female abdomen, ventral. 214. Left second patella and tibia of male, dorsal. 215, 216. Male palpus: 215. Mesal. 216. Ventral.

Scale lines. 1.0 mm.

exist of specimens found between boulders on Mount Washington.

Aculepeira ceropegia (Walckenaer) new combination
Figures 175, 187–197

Aranea ceropegia Walckenaer, 1802, Faune Parisienne, 2: 199. Female specimens from Paris, France, lost. Wiehle, 1931, Tierwelt Deutschlands, 23: 100, figs. 151–155, ♀, ♂. Roewer, 1942, Katalog der Araneae, 1: 783.

Araneus ceropegius:—Bonnet, 1955, Bibliographia Araneorum, 2(1): 454 (European records only).

? *Araneus vachoni* Karol, 1964, Bull. Mus. Nat. d'Hist. Natur., ser. 2, 36: 188. Female holotype from near Ankara, Turkey, in the Muséum National d'Histoire Naturelle, Paris, examined. PROBABLE NEW SYNONYMY.

Note. This is a widespread Eurasian species that has not been found in North America. *Araneus vachoni* appears to be this species: the torn off base of the scape is as wide as that of *A. ceropegia*, the middle area is sclerotized and the abdominal pattern is characteristic. Only by finding a specimen with the scape intact, however, can the synonymy be determined.

Diagnosis. This species is very similar to the American *A. packardi*, having paired, upside-down, comma-shaped marks on the abdomen (Fig. 194). It can be separated from that species by the triangular scape of the female epigynum (which is frequently torn off), by the slightly sclerotized median area of the epigynum (Figs. 188–192) and by the very wide, deep conductor of the male (Fig. 197).

Natural History. According to Wiehle (1931) *A. ceropegia* is found in open areas with the web 50 cm above the ground; it is especially abundant in the foothills of the Alps, the Pyrenees and in the higher mountains to 3000 m. It is known from Scandinavia to the Mediterranean area.

Examined Specimens. Sweden. ♀ (NRS). *Germany.* Bremen, ♀ (SMF); Hessen: Eschwege, ♀ (H. Homann, SMF); Bavaria: Obersdorf, ♀ (SMF). *Austria.* Tirol. Weissenbach, ♂ (H. Wiehle, SMF). *Switzerland.* Zermatt, ♀, ♂ (SMF); Wallis: Frisch, ♀, ♂ (E. Schenkel, AMNH); Uri: Susten Pass, 2232 m, 1875–1876, ♀ (J. H. Emerton, MCZ). *France.* Col de Portet d'Aspet, juv. (E. Crosby, CU); Dept. Pyrenées Hautes: Lac d'Oo, 27 July 1932, ♀ (E. Crosby, CU); Dept. Pyrenées Orientales: Cerdagne many collections, 1976 (H. Zibrowius, MCZ); Dept. Vaucluse: Luberon Mt., July 1976, ♀ (H. Zibrowius, MCZ); near Marseille, Aug. 1976, ♀ (H. Zibrowius, MCZ). *Italy.* Garda, ♀, ♂ (BMNH); Venice, 24 Aug. 1932, ♂ (E. Crosby, AMNH). *Spain.* San Lorenze de El Escorial, ♀ (CU). *Yugoslavia.* Ipek [Pec], ♀ (SMF).

Aculepeira carbonaria (L. Koch)
Figures 198–207

Epeira carbonaria L. Koch, 1869, Z. Ferdinandeum, Tirol, third ser., 14: 168. Female specimens from Kütthai, Finstertal, Tirol., believed lost.

Aranea carbonaria:—Roewer, 1942, Katalog der Araneae, 1: 797.

Araneus carbonarius:—Bonnet, 1955, Bibliographia Araneorum, 2(1): 451 (European records only).

This species is known only from European mountains.

Diagnosis. The coloration is dark (Fig. 203), resembling the American *A. carbonarioides*. *Aculepeira carbonaria* usually lacks the paired light marks on the venter to the side of the median white stripe (Fig. 204). The scape of the epigynum is wider (Figs. 198–201) than that of *A. carbonarioides*, longer than that of *A. ceropegia* (Fig. 200) and the median area of the base is white (Figs. 199, 201); the palpal terminal apophysis tapers to the tip (Fig. 206), unlike that of *A. armida*. The conductor is relatively narrow with a deep distal depression (Fig. 207); it differs from that of *A. ceropegia* but is somewhat similar to that of *A. armida*.

Natural History. Aculepeira carbonaria, as far as is known, is also limited to talus slopes in the high mountains.

Specimens Examined. Austria. Tirol: Stubai, ♀, ♂ (L. Koch, BMNH). *Switzerland.* Wallis: Saas Tal, ♀, ♂ (E. Schenkel,

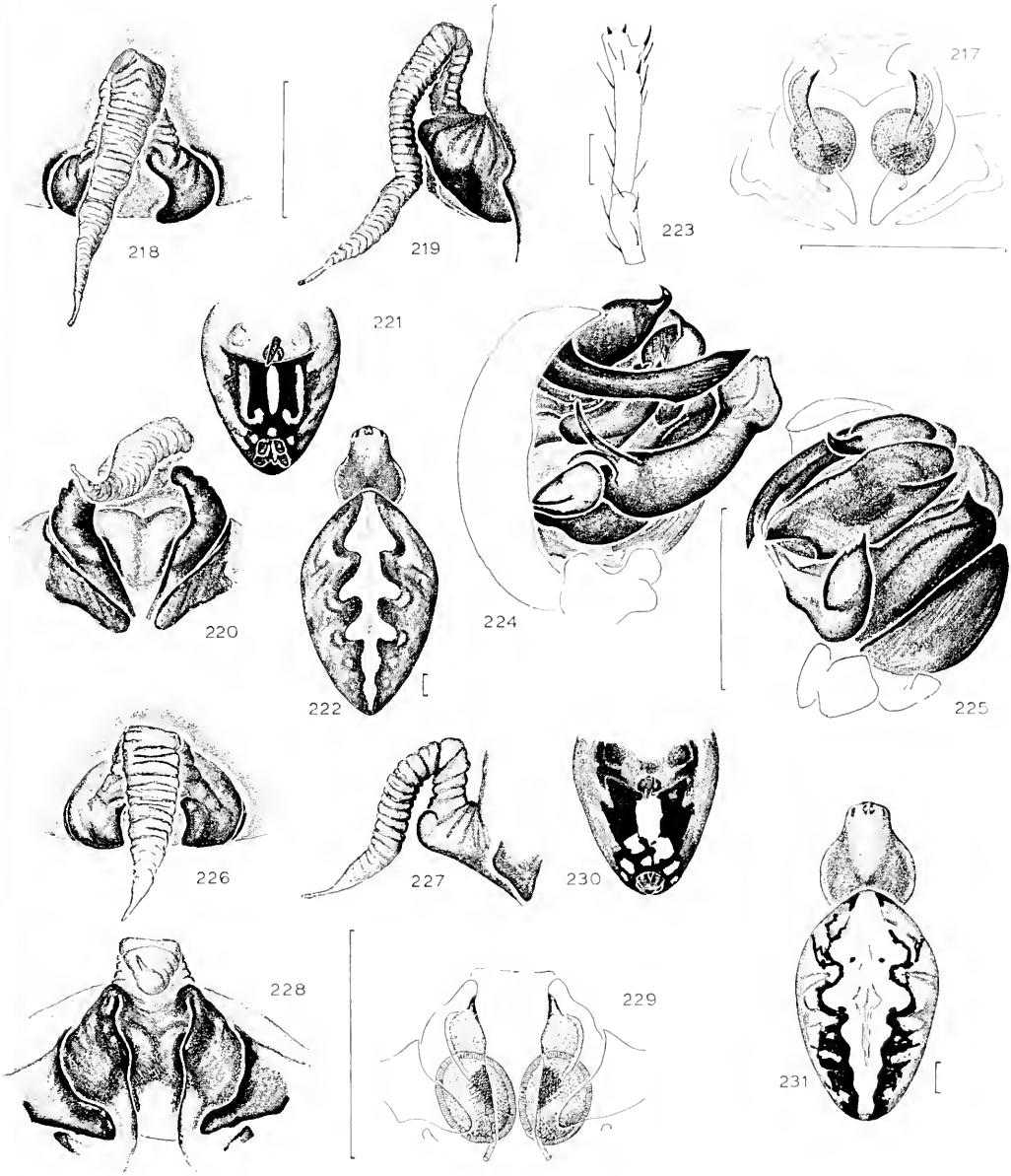


Figure 217. *Aculepeira armida* (Audouin) (France). Epigynum, posterior view, cleared.

Figures 218–225. *A. noseki* (Strand) (Turkey). 218–220. Epigynum: 218. Ventral. 219. Lateral. 220. Posterior. 221. Female abdomen, ventral. 222. Female, dorsal appendages removed. 223. Male left second patella and tibia, dorsal. 224, 225. Male left palpus: 224. Mesal. 225. Ventral.

Figures 226–231. *Aculepeira* sp. (Samarkand). 226–229. Epigynum: 226. Ventral. 227. Lateral. 228. Posterior. 229. Posterior, cleared. 230. Female abdomen, ventral. 231. Female, dorsal, appendages removed.

Scale lines. 1.0 mm.

AMNH); Bern: Gemmi Pass, ♀ (J.H. Emerton, MCZ). *France.* "montagne," ♀ (E. Simon, MCZ).

Aculepeira armida (Audouin), new combination
Figures 208–217

Epeira armida Audouin, 1825 in Savigny, Explication sommaires des Planches d'Arachnides, in Savigny, Description de l'Egypte, p. 126, pl. 2, fig. 8, ♀. Specimens from France, Italy and vicinity of Acre [now northern Israel], lost. I here restrict the type locality to southern France.

Aranea armida:—Roewer, 1942, Katalog der Araneae, 1: 782.

Araneus armidus:—Bonnet, 1955, Bibliographia Araneorum, 2(1): 439.

Note. This Mediterranean species has not been found in America.

Diagnosis. The species can be recognized by the lobed dorsal abdominal band, enclosing a dark mark and having a black band on each side (Fig. 212). It differs from the similar *Neoscona adianta* (Walckenaer) by having a median ventral white spot (Fig. 213); *Neoscona* has two or four paired white marks on the venter. The epigynum differs from related species by the relatively long scape (Fig. 210), by the median lobe on each side of the base (Figs. 208, 209, 211), and by the thin elongate lamellae bent at right angles behind the base in posterior view (Fig. 211). The palpus differs by having the tip of the terminal apophysis wider than the neck (Fig. 215), and by the shallow conductor, which has distally a deeper area (Fig. 216).

Natural History. The species has been collected by sweeping prairies with isolated tufts of high grass in Italy and from grazed fields and brush and cypress-pine woods in Yugoslavia. Wiehle (1931) reports the species from low brush or grasses with the hub located, at most, at 50 cm above the ground. The web has a white, silk-covered hub and the retreat is flat, dish-shaped and open.

Collections Examined. Switzerland. Valais: Valère near Sion, ♀, ♂ (NMB). *France.* Luminy Col de Sugiton near Marseille, 16 June 1976, ♀ (H. Zibrowius, MCZ). *Spain.* San Lorenz de Escorial, ♀, ♂ (CU); Sevilla, ♀ (NMB). *Italy.* Calabria Prov. Aspromonte, ♀ (E. Reimoser, MCZ); Lazio Prov. Monteromano, 21 June 1965, ♂ (P.M. Brignoli). *Sardinia.* ♀, ♂ (SMF). *Yugoslavia.* Istria: 5 km northwest of Vodrijan, 27 June 1962, ♂ (H. & L. Levi, MCZ); Dalmatia: Srebreno near Dubrovnik, 13 June 1962, ♀ (H. & L. Levi, MCZ). *Greece.* ♀ (BMNH). *Tunisia.* El Kairovan, ♂.

Aculepeira noseki (Strand), new combination
Figures 218–225

Araneus similis Nosek, 1905, Ann. Kais. Königl. Naturhist. Hofmus. Wien, 20: 131. Numerous female, male syntypes marked *A. kariae* from Erdschias-Dagh [Erciyas Dağe Mountain] Turkey in very poor physical condition in Naturhistorisches Museum, Wien, examined. (Name preoccupied by *Epeira similis* Taczanowski, 1873 and *Epeira similis* Bösenberg and Lenz, 1894).

Araneus noseki Strand, 1907, Zool. Jahrb. Abt. System., 24: 396. New name for *A. similis* Nosek, preoccupied.

Aranea kariae:—Roewer, 1942, Katalog der Araneae, 1: 788. Roewer cites Strand, 1919, without further citation.

Araneus karapagi Karol, 1966, Comm. Facult. Sci. Univ. Ankara, 10(ser. C): 111, figs. 1–28, ♀. Female from Hakkâri, Karadağ, Turkey, in the Muséum National d'Histoire Naturelle, not examined. NEW SYNONYMY.

Diagnosis. The female differs from *A. armida* in the more pronounced lobes of the abdominal dorsal band, the coloration is less contrasting (Fig. 222), and there are straight lamellae that are posterodorsal from the epigynum (Fig. 220); the male differs by having a half-spear-shaped tip of the terminal apophysis (Fig. 224).

Natural History. This species is also found in talus at and above timberline (K. Thaler, personal communication).

Collections Examined. Turkey. Erzurum-Palandöken, 2400 m elev., 8 Aug. 1970, ♀, ♂ (V. Sbordone, PB); Altiparmek, 2400 m, 30 Aug. 1964, ♀, ♂ (KT); Lasistan, Cigunet Yayla, 2500 m, 20 Aug. 1968, ♀ (H.

Gall, KT); Verschambek, 2800 m, 11 Aug. 1965, ♀ (H. Gall, KT).

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Bulletin OF THE
Museum of
Comparative
Zoology

Systematics and Zoogeography of *Plagiola* (= *Dysnomia* = *Epioblasma*), an Almost Extinct Genus of Freshwater Mussels (Bivalvia: Unionidae) from Middle North America.

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VOLUME [illegible] NUMBER [illegible]
[illegible] APRIL 1973

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

BREVIORA 1952–
BULLETIN 1863–
MEMOIRS 1864–1938
JOHNSONIA, Department of Mollusks, 1941–
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SYSTEMATICS AND ZOOGEOGRAPHY OF *PLAGIOLA* (= *DYSNOMIA* = *EPIOBLASMA*), AN ALMOST EXTINCT GENUS OF FRESHWATER MUSSELS (BIVALVIA: UNIONIDAE) FROM MIDDLE NORTH AMERICA.

RICHARD I. JOHNSON[1]

CONTENTS

Abstract. *Plagiola* (= *Dysnomia* = *Epioblasma*), a genus of Unionidae (Mollusca: Bivalvia) is unique among all freshwater mussels in the extent of sexual dimorphism found among its members. The 17 species recognized here are assigned to 5 subgenera. All but one species, found in the Mobile-Alabama-Coosa river system in Alabama, occur in the Tennessee River system, and that species is clearly derived from one in the latter system. Fourteen of the species are also found in the Cumberland River system. Three of these fourteen are also found in the White River system on the Ozark Plateau in Missouri and Arkansas. These three species, as well as a number of other similarly distributed unionids, afford evidence of a

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relict fauna that may have persisted since the Cretaceous. The post-glacial distribution of several of the species that have found their way beyond the Tennessee and Cumberland river systems suggests that all the species are of Cumberlandian origin.

INTRODUCTION

Among the numerous genera of Unionidae, *Plagiola* is one of the more interesting because of the extent and variety of sexual dimorphism among the 17 species belonging to 5 subgenera. Many of the species vary but slightly, though several have numerous ecophenotypic varients. Some forms, formerly recognized as valid species or subspecies, could not be properly dealt with before the biological species concept was defined. This paper attempts to clarify the synonymy of the species of *Plagiola* and to reconstruct what was, until a short time ago, their distribution. To do this, most specimens in the principal museums were examined. These records are supplemented with some only available in the literature. Almost a dozen of the species are now considered extinct or endangered from pollution, or because their habitats have been, or are being, destroyed by impoundments.

BACKGROUND

The members of *Plagiola* were first monographed and separated from *Unio* by Simpson (1900a: 524), who placed them in the genus *Truncilla* Rafinesque 1820. His designation of *Truncilla triqueter* Rafinesque as the type was invalid, since *Truncilla truncata* Rafinesque had previously been designated as the type by Herrmannsen (1849, 2: 627). Therefore, Ortmann and Walker (1922: 65) designated *Dysnomia* Agassiz 1852 as the next available generic taxon, whose type species was *Unio foliatus* Hildreth (= [*Obliquaria*] *flexuosa* Rafinesque) by subsequent designation (Simpson 1900a: 521). They made this designation since they regarded the type species of both *Plagiola* Rafinesque 1820 (*Obliquaria* (*Plagiola*) *interrupta* Rafinesque) and *Epioblasma* Rafinesque 1831 (*E. biloba* Rafinesque) as unidentifiable, though Frierson (1914) had previously asserted that *biloba* was the female of *foliatus* Hildreth. Thiele (1934), Clench (1959), Morrison (1969) and Stansbery (1973), used *Epioblasma* over *Dysnomia.* Stansbery (pers. com.) assured me that he can recognize *biloba.* To settle this matter, a neotype was chosen for it here, see p. 283. However, Johnson and Baker's (1973:159) selection of a lectotype for *Obliquaria* (*Plagiola*) *interrupta* Rafinesque, which Morrison (1969) had previously asserted as identifiable, makes *Plagiola* the earliest available generic taxon, with *Epioblasma* (=*Dysnomia*) as a subgenus.

These nomenclatorial changes are unfortunate, but we now have *Rules of International Nomenclature* (1964), not available to Ortmann and Walker, which emphasize the identification of the type. As Stansbery (pers. com.) has said, "Ortmann and Walker (1922) did a fine job for their time in consideration of their basic premise that the validity of a name depends upon its identifiability from the original description. I consider the identification of the holotype (if extant) to be the court of last appeal in such matters. If we did not, most of Lamarck's [unionid] names now in use would become *nomina dubia.*"

The most recent revision of the *Rules* [1974. Bull. Zool. Nomencl. *31* (2): 80] under Article 23 states, "A zoologist who considers that the application of the Law of Priority would in his judgment disturb stability or universality or cause confusion is to maintain the existing usage and must refer the case to the Commission for a decision under the plenary powers [Art. 79]."

It is hoped that in this paper, the identity of the specific taxa of *Plagiola* are settled. It is unfortunate that some of these identifications also result in changes on the generic and subgeneric level. However, Morrison (1969) declared *Plagiola* available over *Dysnomia*, and Stansbery has used *Epioblasma* over *Dysnomia* numerous times

in the literature. Since this author is not sure what *is* existing usage in *Plagiola*, this paper is written on the assumption that the Law of Priority has not been totally abrogated.

Simpson (1900a: 516–524) recognized four subgenera within this genus. Ortmann and Walker (1922: 65) created monotypic *Truncillopsis*, based on the former's studies of the very primitive anatomy of *triquetra*. Frierson (1927: 93–96) added three additional subgenera. These were based entirely on conchological characters, merely by selecting a type species for each, without explanation. In spite of this method, two of his subgenera are recognized here, *viz. Plagiola* Rafinesque s. s. [=*Penita* Frierson] and *Torulosa* Frierson [=*Capsaeformis* Frierson].

Walker (1910) constructed an excellent key to the species, as he conceived them. Simpson (1914) augmented his previous arrangement (1900a) with species descriptions. Haas (1969: 477–490), in *Das Tierreich*, wrote on *Dysnomia* [=*Plagiola*]. His subgeneric and specific concepts are those of Frierson, and his descriptions appear to be essentially German translations of Simpson (1914: 2–32). Haas's work is a compilation of the literature on this genus to 1927. Burch (1973, 1975) included the species as recognized by Simpson in a general key to the North American Unionacean clams.

RELEVANT FAUNAL STUDIES

The unionid fauna of the upper Tennessee River system was commented on by Coker (1912), studied extensively by Ortmann (1918), and reexamined by Stansbery (1973) and Stansbery and Clench (1975). The lower Tennessee, below Walden Gorge, to the Muscle Shoals in Lauderdale and Colbert counties, Alabama, was extensively studied by Ortmann (1925) and augmented with notes by van der Schalie (1939b). Morrison (1942) compared the fauna found in the Indian mounds near the Muscle Shoals with the present fauna in the river. Isom (1968) and Isom and Yokley (1968) enumerated the unios of Indian Creek and Bear Creek tributaries of the Tennessee in Alabama. Duck River, a tributary of the lower Tennessee, was carefully studied by Ortmann (1924a), restudied by Isom and Yokley (1968) and re-restudied by van der Schalie (1973).

The Cumberland River unionids were studied by Wilson and Clark (1914). Those of the upper part of the river were examined again, between 1947–49, by Neel and Allen (1964) before the completion of the Wolf Creek Dam.

Studies have been made of the unionid faunas of many of the rivers flowing into the southern side of the Ohio River beyond the Cumberland. These are presented in a west to east arrangement.

The unios of the Tradewater River were listed by Clench and van der Schalie (1944); those of the Green were extensively studied by Ortmann (1926). The Green River species were again listed by Clench and van der Schalie (1944), who also included the Salt River unionids in their paper. The Salt River unionids were listed again by Rosewater (1959). The unionids of the Kentucky River were studied by Danglade (1922), and Ortmann (1913: 290) discussed the species found in the upper Ohio drainage.

Relevant studies of the Ohio River unionids and of those rivers flowing into it on the northern side are presented in a west to east arrangement. The unionid fauna of Kansas was studied by Scammon (1906) and again by Murray and Leonard (1962). Utterback (1915–16) studied that of Missouri, and recently Buchanan (ca. 1976) studied that of the Meramec River basin in the same state. Baker (1928) wrote on the unionids of Wisconsin. Parmalee (1967), in a popular paper on the Unionidae of Illinois, included data on *Plagiola*, as did Starrett (1971) in his work on the Unionacea of the Illinois River. Stein (1881) enumerated the mollusca of Indiana; these were

monographed by Call (1900). Call's work was supplemented by Blatchley and Daniels (1903) and Daniels (1915). The Indiana mollusca were subsequently revised by Goodrich and van der Schalie (1944). Meyer (1974) studied the unionid fauna of the Wabash and White rivers in Indiana, and Clark (1976) examined the unionids of the lower Wabash River. Baker (1922) had previously studied the molluscan fauna of the Big Vermilion River, a large tributary of the Wabash. Goodrich (1932) wrote a handbook on the mollusca of Michigan and included data on *Plagiola.* La Rocque (1967) compiled a work on the Unionidae of Ohio.

Wilson and Clark (1912b) reported on the extensive collection of naiades they made in the Maumee River drainage, which is tributary to Lake Erie. Clark (1977) wrote on the naiades of the St. Joseph River of the Maumee. Ortmann (1924b) in a paper on the distributional features of the naiades in the tributaries of Lake Erie, discussed the post-glacial dispersal of the species, as did Goodrich and van der Schalie (1932), who studied the unionids of the Great Lakes. The post-glacial dispersal of unionids to Lake Erie was again reviewed by Stansbery (1961).

Van der Schalie made further contributions to the understanding of post-glacial dispersion in his papers on the unionid faunas of the Muskegon, Grand (*both* 1941a), St. Joseph (1936) and Huron (1938a) river drainages in Michigan. In a paper discussing the value of mussel distribution in tracing stream confluence, van der Schalie (1945) summarized the data about the post-glacial dispersal of the Unionidae.

The unionid fauna of several drainages of the Mobile-Alabama-Coosa river system have been studied. The unionids of the Cahaba and Tombigbee rivers were examined by van der Schalie (1938b, 1939a), and those of the Coosa River by Hurd (1974).

ZOOGEOGRAPHY

General Considerations

It should be mentioned to the reader unfamiliar with the means of dispersal of the Unionidae, that their mobility is passive—dependent on fishes to which the larval forms, or glochidea, attach themselves for a period of time. Stream capture, and subsequent rupturing of confluences, have therefore played a significant role in determining the geographic distribution of the Unionidae.

The Tennessee and Cumberland river systems are among the world's most ancient. The Tennessee, containing at least 86 species of Unionacea, has the largest assemblage of unionid species found anywhere, followed by the Cumberland River, which has a unionid fauna of at least 78 species.

Ortmann (1924a: 40) recognized among the Unionidae two distinct faunal elements in these two river systems—those belonging to the Interior Basin and found in the Ohio River drainage, and those not found outside the Tennessee and Cumberland river systems. (There are a few exceptions that also occur on the Ozark Plateau). This latter group of species is restricted largely to the Cumberland Plateau and to the Great Allegheny Valley. This area represents the Cumberlandian Region, defined by Ortmann (1924a: 40) as including only the drainages of the Tennessee River system from the headwaters to the vicinity of Muscle Shoals, in Colbert and Lauderdale counties, Alabama; and the Cumberland River system from the headwaters to the vicinity of Clarksville, Montgomery County, Tennessee (Ortmann, 1925: 366). Ortmann (1924a: 40) also discussed the unionid fauna of the Duck River drainage, which is at present a tributary of the Tennessee River system. The upper portion of the Duck River has a fauna that is 38 per cent Cumberlandian, and Ortmann suggested that this was the original fauna and that there had been stream confluence with the

Duck and both the Tennessee and Cumberland river systems long ago.

The distribution of the old Interior Basin fauna in the Tennessee and Cumberland river systems indicates that most of it was present in these rivers, along with the even more ancient Cumberlandian fauna, long before maximum Pleistocene glaciation (which occurred early in the epoch and extended southward roughly to the present Missouri and Ohio rivers). Apparently many members of the former fauna, and some of the latter, repopulated at least the present Ohio and upper St. Lawrence river systems from these sources. Some of the species may also have had refugia elsewhere, as in the Allegheny and Monongahela rivers in Pennsylvania (Ortmann, 1912b).

Originally Ortmann (1924a: 40) regarded as Cumberlandian only those unionid species currently confined to the areas of the Tennessee and Cumberland river systems, as defined above. Later (1925: 370) he suggested there were Cumberlandian species that descended the Tennessee and Cumberland river systems and invaded the Ohio River drainage and the Interior Basin.

Distribution of *Plagiola* below the area Maximum Glaciation

All of the species of *Plagiola*, with the exception of *penita* from the Mobile-Alabama-Coosa river system in Alabama, occur in the Tennessee River system, and only two of these, *torulosa* (Plate 3) and *sampsoni* (Plate 6, fig. B) are missing in the Cumberland River system.

Three species, *triquetra* (Plate 1), *turgidula* and *florentina* (*both* Plate 2), are found not only in the Tennessee and Cumberland river systems, but also in the White River system in Missouri and Arkansas, south of the Ozark Crest, where they may have persisted since before the Cretaceous uplift. One of these species, *triquetra*, is also found north of the Ozark Crest in the Meramec River, Missouri, and in tributaries of the present Missouri River in Kansas.

Another species, *Cumberlandia monodonta* (Say), of the family Margaritiferidae, is found in both the Tennessee and Cumberland river systems and north of the Ozark Crest in the Osage and Gasconade rivers in Missouri. Like *triquetra*, it appears to have had refugia here from glacial destruction. The members of *Cyprogenia* and a number of other unionid species have the same restricted distribution as *florentina* and *turgidula*, but they are beyond the scope of this paper.

Seven species of *Plagiola*—*interrupta* (Plate 7, fig. A), *capsaeformis* (Plate 7, fig. B), *lenior* (Plate 7, fig. C), *haysiana* (Plate 8, fig. A), *arcaeformis* (Plate 8, fig. B), *stewardsoni* (Plate 8, fig. C) and *biemarginata* (Plate 9, fig. A)—are found in both the Tennessee and Cumberland river systems exclusively.

Plagiola penita of the Mobile-Alabama-Coosa river system is derived from *interrupta* of the Tennessee River system. Hayes and Campbell (1894) suggested that the upper Tennessee River formerly flowed through Walden Gorge into the Gulf of Mexico by way of the present Mobile-Alabama-Coosa river system, and that it was diverted to its present course through the Cumberland Plateau in the late Tertiary. Their conclusions, based entirely on physiographic evidence such as the character of the Tennessee-Coosa divide, were substantiated by Simpson (1900b) on the basis of similarities in the unionid faunas of the present river systems.

Johnson (1905) effectively defeated all support for the river capture theory of Hayes and Campbell. The upper Tennessee appears to have held the same course since the close of the Cretaceous. However, "where the smaller tributaries of the Coosa and Tennessee rivers have common divides in the carbonate rocks of the Appalachian Valley, it is highly probable that many captures have occurred and effected the faunal transfers which have been formerly attributed to the Walden Gorge capture." (Hurd, 1974: 137).

Post-glacial Distribution of *Plagiola*

Maximum Pleistocene glaciation occurred early in the epoch, and extended southward to roughly the present Missouri and Ohio rivers. Much of the unionid fauna found on the Cumberland Plateau is the same as that found on the Ozark Plateau, and it is assumed that the latter area was as an important source for the species that repopulated the Mississippi drainage (above the Missouri), as was the former in the repopulation of the Ohio drainage. Ortmann (1913: 351) observed that the unionid fauna of the Ohio River is more numerous downstream. There are some 60 species in the vicinity of Cincinnati, Hamilton County, Ohio, decreasing to 47 species in Pennsylvania. Ortmann suggested that this fauna migrated upstream in glacial and post-glacial time when the present Ohio River was formed. The unionid fauna of the larger tributaries of the Ohio River drainage in Kentucky, beyond the limit of glaciation, is Ohioan. From west to east, the tributaries are: the Tradewater with 17 species, the Green with 50 species, the Salt with 22 species (*all* Clench and van der Schalie, 1944), the Kentucky with 40 species (Danglade, 1922), the Licking with 14 species and the Big Sandy with 12 (*both* Ortmann, 1913).

Plagiola triquetra is the only member of the genus found in the Mississippi River drainage. While it may have spread there from the Ohio River, it is just as likely that it spread from a refugium in the Meramec River system, Missouri. In any event, the present distribution of *triquetra* in Wisconsin clearly illustrates van der Schalie's (1945: 336) suggestion that a connection existed in post-glacial time between the Fox and Wisconsin rivers at Portage, Columbia County, Wisconsin (Plate 1, A).

The presence of *triquetra* in the Illinois River, Illinois, and in the Muskegon, Grand and St. Joseph rivers, on the eastern side of Lake Michigan in the St. Lawrence drainage, supports van der Schalie's (1945: 356) suggestion that before the formation of Lake Michigan the latter rivers were tributaries of the Des Plaines River, which by way of the Chicago outlet, drained into the Mississippi River (Plate 1, B). Although *torulosa* is not currently found in the Mississippi River drainage, the species probably reached the Grand River by the same route as that taken by *triquetra* (Plate 3). If it ever occurred in the Cumberland River system, it now appears to be missing.

It is assumed that *triquetra* spread into the Ohio River system from the Tennessee and Cumberland river systems, though it might have also had refugia in the Allegheny and Monongahela river drainages in western Pennsylvania (Ortmann, 1912b), Fig. 1). The distribution of *triquetra* as well as *torulosa* and *obliquata* in the St. Lawrence River system indicates a former connection between the Wabash and Maumee rivers in the vicinity of Fort Wayne, Allen County, Indiana (Plate 1, C, Plate 3, Plate 4). Like *triquetra*, *torulosa* might have had refugia in western Pennsylvania.

The present distribution of *triquetra*, *torulosa* and *obliquata* in the rivers flowing into Lake Erie also indicates the correctness of Ortmann's (1924b) and van der Schalie's (1945: 362) view that during the Trent Outlet stage of the Great Lakes, when Lake Erie was partially dry, many of the present rivers flowing into western Lake Erie were part of the Greater Maumee River system.

Three species, *flexuosa* (Plate 5), *personata* (Plate 6, fig. A), and *propinqua* (Plate 6, fig. B) have spread from the Tennessee and Cumberland river systems into the Wabash River drainage and the Ohio River. An additional species, *sampsoni* (Plate 6, fig. B), missing from the Cumberland River, has a restricted post-glacial distribution similar to *flexuosa* and *personata*.

OBSERVATIONS AND CONCLUSIONS

1. There are 17 species of *Plagiola*; all but one occur in the Tennessee River system. *P. penita* of the Mobile-Alabama-

Coosa river system is clearly derived from *P. interrupta* and provides evidence of a former confluence between the two river systems in the past.

2. The Cumberland River system has 14 of the 16 species found in the Tennessee River system, lacking only *P. torulosa* and *sampsoni*. Obviously, there has been stream confluence between these ancient river systems.

3. There are six species of *Plagiola* in the upper Duck River drainage of the Tennessee River system; only one, *P. triquetra*, is found outside the Tennessee or Cumberland river systems. Ortmann (1924a: 46), on the basis of this and much more data, suggested that Duck River was originally more directly connected with the Tennessee and Cumberland rivers.

4. Two species of *Plagiola*, *turgidula* and *florentina*, occur only in the upper Tennessee and Cumberland river systems and in the upper White River system south of the Ozark Crest in Missouri. The presence of these species in the latter system as well as *P. triquetra* and several other unionid species (not discussed in this paper), strongly suggests that a number of species have persisted since the Cretaceous uplift.

5. Seven species of *Plagiola*, found in the Tennessee River system, have spread into the formerly glaciated area. Two of these, *P. triquetra* and *torulosa*, may have had Pleistocene refugia in the Allegheny and Monongahela river drainages in the mountainous region of western Pennsylvania. *Plagiola torulosa* and *sampsoni* do not occur in the Cumberland River system. Thus only five species of *Plagiola: triquetra*, *propinqua*, *personata*, *obliquata* and *flexuosa*, may have spread into the once glaciated area from the Cumberland River system.

6. The present distribution of *P. triquetra* in Wisconsin suggests that a connection once existed in post-glacial time between the Fox and Wisconsin rivers at Portage, Columbia County, Wisconsin.

7. The present distribution of *P. triquetra* —in the Illinois River, Illinois, and the Muskegon, Grand (as well as *torulosa* in the latter) and St. Joseph rivers on the eastern side of Lake Michigan in Michigan—indicates that before the formation of Lake Michigan, the latter streams were tributaries of the Des Plaines River, which drained into the Mississippi River by way of the Chicago outlet.

8. The present distribution of *P. triquetra*, *torulosa* and *obliquata* in the St. Lawrence River system indicates that a connection formerly existed in post-glacial time between the Wabash and Maumee rivers in the vicinity of Fort Wayne, Allen County, Indiana.

9. The present distribution of *P. triquetra*, *torulosa* and *obliquata* in the rivers flowing into western and southern Lake Erie indicates that during the Trent Outlet stage of the Great Lakes, when the bed of Lake Erie was partially dry, these rivers were part of the Greater Maumee River system.

10. The most primitive species of *Plagiola*, *triquetra*, appears to be the most abundant as well as the most widely distributed species in the genus. Interestingly, the shells exhibit little morphological variation.

11. Following *Plagiola triquetra*, the most widely distributed species in the genus are *torulosa* and *obliquata*, in that order. The shells of *torulosa* exhibit considerable ecophenotypic variation depending on their environment, while those of *obliquata* show almost no such variation.

12. Three species of *Plagiola*, *arcaeformis*, *stewardiana* and *biemarginata*, appear to be the least abundant as well as the least widely distributed species in the genus. The shells exhibit little morphological variation. All three species are now considered extinct.

ACKNOWLEDGEMENTS

Special thanks are extended to Dr. Joseph Rosewater, National Museum of Natural History, who, in addition to giving me ac-

cess to the collection, had photographs made of all of the relevant types, and to Dr. Arthur H. Clarke for the loan of material. Dr. George M. Davis, Academy of Natural Sciences of Philadelphia, made that collection available and generously loaned types and specimens. Dr. Juan J. Parodiz, Carnegie Museum, Pittsburgh, kindly made that collection available for study. Drs. Henry van der Schalie, John B. Burch and Charlotte Patterson, and Mr. R. W. Hanley, Museum of Zoology, University of Michigan, made the collection in their charge available. Dr. Alan G. Solem, Field Museum, Chicago, graciously loaned specimens and answered questions. Thanks are also extended to Dr. David H. Stansbery, Ohio State Museum, for several data on *Plagiola*, a genus that is also of interest to him; to my colleague, Dr. Kenneth J. Boss; and to the reviewers, for reading the manuscript and making significant suggestions.

SYSTEMATIC SECTION

Abbreviations. The following abbreviations have been used in the text and on the plate captions:

ANSP	Academy of Natural Sciences of Philadelphia, Pennsylvania
BMNH	British Museum (Natural History), London, England
CM	Carnegie Museum, Pittsburgh, Pennsylvania
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts
MZUM	Museum of Zoology, University of Michigan, Ann Arbor, Michigan
OSM	Ohio State Museum, Columbus, Ohio
USNM	National Museum of Natural History, Washington, D. C.

Synonymy. For ease of reference, full citations are included for each taxon, including the type locality and the location of the type when known. References to plates and figures are not included under Lea's Obs. Unio since they are always the same as in the preceding entry. In some instances, lectotypes are selected. Elsewhere in the text, references are abbreviated and require the use of the bibliography. Except for the original references, only relevant citations since 1914 are included here since the earlier ones are available in Simpson (1914).

Descriptions. The measurements are only intended to convey the general size of specimens from a given station, and to indicate sexual differences.

Anatomy and Breeding Season. The available data are cited.

Habitat. Included when known.

Remarks. These are designed to elucidate the differences between the sexes and the species, and include comments on distribution and taxonomy.

Range. The distribution is summarized.

Abundance. The former abundance of the species is based on the number and size of the lots found in the several collections studied. Their present abundance is based on the opinions of Stansbery (1970, 1971, 1976).

Specimens Examined. Most of the records are based on the specimens in the collections mentioned above. These collections contain almost all specimens available for study, and with the exception of the small collection in the Ohio State Museum, all have been personally examined. The records are followed by the initials of the institution in which they were observed. In most instances when records were duplicated only references to the specimens in the Museum of Comparative Zoology were included, though in certain critical cases several references are mentioned. Specimens not seen are credited to the responsible individual or published reference and to the associated institution, if it is known. The published references may be found either under *Synonymy* or under *Literature Cited*, or sometimes under both headings.

Distribution. The various river systems are listed from west to east. East of the Mississippi River this arrangement approxi-

mates the direction of post-glacial dispersal. The records from each river system are arranged from the headwaters to the mouth, with the exception of the Ohio River drainage, which is oppositely arranged to indicate the post-glacial distribution of most species from the Tennessee and Cumberland river systems.

The cumbersome term, Mobile-Alabama-Coosa river system, is used because it reflects the main channel of the river, which was given a different name at each important confluence.

Figures. When available, holotypes, allotypes and lectotypes are generally used to illustrate each species. Where required, several illustrations are included to show ecophenotypic variation. Not included are the pencil sketches of the new species described by the Sicilian nobleman, Marchese A. De Gregorio (1914), who, with abandon, began redescribing the unionids of North America. Some of the data on the plate captions, such as the measurements, are not repeated elsewhere.

The distributional maps are based on Rand McNally and Company's *Commercial Atlas of America* 1912 Edition, plate 21, which indicates United States Inland Waterways.

Key to the Subgenera of *Plagiola*

Because of the pronounced sexual dimorphism occurring in *Plagiola*, this key to the subgenera consists of one section for each sex. The keys to the species in the several subgenera are constructed without special regard for sexual differences. Anyone unfamiliar with this genus should refer to Burch's "Key" (1973 or 1975).

Males

1. Shell with a distinct radial furrow in front of the posterior ridge 2
   Shell without a distinct radial furrow in front of the posterior ridge 4
2. Radial furrow narrow and shallow ..... *Pilea*
   Radial furrow wide and of varying depth 3
3. Shell subrhomboid or subquadrate ..... *Epioblasma*
   Shell oval, obovate, elliptical, subquadrate or trapezoid ..... *Torulosa*
4. Shell long based triangular ..... *Truncillopsis*
   Shell subquadrate, subrhomboid, or elliptical ..... *Plagiola*

Females

1. Marsupial expansion occupying part of the posterior or medial region 2
   Marsupial expansion occupying the entire postbasal region ..... *Torulosa*
2. Marsupial expansion formed by a swelling of the posterior ridge 3
   Marsupial expansion formed by a swelling in front of the posterior ridge and more or less separated from it 4
3. Shell distinctly long based triangular, marsupial swelling not extending below the base line, with conspicuous green rays and mottling ..... *Truncillopsis*
   Shell subquadrate or subrhomboid, marsupial swelling usually extending below the base line, usually with fine green rays that are often broken by growth rests ..... *Plagiola*
4. Marsupial area located medially and extending below the base line as a distinct lobe ..... *Epioblasma*
   Marsupial area in front of the posterior ridge, often separated from it by a narrow sulcus, not extending below the base line ..... *Pilea*

Superfamily **UNIONACEA** Thiele 1935
Family UNIONIDAE (Fleming 1828) Ortmann 1911
Subfamily LAMPSILINAE (Ihering 1901) Ortmann 1910
Genus *Plagiola* Rafinesque

Plagiola Rafinesque 1819, Jour. Phys. Chim. Hist. Nat. (Paris) 88: 426. Species listed: *verrucosa, fasciolaris, leptodon, depressa, flava, obliquatas* [sic], *all* Rafinesque, *all nomina nuda*; 1820, Ann. Gén. des Sci. Physiques, Bruxelles 5: 302. Species listed: *Obliquaria decorticata, O. interrupta, O. depressa, O. lineolata, all* Rafinesque. Type species, *Unio interruptus* Rafinesque 1820, subsequent designation, Herrmannsen, 1847, Indicis Generum Malacozoorum 2: 279.

Penita Frierson 1927, Check list N American naiades, pp. 11, 93. Type species, *Unio penitus* Conrad, original designation, *teste* Errata et Corrigenda.

Description. The most interesting character of *Plagiola* is the remarkable difference between the shells of the male and female. The shells are essentially alike until about one-third to one-half grown, when the development of marsupial swelling begins in the female. This marsupial swelling,

in the post-ventral region, is thinner than the rest of the shell and is often of a somewhat different texture; it may take the form of a widely rounded wing, or be marked off from the rest of the shell by sulci. The swelling is often radially sculptured and toothed at the edge, with remains of the teeth visible along the growth lines. In many species the male has a radial depression in front of the posterior ridge. The shape of the shell is variable, but is generally subovate or subtriangular and is somewhat inflated. The shell is either not sculptured or only covered with low tubercles. The umbonal sculpture is delicate and faintly doubly looped. The periostracum is yellowish or greenish, generally with some green rays.

Anatomy. Discussed by Ortmann (1912a: 354), Simpson (1914: 2) and Utterback (1916: 452 [189]).

The selection of a lectotype for *Obliquaria* (*Plagiola*) *interrupta* Rafinesque 1820 by Johnson and Baker (1973: 159) and its acceptance in this paper over *Unio brevidens* Lea 1831 requires that the species, formerly under the genus *Dysnomia* or *Epioblasma*, be placed in *Plagiola*. This use of *Plagiola* was indicated by Morrison (1969: 24).

Ortmann and Walker (1922: 51) regarded *O.* (*P.*) *interrupta* Rafinesque as unidentifiable and designated *O.* (*P.*) *lineolata* Rafinesque = *securis* Lea as the type species of *Plagiola*. This apparently made *Dysnomia* Agassiz 1852 available. See under remarks to subgenus *Epioblasma*.

Baker (1964: 140) pointed out that whether or not *interrupta* was identifiable, Ortmann and Walker's subsequent designation of *lineolata* as type species was invalid, and that *lineolata* belonged in the genus *Ellipsaria* Rafinesque, the synonymy of which follows:

Ellipsaria Rafinesque 1820, Ann. Gén. des Sci. Physiques, Bruxelles 5: 303. Type species, *Obliquaria ellipsaria* Rafinesque, by tautonymy. Ortmann and Walker (1922: 52) agreed that this taxon is a synonym of *lineolata*. Their conclusion was confirmed by Johnson and Baker (1973: 154, pl. 5, fig. 1), who selected a specimen identified by Rafinesque as neotype.

Crenodonta Schlüter 1838, Kurzgefasstes systematisches Verzeichness meiner Conchyliensammlung . . . . (Halle), p. 33. Species listed: *plicata* Say, *tuberculata* Rafinesque, *securis* Deshayes [=Lea], *trigona* Lea. Type species, *Crenodonta securia* (Deshayes) [=Lea], subsequent designation, Herrmannsen, 1852, Indicis Generum Malacozoorum, Supplementa et Corrigenda, p. 38.

Plagiolopsis Thiele, 1934, Handb. syst. Weichtierk. 3: 834. Type species, *P. securis* (Lea), monotypic.

Thiele concluded that *Plagiola* was equivalent to *Lampsilis* Rafinesque and, unaware of either *Ellipsaria* Rafinesque or *Crenodonta* Schlüter, created an unnecessary taxon.

Ellipsaria is monotypic, and is represented by *E. lineolata* Rafinesque 1820.

Subgenus *Truncillopsis* Ortmann and Walker

Truncillopsis Ortmann and Walker 1922, Occ. Papers, Mus. Zool., Univ. Mich. no. 112, p. 65. Type species, *Truncilla triqueter* Rafinesque, original designation.

Description. Shell long based triangular, covered with conspicuous green rays and mottling, greatly inflated, sharply truncated posteriorly. Disk smooth without any radial furrow. Female with a slight marsupial swelling at the posterior ridge ending at the extreme post-ventral point.

Anatomy. Discussed by Ortmann (1912a: 355), who regarded this monotypic subgenus as the most primitive member of the genus in which the typical features of the genus are barely indicated.

Plagiola (*Truncillopsis*) *triquetra* (Rafinesque)

Plate 10, figures 1–4
Distribution: Plate 1

Truncilla triqueter Rafinesque 1820, Ann. Gén. Sci. Physiques, Bruxelles 5: 300, pl. 81, figs. 1–4 (chutes de l'Ohio [River, near Louisville, Jefferson Co., Kentucky]; lectotype ANSP 20231 selected by Johnson and Baker, 1973, Proc. Acad. Nat. Sci. Phila. 125: 173, pl. 7, fig. 3).

Unio triangularis Barnes 1823, American Jour. Sci. 6: 272, pl. 13, fig. 17, a, b (Detroit River [Michigan]; Bois Blanc Isle [Essex Co., Ontario], figured type Lyceum of Natural History of New York [destroyed by fire]).

Unio cuneatus Swainson 1823, Philos. Mag. Jour., Edinburgh 61: 112 (no locality; type [lost]).

Unio formosus Lea 1831, Trans. Amer. Philos. Soc. 4: 111, pl. 16, fig. 41 (Ohio River; type not in the USNM or ANSP [lost]); 1834, Obs. Unio 1: 121.

Unio triangularis pergibosus Gregorio 1914, Il Nat. Siciliano 22: 40, pl. 4, fig. 4 (Sciota [Scioto] River, Ohio, type presumed to be in Palermo Mus., Sicily [not seen]).

Unio triangularis longiusculus Gregorio 1914, Il Nat. Siciliano 22: 40, pl. 4, fig. 5 (Sciota [Scioto] River, Ohio, type presumed to be in Palermo Mus., Sicily [not seen]).

Truncilla (*Truncilla*) *triquetra* (Rafinesque). Simpson, 1900, Proc. U. S. Natl. Mus. 22: 517; 1914, Cat. Naiades 1: 6.

Truncilla triquetra (Rafinesque). Ortmann 1909, Ann. Carnegie Mus. 5: 118; 1912a, Ann. Carnegie Mus. 8: 355. Wilson and Clark 1912, U. S. Bur. Fisheries, Doc. 757: 55; 1914, U. S. Bur. Fisheries, Doc. 781: 45. Ortmann 1918, Proc. Amer. Philos. Soc. 57: 585; 1919, Mem. Carnegie Mus. 8: 325, pl. 21, figs. 3, 4.

Dysnomia (*Truncillopsis*) *triquetra* (Rafinesque). Ortmann and Walker, 1922, Occ. Papers, Mus. Zool. Univ. Mich., no. 112: 65. Ortmann, 1925, Amer. Mid. Nat. 9: 359. Frierson, 1927, Check list N. American naiades, p. 96. Baker, 1928, Bull. Univ. Wisconsin, no. 1327, p. 296, pl. 86, figs. 5–7, pl. 70, figs. 4–7. La Rocque, 1967, Geol. Surv. Ohio, Bull. 62 (2): 285, fig. 176. Haas, 1969, Das Tierreich, pt. 88, p. 479.

Dysnomia triquetra (Rafinesque). Danglade, 1922, U. S. Bur. Fisheries, Doc. 934, p. 5. Ortmann, 1926, Ann. Carnegie Mus. 17: 182. van der Schalie, 1941, Jour. of Conch. 21: 251. Morrison, 1942, Bur. Amer. Ethnology, no. 129, p. 363. Goodrich and van der Schalie, 1944, Amer. Mid. Nat. 32: 314. Robertson and Blakeslee, 1948, Bull. Buffalo Soc. Nat. Sci. 19: 112, pl. 11, fig. 9. Murray and Leonard, 1962, Univ. Kansas, Mus. Nat. Hist., Misc. Pub. 28, p. 155, pl. 44, figs. 1–4, text fig. 40. Neel and Allen, 1964, Malacologia 1: 450, fig. 63. Starrett, 1971, Illinois Nat. Hist. Surv. Bull. 30: 340, pl. 4, fig. 21. Clarke, 1973, Mal. Review 6: 64.

Description. Shell usually of medium size, reaching up to 80 mm in length. Outline long based triangular. Valves slightly inequilateral, much inflated, solid. Anterior end regularly rounded, posterior end obliquely truncated. Ventral margin slightly curved in males, almost straight in females. Dorsal margin short, almost straight, forming a distinct angle with the obliquely descending posterior margin. Hinge ligament short. Posterior ridge, high, faintly double, sharply angled. Dorsal slope very broad, slightly concave and radially sculptured. Umbos full and high, turned inward and anteriorly over a well-marked lunule, located slightly anterior of the middle of the shell; their sculpture is faint consisting of broken, somewhat doubly-looped ridges. Surface of the shell smooth except for numerous irregular growth rests. Periostracum subshiny, tawny to yellow green, with broken bright green rays and rows of green mottling.

Left valve with two ragged, subcompressed, triangular, pseudocardinal teeth; no interdentum. Two short, straight, elevated, granular lateral teeth. Right valve with two subcompressed, triangular, pseudocardinal teeth. One lateral tooth. Anterior adductor muscle teeth well impressed, posterior ones less so. Pallial line impressed anteriorly. Umbonal cavities deep. Nacre white or silvery.

Male shells grow larger, and are somewhat less sharply triangular than those of the female.

Female shells have a marsupial swelling in the area of the posterior ridge consisting of a slightly elevated, narrowly rounded, radially sculptured ridge that projects just below the ventral margin.

Length mm	Height mm	Width mm	
78	52	45	Little Miami River, Ohio. Male.
46	33	25	Green River, 8 mi. S Campbellsville, Taylor Co., Kentucky. Male.
40	24	22	As above. Female.

Anatomy and Breeding Season. The anatomy was discussed by Ortmann (1912a: 355), who also (1919: 327) determined that the species is bradytictic.

Habitat. Found in riffles with stony and sandy bottoms, in swift currents, usually deeply buried (Baker, 1928: 298).

Remarks. *Plagiola triquetra* (Rafinesque) does not closely resemble any other member of the genus *Plagiola*. It may be distinguished by its long triangular outline, sharply truncated posterior end and rows of green mottling. It might be confused with two other unionids, *Truncilla truncata* Rafinesque or *Alasmidonta marginata* Say, since both have somewhat superficial resemblances to *triquetra*. *T. truncata* is more triangular, with a sharper posterior ridge and a concave dorsal margin, and *A. marginata* lacks distinct pseudocardinal teeth and has no lateral teeth.

Range. Upper White River system, Missouri; Missouri River drainage, Kansas and Missouri; Mississippi River system, Wisconsin and Iowa; Illinois River drainage, Illinois; Tennessee and Cumberland River systems; Green River drainage, Kentucky; Ohio River system from Indiana to Pennsylvania; St. Lawrence River system: Lakes Michigan and Erie.

Reported in Oklahoma by Simpson (1914: 6) but not by Isely (1925).

Abundance. This is the most successful member of the genus in that it is the most widely distributed and most generally abundant. It occupies more of the formerly glaciated region than any other *Plagiola*.

Specimens Examined

White River System

Black River Drainage. *Missouri*: [Black River], Poplar Bluff, [Butler Co.]. (MZUM 81269. This important record, based on a single specimen, has the locality written on the shell, with the additional data [W. A.] Marsh, March 3, 1891).

Mississippi River System

Meramec River Drainage. *Missouri*: Bourbeuse River, 5 mi. S Owensville, Gasconade Co. (MCZ). Meramec and Big rivers (Buchanan [collection sites shown on map, but not listed]).

Osage River Drainage. *Kansas*: Marais des Cygnes River, Ottawa, Franklin Co. (Scammon).

Missouri River Drainage. *Kansas*: Wakarusa River, Lawrence, Douglas Co. (Scammon).

Mississippi River Drainage. *Wisconsin*: Wisconsin River, Sauk Co. (MZUM). *Iowa*: Mississippi River, Davenport, Scott Co.; Mississippi River, Muscatine, Muscatine Co. (*both* MCZ).

Illinois River Drainage. *Illinois*: Kankakee River (Parmalee, 1967). Illinois River, La Salle, La Salle Co.; Illinois River, Fulton Co. (*both* Starrett).

Tennessee River System

Powell River Drainage. *Tennessee*: Powell River, Shawanee, Claiborne Co. (CM).

Clinch River Drainage. *Virginia*: Clinch River, St. Paul, Wise Co.; Clinch River, Dungannon and 1.5 mi. below Speers Ferry bridge, *both* Scott Co.; Clinch River, 1.5 mi. S Dona, Lee Co. (*all* MCZ). *Tennessee*: Clinch River below Kyles Ford bridge, Hancock Co.; Clinch River, 4 mi NW Thorn Hill, Grainger Co.; Clinch River, Clinton, Anderson Co.; (*all* MCZ).

Holston River Drainage. *Virginia*: North Fork, Mendota, Washington Co.; South Fork, Pactolus, Sullivan Co. (*both* CM). *Tennessee*: Holston River, Rogersville, Hawkins Co.; mouth of Holston River, Austins Grist Mill, Knox Co. (*both* MCZ).

French Broad River Drainage. *Tennessee*: Nolichucky River, Chunns Shoals, Hamblen Co. (CM).

Tennessee River Drainage. *Tennessee*: Tennessee River, Knoxville, Knox Co. (MCZ).

Paint Rock River Drainage. *Alabama*: Paint Rock River, Paint Rock, Jackson Co. (CM).

Flint River Drainage. *Alabama*: Flint River, Maysville, Madison Co. (CM).

Elk River Drainage. *Tennessee*: Elk River, Fayetteville, Lincoln Co. (MCZ).

Tennessee River Drainage. *Alabama*: Tennessee River, Muscle Shoals, between

Colbert and Lauderdale Cos. (CM). Not found by Morrison (1942: 363) in the Pickwick Basin mounds.

Bear Creek Drainage. *Alabama*: Bear Creek, Burleson, Franklin Co. (CM).

Duck River Drainage. *Tennessee*: Duck River, Wilhoite, Marshall Co.; Duck River, Hardinsons Mill, Maury Co., 12 mi. NW Lewisburg, Marshall Co.; Duck River, Columbia, Maury Co. (*all* MCZ).

Cumberland River System

Cumberland River Drainage. *Kentucky*: Beaver Creek, E Rowena Ferry, Russell Co. (MCZ). *Tennessee*: Cumberland River, Goodall Island, Smith Co. (Wilson and Clark).

Obey River Drainage. *Tennessee*: Obey River, Duncan Ford, 4 mi. SE Lilydale, Pickett Co. (MCZ); Obey River, Celina, Clay Co. (Wilson and Clark).

Cumberland River Drainage. *Tennessee*: Cumberland River, Nashville, Davidson Co. (MCZ).

Ohio River System

Wabash River Drainage. *Illinois*: Little Wabash River, Wayne Co. (MCZ). *Indiana*: West Fork, White River, Indianapolis, Marion Co.; White River, Rockford, Jackson Co. (*both* MCZ). *Ohio*: Big Beaver Creek (CM); Wabash River, Recovery; *both* Mercer Co. (MCZ). *Indiana*: Salmonia River, Grant Co.; Wabash River, Lafayette, Tippecanoe Co. (*both* MCZ).

Green River Drainage. *Kentucky*: Green River, 8 mi. S Campbellsville, Taylor Co.; Green River, Greensburg, Green Co.; Green River, Rio and Munfordville, *both* Hart Co.; Green River, Mammoth Cave, Edmondson Co.; West Fork, Drakes Creek, Massey Mill, Warren Co.; (*all* MCZ).

Salt River Drainage. *Kentucky*: Rolling Fork, Salt River, Raywick, Marion Co. (MCZ).

Ohio River Drainage. *Kentucky*: Falls of the Ohio River, near Louisville, Jefferson Co. (Rafinesque). *Ohio*: Ohio River, Cincinnati, Hamilton Co. (MCZ).

Miami River Drainage. *Ohio*: Little Miami River (MCZ); Miami River (CM).

Scioto River Drainage. *Ohio*: Olentangy River, Delaware, Delaware Co.; Scioto River, Columbus, Franklin Co.; Big Darby Creek, 4 mi. S Orient; Scioto River, Circleville; *both* Pickaway Co. (*all* MCZ).

Little Kanawha River Drainage. *West Virginia*: Little Kanawha River, Burnsville, Braxton Co.; Little Kanawha River, Grantsville, Calhoun Co.; North Fork, Hughes River, Cornwallis, Richie Co. (*all* CM).

Muskingum River Drainage. *Ohio*: Tuscarawas River, New Philadelphia, Tuscarawas Co.; Mohican River, above confluence with Kolosing River, Newcastle Twp., Coshocton Co. (*both* MCZ).

Ohio River Drainage. *Ohio*: Ohio River, Stubenville, Jefferson Co. (MCZ).

Big Beaver River Drainage. *Ohio*: Mahoning River, near Garretsville, Portage Co. (MCZ). *Pennsylvania*: Shenango River, Shenango; Pymatuning, Pymatuning Township, *both* Mercer Co. (*both* CM).

Allegheny River Drainage. *Pennsylvania*: Leboeuf Creek, Erie Co.; Conneaut Outlet, Crawford Co.; French Creek, Venango Co. (*all* CM); Allegheny River, Kelly and Aladdin, *both* Armstrong Co. (*both* CM).

Monongahela River Drainage. *West Virginia*: West Fork River, Lightburn, Lewis Co.; West Fork River, Lynch Mines, Harrison Co. (*both* CM). *Pennsylvania*: Dunkards Creek, Mt. Morris, Greene Co. (MCZ).

St. Lawrence River System

Great Lakes Drainage. (Lake Michigan) *Wisconsin*: Fox River, Omro, Winnebago Co. (Baker). *Michigan*: St. Joseph River, 2 mi. S Leonidas, St. Joseph Co. (MZUM); Grand River, Grand Rapids, Kent Co. (MCZ); Muskegon River, 3 mi. below Newaygo, Newaygo Co. (MZUM). (Lake Huron) *Michigan*: Lake Huron (Goodrich, 1932). (Lake Erie) *Ontario*: Sydenham River, 1.8 mi. NE Shetland, Lamberton Co. (Clarke). *Michi-*

gan: Lake St. Clair (Goodrich, 1932). *Ontario*: Bois Blanc Isle, Essex Co. (Barnes); Lake Erie, Rondeau Bay, Kent Co. (MCZ). *Michigan*: Huron River, 1 mi. S Milford, Oakland Co.; Huron River, E Buck Lake, Livingston Co.; Huron River, Rockwood; Lake Erie, La Plaisance Bay; *both* Monroe Co. (*all* MZUM). *Ohio*: Auglaize River (MCZ). Swan Creek, Toledo, Lucas Co. (CM). Lake Erie, Put-in Island, Ottawa Co. (Wilson and Clark). Sandusky River, Fremont, Sandusky Co. (CM). Grand River, Painsville, Lake Co. (MCZ). *Pennsylvania*: Lake Erie, Presque Isle Bay, Erie, Erie Co. (CM).

Subgenus *Plagiola* s. s. Rafinesque

Type species, *Unio interruptus* Rafinesque 1820; subsequent designation, Herrmannsen 1847, 1: 279.

Description. Shell subquadrate, subrhomboid, or elliptical somewhat truncated posteriorly. Male smooth on the disk without any radial furrow. Female with a marsupial swelling in front of the post basal point; swelling may or may not extend below the ventral margin, but it is marked by two distinct sulci.

KEY TO THE SPECIES OF *PLAGIOLA* S. S.

1. Shell not much inflated, marsupial swelling extending below the base 2
   Shell greatly inflated, marsupial swelling not extending below the base ..... *arcaeformis*
2. Shell moderately thick, rays generally broken, sometimes not rayed 3
   Shell very thin and delicate with fine green rays ..... *lenior*
3. Posterior slope acutely angled, from the Mobile-Alabama-Coosa river system ..... *penita*
   Posterior slope not acutely angled, from the Tennessee or Cumberland river systems ..... *interrupta*

Plagiola (*Plagiola*) *interrupta* (Rafinesque) Plate 10, figures 5–7 Distribution: Plate 7, figure A

Obliquaria (*Plagiola*) *interrupta* Rafinesque 1820, Ann. Gén. Sci. Physiques, Bruxelles 5: 320 (le Kentuky et Ohio [Rivers]. Lectotype ANSP 20257, selected by Johnson and Baker, 1973, Proc. Acad. Nat. Sci. Phila. 125: 159, pl. 7, fig. 4 and the type locality restricted to the Cumberland River).

Unio brevidens Lea 1831, Trans. Amer. Philos. Soc. 4: 75, pl. 6, fig. 6 (Ohio; Cumberland River, Tennessee [*teste* errata sheet]; figured type [lost]; male and female specimens, subsequently identified by Lea, USNM 85349). 1834, Obs. Unio 1: 85.

Unio interruptus (Rafinesque). Conrad, 1834, New Fresh Water Shells U. S., p. 69; 1838, Monography Unionidae, no. 10, p. 88, pl. 48.

Truncilla brevidens (Lea). Simpson, 1900, Proc. U. S. Natl. Mus., 22: 517; 1914, Cat. Naiades 1: 7. Wilson and Clark, 1914, U. S. Bur. Fisheries Doc. no. 781: 45.

Truncilla interrupta (Rafinesque). Ortmann, 1918, Proc. Amer. Philos. Soc. 57: 586.

Dysnomia (*Truncillopsis*) *brevidens* (Lea). Ortmann and Walker, 1922, Occ. Papers, Mus. Zool., Univ. Mich. no. 112, p. 66. Ortmann, 1925, Amer. Midland Nat. 9: 360.

Dysnomia (*Penita*) *brevidens* (Lea). Frierson, 1927, Check list N American naiades, p. 94. Haas, 1969, Das Tierreich, pt. 88, p. 482.

Dysnomia brevidens (Lea). Morrison, 1942, Bur. Amer. Ethnology, Bull. no. 129, p. 363. Neel and Allen, 1969, Malacologia 1: 448, figs. 59–62.

Description. Shell of medium size, reaching over 80 mm in length, though often not exceeding 50 mm in length. Outline of male rhomboid or subtriangular; of female subquadrate. Valves somewhat inequilateral; males not much inflated; females greatly inflated, especially old individuals; solid. Anterior end regularly rounded; posterior one more broadly rounded. Ventral margin slightly curved. Dorsal margin of male straight, forming an obtuse angle with the obliquely descending posterior margin. Dorsal margin of female broadly curved merging imperceptably with the rounded posterior margin. Hinge ligament prominent. Posterior ridge broadly curved and faintly double in the male; the posterior ridge of the female becomes a rather sharply elevated marsupial swelling, toothed below and marked with the remains of former teeth, separated from the rest of the shell by two distinct sulci. It often projects well below the base and has a semicircular outline on it. Dorsal slope flat, broad, sometimes with radial sculpture. Umbos much elevated, elongated, located

anteriorly, their sculpture consisting of feeble, double looped bars. Surface of the disk smooth or clothlike. Periostracum yellowish, tawny, or tawny brown, with narrow, broken, radial green rays, sometimes broken into large dots, especially posteriorly.

Left valve with two ragged pseudocardinal teeth, triangular, and of about equal size; the anterior tooth narrow, straight, directed obliquely forward slightly widening toward the anterior end; the posterior tooth triangular; the space between them triangular and extending to the hinge. Interdentum very short and narrow. Two nearly straight, very short, heavy, obliquely sculptured lateral teeth. Right valve with two pseudocardinal teeth, the anterior tooth small and parallel with the hinge, the posterior tooth long, high, parallel to the anterior one, separated from the interdentum by a deep pit. One well-developed lateral tooth, often with a parallel vestigial tooth below it. Umbonal cavities very shallow. Anterior and posterior adductor muscle scars well impressed, pallial line distinct. The marsupial area of the female has a rounded radial furrow. Nacre white.

Male shells are rhomboid or subtriangular in outline, moderately inflated, and flattened on the disk.

Female shells are subquadrate, rounded behind, and greatly inflated. When about one-third grown the marsupial swelling becomes sharply elevated, and decidedly separated from the rest of the shell by two distinct sulci.

Length mm	Height mm	Width mm	
70	54	37	Cumberland River, Tennessee. Male.
64	49	42	As above. Female.

Habitat. The species appears to occur in moderate-sized, clear streams with a rocky bottom, avoiding the smaller tributaries. (Wilson and Clark, 1914: 45).

Remarks. Male shells of *Plagiola interrupta* (Rafinesque) can usually be separated from the shells of the other members of the subgenus *Plagiola* s. s. by the tendency of the green rays, which are often present on the entire surface, to be broken into dots. In *P. lenior* the rays are confined to the posterior region and are not broken. The shell of *interrupta* is rhomboid, subtriangular or subquadrate in outline, whereas that of *lenior* is elliptical; both are flattened on the disk, but the latter is smaller, and has a thin, delicate shell. *P. interrupta* is easily separated from *P. arcaeformis*, as the latter is always much more inflated, has a stronger posterior ridge, and a characteristic emarginate posterior margin.

Female shells of *P. interrupta* resemble those of *arcaeformis* except the latter's shells are much more inflated. The sulci of *interrupta* are much more acute, and while its marsupial swelling extends below the base, the swelling in *arcaeformis* does not; instead the base is remarkably flattened. *P. lenior* has a marsupial swelling similar to that of *interrupta*, but the former has such a thin, delicate, small shell it is unlikely to be mistaken for the latter.

Old, mature specimens of both sexes of *P. interrupta* from the Cumberland River, and the Holston River of the Tennessee River system, closely resemble those of *penita* of similar maturity from the Mobile-Alabama-Coosa river system, but they can be separated morphologically. In general, the male of *interrupta* is more rhomboid and flatter on the disk than is *penita*, and the former is covered with green rays which are broken into dots. In both sexes, if rayed at all, those of *penita* are more delicate and any dots are finer. Females of *interrupta* differ from those of *penita* in that the marsupial swelling is marked by two acute sulci, whereas the posterior one in *penita* is obscure or absent, and the dorsal slope of the latter is much more oblique.

The taxa *interrupta* and *brevidens* have both been used for this species. Say (1834: no. 6 [no pagination]) and Conrad (1834: 69 and 1838, no. 10, p. 88, pl. 48) recognized *interrupta* Rafinesque; however,

Simpson (1900a: 517; 1914: 7) did not. Ortmann and Walker (1922: 66) argued *interrupta* could not be recognized from the original description; Frierson (1927: 79) insisted *interrupta* is *Lampsilis menkiana* (Lea) 1836; and Morrison (1969: 24) asserted that *Obliquaria* (*Plagiola*) *interrupta* Rafinesque 1820 = *Unio brevidens* Lea 1831. The present emphasis on the identification of the type as the final criterion in determining the availability of a taxon requires that Rafinesque's name be recognized.

Range. Tennessee River system, Virginia, Tennessee and Alabama; Cumberland River system, Kentucky and Tennessee.

Abundance. The number of specimens in the collections studied indicate this species must once have been relatively abundant. It is considered "threatened" by Stansbery (1976: 43, 49).

Specimens Examined

Tennessee River System

Powell River Drainage. *Virginia*: Powell River, 2.5 mi. S and 7 mi. SW, Jonesville, *both* Lee Co. (*both* MCZ). *Tennessee*: Powell River, 8–10 mi. N Tazwell, Claiborne Co.; Powell River [town of] Powell River, Campbell Co. (*both* MCZ).

Clinch River Drainage. *Virginia*: Clinch River, Hill Station, 5.5 mi. below Fort Blackmore, Scott Co.; Station Creek, Lee Co. (*both* MCZ). *Tennessee*: Clinch River, below Kyles Ford bridge, Clinch River, Sneedsville, *both* Hancock Co. (*both* MCZ); Clinch River, Clinton, Clinch River, Edgmoor, *both* Anderson Co. (*both* MCZ).

Holston River Drainage. *Tennessee*: Holston River, Austins Grist Mill, Knox Co. (MCZ).

French Broad River Drainage. *Tennessee*. Nolichucky River (MCZ).

Tennessee River Drainage. *Tennessee*: Tennessee River, Knoxville, Knox Co. (MCZ).

Elk River Drainage. *Tennessee*: Lower Elk River (Conrad); Elk River, 4 mi. ESE Fayetteville, Lincoln Co. (MCZ).

Tennessee River Drainage. *Alabama*: Tennessee River, Muscle Shoals, Colbert and Lauderdale Cos. (CM, MZUM); Tennessee River, Tuscumbia, Colbert Co. (MCZ); Pickwick Basin, mounds between Barton, Colbert Co. and Waterloo, Lauderdale Co. (Morrison, USNM).

Duck River Drainage. *Tennessee*: Duck River, Wilhoite, Marshall Co. (MZUM, CM); Duck River, Hardinsons Mill, Mauray Co., 12 mi. NW Lewisburg, Marshall Co. (MCZ); Duck River, Columbia, Mauray Co. (Hinkley and Marsh).

Cumberland River System

Cumberland River Drainage. *Kentucky*: Cumberland River, Burnside (MCZ); Big South Fork, opposite Parkers Lake Station (Wilson and Clark); *both* Pulaski Co.; Beaver Creek, E Rowena Ferry, Russell Co. (MCZ).

Caney Fork Drainage. *Tennessee*: Caney Fork, Putnam Co. (Wilson and Clark).

Stones River Drainage. *Tennessee*: Stones River, Murfreesboro, Rutherford Co; Stones River, 1.2 mi. W Couchville, Davidson Co.; (both MCZ).

Cumberland River Drainage. *Tennessee*: Cumberland River, Nashville, Davidson Co. (USNM).

Plagiola (*Plagiola*) *penita* (Conrad)

Plate 10, figures 8–15

Distribution: Plate 9, figure B

Unio penitus Conrad 1834, New fresh water shells United States p. 33, pl. 5, fig. 1 (Alabama River, near Claiborne [Monroe Co.], Alabama; figured holotype ANSP 59860).

Unio metastriatus Conrad 1838, Monography Unionidae, no. 11 [back cover]; 1840, *Ibid.*, no. 12, p. 104, pl. 57, fig. 2 (Black Warrior River, Blounts Springs, [Blount Co.], Alabama; figured types [lost]).

Unio othcaloogensis Lea 1857, Proc. Acad. Nat. Sci. Phila. 9: 32 (Othcalooga [Oothkalooga] Creek, Gordon Co., Georgia); 1858, Jour. Acad. Nat. Sci. Phila. (2) 4: 74, pl. 14, fig. 54, figured holotype USNM 84615; 1858, Obs. Unio 6: 74.

Unio compactus Lea. 1859, Proc. Acad. Nat. Sci. Phila. 11: 154 (Etowah River; Conasauga River; *both* Georgia); 1859, Jour. Acad. Nat. Sci. Phila. (2) 4: 218, pl. 28, fig. 98, figured holotype USNM 84447 from the former locality; 1859, Obs. Unio 7: 36.

Unio modicellus Lea 1859, Proc. Acad. Nat. Sci. Phila. 11: 171 (Conasauga River; Chattanooga [=Chattooga] River; *both* Georgia); 1860, Jour. Acad. Nat. Sci. Phila. (2) 4: 347, pl. 57, fig. 172, figured holotype USNM 84841 from the former locality; 1860, Obs. Unio 8: 29.

Truncilla penita (Conrad). Simpson 1900, Proc. U. S. Natl. Mus. 22: 518; 1914, Cat. Naiades 1: 8.

Dysnomia (*Penita*) *penita* (Conrad). Frierson, 1927, Check list N American naiades, p. 93; Haas, 1969, Das Tierreich, pt. 88, p. 481; Hurd, 1974, Ph. D. thesis, p. 97.

Epioblasma penita (Conrad). Stansbery, 1976, Bull. Alabama Mus. Nat. Hist., no. 2: 43, 48, fig. on p. 49.

Truncilla metastriata (Conrad). Simpson, 1900, Proc. U. S. Natl. Mus. 22: 519; 1914, Cat. Naiades 1: 10.

Dysnomia (*Penita*) *metastriata* (Conrad). Frierson, 1927, Check list N American naiades, p. 93. Haas, 1969, Das Tierreich, pt. 88, p. 482. van der Schalie, 1938, Occ. Papers Mus. Zool., Univ. Mich., no. 392, p. 16; 1939, *Ibid.*, no. 407, p. 4; Hurd, 1974, Ph. D. thesis, p. 95.

Truncilla othcaloogensis (Lea). Simpson, 1900, Proc. U. S. Natl. Mus. 22: 521; 1914, Cat. Naiades 1: 17.

Dysnomia (*Penita*) *othcaloogensis* (Lea). Frierson, 1914, Check list N American naiades, p. 94. Haas, 1969, Das Tierreich, pt. 88, p. 484. van der Schalie, 1938, Occ. Papers, Mus. Zool., Univ. Michigan, no. 392, p. 16. Hurd, 1974, Ph. D. thesis, p. 96.

Truncilla compacta (Lea). Simpson, 1900, Proc. U. S. Natl. Mus. 22: 518; 1914, Cat. Naiades 1: 9.

Truncilla modicella (Lea). Simpson, 1900, Proc. U. S. Natl. Mus. 22: 518; 1914, Cat. Naiades 1: 11.

Dysnomia (*Penita*) *modicella* (Lea). 1927, Check list N American naiades, p. 94. Haas, 1969, Das Tierreich, pt. 88, p. 484.

Description. Shell of medium size reaching 60 mm in length. Outline of male rhomboid or subtriangular, of female subrhomboid or quadrate. Valves somewhat inequilateral, males usually moderately inflated, females considerably inflated, solid. Anterior end regularly rounded, posterior end more broadly rounded. Ventral margin slightly curved. Dorsal margin of male straight, forming an obtuse angle with the obliquely descending posterior margin. Dorsal margin of female broadly curved merging imperceptably with the rounded posterior margin. Hinge ligament prominent. Posterior ridge broadly curved, sometimes quite imperceptable in the male. When about one-half grown, the posterior ridge of the female often becomes a rather sharply-elevated, narrow, rounded marsupial swelling, often slightly toothed below, and sometimes marked with the remains of former teeth, separated from the anterior of the shell by a sulcus. The marsupial swelling often projects below the base line, and when it does is rather long and has a semicircular outline on it. Dorsal slope flat and narrow, sometimes with radial sculpture. Umbos much elevated, located anteriorly, their sculpture not observed. Surface of the disk smooth. Periostracum yellowish, tawny, or tawny brown, often with broken radial green lines, sometimes broken into inconspicuous dots, arrowhead markings or darker color arranged radially on the posterior part.

Left valve with two ragged pseudocardinal teeth, triangular and of about equal size; the anterior tooth is narrow, straight, directed obliquely forward, slightly widening toward the anterior end; the posterior tooth is triangular, the space between them is triangular and extending to the hinge. Interdentum very short and narrow. Two nearly straight, short, heavy, obliquely sculptured lateral teeth. Right valve with two pseudocardinal teeth, the anterior tooth small, parallel to the hinge, the posterior tooth long, high, parallel to the anterior one, separated from the interdentum by a deep pit. One well-developed lateral tooth often with a parallel vestigial tooth below. Umbonal cavities very shallow. Anterior and posterior muscle scars well impressed, pallial line distinct. The marsupial area of the female showing a rounded radial furrow. Nacre white, or bluish white.

Male shells are rhomboid or subtriangular in outline, and moderately inflated.

Female shells are subrhomboid or quadrate, subtruncated behind and often greatly inflated. When about one-third grown the marsupial area becomes swollen and elevated, separated from the anterior part of the shell by a distinct sulcus.

Length mm	Height mm	Width mm	
25	19	13	Conasauga River, 4.3 mi. W Eton, Murray Co., Georgia. Male.
21	15	11.5	As above. Female.
58	42	36	Alabama River, Selma, Autauga Co., Alabama. Male.
45	25	25	As above. Female.

Remarks. Plagiola penita (Conrad) of the Mobile-Alabama-Coosa river system resembles *P. interrupta* of the Tennessee and Cumberland river systems. Males of the former are, in general, more quadrate, or proportionally higher than those of *interrupta. P. penita* remain quadrate, or subtriangular, throughout their range though specimens from the upper reaches of the Coosa River drainage do not grow very large and are often rayless. *P. interrupta* from the upper reaches of headwater streams become rather more rhomboid and flattened on the disk than specimens from elsewhere, though still growing up to 50 mm in length and exhibiting distinct green rays broken into dots.

Females of *P. penita* and *interrupta*, from those habitats where each reach their maximum size, rather closely resemble one another; the marsupial swelling of both is marked from the disk by an anterior sulcus, while the latter also has a sharp posterior sulcus that is slight, or lacking, in *penita. P. penita* has a posterior margin that slopes more obliquely than that of *interrupta*; this renders the dorsal slope of the former much narrower. Females of *penita* from the upper reaches of the Coosa River drainage are usually small, rayless, and appear barely to reach sexual maturity. These were recognized as *othcaloogensis* by Hurd (1974: 96) who followed the usage of authors since Simpson (1914: 8). The localities of the lots, included under this taxon by Hurd, in the Museum of Comparative Zoology, are with their catalogue numbers, since the latter are the only data given by him. (See under Specimens Examined.) Simpson (1914: 9) recognized *compactus* (included with *modicellus* under *othcaloogensis* by Hurd), and noted that female shells are generally, though not always, shorter than those of *penita*; that they are rather narrower and more compressed in front, and that the posterior end is somewhat evenly rounded instead of being obliquely truncate. Simpson (1914: 10) suggested that *U. metastriatus* Conrad was nothing more than a variety of *compactus*, in which case the later taxon would have priority. The former was recognized as a valid species by Hurd (1974: 95). Stansbery (1976: 49) recognized both *metastriata* and *penita* as valid and said of the latter, "This species is very similar to, yet distinct from *Epioblasma metastriata*," without further elucidation.

The female shells of *penita* are variable as to the extent of the marsupial swelling. Variation in the amount of inflation of the valves occurs in both sexes. Specimens from the larger rivers tend to attain greater size, are more inflated and are more often rayed than those occurring in smaller headwater streams. In the latter, shells are small, not greatly inflated, almost always rayless and with a smooth yellow periostracum. When rayed at all, those of *penita* are narrower and more delicate than those of *interrupta* from the Tennessee and Cumberland river systems. When the rays of the former are broken into dots, they are much finer than those of *interrupta*.

Van der Schalie (1938a: 27) noted that no *Dysnomia* [*Plagiola*] occur in the river systems on either side of the Mobile-Alabama-Coosa river system and correctly suggested that it, and a number of other genera, arrived there through a former confluence with the Tennessee River system.

Range. Mobile-Alabama-Coosa river system, Georgia, Alabama, and Mississippi.

Abundance. The number of specimens in the collections studied indicate this species must have been relatively abundant. Hurd (1974: 170–180), during 1971–73, made an extensive survey of the Coosa River drainage for Unionidae. He collected at 194 stations but found only 28 specimens of *Plagiola* from four localities, all of which he regarded as *othcaloogensis* (pp. 42, 96). Stansbery (1976: 43, 48, 49) lists *othcaloogensis* and *penita* as having an "endangered status" and *metastriata* as having a "threatened status."

Specimens Examined

Mobile-Alabama-Coosa River System

Conasauga River Drainage. *Georgia*: Conasauga River, Beaverdale, Whitfield Co. (MCZ 200353); Conasauga River, Upper Kings Bridge (MCZ 933788); Conasauga River, Lower Kings Bridge (MCZ); Conasauga River, 4.3 mi. W Eton (MCZ 36620 & 214237); *all* Murray Co. Conasauga River, Fikes Ford, 1.4 mi. N Resaca, Gordon Co. (MCZ).

Oothkalooga Creek Drainage. *Georgia*: Oothkalooga Creek, Gordon Co. (Lea, USNM).

Oostanaula River Drainage. *Georgia*: Oostanaula River, Rome, Floyd Co. (MCZ).

Etowah River Drainage. *Georgia*: Etowah River, Rome, Floyd Co. (MCZ).

Chattooga River Drainage. *Georgia*: Chattooga River (MCZ 16348, 16532, 28711, 28809).

Coosa River Drainage. *Alabama*: Mill Creek (MCZ 51518, 16444); Coosa River, Stackland (MCZ); *both* Cherokee Co. Coosa River, Gadsden, Etowah Co. (MCZ). Coosa River, old lock 5, 6 mi. SW, Lincoln; Coosa River, Fort William Shoals; *both* Talladega Co. Coosa River, Weduska Shoals and Three Island Shoals, *both* Shelby Co. Coosa River, Wetumpka, Elmore Co. (*all* MCZ).

Cahaba River Drainage. *Alabama*: Cahaba River, Henry Ellen, Lovick, Grants Mill, and E. Merkel, *all* Jefferson Co. (*all* MZUM); Buck Creek, Helena (MCZ, MZUM); Cahaba River, Nunley Ford (MZUM); *both* Shelby Co.; Cahaba River, Lily Shoals (MCZ), and 10 mi. above Centerville (MZUM), *both* Bibb Co.; Cahaba River, 8 mi. N Sprott, and 5 mi. NE Marion, *both* Perry Co. (*both* MZUM).

Alabama River Drainage. *Alabama*: Alabama River, Selma, Dallas Co. (MCZ); Alabama River, near Claiborne, Monroe Co. (Conrad).

Black Warrior River Drainage. *Alabama*: Black Warrior River, Blounts Springs, Blount Co. (Conrad); Black Warrior River, Squaw Shoals, Jefferson Co.; Black Warrior River, Tuscaloosa Co. (*both* MCZ);

Tombigbee River Drainage. *Mississippi*: East Fork Tombigbee River, 3 mi. W Smithville, Monroe Co. (OSM, MCZ). *Alabama*: Tombigbee River, Epes, Sumter Co. (MZUM).

Plagiola (*Plagiola*) *arcaeformis* (Lea)

Plate 11, figures 1–4
Distribution: Plate 8, figure B

Unio arcaeformis Lea 1831, Trans. Amer. Philos. Soc. 4: 116, pl. 17, fig. 44 (Tennessee River; figured type [lost], male and female specimens subsequently identified by Lea USNM 84422); 1834, Obs. 1: 126.

Unio nexus Say 1831, Transylvania Jour. Medicine 4: 527 (Cumberland River, Nashville [Davidson Co.], Tennessee); 1834, Amer. Conch., no. 6, pl. 51, figured type [lost].

Truncilla arcaeformis (Lea). Simpson, 1900, Proc. U. S. Natl. Mus. 22: 519; 1914, Cat. Naiades 1: 12. Wilson and Clark, 1914, U. S. Bur. Fisheries Doc. 781, p. 46. Ortmann, 1918, Proc. Amer. Philos. Soc. 57: 586.

Dysnomia (*Truncillopsis*) *arcaeformis* (Lea). Ortmann, 1925, Amer. Mid. Nat. 9: 359.

Dysnomia (*Penita*) *arcaeformis* (Lea). Frierson, 1927, Check list N American naiades, p. 94. Haas, 1969, Das Tierreich, pt. 88, p. 482.

Dysnomia arcaeformis (Lea). Morrison, 1942, Bur. Amer. Ethnology Bull. 129, p. 363. Stansbery, 1970, Malacologia 10: 19, pl. 1, figs. 5, 6; 1971, Symposium of rare and endangered Moll. U. S., p. 18a, figs. 1–2.

Description. Shell of medium size, reaching 70 mm in length. Outline of shell sub-

quadrate or subrhomboid. Valves inequilateral, greatly inflated, females especially so, solid. Anterior end regularly rounded; posterior end more broadly rounded. Ventral margin slightly curved in males, with a slight emargination before the posterior ridge; quite straight in females. Dorsal margin straight forming an obtuse angle with the obliquely descending, emarginate, posterior margin. Hinge ligament prominent. Posterior ridge full, high, double or triple, subangulate, subtruncate behind the ridge. When about half grown the posterior ridge of the female becomes a marsupial swelling, slightly toothed below, marked with faint tooth sculpture at rest lines and with faint radial sculpture, separated from the rest of the shell by two distinct but broad sulci. Marsupium much flattened below, does not project below the base which is remarkably flattened. On the dorsal slope above the upper posterior ridge is usually a shallow radial furrow. Umbos full, much elevated, almost touching one another, located anteriorly, their sculpture consisting of undulating ridges. Surface of the shell smooth, or cloth-like. Periostracum tawny to yellowish-green, usually with delicate green rays over the entire surface.

Left valve with two ragged pseudocardinal teeth, triangular, and of about equal size, the space between them triangular and extending to the hinge. Interdentum very short and narrow. Two nearly straight, very short, heavy, obliquely sculptured lateral teeth. Right valve with one large pseudocardinal tooth, sometimes with a smaller tooth before or behind it. When present, the anterior tooth is small and parallel with the hinge. The pit before the interdentum is deep. One well-developed lateral tooth, sometimes with a vestigial tooth below. Umbonal cavities moderately deep. Anterior and posterior adductor muscle scars well impressed. Pallial line distinct. The marsupial area of the female is much thinner than the surrounding shell and has a rounded radial furrow. Nacre white.

Length mm	Height mm	Width mm	
52	40	38	Cumberland River, Tennessee. Male.
70	48	64	Tennessee River, Tennessee. Female.

Remarks. Plagiola arcaeformis (Lea) may be distinguished from any other member of the genus by the extreme inflation of both the male and female shells, by the radial furrow above the posterior ridge and by the emarginate posterior margin.

Both male and female shells are considerably alike in outline, though the latter are less elevated and more inflated. Old females are extraordinarily inflated. The marsupial swelling is considerably inflated toward the base, but is remarkably flattened so that it scarcely projects below the base.

Young males of *arcaeformis* might possibly be mistaken for *P. turgidula,* except the latter is not as high or inflated and has a shallow radial furrow below rather than above the posterior ridge.

Range. Tennessee River system, Tennessee and Alabama; Cumberland River system, Kentucky and Tennessee.

Abundance. Generally not found in great numbers, but reported to be locally abundant in the Holston River drainage of the Tennessee River system by Ortmann (1918: 586). "The entire range of this species is now under a series of impoundments. It has not been collected in over half a century and hence is presumed extinct," (Stansbery, 1976: 43, 50).

Specimens Examined

Tennessee River System

Clinch River Drainage. *Tennessee*: Clinch River, Clinch River Station, Claiborne Co. (CM); Clinch River, Oakman, Grainger Co. (CM); Clinch River, Clinton, Anderson Co. (MCZ).

Holston River Drainage. *Tennessee*: Holston River, near Rogersville (MCZ);

Holston River, Austin Mill (CM), *both* Hawkins Co.; Holston River, 4 mi. above Morristown, Hamblen Co. (MZUM); Holston River, Holston Station; Holston River, Turley Mill, Noeton; *both* Grainger Co. (*both* CM). Holston River, Gant Island, nr. Straw Plains, Jefferson Co. (MZUM); mouth of Holston River, Austins Grist Mill; Holston River, Knoxville; *both* Knox Co. (*both* MCZ).

French Broad River Drainage. *Tennessee*: French Broad River, Boyd Creek, Sevier Co. (CM).

Tennessee River Drainage. *Tennessee*: Tennessee River, Knoxville, Knox Co. (MCZ). *Alabama*: Tennessee River, Bridgeport, Jackson Co. (MCZ); Tennessee River, Florence, Lauderdale Co. (MCZ); Tennessee River, Tuscumbia, Colbert Co. (MCZ); Pickwick Basin, mounds between Barton, Colbert Co. and Waterloo, Lauderdale Co. (Morrison, USNM).

Cumberland River System

Cumberland River Drainage. *Kentucky*: Cumberland River (MCZ); Big South Fork of Cumberland River, 2 mi. above Burnside, Pulaski Co. (Wilson and Clark). *Tennessee*: Cumberland River, Nashville, Davidson Co. (Say).

Plagiola (*Plagiola*) *lenior* (Lea)

Plate 11, figures 5–6

Distribution: Plate 7, figure C

Unio lenis Lea 1840, Proc. Amer. Philos. Soc. 1: 286 (Stones River, Tennessee), *non* Conrad 1840. Changed to:

Unio lenior Lea 1842, Trans. Amer. Philos. Soc. 8: 204, pl. 12, fig. 18, figured holotype USNM 86130; 1842, Obs. Unio 3: 42.

Truncilla lenior (Lea). Simpson, 1900, Proc. U. S. Natl. Mus. 22: 518; 1914, Cat. Naiades 1: 11. Ortmann, 1918, Proc. Amer. Philos. Soc. 57: 587.

Dysnomia (*Truncillopsis*) *lenior* (Lea). Ortmann, 1924, Amer. Mid. Nat. 9: 34; 1925, Amer. Mid. Nat. 9: 360.

Dysnomia (*Penita*) *lenior* (Lea). Frierson, 1927, Check list N American naiades, p. 94. Haas, 1969, Das Tierreich, pt. 88, p. 484.

Dysnomia lenior (Lea). Stansbery 1970, Malacologia 10: 19, pl. 2, figs. 3, 4; 1971, Symposium of rare and endangered moll. U. S. p. 18f, figs. 3, 4.

Description. Shell usually of small size, reaching almost 40 mm in length. Outline of male subelliptical; of female subquadrate, a little narrower anteriorly. Valves inequilateral, subinflated to inflated, thin and delicate. Anterior end regularly rounded, posterior end of male slightly more broadly rounded; subtruncate in females. Ventral margin slightly curved. Dorsal margin almost straight, forming a slight angle with the obliquely descending posterior margin. Posterior ridge triple. Dorsal slope slightly rounded. Below the third ridge in females is a radially sculptured, toothed, raised marsupial swelling separated from the rest of the shell by two sulci, the more posterior one acute, ending in an emargination below the middle of the posterior slope. The marsupium projects slightly below the base and has a semicircular outline that extends posteriorly beyond it. Umbos slightly elevated, located toward the anterior third of the shell, their sculpture consisting of doubly-looped bars. Surface of the shell smooth with delicate growth lines. Periostracum subshiny, pale ashy-greenish, or yellowish green, with numerous, narrow green rays posteriorly.

Left valve with two delicate, subcompressed, pseudocardinal teeth; no interdentum. Two short, delicate, lateral teeth. Right valve with one pseudocardinal and one lateral tooth. Umbonal cavities very shallow. Anterior adductor muscle scars well impressed, posterior ones less so. Pallial line faint. The shell is thin, especially so in the marsupial furrow of the female. Nacre bluish white.

Length mm	Height mm	Width mm	
38	23	15	Eastern Tennessee. Male.
28	18	14	Stones River, Tennessee. Female. Identified by Lea.

Remarks. *Plagiola lenior* (Lea) is dis-

tinguished from other members of *Plagiola* by its thin shell and delicate green rays, which are restricted to the posterior end. The male might be mistaken for a young, pale colored *Villosa nebulosa* (Conrad), except that it has fine denticles on the posterior margin. The female has, in addition to the delicate shell, an acute sulcus behind the marsupial swelling that ends in an emargination below the middle of the posterior slope.

Range. Tennessee River system, Virginia, Tennessee and Alabama. Cumberland River system, restricted to Stones River, Tennessee.

Abundance. A rare species that appears to be somewhat locally abundant in the Paint Rock River, Alabama (Ortmann, 1918: 587). "The last known population of this species is now covered by the Priest Reservoir on the Stones River in Tennessee," (Stansbery, 1970: 19). It was last collected in the Stones River by Stansbery and Jenkinsen in 1965. Considered to be extinct in the Clinch River, above Norris Dam, Tazewell, Clairbone Co., Tennessee (Stansbery, 1972: 22). Listed as "extirpated" by Stansbery (1976: 43.50).

Specimens Examined

Tennessee River System

Powell River Drainage. *Virginia*: Powell River, Dickson Ford, 3 mi. SE Jonesville, Lee Co. (MZUM).

Clinch River Drainage. *Virginia*: Clinch River, Speers Ferry, (CM); Clinch River, Maness (MZUM); *both* Scott Co.

Holston River Drainage. *Tennessee*: North Fork, Holston River, Rotherwood, Hawkins Co. (CM); South Fork, Holston River, Pactolus, Sullivan Co. (CM); Holston River, Church Hill, Hawkins Co. (MCZ); Holston River nr. Knoxville, Knox Co. (Andrews, Walker colln. UZUM).

Paint Rock River Drainage. *Tennessee*: Paint Rock River, Holly Tree, Trenton, Paint Rock, *all* Jackson Co. (*all* CM); Paint Rock River, Woodville Jackson Co. (USNM, MZUM).

Duck River Drainage. *Tennessee*: Duck River, Columbia, Maury Co. (Hinkley and Marsh).

Cumberland River System

Stones River Drainage. *Tennessee*: Cumberland River ([written on shell] USNM) Stones River, 1.2 mi. W Couchville, Davidson Co. (MCZ).

Subgenus *Torulosa* Frierson

Torulosa Frierson 1927, Check list N American naiades, pp. 11, 94. Type species, *Amblema torulosa* Rafinesque, original designation, *teste* Errata et Corrigenda.

Capsaeformis Frierson 1927, Check list N American naiades, pp. 11, 95. Type species, *Unio capsaeformis* Lea, original designation, *teste* Errata et Corrigenda.

Description. Shell usually ovate, obovate or elliptical, occasionally triangular, male shell with a wide radiating depression, of varying depth, in front of the posterior ridge. The depression usually ends in an emargination. Female with a thin, compressed or subcompressed marsupial swelling that occupies the entire post-basal region.

Anatomy. In his discussion of the anatomy of *rangiana* (= *torulosa*), *florentina* and *capsaeformis*, Ortmann (1912a: 358–360) mentions no differences that would indicate any of these species should be placed in different subgenera.

Discussion. Frierson (1927) did not give descriptions of any of his new subgenera, but merely cited type species. He arbitrarily created subgenera for every assemblage of four or five species in genera of any size. Of the species recognized in this paper that would fall into *Capsaeformis*—namely *capsaeformis*, *florentina* and *turgidula*—all that can be said to differentiate them from other *Torulosa* is that they have thinner, smaller shells and that the radial depression in front of the posterior ridge in

capsaeformis and *florentina* is often faint. These minor conchological characters do not warrant the use of *Capsaeformis* as a subgenus.

KEY TO THE SPECIES OF *TORULOSA*

1. Shell elliptical, ovate, or obovate 2
   Shell subtriangular, subrhomboid, subquadrate or trapezoid 5
2. Shell thin, small, with a smooth surface 3
   Shell thick, often large, generally with some nodules ..... *torulosa*
3. Surface light yellow, honey colored, or yellowish green 4
   Surface green or greenish brown ..... *capsaeformis*
4. Rays distributed evenly over the entire surface ..... *turgidula*
   Rays somewhat darker in the radial depression ..... *florentina*
5. Radial furrow oblique 6
   Radial furrow subvertical ..... *biemarginata*
6. Furrow wide and shallow, periostracum shiny ..... *sampsoni*
   Furrow narrow and deep, periostracum subshiny ..... *propinqua*

Plagiola (*Torulosa*) *torulosa* (Rafinesque)

Plate 11, figures 7–11
Plate 12, figures 1–5
Distribution: Plate 9, figure A

Amblema torulosa Rafinesque 1820, Ann. Gén. Sci. Physiques, Bruxelles 5: 314, pl. 82, figs. 11, 12 (l'Ohio et le Kentuky [Rivers]; holotype ANSP 20218 from the Kentucky River, refigured by Johnson and Baker, 1973, Proc. Acad. Nat. Sci. Phila. 125: 173, pl. 7, fig. 5).

Amblema torulosa angulata Rafinesque 1820, Ann. Gén. Sci. Physiques, Bruxelles 5: 315 (l'Ohio et le Kentuky [Rivers]; type [lost]).

Amblema gibbosa Rafinesque 1820, Ann. Gén. Sci. Physiques, Bruxelles 5: 315 (l'Ohio et les rivières adjacentes; lectotype ANSP 20232 from the Ohio River, selected by Johnson and Baker, 1973, Proc. Acad. Nat. Sci. Phila. 125: 156, pl. 7, fig. 6) [also the varieties: *olivacea*, *radiata* and *difformis*; all types lost].

Unio perplexus Lea, 1831, Trans. Amer. Philos. Soc. 4: 112, pl. 17, fig. 42 (Ohio River [Cincinnati, Hamilton Co., Ohio]), figured holotype USNM 84324; 1834, Obs. Unio 1: 122.

Unio gibbosus perobliquus Conrad 1836, Monography Unionidae, no. 6, p. 51, pl. 27, fig. 2 (Wabash River, Indiana; Detroit River, Michigan, type lost). The prominent knobs on the middle of the shell suggest the figured specimen came from the former locality and not from the Great Lakes drainage, where knobs are usually lacking. The type locality is here restricted to the Wabash River, Indiana.

Unio perobliquus Conrad, 1837, Monography Unionidae, no. 8 [back cover].

Unio rangianus Lea 1838, Trans. Amer. Philos. Soc. 6: 95, pl. 18, fig. 56 (Ohio River, near Cincinnati [Hamilton Co.]; Mahoning River, near Poland [Mahoning Co.]; *both* Ohio); type [lost]. Lectotype, here selected, USNM 84798 (pl. 12, Fig. 3), USNM 84798 from the latter locality; 1838, Obs. Unio 2: 95.

Unio cincinnatiensis Lea 1840, Proc. Amer. Philos. Soc. 1: 285 (Ohio River, Cincinnati [Hamilton Co.], Ohio); 1842, Trans. Amer. Philos. Soc. 8: 194, pl. 8, fig. 4, figured holotype USNM 84199; 1842, Obs. Unio. 3: 32.

Unio obliquus Potiez and Michaud 1844, Galérie Moll. Cat. Mus. Douai 2: 153, pl. 48, figs. 3, 4 (l'Ohio [River]); figured type in Mus Douai [not seen], *non* Lamarck 1820.

Unio phillipsii Reeve 1864, Conch. Iconica 16, *Unio*, pl. 4, species 15 (North America), figured holotype BMNH 196481, *non* Conrad 1835.

Unio gubernaculum Reeve, 1865, Conch. Iconica 16, *Unio*, pl. 28, species 146 (Hab.?), figured holotype BMNH 1965203.

Truncilla (*Scalenaria*) *sulcata delicata* Simpson 1900, Proc. U. S. Natl. Mus. 22: 520 (Detroit River, [Amherstburg, Essex Co., Ontario]; holotype USNM 160853 [only specimen]); 1914, Cat. Naiades 1: 16. Approaches *rangiana* (Lea), *teste*.

Dysnomia sulcata delicata Simpson Morrison, 1942, Bur. Amer. Ethnology Bull. no. 129, p. 364. La Rocque, 1967, Geol. Survey Ohio, Bull. no. 62 (2): 280.

Truncilla (*Pilea*) *perplexa* (Lea). Simpson, 1900, Proc. U. S. Natl. Mus. 22: 522; 1914, Cat. Naiades 1: 24.

Dysnomia perplexa (Lea). Goodrich and van der Schalie, 1944, Amer. Mid. Nat. 32: 314.

Truncilla torulosa (Rafinesque). Ortmann, 1918, Proc. Amer. Philos. Soc. 57: 589. Ball, 1922, Ecology 3: 115.

Dysnomia (*Pilea*) *torulosa* (Rafinesque). Ortmann and Walker, 1922, Occ. Papers, Mus. Zool., Univ. Mich., no. 112, p. 69. Ortmann, 1925, Amer. Mid. Nat. 9: 363. La Rocque, 1967, Geol. Survey Ohio, Bull. 62 (2): 280, fig. 173.

Dysnomia torulosa (Rafinesque). Ortmann, 1926, Ann. Carnegie Mus. 17: 182. Morrison, 1942, Bur. Amer. Ethnology, Bull. 129, p. 364. Stansbery 1970, Malacologia 10: 20.

Dysnomia (*Torulosa*) *torulosa* (Rafinesque). Frierson, 1927, Check list N American naiades, p. 94. Haas, 1969, Das Tierreich, pt. 88, p. 485.

Truncilla (*Pilea*) *perplexa rangiana* (Lea). Simp-

son, 1900, Proc. U. S. Natl. Mus. 22: 523. Ortmann, 1909, Ann. Carnegie Mus. 5: 188. Simpson, 1914, Cat. Naiades 1: 25.

Truncilla rangiana (Lea). Ortmann, 1912, Ann. Carnegie Mus. 8: 358, fig. 28 (anatomy); 1919, Mem. Carnegie Mus. 9: 331, pl. 21, figs. 5–7. Ball, 1922, Ecology 3: 117. Danglade, 1922, U. S. Bur. Fisheries. Doc. no. 934: 5.

Dysnomia (Torulosa) rangiana (Lea). Frierson, 1927, Check list N American naiades, p. 95.

Dysnomia perplexa rangiana (Lea). Goodrich, 1932, Moll. Mich. p. 113. van der Schalie, 1941, Jour. Conch. 21: 251.

Dysnomia (Pilea) torulosa rangiana (Lea). La Rocque, 1967, Geol. Survey Ohio, Bull. 62 (2): 283.

Dysnomia (Torulosa) torulosa rangiana (Lea). Haas, 1969, Das Tierreich, pt. 88, p. 486.

Truncilla (Pilea) perplexa cincinnatiensis (Lea). Simpson, 1900, Proc. U. S. Natl. Mus. 22: 523; 1914, Cat. Naiades 1: 26.

Dysnomia (Torulosa) torulosa cincinnatiensis (Lea). Frierson, 1927, Check list N American naiades, p. 94. Haas, 1969, Das Tierreich, pt. 88, p. 486.

Dysnomia torulosa cincinnatiensis (Lea). Morrison, 1942, Bur. Amer. Ethnology, Bull. no. 129: 365.

Dysnomia (Pilea) torulosa cincinnatiensis (Lea). La Rocque, 1967, Geol. Survey Ohio, Bull. 62 (2): 283.

Truncilla torulosa gubernaculum (Reeve). Ortmann, 1918, Proc. Amer. Philos. Soc. 57: 590. Ball, 1922, Ecology 3: 114.

Dysnomia torulosa gubernaculum (Reeve). Ortmann, 1926, Ann. Carnegie Mus. 17: 182. Stansbery, 1971. Symposium of rare and endangered moll. U. S., p. 18f, figs. 49, 50.

Dysnomia (Torulosa) torulosa gubernaculum (Reeve). Frierson, 1927, Check list N American naiades, p. 95.

Epioblasma torulosa gubernaculum (Reeve). Stansbery, 1972, Amer. Mal. Union, Bull. for 1972, p. 22.

Description. Shell of medium size, reaching almost 90 mm in length. Outline irregularly ovate, elliptical or obovate. Valves inequilateral, subinflated to inflated, solid. Anterior end regularly rounded, posterior end of male slightly produced; more broadly rounded in females. Ventral margin slightly curved. Dorsal margin curved forming an indistinct angle with the obliquely descending posterior margin. Hinge ligament short. Posterior ridge of the male rather low, narrowly rounded, separated from a similar medial ridge by a broad furrow of varying depth that ends in an emargination between the somewhat produced ridges. Both the ridges and the furrow vary from being smooth to having elevated knobs. The marsupial swelling in the female is sometimes marked by a number of small radial furrows, but the ridges become obscure. The rounded marsupial swelling extends from the middle of the base to the upper part of the posterior end. Umbos full, somewhat turned over a small lunule, located toward the anterior third of the shell, their sculpture feeble and corrugated. Surface of the shell with many distinct growth lines. Periostracum smooth and shiny, tawny, yellowish green, or straw colored, usually with numerous green rays.

Left valve with two triangular pseudocardinal teeth; slight interdentum. Two long, almost straight, lateral teeth. Right valve with one large pseudocardinal tooth with a smaller tooth before it. One lateral tooth, sometimes with a vestigial tooth below. Umbonal cavity shallow. Anterior and posterior adductor muscle scars and pallial line, well impressed. The shell is thin in the marsupial region of the female especially toward the margin. Nacre white to salmon-red.

Male shells are generally irregularly ovate with a rather wide radial furrow of varying depth ending in a broad sinus, often bluntly pointed behind.

Female shells are generally obovate, larger than the male, having a large, flattened, rounded marsupial swelling extending from the middle of the base to near the upper part of the posterior end, which is thin and often a darker green than the rest of the shell.

Length mm	Height mm	Width mm	
68	57	42	Wabash River, Indiana. Male.
85	59	38	As above. Female.

Habitat. Lives in coarse sand and gravel, in current, and in water from a few inches to 4 to 6 feet (Parmalee:1967: 62).

Remarks. Plagiola torulosa (Rafinesque) exhibits considerable ecophenotypic variation as to sculpture, or the lack of it, and to obesity. Ball (1922: 116) convincingly showed the relationship in this species between strong tubercle development and large stream-flow and between the lack of tubercles and small stream flow, as well as *torulosa*'s tendency to be more compressed in smaller streams. Ortmann (1918: 590) had previously noted that in the Tennessee River, "the typical *torulosa* has a radial row of prominent knobs across the middle of the shell. But these knobs vary greatly, and in the upstream direction, they have a tendency to become reduced, finally disappearing, thus passing into the condition seen in the next form [*gubernaculum* Reeve]. From the typical *torulosa*, this variety differs by the poorly developed, or wanting, knobs, and by the rather more compressed shell. This is the headwaters form of *torulosa* and begins to take place in the [Tennessee River] in the vicinity of Knoxville [Knox Co., Tennessee]." Ortmann further observed the variance of tubercules and obesity in relationship to stream size in the Ohio River system (1918: 590) and in the Green River (1926: 182).

Though Ortmann recognized clinal variation in *torulosa*, and Ball carefully documented it, some taxa (applied to ecophenotypic varients of *torulosa*) continue to be promulgated in the literature as if they referred to subspecies. *E. torulosa*, like many other unionid species when found in large lakes, show some ecophenotypic variation. Often these forms have been named; in this case, *Dysnomia sulcata delicata* Simpson.

Ortmann (1926: 182) mentioned that Walker had specimens of *torulosa* from the Cumberland River. "According to the labels, they have gone through the hands of Wetherby and Marsh, and probably were collected by Dr. Lindsey in 1877." Additional specimens from this lot in the Museum of Zoology, University of Michigan are now in the Museum of Comparative Zoology 236769. Since this species appears to have been relatively abundant [illegible] located, and as it was not found [illegible] the extensive Cumberland River collecting reported by Wilson and Clark (1914), this record is regarded as spurious.

Range. Tennessee River system, Tennessee and Alabama; Ohio River system: from Illinois to Pennsylvania, including the Wabash, Green, Licking and Kentucky River drainages; St. Lawrence River system: Lakes Michigan, Huron, and Erie.

Abundance. Still occasionally collected in commercial operations on the lower Ohio River (Kentucky-Illinois) (Parmalee 1967: 62) and from the Nolichucky River near its mouth in western Tennessee. Persists in smaller streams in the Ohio and lower Great Lakes systems [Stansbery as *D. t. rangiana*] and in the Clinch River, Tennessee [Stansbery as *D. t. gubernaculum*]. Gone throughout the rest of its previous range (Stansbery, 1970; 20). *Epioblasma torulosa torulosa* is listed as "extirpated" by Stansbery (1976: 43, 51).

SPECIMENS EXAMINED

TENNESSEE RIVER SYSTEM

Powell River Drainage. *Virginia*: Powell River, Jonesville, Lee Co. (MCZ); Powell River, Shawanee, Clairborne Co. (CM).

Clinch River Drainage. *Virginia*: Clinch River, Dungannon (CM); Clinch River, Hill Station, 5.5 mi. below Fort Blackmore (MCZ); Clinch River, Clinchport (MCZ); *all* Scott Co. *Tennessee*: Clinch River, Kyles Ford, Hancock Co. (MZUM); Clinch River, Union Co.; Clinch River, Clinton, Anderson Co. (*both* MCZ).

Holston River Drainage. *Virginia*: North Fork, Holston Bridge, Scott Co. (CM). *Tennessee*: Holston River, McBee Ford, Hodges, Jefferson Co.; mouth of Holston River, Austins Grist Mill, Knox Co. (*both* MCZ).

French Broad River Drainage. *Tennessee*: Nolichucky River, 3.5 mi. SE Warrensburg, Greene Co. (MCZ); Nolichucky River, Chunns Shoals, Hamblen Co. (CM).

Tennessee River Drainage. *Tennessee*: Tennessee River near Knoxville, Knox Co. (MCZ); Tennessee River, Chattanooga, Hamilton Co. (CM).

Paint Rock River Drainage. *Alabama*: Paint Rock River, Poplar Bluff Ridge, Madison Co. (MCZ).

Tennessee River Drainage. *Alabama*: Tennessee River, 6 mi. E Decatur Morgan Co. (MZUM).

Elk River Drainage. *Alabama*: Elk River, Fayetteville, Lincoln Co. (MZUM).

Tennessee River Drainage. *Alabama*: Tennessee River, Muscle Shoals, Colbert and Lauderdale Cos. (MCZ, CM); Tennessee River, Florence, Lauderdale Co. (MCZ, USNM); Tennessee River, Tuscumbia, Colbert Co. (USNM); Pickwick Basin, mounds between Barton, Colbert Co. and Waterloo, Lauderdale Co. (Morrison, USNM).

Ohio River System

Ohio River Drainage. *Illinois*: Ohio River, Metropolis, Massac Co. (Parmalee, 1967).

Wabash River Drainage. *Indiana*: Eel River, N Manchester, Montgomery Co. (MCZ); Blue River, Morristown (MZUM); Conn Creek, Waldron; East Fork Flat Rock Creek, [town of] Flat Rock Creek (*both* MCZ); *all* Shelby Co. [Mississinewa River], Albany, Delaware Co. (USNM); White River, Indianapolis, Marion Co. (MZUM); White River, Rockford, Jackson Co. (CM). Wabash River, Delphi; Wild Cat Creek; *both* Carroll Co. (*both* MCZ). Wabash River, Lafayette, Tippecanoe Co. (MCZ). Wabash River, New Harmony, Posey Co. (USNM).

Green River Drainage. *Kentucky*: Green River, 8 mi. S Campbellsville, Taylor Co. (MCZ); Green River, Greensburg, Green Co. (MZUM); Mamouth Cave, Edmondson Co. (MCZ); Drakes Creek, 1 mi. SE Mt. Victor (MZUM); Barren River, Bowling Green (MCZ); *both* Warren Co.

Kentucky River Drainage. *Kentucky*: Kentucky River (Rafinesque and Danglade).

Licking River Drainage. *Kentucky*: Licking River (MCZ).

Ohio River Drainage. *Ohio*: Ohio River, Cincinnati, Hamilton Co. (MCZ).

Little Miami River Drainage. *Ohio*: Little Miami River (MCZ).

Scioto River Drainage. *Ohio*: Scioto River, Columbus, Franklin Co.; Big Darby Creek, 4 mi. S Orient (*both* MCZ); Scioto River, Circleville (USNM); *both* Pickaway Co.; Scioto River, Chillicothe, Ross Co. (USNM).

Muskingum River Drainage. *Ohio*: Tuscarawas River, New Philadelphia, Tuscarwas Co. (MCZ).

Ohio River Drainage. *Ohio*: Ohio River, Marietta, Washington Co. (MZUM).

Big Beaver River Drainage. *Ohio*: [Little Mahoning River], Newton Falls, Trumbull Co. (MZUM); Mahoning River, near Garrettsville, Portage Co. (MCZ); Mahoning River, near Poland, Mahoning Co. (Lea). *Pennsylvania*: Shenango River, Pulaski and Harbor Bridge; *both* Lawrence Co. (*both* CM).

Allegheny River Drainage. *Pennsylvania*: Allegheny River, Warren, Warren Co. (MCZ); Allegheny River, Hickory and Tionesta, *both* Forest Co.; Allegheny River, Walnut Bend, Venango Co.; French Creek, Meadville and Cochranton, *both* Crawford Co.; French Creek, Utica, Venango Co.; Allegheny River, Templeton, Johnetta, Godfrey, and Aladdin; *all* Armstrong Co. (*all* CM).

Monongahela River Drainage. *West Virginia*: West Fork Lynch Mines, Harrison Co. (CM).

St. Lawrence River System

Great Lakes Drainage. (Lake Michigan) *Michigan*: Grand River, Grand Rapids, Kent Co. (MCZ). (Lake Huron) *Michigan*: Black River, 1.5 mi. W Amadore, Salinac Co. (MZUM). (Lake Erie)

Michigan: Clinton River, Pontiac, Oakland Co. (MZUM). *Ontario*: Syndenham River, 1.8 mi. NE Shetland, Lambton Co. (Clarke); Detroit River [=Lake Erie], Amherstburg (USNM); Detroit River, Bois Blanc Isle (MZUM); *both* Essex Co. *Michigan*: Huron River, Huron Park, Wayne Co.; River Raisin, Petersburg, Monroe Co. (*both* MZUM). *Indiana*: St. Marys River (MZUM).

Plagiola (*Torulosa*) *sampsoni* (Lea)
Plate 12, figures 6, 7
Distribution: Plate 6, figure B

Unio sampsonii Lea 1861, Proc. Acad. Nat. Sci. Phila. 13: 392 (Wabash River, New Harmony [Posey Co.], Indiana); 1862, Jour. Acad. Nat. Sci. Phila. (2)5: 192, pl. 25, fig. 261, figured holotype UNSM 84802; 1863, Obs. Unio 9: 14.

Truncilla (*Pilea*) *sampsoni* (Lea). Simpson, 1900, Proc. U. S. Natl. Mus. 22: 523; 1914, Cat. Naiades 1: 27.

Truncilla sampsoni (Lea). Ball, 1922, Ecology 3: 117.

Dysnomia (*Torulosa*) *sampsoni* (Lea). Frierson, 1927, Check list N American naiades, p. 95. Haas, 1969, Das Tierreich, pt. 88, p. 486.

Dysnomia sampsoni (Lea). Goodrich and van der Schalie, 1944, Amer. Mid. Nat. 32: 314. Parmalee, 1967, Illinois State Mus., Popular Sci. Ser. 8: 92, pl. 30 E. Stansbery, 1970, Malacologia 10: 20, pl. 2, fig. 6; 1971, Symposium of rare and endangered moll. U. S., p. 18b, fig. 18.

Description. Shell of medium size, seldom reaching over 50 mm in length. Outline subquadrate or trapezoid. Valves inequilateral, inflated, solid. Anterior end regularly rounded, posterior end of the male somewhat pointed, rather broadly rounded in females. Ventral margin straight or slightly curved. Dorsal margin usually sufficiently straight to form an angle with the obliquely descending posterior slope, but sometimes rounded and joining the posterior margin imperceptibly. Hinge ligament short. Posterior ridge low, narrowly rounded, separated from a somewhat broader medial ridge by a distinct furrow that ends in an emargination between the somewhat produced ridges in most males, though in some males the furrow ends in a straight line; in females it is broadly rounded. The ridges are occasionally slightly knobbed, but the furrow is always smooth. The marsupial swelling in the female is infrequently marked by a number of small radial furrows. The rounded marsupial swelling extends from the middle of the base to the upper part of the posterior end. Umbos high and full, turned over a small wide lunule, located toward the anterior third of the shell, their sculpture feeble and corrugated. Surface of the shell rather smooth, usually with a concentric constriction at the rest marks. Periostracum smooth, usually shiny, though sometimes s lky, yellowish green or straw colored with numerous green rays.

Left valve with two triangular pseudocardinal teeth; slight interdentum. Two moderately long, almost straight, lateral teeth. Right valve with one large pseudocardinal tooth with a smaller tooth before and after it. One lateral tooth, sometimes with a vestigial tooth below. Umbonal cavity shallow. Anterior and posterior muscle scars and pallial line well impressed. Nacre bluish white to salmon.

Usually female shells do not differ greatly in outline from the male. The female marsupial swelling is usually just a little produced, not differing in color or texture from the rest of the shell.

Length mm	Height mm	Width mm	
45	42	28	Lower Wabash River, Indiana. Male. (USNM).
52	50	34	As above. Female.

Habitat. Lives in sand and gravel bars, never in mud. (Lea).

Remarks. Plagiola sampsoni (Lea) most closely resembles *P. torulosa* (Rafinesque), but it differs from the latter in that it does not reach such large size, it is almost always devoid of knobs, and both the male and female shells are subquadrate or trapezoid in outline (a characteristic that does not vary

much because of sexual differences). The outline of the male *torulosa* is ovate and that of the female obovate; the marsupial swelling of the female is darker than the rest of the shell, whereas in *sampsoni* it is the same color as the rest of the shell. *P. sampsoni* also resembles *P. propinqua* in that it is generally without knobs. However, male shells of the latter are subtriangular in outline while those of the female are subelliptical. The periostracum of *sampsoni* is generally shiny while that of *propinqua* is almost always subshiny.

Call (1900: 476) included *sampsoni* under the synonymy of *Unio perplexus* [= *torulosa*]. Goodrich and van der Schalie (1944: 314) suggested that *sampsoni* might be a large river form or variant of *Dysnomia perplexa*, though they admitted there were characters that might entitle it to specific rank. Stansbery (1970: 20, pl. 2, fig. 6) thought *sampsoni* might be simply a variant of the subspecies he recognized as *Dysnomia torulosa rangiana* (Lea). As pointed out above, both the male and female shell of *sampsoni* have sufficient characters to separate it from the other *Plagiola*.

Range. Tennessee River system, Tennessee. Ohio River system: lower Wabash River drainage, Indiana; Ohio River drainage to Cincinnati, Hamilton Co., Ohio.

Abundance. This species was not mentioned by Ortmann (1918, 1925) or Morrison (1942) in their studies of the unionids of the Tennessee River system. Ball (1922: 117) had only three specimens without locality data, which could not be presently located in the Carnegie Museum. It is presumed to be known from the Tennessee River system, from a male and female specimen in the Museum of Comparative Zoology merely labeled, "Tennessee."

Formerly found in fair numbers in the lower Wabash River, Indiana. Not located there by Meyer (1974) or Clark (1976). Considered extinct by Stansbery (1970: 20).

Specimens Examined

Tennessee River System

Tennessee River Drainage. *Tennessee*: Tennessee (MCZ. Locality as well as the collector, Steward, written on the male and female shells).

Ohio River System

Wabash River Drainage. *Indiana*: White River (MZUM). Wabash River, New Harmony (MZUM, USNM, ANSP); Grand Chain (USNM); *both* Posey Co. *Illinois.* Wabash River, 'Little Chains,' [archaeological site], 10 mi. above confluence with the Ohio River, White Co. (Parmalee).

Ohio River Drainage. *Ohio*: Ohio River (ANSP); Ohio River, Cincinnati, Hamilton Co. (MCZ).

Plagiola (*Torulosa*) *propinqua* (Lea)

Plate 12, figures 8, 9

Distribution: Plate 6, figure B

Unio propinquus Lea, 1857, Proc. Acad. Nat. Sci. Phila. 9: 83 ([Tennessee River], Florence [Lauderdale Co.]; [Tennessee River] Tuscumbia [Colbert Co.]; *both* Alabama); 1861, Jour. Acad. Nat. Sci. Phila. (2) 5: 63, pl. 5, fig. 212, figured holotype USNM 84332 from the former locality; 1862, Obs. Unio 8: 67.

Truncilla (*Pilea*) *propinqua* (Lea). Simpson, 1900, Proc. U. S. Natl. Mus. 22: 523; 1914, Cat. Naiades 1: 27.

Truncilla propinqua (Lea). Ortmann, 1918, Proc. Amer. Philos. Soc. 57: 589. Ball, 1922, Ecology 3: 113.

Dysnomia (*Pilea*) *torulosa propinqua* (Lea). Ortmann, 1925, Amer. Mid. Nat. 9: 363.

Dysnomia (*Torulosa*) *propinqua* (Lea). Frierson, 1927, Check list N American naiades, p. 95. Haas, 1969, Das Tierreich, pt. 88, p. 487.

Dysnomia propinqua (Lea). Morrison, 1942, Bur. Amer. Ethnology, Bull. no. 129, p. 365. Stansbery, 1970, Malacologia 10: 20, pl. 2, fig. 5; 1971, Symposium of rare and endangered moll. U. S., p. 18b, fig. 17.

Description. Shell of medium size, seldom reaching over 60 mm in length. Outline subtriangular, subelliptical or subquadrate. Valves very inequilateral, inflated,

solid. Anterior end regularly rounded, posterior end of male more broadly rounded, sometimes somewhat pointed; posterior more broadly and evenly rounded in females. Ventral margin curved. Dorsal margin sometimes sufficiently straight to form an angle with the obliquely descending posterior margin, but often rounded and joining the posterior margin imperceptibly. Hinge ligament short. Posterior ridge low, narrowly rounded, median ridge full or rounded, sometimes the ridges are slightly knobbed. Dorsal slope usually rounded. The radial furrow that separates the ridges varies in both depth and width, but it is usually rather deep, especially in the male. Umbos full and high, somewhat turned over a small wide lunule, located in the anterior quarter of the shell, their sculpture is feebly corrugated. Surface of the shell with many distinct growth rests. Periostracum varying from straw-colored or tawny to yellow green with feeble green rays, subshiny or somewhat silky.

Left valve with two chunky triangular pseudocardinal teeth; slight interdentum. Two short, slightly curved lateral teeth. Right valve with one large triangular pseudocardinal tooth usually with a smaller tooth before and behind it. One lateral tooth, sometimes with a vestigial tooth below. Umbonal cavities shallow. Anterior and posterior adductor muscle scars, and pallial line, well impressed. Nacre bluish white, rarely pinkish.

Male shells subtriangular, with the radial furrow usually deep, ending in a narrow sinus below.

Female shells subelliptical or subquadrate, the marsupial swelling rounded and moderately produced, the radial furrow becoming obscure posteriorly. Marsupial swelling sometimes darker than the rest of the shell.

Remarks. *Plagiola propinqua* (Lea) bears some resemblance to *P. torulosa*, and though the former may be slightly knobbed, it is generally smooth. The male of *propinqua* is subtriangular in outline, while that of *torulosa* is generally irregularly [illegible] the posterior ridge of the former [illegible] obliquely angled, and the radial furrow is narrower and deeper than in *torulosa*. The female of *propinqua* is subelliptical in outline, while the *torulosa* female is produced posteriorly and obovate. The radial furrow of *propinqua* is narrow and deep except in the post-basal region where there is some marsupial swelling. The posterior end of the female *torulosa* is without a radial furrow, but is instead a large flattened marsupial swelling that extends from the middle of the ventral margin to the upper part of the posterior margin. While the marsupial area of *propinqua* is usually the same color as the rest of the shell, that of *torulosa* is often a darker green.

Simpson (1914: 24) correctly recognized *propinqua* as a distinct species, but Ortmann (1925: 363) in interpreting the data of Ball (1922: 115) regarded *propinqua* as merely a *torulosa* with the tubercules very poorly developed or absent. Morrison (1942: 365) examined thousands of *torulosa* and *propinqua* specimens from Indian mounds of the Pickwick Landing Basin, Colbert and Lauderdale counties, Alabama and found no integrades between them.

Range. Tennessee River system, Tennessee and Alabama; Cumberland River system, Tennessee; Ohio River system: from the lower Wabash River drainage, Indiana to the Ohio River, Cincinnati, Hamilton County, Ohio.

Abundance. This species was not found by Wilson and Clark (1914) in the Cumberland River system. Considered extinct by Stansbery (1976: 43, 51).

Specimens Examined

Tennessee River System

Clinch River Drainage. *Tennessee*: Clinch River, Clinton and Edgemoor, *both* Anderson Co. (*both* CM).

Holston River Drainage. *Tennessee*: mouth of Holston River, Austins Grist Mill, Knox Co. (MCZ; MZUM).

Tennessee River Drainage. *Tennessee*: Tennessee River, Knoxville, Knox Co. (MCZ); *Alabama*: Tennessee River, Muscle Shoals, Colbert and Lauderdale Cos. (CM); Tennessee River, Florence, Lauderdale Co. (MCZ, MZUM); Tennessee River, Tuscumbia, Colbert Co. (MCZ); Pickwick Basin, mounds between Barton, Colbert Co. and Waterloo, Lauderdale Co. (Morrison, USNM).

CUMBERLAND RIVER SYSTEM

Cumberland River Drainage. *Tennessee*: Cumberland River (Simpson, 1914: 27; MZUM; MCZ). [Cumberland River], Nashville, [Davidson Co.] (MCZ, data written on the shells).

OHIO RIVER SYSTEM

Wabash River Drainage. *Indiana*: White River (MZUM); Wabash River, New Harmony, Posey Co. (MCZ; MZUM).

Ohio River Drainage. *Ohio*: Ohio River, Cincinnati, Hamilton Co. (MCZ).

Plagiola (*Torulosa*) *biemarginata* (Lea)
Plate 13, figures 1, 2
Distribution: Plate 9, figure A

Unio biemarginatus Lea 1857, Proc. Acad. Nat. Sci. Phila. 9: 83 ([Tennessee River], Florence [Lauderdale Co.], Alabama); 1866, Jour. Acad. Nat. Sci. Phila. (2) 6: 47, pl. 16, fig. 45, figured holotype USNM 84608; 1867, Obs. Unio 11: 51.

Truncilla (*Pilea*) *biemarginata* (Lea). Simpson, 1900, Proc. U. S. Natl. Mus. 22: 524; 1914, Cat. Naiades 1: 28.

Dysnomia (*Pilea*) *biemarginata* (Lea). Ortmann, 1925, Amer. Midland Nat. 9: 361.

Dysnomia (*Torulosa*) *biemarginatus* (Lea). Frierson, 1927, Check list N American naiades, p. 95. Haas, 1969, Das Tierreich, pt. 88, p. 487.

Dysnomia biemarginata (Lea). Morrison, 1942, Bur. Amer. Ethnology, Bull. no. 129: 364. Stansbery, 1970, Malacologia 10: 20; 1971, Symposium of rare and endangered moll. U. S., p. 18b, figs. 13, 14.

Description. Shell usually small, seldom reaching more than 50 mm in length. Outline subtriangular, subrhomboid, or irregularly obovate. Valves not much inflated, solid, inequilateral. Anterior end regularly rounded, posterior end of male less broadly rounded, subtruncated; more broadly and more evenly rounded in females. Ventral margin of male curved, of female almost straight before the marsupial swelling. Dorsal margin of male long, forming a sharp angle with the obliquely descending posterior margin; of female short forming a less sharp angle with the obliquely descending posterior margin. Hinge ligament rather long. Posterior ridge of male with a sharp, biangulate, posterior ridge ending in a biangulation below, median ridge full and rounded, the radial depression between the ridges wide and shallow. Dorsal slope concave. Posterior ridge of the female faintly biangulate, the radial depression between it and the medial ridge shallow and fading out on the marsupial swelling. Umbos moderately full and inflated, located slightly anterior of the middle, their sculpture not observed. Surface of the shell with strong and irregular growth rests. Periostracum yellowish green, with numerous green rays of varying width over the entire surface.

Left valve with two chunky triangular pseudocardinal teeth; slight interdentum. Two long, almost straight, lateral teeth. Right valve with one large triangular pseudocardinal tooth, usually with a much smaller tooth before and behind it. One lateral tooth. Umbonal cavities shallow. Anterior and posterior adductor muscle scars and pallial line well impressed. Shell thinner posteriorly in both sexes. Nacre bluish white to creamy.

Male shells are subtriangular, or subrhomboid, with a sharply biangulate posterior ridge that ends posteriorly in a biangulation. There is a wide shallow radial depression before a full rounded medial ridge.

Female shells are obovate, having a large flattened, rounded marsupial swelling extending from the middle of the base to the upper part of the posterior end. The radial

depression between the faintly biangulate posterior ridge and the medial ridge is shallow and fades out on the marsupial swelling which is darker than the rest of the shell.

Length mm	Height mm	Width mm	
50	38	27	Tennessee River, Muscle Shoals, Colbert and Lauderdale Cos., Alabama. Male.
38	28	17	As above. Female.

Remarks. *Plagiola biemarginata* (Lea) bears a resemblance to both *P. perplexa* and *propinqua.* It is smaller than both of them, and is not knobbed as *perplexa* often is. It may be distinguished easily from *propinqua,* which has a much higher shell in relation to length. While close to the same proportions as *perplexa, biemarginata* is easily separated from it by the decidedly more acutely biangulate posterior ridge, which ends in a sharper biangulation at the posterior end in males, and has a concave dorsal slope. The wide green rays on both sexes of *biemarginata* distinguish it from *perplexa* and *propinqua.*

Range. Tennessee River system, Tennessee and Alabama; Cumberland River system, Big South Fork, Kentucky.

Abundance. Considered extinct by Stansbery (1970: 20; 1976: 43, 50).

SPECIMENS EXAMINED

TENNESSEE RIVER SYSTEM

Clinch River Drainage. *Tennessee*: Clinch River, "The Rounds," Hancock Co. (MCZ).

Holston River Drainage. *Tennessee*: Holston River, Knox Co. (MCZ).

Sequatchie River Drainage. *Tennessee*: Sequatchie River (MZUM).

Paint Rock River Drainage. *Alabama*: Paint Rock River, Paint Rock, Jackson Co. (MZUM).

Flint River Drainage. *Alabama*: Flint River (MZUM).

Elk River Drainage. *Tennessee*: [illegible] River, Fayetteville, Lincoln Co. ([illegible]).

Tennessee River Drainage. *Alabama*: Tennessee River, Muscle Shoals, Colbert and Lauderdale Cos.; Tennessee River, Florence, Lauderdale Co.; Tennessee River, Tuscumbia, Colbert Co.; (*all* MCZ); Pickwick Basin, mounds between Barton, Colbert Co. and Waterloo, Lauderdale Co. (Morrison, USNM).

CUMBERLAND RIVER SYSTEM

Cumberland River Drainage. *Kentucky*: Big South Fork, Burnside, Pulaski Co. (MZUM).

Plagiola (*Torulosa*) *capsaeformis* (Lea)
Plate 13, figures 3, 4
Distribution: Plate 7, figure B

Unio capsaeformis Lea 1834, Trans. Amer. Philos. Soc. 6: 31, pl. 2, fig. 4 (Cumberland River [Tennessee], figured holotype MCZ 178570); 1834, Obs. Unio 1: 143.

Truncilla (*Pilea*) *capsaeformis* (Lea). Simpson, 1900, Proc. U. S. Natl. Mus. 22: 524; 1914, Cat. Naiades 1: 29.

Truncilla capsaeformis (Lea). Ortmann, 1912, Ann. Carnegie Mus. 8: 359 [anatomy mistakenly described under *florentina*]; 1913, Proc. Amer. Philos. Soc. 52: 311. Goodrich, 1913, Nautilus 27: 95.

Dysnomia (*Pilea*) *capsaeformis* (Lea). Ortmann, 1924, Amer. Mid. Nat. 9: 38; 1925, Amer. Mid. Nat. 9: 362.

Dysnomia (*Capsaeformis*) *capsaeformis* (Lea). Frierson, 1927, Check list N American naiades, p. 95. Haas, 1969, Das Tierreich, pt. 88, p. 487.

Dysnomia capsaeformis (Lea). Wilson and Clark, 1914, U. S. Bur. Fisheries, Doc. 781, p. 46. Morrison, 1942, Bur. Amer. Ethnology, Bull. no. 129, p. 364. Neel and Allen, 1964, Malacologia 1: 448. Van der Schalie, 1973, Sterkiana, no. 52, pp. 46, 48, 50, 51.

Epioblasma capsaeformis (Lea). Stansbery, 1972, Amer. Mal. Union, Bull. for 1972, p. 22.

Description. Shell of medium size, reaching about 70 mm in length. Outline elliptical or irregularly obovate. Valves somewhat inequilateral, subinflated, subsolid. Anterior end regularly rounded, posterior end of male slightly produced; more broad-

ly rounded in females. Ventral margin slightly, but uniformly, curved in the male; almost straight in females to the sulcus, behind which the marsupial swelling extends well below the base. Dorsal margin straight, forming an angle with the obliquely descending posterior margin. Hinge ligament short. Posterior ridge of the male, double, but faint, ending in a slight biangulation posteriorly; ridge scarcely visible in females. There is sometimes a faint radial depression in front of the lower posterior ridge of the male. The considerable marsupial swelling of the female is usually marked by a sulcus before and behind and is sometimes finely toothed on the margin. Umbos quite full and elevated, located slightly anterior of the middle in the male, and in the anterior third of the shell in the female; umbonal sculpture not observed. Surface of the shell with uneven growth lines. Periostracum subshiny, yellowish green with numerous fine green rays over the entire surface, marsupial area of the female usually dark green, sometimes blackish.

Left valve with two, chunky, triangular pseudocardinal teeth; slight interdentum. Two short, slightly curved lateral teeth. Right valve with one large triangular pseudocardinal tooth, usually with a smaller tooth before it that is parallel to the hinge line. One lateral tooth, sometimes with a vestigial tooth below. Umbonal cavities shallow. Anterior adductor muscle scars well impressed, posterior ones shallow. Pallial line distinct anteriorly. Nacre bluish white. Shell heavier anteriorly, posterior end of females especially thin and iridescent.

Male shells irregularly elliptical, with a double, but faint, posterior ridge, which ends in a slight biangulation, near the median.

Female shells irregularly obovate with a thin, slightly inflated, marsupial swelling, which may be considerably produced and extended well below the base, often marked by two distinct sulci, sometimes toothed on the margin.

Length mm	Height mm	Width mm	
60	40	24	Duck River, Milltown, Marshall Co., Tennessee. Male.
60	43	21	As above. Female.

Remarks. *Plagiola capsaeformis* (Lea) bears some resemblance both to *P. perplexa* and *florentina.* Only the female resembles *perplexa*, but that of *capsaeformis* is always smaller, thinner and without knobs. Both the male and female of *capsaeformis* resemble *florentina*, but the male of the former is longer, lower and less swollen than that of *florentina.* In the *capsaeformis* female the marsupial swelling is darker than the rest of the shell, while in *florentina* the periostracum (in both sexes) is a uniform honey yellow or yellowish brown. The green rays of the latter are more evenly distributed.

Range. Tennessee River system, Virginia, Tennessee and Alabama; Cumberland River system, Kentucky and Tennessee.

Abundance. The number of specimens seen in collections indicates this species must have been abundant, especially in the Tennessee River system.

Specimens Examined

Tennessee River System

Powell River Drainage. *Virginia*: Powell River, 2.5 mi. S Jonesville, Lee Co. *Tennessee*: Powell River, Shawnee (CM); Powell River, 8–10 mi. N Tazewell (MCZ); *both* Claiborne Co.; Powell River, Greens Ford, 2 mi. NW Long Hollow, Union Co. (MCZ).

Clinch River Drainage. *Virginia*: Clinch River, Cedar Bluff, Tazewell Co. (CM); Clinch River, Cleveland, Russell Co. (MCZ); Clinch River, Dungannon, Clinchport, and below Speers Ferry Bridge, *all* Scott Co. (*all* MCZ); Clinch River, 1.5 mi.

S Dona, Lee Co. (MCZ). *Tennessee*: Clinch River, Kyles Ford, and "The Rounds," *both* Hancock Co. Clinch River, 4 mi. NW Thorn Hill, Grainger Co.; Clinch River, Clinton, Anderson Co. (*all* MCZ).

Holston River Drainage. *Virginia*: North Fork, Mendota, Washington Co. (CM); North Fork, Hilton, Scott Co. (MCZ). *Tennessee*. North Fork, Clouds Ford, 2 mi. W Morrison (MCZ); South Fork, Pactolus (CM); *both* Sullivan Co.; mouth of Holston River, Austins Grist Mill, Knox Co. (MCZ).

French Broad River Drainage. *North Carolina*: French Broad River, Asheville, Buncombe Co. (MZUM). *Tennessee*: Nolichucky River, 3.5 mi. SE Warrensburg, Green Co.

Tennessee River Drainage. *Tennessee*: Tennessee River, near Knoxville, Knox Co. (*both* MCZ); Little Tennessee River, Coytee, Loundon Co. (MZUM).

Paint Rock River Drainage. *Alabama*: Paint Rock River, Princeton, Holly Tree, and Trenton (*all* MCZ); between New Hope and Paint Rock (CM); *all* Jackson Co.

Flint River Drainage. *Alabama*: Flint River, Gurley, Madison Co. (MCZ).

Limestone Creek Drainage. *Alabama*: Limestone Creek, Mooresville, Limestone Co. (MZUM).

Elk River Drainage. *Tennessee*: Elk River, Winchester, Franklin Co. (MCZ); Richland Creek, Wales, Giles Co. (CM). *Alabama*: Elk River, Fayetteville, Lincoln Co. (MCZ).

Tennessee River Drainage. *Alabama*: Shoals Creek, Lauderdale Co.; Tennessee River, Muscle Shoals, Colbert and Lauderdale Cos. (*both* MCZ); Pickwick Basin, mounds between Barton, Colbert Co. and Waterloo, Lauderdale Co. (Morrison, USNM).

Bear Creek Drainage. *Alabama*: Bear Creek, Burleson, Franklin Co. (CM).

Duck River Drainage. *Tennessee*: Duck River, Shelbyville, Bedford Co. (MZUM); Duck River, Wilhoite; Duck River, below Lillard Mill, Miltown; Duck River, Hardinsons Mill, 12 mi. NW Lewisburg; *all* Marshall Co. (*all* MCZ); Duck River, Leftwich (CM) and Columbia (MCZ), *both* Maury Co.

CUMBERLAND RIVER SYSTEM

Cumberland River Drainage. *Kentucky*: Cumberland River, below Cumberland Falls, Whitely Co.; Rockcastle River, Mt. Victory; (*both* MZUM); Big South Fork, Parkers Lake Station (Wilson and Clark) and above Burnside (MZUM); *all* Pulaski Co.; Cumberland River, Horseshoe Bottom (MZUM); Beaver Creek, E Rowena Ferry (MCZ); *both* Russell Co. Cumberland River, Neeleys Ferry, Cumberland Co. (MZUM).

Obey River Drainage. *Tennessee*: Obey River, Pryor Bend, Pickett Co. (MCZ).

Caney Fork Drainage. *Tennessee*: Caney Fork [Smith Co.], (Wilson and Clark).

Harpeth River Drainage. *Tennessee*: Harpeth River, 10 mi. W Franklin, Williamson Co.; Harpeth River, Davidson Co. (*both* MCZ).

Plagiola (*Torulosa*) *florentina* (Lea)
Plate 13, figures 5–14
Distribution: Plate 2

Unio florentinus Lea 1857, Proc. Acad. Nat. Sci. Phila. 9: 83 ([Tennessee River], Florence, [Lauderdale Co.], Alabama; Cumberland River, Tennessee); 1861, Jour. Acad. Nat. Sci. Phila. (2) 5: 64, pl. 5, fig. 213, figured holotype USNM 84948 from the former locality; 1862, Obs. Unio 8: 68.

Unio saccatus Küster 1862, Conch. Cabinet (2) 9, pt. 2, p. 263, pl. 89, fig. 2 (Tennessee, figured type, location unknown).

Unio sacculus Reeve 1864, Conch. Iconica 16, *Unio*, pl. 15, species 67 (North America, figured type, British Mus. Nat. Hist. [lost]). Anthony, 1865, Amer. Jour. Conch. 1: 157, pl. 12, fig. 3 (Tennessee, figured holotype MCZ 161898). Anthony sent H. Cuming a specimen of his species before publication, which Reeve described before Anthony.

Truncilla walkeri Wilson and Clark 1914, U. S. Bur. Fisheries, Doc. no. 781, p. 46, pl. 1, fig. 1

(East Fork of Stones River, near Walterville [=Walterhill, Rutherford Co.], Tennessee, since the two figured syntypes could not be located in the USNM, a lectotype is here selected from a series of syntypes in the Museum of Zoology, University of Michigan 90729, pl. 13, fig. 9). Ortmann, 1918, Proc. Amer. Philos. Soc. 57: 592.

Truncilla curtisii Frierson and Utterback 1916, Amer. Mid. Nat. 4: 453 (190), pl. 6, fig. 14a–d, pl. 28, fig. 109 A–D (White River, Hollister, [Taney Co.], Missouri, the two figured syntypes are lost, a lectotype is here selected from a series collected by Frierson and Utterback in the White River, Forsyth, Taney Co., Missouri, Museum of Zoology, University of Michigan 90748, pl. 13, fig. 10).

Truncilla (Pilea) florentina (Lea). Simpson, 1900, Proc. U. S. Natl. Mus. 22: 524 [partim]; 1914, Cat. Naiades 1: 30 [partim]. Wilson and Clark, 1914, U. S. Bur. Fisheries, Doc. 781, p. 46.

Dysnomia (Pilea) florentina (Lea). Ortmann, 1925, Amer. Mid. Nat. 9: 362.

Dysnomia (Capsaeformis) florentina (Lea). 1927, Check list N American naiades, p. 95. Haas, 1969, Das Tierreich, pt. 88, p. 488.

Description. Shell of medium size, seldom reaching over 60 mm in length. Outline elliptical or irregularly obovate. Valves somewhat inequilateral, subinflated, subsolid. Anterior end regularly rounded, posterior end of male slightly produced; posterior more broadly rounded in females. Ventral margin slightly but uniformly curved in the male; almost straight in females to the sulcus, behind which the marsupial swelling extends well below the base. Dorsal margin straight, forming an angle with the obliquely descending posterior margin. Hinge ligament short. Posterior ridge of the male, double, but faint, ending in a slight biangulation posteriorly; ridge scarcely visible in females. There is a wide shallow radial depression in front of the full, lower posterior ridge in the male. The considerable marsupial swelling of the female is usually marked by a sulcus before and behind and is sometimes finely toothed on the margin.

Umbos quite full and elevated, located slightly anterior of the middle in the male, and in the anterior third of the shell in the female, umbonal sculpture not observed. Surface of the shell with uneven growth lines. Periostracum subshiny, yellow, honey yellow, brownish yellow or whitish with numerous green rays more or less uniformly distributed over the entire surface.

Left valve with two chunky triangular pseudocardinal teeth; slight interdentum. Two short slightly curved lateral teeth. Right valve with one large triangular pseudocardinal tooth, usually with a smaller tooth before it that is parallel to the hinge line. One lateral tooth, sometimes with a vestigial tooth below. Umbonal cavities shallow. Anterior adductor muscle scars well impressed, posterior ones shallow. Pallial line distinct anteriorly. Nacre bluish white. Shell heavier anteriorly, posterior end of females especially thin and irridescent.

Male shells irregularly elliptical, with a double posterior ridge that ends in a slight bimargination near the median. There is a wide, shallow, radial depression in front of the full, lower posterior ridge.

Female shells irregularly obovate with a thin, slightly inflated marsupial swelling, which may be considerably produced and extended well below the base, often marked by two distinct sulci, toothed on the margin.

Length mm	Height mm	Width mm	
54	39	24	Stones River, 7 mi. NE Murfreesboro, Rutherford Co., Tennessee. Male.
49	38	21	As above. Female.

Remarks. Plagiola florentina (Lea) most closely resembles *P. capsaeformis.* The male of the former is shorter, higher and more swollen than that of *capsaeformis* and has a distinct wide shallow radial depression in front of the lower posterior ridge. This depression is very faint or wanting in *capsaeformis.* The female *florentina* has more strongly developed and more numerous denticulations on the margin of the marsupial expansion, and is more convex than *capsaeformis.* The two species are most readily separated by the color of the

surface—*florentina* is light yellow, honey colored, yellowish brown, or whitish, and is rather uniformly rayed over the entire surface; *capsaeformis* is green or greenish brown, and while the male is rather uniformly rayed, the marsupial area of the female is a darker green.

Ortmann (1918: 592) noted that *walkeri* was a large, compressed *florentina*, and that it was probably only an ecophenotypic variant. He later (1924a: 36) concluded from the measurements of numerous samples that the obesity or diameter of the shell changed with the size of the river—the larger rivers have the more swollen *florentina*, and the smaller rivers have the more compressed *walkeri*. In spite of Ortmann's observations, *walkeri* has continued to be promulgated in the literature as if it had nomenclatorial standing.

Truncilla curtisi Frierson and Utterback from the Ozark Plateau was recognized by Stansbery (1971: 18e) as a subspecies on the basis that his specimens were nearly white (pers. comm.). Utterback (1916: 453 [190]) mentioned that the epidermis of his specimens was yellowish brown and finely and obscurely radiate all over. Because of its geographical isolation, *curtisi* might be recognized as a subspecies as presently understood, but this does not seem warranted on morphological differences.

Anatomy. Described by Utterback (1916: 453 [190]).

Range. Upper White River system, Missouri; Tennessee River system, Virginia, Tennessee, and Alabama; Cumberland River system, Kentucky and Tennessee.

Abundance. "Now restricted in the Cumberland River system to the lower Stones and Red Rivers [as *D. f. walkeri*] and apparently gone from the entire Tennessee River system save the South Fork of the Holston in Virginia," (Stansbery 1970: 20). Collected in small numbers in the Black River, Missouri by C. B. Stein in 1964. Listed as "extirpated" by Stansbery (1976: 43, 51).

Specimens Examined

White River System

White River Drainage. *Missouri*: White River, Hollister, (Utterback); White River, Forsyth, (MZUM); *both* Taney Co.

Black River Drainage. *Missouri*: Black River, Hendrickson, Butler Co. (MCZ, OSM).

Tennessee River System

Holston River Drainage. *Virginia*: Middle Fork, Chilhowie, Smyth Co. (CM; Stansbery, OSM); Middle Fork, 3.7 mi. S Glade Spring (MCZ); South Fork, Barron (CM); *both* Washington Co. *Tennessee*: South Fork, Emmett, Sullivan Co.; Holston River, Holston Station, Grainger Co.; Holston River, Knox Co. (*all* CM).

Flint River Drainage. *Alabama*: Flint River, Maysville and Gurley; Hurricane Creek, Gurley; *all* Madison Co. (*all* CM).

Limestone Creek Drainage. *Alabama*: Limestone Creek, Mooresville, Limestone Co. (MZUM).

Tennessee River Drainage. *Alabama*: Tennessee River, Muscle Shoals, Colbert and Lauderdale Cos. (CM); Cypress Creek, Florence, (MZUM); Tennessee River, Florence, (MCZ); *both* Lauderdale Co. Pickwick Basin, mounds between Barton, Colbert Co. and Waterloo, Lauderdale Co. (Morrison, USNM).

Bear Creek Drainage. *Alabama*: Bear Creek, Burleston, Franklin Co. (MZUM).

Duck River Drainage. *Tennessee*: Duck River, Lillards Mills, Wilhoite, Marshall Co. (CM); Duck River, Columbia, Maury Co. (MCZ).

Cumberland River System

Cumberland River Drainage. *Kentucky*: Buck Creek, 2.1 mi. NE Mt. Victory (MCZ); Cumberland River, Burnside (CM); *both* Pulaski Co.; Beaver Creek, near mouth, (MZUM); Cumberland River, Indian Creek Bar (Wilson and Clark);

Cumberland River, Horseshoe Bottom, 5 mi. S Jamestown (MZUM); *all* Russell Co.

Obey River Drainage. *Tennessee*: Obey River, Duncan Ford, 4 mi. SE Lilydale, Pickett Co. (MCZ).

Stones River Drainage. *Tennessee*: East Fork, Stones River, Walterhill; Stones River, 7 mi. NNE Murfreesboro; *both* Rutherford Co. (*both* MCZ); Stones River, 1.2 mi. W Couchville, Davidson Co. (MCZ).

Harpeth River Drainage. *Tennessee*: Harpeth River, Belleview, Davidson Co. (CM).

Red River Drainage. *Tennessee*: Lower Red River [Montgomery Co.] (Stansbery, OSM).

Plagiola (*Torulosa*) *turgidula* (Lea)
Plate 14, figures 1–6
Distribution: Plate 2

Unio turgidulus Lea 1858, Proc. Acad. Nat. Sci. Phila. 10: 40 (Cumberland River, Tennessee; [Tennessee River], Florence, [Lauderdale Co.], Alabama); 1861, Jour. Acad. Nat. Sci. Phila. (2) 5: 62, pl. 5, fig. 211, figured holotype USNM 84946 from the former locality; 1862, Obs. Unio 8: 66.

Unio nux Küster 1861, Conch. Cabinet (2) 9, pt. 2, p. 218, pl. 73, fig. 2 (Alabama, figured type, [location unknown]) *non* Lea 1852.

Unio deviatus Reeve 1864, Conch. Iconica 16, Unio, pl. 15, species 61 ([Tennessee], figured holotype British Mus. Nat. Hist. 1965210). Anthony, 1865, Amer. Jour. Conch. 1: 156, pl. 12, fig. 2 (Tennessee, figured holotype MCZ 161895). Anthony sent H. Cuming a specimen of his species before publication, which Reeve described before Anthony.

Truncilla lefevrei Utterback 1916, Amer. Mid. Nat. 4: 455 [192], pl. 6, figs. 13 a–d, pl. 28, figs. 108 A–D (Black River, Williamsville, [Wayne Co.], Missouri, figured syntypes [lost]).

Truncilla (*Pilea*) *deviata* (Reeve). Simpson, 1900, Proc. U. S. Natl. Mus. 22: 524; 1914, Cat. Naiades 1: 32.

Truncilla (*Pilea*) *florentina* (Lea). Simpson, 1900, Proc. U. S. Natl. Mus. 22: 524 [partim]; 1914, Cat. Naiades 1: 32 [partim].

Truncilla turgidula (Lea). Ortmann, 1918, Proc. Amer. Philos. Soc. 57: 590.

Dysnomia (*Pilea*) *turgidula* (Lea). Ortmann and Walker, 1922, Occ. Papers, Mus. Zool., Univ. Michigan no. 112, p. 69. Ortmann, 1924, Amer. Mid. Nat. 9: 34; 1925, Amer. Mid. Nat. 9: 361.

Dysnomia (*Capsaeformis*) *turgidula* (Lea). Frierson, 1927, Check list N American naiades, p. 95. Haas, 1969, Das Tierreich, pt. 88, p. 490.

Dysnomia biemarginata turgidula (Lea). Stansbery, 1970, Malacologia 10: 20.

Dysnomia turgidula (Lea). Stansbery 1971, Symposium of rare and endangered moll. U. S., p. 18b, fig. 19. Van der Schalie, 1973, Sterkiana no. 52, p. 52.

Dysnomia (*Capsaeformis*) *lefevrei* (Utterback). Frierson, 1927, Check list N American naiades, p. 95. Haas, 1969, Das Tierreich, pt. 88, p. 489.

Description. Shell rather small, seldom reaching more than 40 mm in length. Outline elliptical, ovate or obovate. Valves inequilateral, solid, slightly inflated. Anterior end regularly rounded; posterior end of male rather pointed, of female more broadly rounded. Ventral margin curved in males, almost straight in females before the marsupial swelling. Dorsal margin slightly curved forming an indistinct angle with the obliquely descending posterior margin. Hinge ligament short. Posterior ridge of the male, double, somewhat raised, ending posteriorly in a slight biangulation. The ridges of the female fade out on the marsupial swelling. Dorsal slope slightly concave. The male has a rather wide, shallow, radial furrow, which ends in an emargination. The medial ridge is only slightly developed, and both it and the radial furrow are obscured in females by marsupial swelling. Umbos moderately full and elevated, located in the anterior third of the shell; umbonal sculpture not observed. Surface of the shell with irregular growth lines, which are especially strong on the female posteriorly. Periostracum rather shiny, yellowish green, with numerous fine green rays over the entire surface.

Left valve with two small, rough, subcompressed pseudocardinal teeth. No interdentum. Two short, straight, lateral teeth. Right valve with one small, triangular, pseudocardinal tooth, with a second tiny tooth before it that is parallel to the hinge line. One lateral tooth. Umbonal

cavities shallow. Anterior adductor muscle scars well impressed; posterior scars faint. Pallial line distinct anteriorly. Nacre bluish white. Shell heavier anteriorly, posterior end of females especially thin and irridescent.

Male shells are elliptical or ovate, with a distinct raised double posterior ridge, which ends in a biangulation near the base. Before the ridge is a wide shallow radial furrow and faint medial ridge.

The female is somewhat obovate, and while the marsupial swelling obliterates the radial furrow and the medial and posterior ridges, there is a tendency for the shell to be somewhat concave in the region of the posterior ridges. The surface of the marsupial swelling is not different from the rest of the shell, the feeble green rays are rather evenly distributed in both sexes.

Length mm	Height mm	Width mm	
41	29	22	Holston River, Knox Co., Tennessee. Male.
39	25	18	Tennessee. Female. Holotype of *Unio deviatus* Anthony.

Remarks. Plagiola turgidula (Lea) most closely resembles *P. biemarginata*, but the former has a more delicate, more elongate shell. The male of *turgidula* differs from that of *biemarginata*, in that the former has a less pronounced posterior and medial ridge and the radial furrow is not as deep as in the latter. Further, the posterior ridge of *turgidula* ends higher on the posterior margin than does that of *biemarginata*.

The female *turgidula* resembles the females of the other members of subgenus *Capsaeformis*, with its inflated, outcurved, marsupial expansion in the area occupied by the radial furrow in the male. However in *turgidula* alone is there no color difference between the disk and the marsupial swelling. Light green rays uniformly cover the entire surface, except sometimes the extreme anterior.

The male of this species was described by Lea and the female, later, by Reeve. Walker (1910: 81) was first to recognize the two sexes as the same species. This is the species described by Utterback as *lejeunerei* from the Ozark Plateau. He refers to the male shell as having a post-umbonal ridge, rather biangulated and with a very slight radial furrow in front. *P. turgidula* had been collected before 1914 on the Ozark Plateau from Spring Creek, Hardy, Sharp County, Arkansas, and so noted by Simpson (1914; 1: 32).

The presence of *P. turgidula*, like that of *florentina* on the Ozark Plateau, is evidence of a former connection of that area with the Cumberland Plateau.

Anatomy. Described by Utterback (1916: 457 [192]).

Range. Upper White River system, Missouri and Arkansas; Tennessee River system, Tennessee and Alabama; Cumberland River system.

Abundance. This species is known from the Cumberland River, only on the authority of Lea and from a specimen, so labeled, in the British Museum (Nat. Hist.). It was once widely distributed throughout the Tennessee River system, but according to Stansbery (pers. comm.), it is now restricted to the Duck River, in the vicinity of Normandy, Bedford County, Tennessee.

Listed a "extirpated" by Stansbery (1976: 43, 51).

Specimens Examined

White River System

White River Drainage. *Missouri*: White River, Moores Ferry [not located, but probably in Stone or Taney Co.] (MZUM).

Black River Drainage. *Arkansas*: [Spring River], Hardy, Sharp Co. (MZUM; MCZ, *ex* MZUM; Field Museum, Chicago). *Missouri*: Black River, Williamsville, Wayne Co. (Utterback).

Tennessee River System

Clinch River Drainage. *Tennessee*: Clinch River (MCZ); Emory River, Harriman, Roane Co. (CM).

Holston River Drainage. *Tennessee*: Holston River, Rogersville (MZUM); Holston River, Austin Mill (CM); *both* Hawkins Co.; mouth of Holston River, Austins Grist Mill, Knox Co. (MCZ).

Elk River Drainage. *Tennessee*: Elk River (Stansbery, OSM).

Tennessee River Drainage. *Alabama*: Shoals Creek (Hinkley and Marsh); Tennessee River, Florence (Lea, USNM); *both* Lauderdale Co.

Bear Creek Drainage. *Alabama*: Bear Creek, Burleson, Franklin Co. (CM).

Duck River Drainage. *Tennessee*: Duck River, Normandy (Stansbery, OSM); Shelbyville (CM); *both* Bedford Co. Duck River, Columbia, Maury Co. (Hinkley and Marsh).

CUMBERLAND RIVER SYSTEM

Cumberland River Drainage. Cumberland River (Lea, USNM; BMNH).

Subgenus *Pilea* Simpson

Pilea Simpson 1900, Proc. U. S. Natl. Mus. 22: 522. Type species, *Unio personatus*, original designation.

Scalenilla Ortmann and Walker 1922. Occ. Papers, Mus. Zool., Univ. Mich. no. 112, p. 68. Type species, *Unio sulcatus* Lea, original designation.

Obliquata Frierson, 1927, Check list N American naiades, pp. 10, 52. Type species, *Obliquaria* (*Scalenaria*) *obliquata* Rafinesque, original designation, *teste* Errata et Corrigenda.

Description. Shell subtriangular or subquadrate. "Male shell with a wide, shallow, radiating depression in front of the posterior ridge, that of the female with a rounded, foliaceous swelling at the posterior base. Animal with post basal flap of mantle of female very heavy; ovisacs not extending to the top of the marsupium." (Simpson).

Remarks. Frierson (1927: 96) restricted Simpson's subgenus *Pilea* to include *personatus* and *sulcatus* (= *obliquata*), but *haysianus* is now also included on the basis of shell morphology. All three of these species tend to be proportionally higher in relationship to length than any others in the genus. They all have relatively heavy shells, and have periostraca that are similarly shiny or subshiny, greenish yellow, or chestnut, with very fine green rays. Unlike other members of *Plagiola* they sometimes have purple or flesh-colored nacre. The depression in front of the posterior ridge in the male is a raised marsupial swelling in the female.

KEY TO THE SPECIES OF *PILEA*

1. Shell subtriangular, subquadrate, or suborbicular 2
   Shell subtrapezoid or subquadrate, nacre white ..... *personata*
2. Periostracum subshiny, yellowish brown or greenish, nacre usually purplish ..... *obliquata*
   Periostracum shiny, tawny to chestnut, nacre purplish ..... *haysiana*

Plagiola (*Pilea*) *personata* (Say)
Plate 14, figures 7–9
Distribution: Plate 6, figure B

Unio personatus Say 1829, New Harmony [Indiana] Disseminator 2 (20): 309 (Wabash River, [Indiana]; neotype MCZ 5763 from the Cumberland River, Tennessee, selected by Johnson and Baker, 1973, Proc. Acad. Nat. Sci. Phila. 125: 166, pl. 8, fig. 5).

Unio pileus Lea 1831, Trans. Amer. Philos. Soc. 4: 119, pl. 18, fig. 47 (Ohio River, near Cincinnati [Hamilton Co.], Ohio, figured holotype USNM 84602a); 1834, Obs. Unio 1: 129.

Unio capillaris Lea 1834, Trans. Amer. Philos. Soc. 5: 29, pl. 2, fig. 2 (Ohio, figured type [lost], specimen subsequently identified by Lea USNM 84602); 1834, Obs. Unio 1: 141.

Trincilla (*Pilea*) *personata* (Say). Simpson, 1900, Proc. U. S. Natl. Mus. 22: 522; 1914, Cat. Naiades 1: 23; 1903, Daniels, 27th Ann. Rept. Dept. Geol. and Nat. Res. of Indiana, p. 646.

Dysnomia (*Pilea*) *personata* (Say). Ortmann, 1925, Amer. Mid. Nat. 9: 361. Frierson, 1927, Check list N American naiades, p. 96, Haas, 1969, Das Tierreich, pt. 88, p. 480.

Dysnomia personata (Say). Morrison, 1942, Bur. Amer. Ethnology, Bull. no. 129, p. 364. Goodrich and van der Schalie, 1944, Amer. Mid. Nat. 32: 314. La Rocque, 1967, Geol. Surv. Ohio, Bull. no. 62 (2): 278, fig. 169. Stansbery, 1970, Malacologia 10: 19; 1971, Symposium of rare and endangered moll. U. S., p. 18a, figs. 11, 12.

Description. Shell of medium size, reach-

ing up to 65 mm in length. Outline subtriangular or subquadrate. Valves inequilateral, solid, inflated. Anterior end regularly rounded, sometimes subtruncate in the male; posterior end of male regularly rounded or subtruncate; posterior in females slightly produced above the median. Ventral margin curved with a slight emargination posteriorly in the male. Dorsal margin straight, forming an angle with the obliquely descending posterior margin. Hinge ligament short. Posterior ridge faintly double in males, ending in a slight bimargination, separated from a faint medial ridge by a narrow radial sulcus, which ends in a slight emargination. The area of the sulcus is a raised swelling marked by denticulations in the female. Dorsal slope slightly concave. Umbos full, somewhat elevated and prominent, slightly turned over a distinct lunule, located near the middle of the male shell and in the anterior third of the female. Surface of the shell irregularly concentrically sculptured. Periostracum often silky or clothlike, greenish yellow, brownish, or greenish brown in old shells, usually with faint wavy green rays over most of the surface.

Left valve with two chunky triangular pseudocardinal teeth; slight interdentum. Two short, almost straight, lateral teeth. Right valve with one large triangular pseudocardinal tooth, usually with a small tooth before it, and sometimes with a much smaller tooth after it. One lateral tooth, sometimes with a vestigial tooth below. Umbonal cavities shallow. Anterior and posterior muscle scars well impressed. Pallial line distinct anteriorly. Nacre white or flesh colored. Shell heavier anteriorly, marsupial area of the female quite thin.

Male shells are subtriangular with a double posterior ridge that ends in a biangulation in front of which is a narrow, shallow radial depression that ends in a slight emargination.

Female shells are subquadrate, the marsupial swelling occupies the place of the radial depression. It is rather small, and only slightly inflated, but it is radially sculptured, denticulated, thin and excavated within. Reaches the same size as the male shell.

Length mm	Height mm	Width mm	
47	47	30	Ohio River, Cincinnati, Hamilton Co., Ohio. Male.
53	48	35	As above. Female.

Habitat. Lives in deeper water [deeper than what?] *teste* Morrison (1942: 364).

Remarks. *Plagiola personata* (Say) most closely resembles *P. obliquata.* Both the male and the female of the former have proportionally higher shells. The radial furrow in the male *personata* is more developed than is that of *obliquata.* The female of *personata* has a slightly raised marsupial swelling, whereas that of *obliquata* is separated from the rest of the shell by two distinct sulci.

Range. Tennessee River system, Tennessee and Alabama; Cumberland River system, Tennessee; Ohio River system, from the lower Wabash drainage to Cincinnati, Hamilton County, Ohio.

Abundance. "I know of no collections of this species made in this century. It is presumed extinct." (Stansbery, 1976: 43, 50)

Specimens Examined

Tennessee River System

Clinch River Drainage. *Tennessee*: Clinch River (MCZ, MZUM).

Tennessee River Drainage. *Alabama*: Tennessee River, Muscle Shoals, Colbert and Lauderdale Cos. (CM); Tennessee River, Florence, Lauderdale Co. (MCZ, MZUM); Pickwick Basin, mounds between Barton, Colbert Co. and Waterloo, Lauderdale Co. (Morrison, USNM).

Cumberland River System

Cumberland River Drainage. *Tennessee*: Cumberland River (MCZ); Cumberland River, near Priestly Shoals, Davidson Co. (MZUM).

Ohio River System

Wabash River Drainage. *Indiana*: White River (MZUM); Wabash River (MCZ); Wabash River, New Harmony, Posey Co. (Daniels).

Ohio River Drainage. *Ohio*: Ohio River, Cincinnati, Hamilton Co. (MCZ, OSM, MZUM).

Plagiola (*Pilea*) *obliquata* (Rafinesque)
Plate 14, figures 10–12
Distribution: Plate 4

Obliquaria obliquata Rafinesque 1820, Ann. Gén des Sci. Physiques, Bruxelles 5: 309 (le Kentuky [River]; lectotype ANSP 20226, selected by Johnson and Baker, 1973, Proc. Acad. Nat. Sci. Phila. 125: 163, pl. 7, fig. 1).

Unio sulcatus Lea 1829, Trans. Amer. Philos. Soc. 3: 430, pl. 9, fig. 12 (Ohio, figured holotype USNM 84803); 1834, Obs. Unio 1: 44.

Unio ridibundus Say, 1829, New Harmony [Indiana] Disseminator 2 (5): 308; 1830, Amer. Conch. no. 1, pl. 5 (Cumberland River [Tennessee], figured type [lost]).

Unio perplexus Say 1829, New Harmony [Indiana] Disseminator 2 (5): 309; 1830, American Conch. no. 1 [letterpress to pl. 5] (Cumberland River [Tennessee], type [lost]), *non* Lea 1831.

Unio flagellatus Say 1830, Amer. Conch. no. 1 [letterpress to pl. 5]. Listed as a synonym of *Unio sulcatus* Lea.

Unio pectitis Conrad 1853, Proc. Acad. Nat. Sci. Phila. 6: 255 [nomen nudum]; 1854, Jour. Acad. Nat. Sci. Phila. (2) 2: 297, pl. 27, fig. 4 (Wabash River [Indiana], type not located).

Unio stewardsonii stewensoni Gregorio 1914, Il Nat. Siciliano 22: 45, pl. 6, fig. 3 (no locality, type presumed to be in Palermo Mus., Sicily [not seen]).

Unio propesulcatus Gregorio 1914, Il Nat. Siciliano 22: 60, pl. 10, fig. 2 (Cumberland River, Tennessee, type presumed to be in Palermo Mus., Sicily [not seen]).

Truncilla (*Scalenaria*) *sulcata* (Lea). Simpson, 1900, Proc. U. S. Natl. Mus. 22: 520; 1914, Cat. Naiades 1: 14.

Truncilla sulcata (Lea). Wilson and Clark, 1912, U. S. Bur. Fisheries, Doc. 757: 31, 37, 38, 55. Wilson and Clark, 1914, U. S. Bur. Fisheries, Doc. 781: 46. Walker, 1918, Mus. Zool., Univ. Mich., Misc. Pub. no. 8: 186.

Dysnomia (*Scalenilla*) *sulcata* (Lea). Ortmann and Walker, 1922, Occ. Papers, Mus. Zool., Univ. Mich., no. 112, p. 68. Ortmann, 1925, Amer. Mid. Nat. 9: 360. La Rocque, 1967, Geol. Surv. Ohio, Bull. no. 62 (2): 278, fig. 171.

Dysnomia (*Pilea*) *sulcata* (Lea). Frierson 1927, Check list N American naiades, p. 96. Haas, Das Tierreich, pt. 88, p. 480.

Dysnomia sulcata (Lea). Morrison, 1942, Bur. Amer. Ethnology, Bull. no. 129, p. 364. Goodrich and van der Schalie, 1944, Amer. Mid. Nat. 32: 314. Neel and Allen, 1964, Malacologia 1: 450. Stansbery, 1970, Malacologia 10: 19; 1971, Symposium of rare and endangered moll. U. S., p. 18e, figs. 43, 44. Clark, 1977, Sterkiana, nos. 65, 66, p. 27, fig. 19.

Dysnomia sulcata perobliquus Stansbery, 1970, Malacologia 10: 19, *non* Conrad 1836.

Description. Shell of medium size, reaching up to 70 mm in length. Outline subtrapezoid or quadrate. Valves very inequilateral, inflated, solid. Anterior end of male decidedly subtruncate, regularly rounded in the female; posterior end of male somewhat produced and pointed, truncate in the female. Ventral margin broadly curved in males, almost straight in females. Dorsal margin long and almost straight, forming an angle with the obliquely descending posterior margin. Hinge ligament rather long. Posterior ridge of the male double, rather low and faint, separated by a wide faint radial furrow before another faint ridge. Posterior ridge of female, somewhat obscured before a sharp sulcus before the marsupial swelling. Dorsal slope of male very narrow, wider in the female. Umbos full, elevated and prominent, turned over a small lunule, located at the extreme anterior end, their sculpture consisting of a few corrugations. Surface of the shell with numerous strong growth rests. Periostracum smooth and shiny, or subshiny, yellowish, greenish yellow or brownish, usually feebly rayed over the entire surface.

Left valve with two chunky triangular, pseudocardinal teeth; slight interdentum. Two short straight lateral teeth. Right valve with one large triangular pseudocardinal tooth, usually with a much smaller tooth before and behind it. One lateral tooth, sometimes with a vestigial tooth below. Anterior and posterior muscle scars and pallial line well impressed. Shell thinner posterior-

ly in the female in the area of the marsupial swelling. Nacre purplish, pink, bluish white or white.

Male shells are usually much larger than those of the female, and are subtrapezoid. The dorsal and ventral margins are curved, but the anterior margin is subtruncate. The posterior end is pointed bluntly above, and is slightly truncate below. The lower posterior ridge is rather widely separated from the medial ridge by a faint furrow.

Female shells are subquadrate, and truncated posteriorly. The marsupial area, which occupies the space between the lower posterior and medial ridges in the male, is inflated, rounded and separated from the rest of the shell by two sulcations, the more posterior being the more acute and ending in a more acute emargination. The marsupial area is toothed and is sculptured by former teeth at rest stops.

Length mm	Height mm	Width mm	
55	41	33	Ohio River, Cincinnati, Hamilton Co., Ohio. Male.
35	28	24	Cumberland River, Tennessee. Female.

Remarks. Plagiola obliquata (Rafinesque) most closely resembles *P. personata*, under which see: *Remarks*. The male shell of *personata* is subtriangular, while that of *obliquata* is subtrapezoid. The umbos of the latter project much farther forward than do those of the male *personata* or of the female *obliquata*, often reaching the extreme anterior end as in *Pleurobema clava* (Lamarck). The female of *obliquata* has a marsupial swelling that is separated from the rest of the shell by two distinct sulci.

Stansbery (1970: 19) regarded *Unio gibbosus perobliquus* Conrad as a geographically isolated subspecies from the streams tributary to western Lake Erie and Lake St. Clair on the basis of its having a white nacre. Nacre color appears to be an ecophenotypic variation which changes from purple to white throughout the range of *P. obliquata*. The figured type of *perobliquus* is *P. torulosa* (Rafinesque).

Ortmann and Walker (1922: 65) pointed out that the original description of *obliquata* applied as well to *Pleurobema pyramidatum* (Lea) as to *Unio sulcatus* Lea, and made the reasonable suggestion that *obliquata* be dropped as unidentifiable. Frierson (1927: 53) argued that *obliquata* was *pyramidatum* (Lea). He was followed by Haas (1969: 297) and Morrison (1969: 24). Since the lectotype of *obliquata* is *sulcata* (Lea), the former taxon must, unfortunately, replace Lea's well-known name.

Morrison (1969: 24) mentioned that *Unio sulcatus* Lea 1829 is preoccupied, and indicated that this taxon should be replaced by *Plagiola ridibundus* (Say) 1829. Morrison did not say by whom *sulcatus* was preoccupied and a careful search of the literature did not afford the answer, but this is now of no interest here.

Range. Tennessee River system, Tennessee and Alabama; Cumberland River system, Kentucky and Tennessee; Ohio River system: Wabash River Drainage, and Ohio River, to the Scioto River drainage, Ohio; St. Lawrence River system: Lake Erie drainage.

Abundance. As early as 1912, Wilson and Clark (p. 31) were able to find only one live specimen of *P. obliquata* in an extensive survey of the Maumee River drainage. Still occasionally found in streams tributary to western Lake Erie or Lake St. Clair (Stansbery, 1970: 19 as *D. sulcata perobliquus*), and the Green River, Kentucky (Stansbery, 1971: 18e). *Epioblasma sulcata sulcata* is listed as "extirpated" by Stansbery (1976: 43, 50).

Specimens Examined

Tennessee River System

Tennessee River Drainage. *Alabama*: Tennessee River, Muscle Shoals, Lauderdale and Colbert Cos. (CM); Tennessee River, Florence, Lauderdale Co. (MZUM); Tennessee River, Tuscumbia, Colbert Co. (MCZ); "Mound about 3 mi. WSW Gravelly Springs, Lauderdale Co., only this speci-

men found in all mounds studied" (Morrison, 1942).

Cumberland River System

Cumberland River Drainage. *Kentucky*: Cumberland River, Burnside, Pulaski Co.; Cumberland River, Neeleys Ford, 4 mi. S Burksville, Cumberland Co.; (*both* MZUM). *Tennessee*: Cumberland River, Fort Blount, 6 mi. SW Jamesboro, Jackson Co. (MZUM); Cumberland River, Goodall Island, Smith Co. (Wilson and Clark).

Caney Fork Drainage. *Tennessee*: Caney Fork, Buffalo Valley, Putnam Co. (Wilson and Clark).

Cumberland River Drainage. *Tennessee*: Cumberland River, Nashville, Davidson Co. (MCZ); Cumberland River, Halfpone Bar, Cheatham Co. (Wilson and Clark).

Harpeth River Drainage. *Tennessee*: Harpeth River (MZUM).

Ohio River System

Ohio River Drainage. *Illinois*: Ohio River (Baker).

Wabash River Drainage. *Indiana*: White River (MCZ); West Fork, White River (Daniels); White River, Indianapolis (MZUM); *both* Marion Co.; White River, Rockford, Jackson Co. (Daniels); Wabash River, Lafayette, Tippecanoe Co. (MCZ and MZUM); Wabash River, New Harmony, Posey Co. (MZUM).

Green River Drainage. *Kentucky*: Green River, Glenmore, Warren Co. (OSM); Green River, Rochester, Butler Co. (MCZ; MZUM).

Kentucky River Drainage. *Kentucky*: Kentucky River (Rafinesque).

Ohio River Drainage. *Ohio*: Ohio River, Cincinnati, Hamilton Co. (MCZ).

Licking River Drainage. *Kentucky*: Licking River (MCZ).

Scioto River Drainage. *Ohio*: Scioto River (MZUM).

St. Lawrence River System

Great Lakes Drainage. (Lake Erie) *Ohio*: Blanchard River, Findlay, Hancock Co. (MZUM); Fish Creek, Williams Co. (Clark, 1977: 21). *Indiana*: St. Joseph River (MZUM); St. Marys River (Wilson and Clark); Maumee River (MCZ, MZUM); *both* Fort Wayne, *all* Allen Co. *Ohio*: Maumee River, 4 mi. below Defiance; Auglaise River, 4 mi. above Defiance; *both* Defiance Co. (*both* Wilson and Clark). Lake Erie, Putin Bay, Ottawa Co. (Wilson and Clark). *Michigan*: Otter Creek, Monroe Co. (MZUM). Lake St. Clair (Stansbery, 1970). Detroit River, Belle Island, Wayne Co. (MZUM). *Ontario*: Detroit River, Bois Blanc Isle, Essex Co. (MZUM). *Michigan*: Lake Erie, near Stony Creek; River Rasin; Lake Erie, La Plaisance Bay; *all* Monroe Co. (*all* MZUM). *New York*: Niagara River (MZUM).

Plagiola (*Pilea*) *haysiana* (Lea)
Plate 15, figures 1–4
Distribution: Plate 8, figure A

Unio haysianus Lea 1834, Trans. Amer. Philos. Soc. 5: 35, pl. 3, fig. 7 (Cumberland River [Tennessee], figured type [lost], male specimen, subsequently identified by Lea, USNM 84613 from the Cumberland River, Nashville, Davidson Co., Tennessee); 1834, Obs. Unio 1: 147.

Unio sowerbyanus Lea 1834, Trans. Amer. Philos. Soc. 5: 68, pl. 10, fig. 28 (Tennessee, figured type [lost], 4 male specimens, subsequently identified by Lea, MCZ 178886 from the Caney Fork of the Cumberland River, Tennessee); 1834, Obs. Unio 1: 180.

Truncilla (*Scalenaria*) *haysiana* (Lea). 1900, Proc. U. S. Natl. Mus. 22: 520; 1914, Cat. Naiades 1: 16.

Truncilla haysiana (Lea). Wilson and Clark, 1914, U. S. Bur. Fish. Doc. no. 781, p. 46. Ortmann, 1912, Ann. Carnegie Mus. 8: 357; 1913, Proc. Amer. Philos. Soc. 52: 311; 1918, Proc. Amer. Philos. Soc. 57: 587.

Dysnomia (*Scalenilla*) *haysiana* (Lea). Ortmann, 1925, Amer. Mid. Nat. 9: 361.

Dysnomia (*Penita*) *haysiana* (Lea). Frierson, 1927, Check list N American naiades, p. 94. Haas, 1969, Das Tierreich, pt. 88, p. 483.

Dysnomia haysiana (Lea). Morrison, 1942, Bur. Amer. Ethnology, Bull. no. 129, p. 364. Neel and Allen, 1964, Malacologia 1: 450, fig. 60. Stansbery 1970, Malacologia 10: 19; 1971, Symposium of rare and endangered moll. U. S., p. 18e, figs. 45, 46.

Epioblasma haysiana (Lea). Stansbery, 1972, Amer. Mal. Union, Bull. for 1972, p. 22.

Description. Shell usually of small size, reaching up to 40 mm in length. Outline subtriangular or suborbicular. Valves inequilateral, somewhat inflated, solid. Anterior end regularly rounded, posterior end of male somewhat elongate and slightly more broadly rounded; more broadly rounded in the female. Ventral margin curved. Dorsal margin curved merging almost imperceptibly with the obliquely descending posterior margin. Hinge ligament short. Posterior ridge of the male faint, but double, broadly curved or flat, merging into a flat dorsal slope; ridge elevated into a marsupial swelling in females. There is a broad, shallow radial furrow before a medial ridge in the male; the furrow is narrow and deep in the female. The posterior end of the male shows vestiges of teeth along the growth rests; these are prominent in the female especially on the marsupial swelling. Umbos full and high, located somewhat anteriorly, feebly sculptured. Surface of the shell smooth anteriorly, but sometimes rendered subnodulous by deep growth rests. Periostracum very shiny, especially anteriorly, tawny to chestnut, with a few greenish rays in the radial furrow and on the disk.

Left valve with two chunky, triangular pseudocardinal teeth of about equal size with a sharp, deep, triangular pit between them extending to the hinge line; interdentum short but wide. Two short straight lateral teeth. Right valve with one large, triangular, pseudocardinal tooth, sometimes with a vestigial tooth anterior to it. One well-developed lateral tooth, with a vestigial tooth below. Umbonal cavities shallow. Anterior and posterior muscle scars and pallial line well impressed. Marsupial area of the female thinner and somewhat excavated. Nacre usually purple, but sometimes white and iridescent posteriorly.

Male shells are subtriangular, often as high or higher than long. The radial furrow in front of the posterior ridge is broad and shallow. The posterior end has vestiges of teeth along the growth lines.

Female shells are suborbicular, less long than high. The posterior ridge is inflated, and extends below the ventral margin. The radial furrow in front of the posterior ridge is narrow, sharp and deep. The posterior end has more vestiges of sharper teeth along the growth lines than does the male.

Length mm	Height mm	Width mm	
40	31	21	Clinch River, Union Co., Tennessee. Male.
30	25	17	As above. Female.

Anatomy. Discussed by Ortmann (1912, 357).

Remarks. Plagiola haysiana (Lea) is easily distinguished from the other members of the genus by its polished, tawny to chestnut periostracum, its small size, its unusually thick and heavy shell, and its usually purplish nacre.

Lea described the female of this species as *U. haysianus* and the male as *U. sowerbyanus.*

Range. Tennessee River system, Virginia, Tennessee and Alabama; Cumberland River system, Kentucky and Tennessee.

Abundance. Now restricted to the Clinch River between St. Paul, Wise County, to Dungannon, Scott County, Virginia, a distance of only about 10 miles (Stansbery, 1970: 19). Listed as "extirpated" by Stansbery (1976: 43, 50).

Specimens Examined

Tennessee River System

Powell River Drainage. *Virginia*: Powell River, 2.5 mi. S Jonesville; Wallens Creek; Powell River, Lyttons Mill (*all* MCZ); Powell River, Pennington Gap (CM); *all* Lee Co.

Clinch River Drainage. *Virginia*: Clinch River, Raven, Tazewell Co. (CM); Clinch River, Cleveland, Russell Co. (MCZ); Clinch River, Saint Paul, Wise Co. (Stansbery, OSM); Clinch River, Dungannon, Scott Co. (MCZ). *Tennessee*: Clinch

River, Union Co.; Clinch River, Clinton, Anderson Co. (*both* MCZ).

Holston River Drainage. *Virginia*: North Fork, Hilton, Scott Co. (CM). *Tennessee*: South Fork, Pactolus, Sullivan Co. (CM); Mouth of Holston River, Austins Grist Mill, Knox Co. (MCZ).

Tennessee River Drainage. *Tennessee*: Tennessee River, near Knoxville, Knox Co. (MCZ).

Little River Drainage. *Tennessee*: mouth of Little River, Little River Shoals, Blount Co. (MCZ).

Little Tennessee River Drainage. *Tennessee*: Little Tennessee River, Monroe Co. (MCZ); Little Tennessee River, Coytee, Loudon Co. (MZUM).

Elk River Drainage. *Tennessee*: Elk River, Fayetteville, Lincoln Co. (MCZ). *Alabama*: Lower Elk River (Conrad).

Tennessee River Drainage. *Alabama*: Tennessee River, Florence, Lauderdale Co.; Tennessee River, Tuscumbia, Colbert Co. (*both* MCZ); Pickwick Basin, mounds between Barton, Colbert Co. and Waterloo, Lauderdale Co. (Morrison, USNM).

Cumberland River System

Cumberland River Drainage. *Kentucky*: Big South Fork, above Burnside and Parkers Lake Station; *both* Pulaski Co. (*both* MCZ). *Tennessee*: Cumberland River, Goodall Island, Smith Co. (Wilson and Clark).

Caney Fork Drainage. *Tennessee*: Caney Fork, [Smith Co.] (MCZ).

Cumberland River Drainage. *Tennessee*: Cumberland River, Nashville, Davidson Co. (MCZ; USNM); Cumberland River, Clarksville, Montgomery Co. (Wilson and Clark).

Subgenus *Epioblasma* Rafinesque

Epioblasma Rafinesque 1831, Cont. Monog. Bivalve Shells River Ohio, p. 2. Type species, *Epioblasma biloba* Rafinesque, monotypic.

Dysnomia Agassiz 1852, Arch. für Naturgesch. 18: 43. First species listed, [*Obliquaria*] *flexuosa* [Rafinesque] = *Unio foliatus* Hildreth [*teste* Agassiz]. Type species, *Unio foliatus* Hildreth, subsequent designation, Simpson, 1900, Proc. U. S. Natl. Mus. 22: 521.

Description. Shell subrhomboid, subquadrate or subtriangular. "Shell of the male with a posterior and central radiating ridge, with a wide, flattened space between them; that of the female with a greatly produced inflation, which is but a little behind the center of the base and which is a continuation of the central ridge" (Simpson, 1914: 18).

Remarks. The availability of *Epioblasma* over *Dysnomia* becomes of nugatory interest once both of these names are reduced to subgeneric standing under *Plagiola*. The availability of *Epioblasma* is dependent on the identification of *E. bioloba*. Frierson (1914: 7) asserted that *E. bioloba* Raf. = *U. foliatus* Hild. [=*flexuosa* Raf.]. In reply to Frierson, Ortmann and Walker (1922: 71) gave a number of palpable reasons why *bioloba* was not recognizable to them. In the index to his *Check list of North American naiades*, Frierson (1927: 101) indicated that *bioloba* belonged in the synonymy of *Dysnomia flexuosa* (Raf.) although he neglected to include it in the synomymy of the latter. He apparently forgot he had previously asserted the availability of *Epioblasma* over *Dysnomia*. Thiele (1934: 837), Clench (1959: 1157), Morrison (1969: 24), and Stansbery (1972: 22) recognize *Epioblasma*. The latter said (1973, pers. comm.), "*Epioblasma* [*bioloba*] Rafinesque 1831 is clearly the female of [*Obliquaria*] *flexuosa* Rafinesque 1820."

Van der Schalie (1973: 49) partially requoted Ortmann and Walker as to why *bioloba* is unrecognizable, merely reasserting their position. While no one has made any contribution to the subject of *bioloba*'s recognizability since Ortmann and Walker, most subsequent published opinions, as noted above, are that *bioloba* is identifiable and is the female of *flexuosa*.

The type and an authentic specimen sent to Férussac of *bioloba* are both lost (Johnson and Baker, 1973: 149), therefore in the

interests of stability of nomenclature, the "exceptional circumstances" [Int. Code Zool. Nomen., 1964, Art. 75 (a) (i)] described above require that a neotype be selected for *bioloba*. This is done under *Plagiola* (*Epioblasma*) *flexuosa* (Rafinesque).

KEY TO THE SPECIES OF *EPIOBLASMA*

Medial ridge considerably elevated ..... *flexuosa*
Medial ridge not much elevated ..... *stewardsoni*

Plagiola (*Epioblasma*) *flexuosa* (Rafinesque)

Plate 15, figures 5–8
Distribution: Plate 5

Obliquaria flexuosa Rafinesque 1820, Ann. Gén. Sci. Physiques, Bruxelles 5: 306 (le Kentuky, Salt-river et Green-river; lectotype ANSP 20249 from the Kentucky River, selected by Johnson and Baker, 1973, Proc. Acad. Nat. Sci. Phila. 125: 163, pl. 7, fig. 2).

Unio foliatus Hildreth 1828, American Jour. Sci. 14: 284, fig. 16 (Ohio; known only from the figured type [lost]).

Epioblasma biloba Rafinesque 1831, Cont. Monog. Bivalve Shells River Ohio, p. 2 (Green River and Kentucky River; type lost, *teste* Johnson and Baker, 1973, Proc. Acad. Nat. Sci. Phila. 125: 149). Neotype, here selected, ANSP 56571, pl. 15, fig. 7, and the type locality restricted to the Ohio River, near Cincinnati, Hamilton Co., Ohio).

Truncilla lewisi Walker 1910, Nautilus 24: 42, pl. 3, fig. 3 female; figs. 4, 5 male (Holston River, Tennessee, the figured female syntype is, here selected, lectotype MZUM 91456, pl. 15, fig. 8). Simpson, 1914, Cat. Naiades 1: 20. Ortmann, 1918, Proc. Amer. Philos. Soc. 57: 588.

Truncilla foliata (Hildreth). Simpson, 1900, Proc. U. S. Natl. Mus. 22: 521; 1914, Cat. Naiades 1: 18.

Dysnomia (*Dysnomia*) *flexuosa* (Rafinesque). Ortmann and Walker, 1922, Occ. Papers, Mus. Zool. Univ. Michigan no. 122, p. 70. Ortmann, 1926, Ann. Carnegie Mus. 17: 183. Frierson, 1927, Check list N American naiades, p. 93. Goodrich and van der Schalie, 1944, Amer. Mid. Nat. 32: 314. La Rocque 1967, Geol. Surv. Ohio, Bull. 62 (2): 275, fig. 167. Haas, 1969, Das Tierreich, pt. 88, p. 478. Stansbery, 1970, Malacologia 10: 19, pl. 1, figs. 1, 2; 1971, Symposium of rare and endangered moll. U. S., p. 18a, figs. 5, 6.

Dysnomia (*Dysnomia*) *lewisi* (Walker). Frierson, 1927, Check list N American naiades, p. 93. Haas, 1969, Das Tierreich, pt. 88, p. 479.

Dysnomia flexuosa lewisi (Walker). Morrison, 1942, Bur. Amer. Ethnology, Bull. no. 129, p. 366.

Dysnomia lewisi (Walker). Neel and Allen, 1964, Malacologia 1: 450, figs. 61, 66. Stansbery 1970, Malacologia 10: 19; 1971, Symposium of rare and endangered moll. U. S., p. 18a, fig. 7 [fig. 8, after Walker, is a male of *E. stewardsoni*].

Description. Shell of medium size, reaching up to 75 mm in length. Outline of male subrhomboid or quadrate; outline of female, depending on the extent of marsupial swelling, subtriangular. Valves equilateral, slightly inflated, solid. Anterior end of the male shell regularly rounded, forming an obtuse angle at its junction with the basal emargination. Anterior end of the female regularly rounded, becoming straight and obliquely descending beyond the base line. Posterior end of the male subtruncated; that of the female somewhat extended and pointed. Ventral margin of the male with two slight emarginations; one considerable emargination in females. Dorsal margin broadly curved in males; margin short and straight in females, forming an obtuse angle with the obliquely descending posterior margin. Hinge ligament prominent. Posterior ridge distinct, rounded toward the umbos, becoming flattened and somewhat double as it approaches the posterior end, where it terminates in a slight biangulation projecting a little beyond the posterior and basal lines. Dorsal slope narrow and slightly concave. In front of a median groove is a strong anterior ridge that becomes more pronounced as it approaches the base, where it terminates in an angle slightly backward, at, or a little behind, the middle of the base. In the female this anterior ridge becomes an enormously produced lobe, or winglike marsupial swelling. Umbos laterally compressed, only slightly elevated above the hinge line, located near the middle of the shell, their sculpture faint and corrugated. Surface of the shell with uneven concentric sculpture. Periostracum uniformly pale brownish green or brownish, with faint green rays,

except for the female's marsupial swelling, which may be dark green.

Left valve with two ragged pseudocardinal teeth, triangular and of about equal size; the anterior tooth narrow, straight, directed obliquely forward, slightly widening toward the anterior end; the posterior tooth triangular; the space between them triangular and extending to the hinge. Interdentum rather long, narrow, rounded and parallel to the hinge. Two nearly straight, granular, lateral teeth, bent obliquely downward from the hinge line. Right valve with two pseudocardinal teeth, the anterior tooth small but well developed; the posterior tooth long and triangular, separated from the interdentum by a deep groove. One well developed lateral tooth, often with a parallel vestigial tooth below. Umbonal cavities rather shallow. Anterior and posterior muscle scars well impressed. Pallial line distinct. Nacre white.

Although the wide radial furrow of the male is usually a little deeper than in the female, the shells of the two sexes are essentially alike until they are about one-third grown. Then the female begins to develop a rounded, prolonged marsupial swelling, which points backward, almost at the middle of the ventral margin. The swelling is scarcely, if at all, radially sculptured, but it is thin, winglike and gapes slightly.

Length mm	Height mm	Width mm	
71	58	41	Wabash River, Indiana. Male.
76	68	41	As above. Female.
37	30	27	Holston River, Austins Grist Mill, Knox Co., Tennessee. Male.
51	49.5	25	Holston River, Tennessee. Female. Lectotype of *Truncilla lewisi.*

Anatomy. Known only from a brief description, based on an imperfect dry specimen, by Lea (1863, Jour. Acad. Nat. Sci. Phila. (2) 5: 443; 1863, Obs. Unio 10: 79).

Habitat. Call (1898: 511) observed that in the Ohio River this species was found on muddy bottoms in deeper water, while Stansbery (1970: 19) suggested that *flexuosa* was, "apparently a species of shallow riffles in big rivers," which it was in the Tennessee and Cumberland River systems.

Remarks. The pronounced sexual dimorphism shown in the shells of *Plagiola flexuosa* (Rafinesque), reflecting the special use of the gills as marsupia, make it one of the world's more remarkable species of Unionacea. It cannot be confused with any other member of the genus save *P.* (*E.*) *stewardsoni*, under which see *Remarks.* Walker described the form of *flexuosa* found in the Tennessee and Cumberland river systems as *lewisi* on the basis that the male of the latter did not grow as large or have a shell as heavy as that of the former. The female, he said, "besides being uniformly smaller, more delicate and smoother than [*flexuosa*], is especially characterized by the difference in the marsupial expansion, which is triangular and comparatively narrow at the extremity and of a different texture from the body of the shell [being thin and dark green]. In [*flexuosa*] this expansion is broadly rounded and is of the same texture as the remainder of the valve."

Truncilla lewisi is regarded here as merely an ecophenotypic variant. *Plagiola flexuosa* does not grow as large in the Tennessee and Cumberland river systems, where it lives on shallow riffles. It seems to have found in the muddy Ohio River, where it spread in post-glacial time, a favorable environment where it could achieve larger size. While Ohio River females do not usually have green marsupial swellings, one in the Museum of Comparative Zoology, no. 5358, does have the green marsupial swelling and is indistinguishable from females from the Tennessee and Cumberland river systems.

Specimens of *Plagiola flexuosa*, Museum of Comparative Zoology 221711, from the, "Ohio River, Stubenville, Ohio, C. M. Wheatley, 1856," and so labeled in the shells, extend the range of this species farther up the Ohio than was previously authenticated. While no specimens of this species have been found in the Kentucky,

Salt and Green rivers, since it was reported from them by Rafinesque, these localities fall within the known range of the species.

Range. Tennessee River system, Tennessee and Alabama; Cumberland River system, Kentucky; Ohio River system; from the lower Wabash River, Indiana to the Ohio River, Jefferson Co., Ohio.

Abundance. No collection has very many examples of this rare shell. Found sparingly in the Pickwick Basin mound deposits by Morrison (1942: 366). "Recorded from both the Tennessee and Cumberland River systems up until the construction of Wolf Creek Dam on the Cumberland [collected by Neel and Allen 1947–49] and the TVA Dams on the Tennessee. It has not been collected in over 20 years and hence is presumed extinct." (Stansbery, 1970, 19 as *lewisi*). Once locally abundant in the Ohio River, near Cincinnati, Hamilton County, Ohio. "This species has not been collected since 1900 [in the Ohio River] and is presumed extinct" (Stansbery, 1970: 19). Both *lewisi* and *flexuosa* are listed as "extirpated" by Stansbery (1976: 43, 50).

Specimens Examined

Tennessee River System

Powell River Drainage. *Tennessee*: Powell River, Combs, Claiborne Co. (CM, single male).

Clinch River Drainage. *Tennessee*: Clinch River (MCZ).

Holston River Drainage. *Tennessee*: Holston River, Holston Station, Grainger Co. (CM, single male); mouth of Holston River, Austins Grist Mill, Knox Co. (MCZ).

Tennessee River Drainage. *Alabama*: Tennessee River, Tuscumbia, Colbert Co. (USNM); Pickwick Basin, mounds between Barton, Colbert Co. and Waterloo, Lauderdale Co. (Morrison, USNM).

Cumberland River System

Cumberland River Drainage. *Kentucky*: Cumberland River, Port Burnside, Pulaski Co. (MZUM); Cumberland River, Rowena Ferry; Cumberland River, Long Bottom, just below Wolf Creek Dam, *both* Russell Co. (*both* MZUM).

Ohio River System

Wabash River Drainage. *Indiana*: White River (USNM); Wabash River (MCZ); Wabash River, New Harmony, Posey Co. (MZUM).

Green River Drainage. *Kentucky*: Green River (Rafinesque).

Salt River Drainage. *Kentucky*: Salt River (Rafinesque).

Kentucky River Drainage. *Kentucky*: Kentucky River (Rafinesque).

Ohio River Drainage. *Ohio*: Ohio River, Cincinnati, Hamilton Co. (MCZ). *Kentucky*: Fort Ancient Aspect, Campbell Co. [from Indian Midden] (USNM). *Ohio*: Ohio River, Steubenville, Jefferson Co. (MCZ).

Plagiola (*Epioblasma*) *stewardsoni* (Lea)
Plate 15, figures 9, 10
Distribution: Plate 8, figure C

Unio stewardsoni Lea, 1852, Trans. Amer. Philos. Soc. 10: 278, pl. 23, fig. 36 ([Tennessee] River, Chattanooga [Hamilton Co.], Tennessee; figured holotype ANSP 56572); 1852, Obs. Unio 5: 34.

Truncilla stewardsoni (Lea). Simpson, 1900, Proc. U. S. Natl. Mus. 22: 521; 1914, Cat. Naiades 1: 21. Ortmann, 1918, Proc. Amer. Philos. Soc. 57: 588.

Dysnomia (*Dysnomia*) *stewardsoni* (Lea). Ortmann, 1925, Amer. Mid. Nat. 32: 364. Frierson, 1927 Check list N American naiades, p. 93. Haas, 1969, Das Tierreich, pt. 88, p. 478.

Dysnomia stewardsoni (Lea). Morrison, 1942, Bur. Amer. Ethnology, Bull. no. 129, p. 365. Stansbery, 1970, Malacologia 10: 19, pl. 1, figs. 3, 4; 1971, Symposium of rare and endangered moll. U. S., p. 18a, figs. [8 as male of *lewisi*] 9, 10; Hurd, 1974, Ph.D. thesis, p. 97.

Description. Shell of small size, usually not exceeding 45 mm in length. Outline of shell irregularly rhomboid. Valves subequilateral, subcompressed, solid. Anterior end of the male shell regularly rounded forming an obtuse angle at its junction with the basal emargination. Anterior end of the female regularly rounded but becoming

straight and obliquely descending somewhat beyond the base line. Posterior end of the male subtruncated; that of the female slightly extended. Ventral margin of the male emarginate; female margin more considerably emarginate. Dorsal margin broadly curved in males; short and straight in females, forming an obtuse angle with the obliquely descending posterior margin. Hinge ligament prominent. Posterior ridge distinct and rounded, becoming slightly biangulate as it approaches the posterior end, where it terminates in a slight projection. Dorsal slope narrow and slightly concave. In front of a median groove there is a rounded anterior ridge that becomes somewhat pronounced as it approaches the base, where it terminates in a slight angle slightly backward, at, or a little behind, the middle of the ventral margin. In the female this anterior ridge becomes a produced, broadly rounded marsupial swelling. Umbos laterally compressed, only slightly elevated above the hinge line, located near the middle of the shell, their sculpture not observed. Surface of the shell with uneven concentric sculpture. Periostracum greenish yellow to brownish, with faint green rays. Marsupial expansion of the female sometimes dark and greenish.

Left valve with two ragged pseudocardinal teeth, triangular, and of about equal size; the anterior tooth narrow, straight, directed obliquely forward, slightly widening toward the anterior end; the posterior tooth triangular; the space between them triangular and extending to the hinge. Interdentum rather long, narrow, rounded, and parallel to the hinge. Two nearly straight, granular, lateral teeth, bent obliquely down from the hinge line. Right valve with two pseudocardinal teeth, the anterior tooth small and very slightly elevated above the hinge line, the posterior tooth long, high and triangular, separated from the interdentum by a groove. One well-developed lateral tooth, often with a parallel vestigial tooth below. Umbonal cavities rather shallow. Anterior and posterior adductor muscle scars well impressed. Pallial line distinct in males, distinct anteriorly only in females. Nacre white.

Although the wide radial furrow of the male being a very little bit deeper than in the female, the shells of the two sexes are essentially alike until they are about two-thirds grown. Then the female begins to develop a rounded, prolonged marsupial swelling which points backward, almost at the middle of the base. The swelling is often faintly radially sculptured, and is thin and winglike.

Length mm	Height mm	Width mm	
40	28	16	Holston River, Knoxville, Knox Co., Tennessee. Male.
32	27	16	As above. Female.
31	29	13	[Tennessee] River, Chattanooga [Hamilton Co.], Tennessee. Female. Holotype of *U. stewardsoni* Lea.

Remarks. Plagiola stewardsoni (Lea) and *flexuosa* are clearly sibling species. The former differs from *flexuosa* in several ways: It does not attain as large a size, the male shell is more quadrate, and the radial furrow is not as distinct or as deep. In the female of *stewardsoni*, the radial furrow is quite feeble and runs into the marsupial swelling, where it is generally obliterated, while in *flexuosa* the furrow continues to the base of the shell behind the marsupial swelling. The posterior ridge of *stewardsoni* is not produced posteriorly, which renders the ventral emargination proportionally more acute than in *flexuosa*. The marsupial swelling of *stewardsoni* is not as exaggerated as in *flexuosa*, but it also tends to be darker, often greenish, as in *flexuosa* specimens from the Tennessee and Cumberland river systems.

The two records listed by Hurd (1974: 97, 116) from the Coosa River drainage of the Mobile-Alabama-Coosa river system: "Coosa River, Al." (MZUM 90564) and "Etowah River, Ga." (MZUM 90565), as

suggested to Hurd by van der Schalie, are doubtless spurious.

Range. Restricted to the Tennessee and Cumberland river systems, Tennessee and Alabama.

Abundance. A rare species that has never been found in great numbers. This fact was noted by Ortmann (1918: 588) and by Morrison (1942: 365) who found it sparingly in the Pickwick Basin mound samples. "A rare species even before the impoundments and apparently not collected in the last half century. It is presumed extinct" (Stansbery, 1976: 43, 50).

Specimens Examined

Tennessee River System

Clinch River Drainage. *Tennessee*: Clinch River (MCZ); Clinch River, Clinton (CM); *both* Anderson Co.

Holston River Drainage. *Tennessee*: Holston River, Holston Station, Grainger Co.; Holston River, Mascot; Holston River, McMillan (*all* CM); mouth of Holston River, Austins Grist Mill (MCZ); *all* Knox Co.

French Broad River Drainage. *Tennessee*: Nolichucky River (MCZ).

Tennessee River Drainage. *Tennessee*: Tennessee River, Knoxville, Knox Co. (MCZ).

Little River Drainage. *Tennessee*: mouth of Little River, Little River Shoals, Blount Co. (MCZ).

Tennessee River Drainage. *Tennessee*: Tennessee River, Chattanooga, Hamilton Co. (Lea, USNM; MZUM). *Alabama*: Tennessee River, Bridgeport, Jackson Co. (MCZ); Tennessee River, Florence, Lauderdale Co.; Tennessee River, Tuscumbia, Colbert Co. (*both* USNM); Pickwick Basin, mounds between Barton, Colbert Co. and Waterloo, Lauderdale Co. (Morrison, USNM).

Cumberland River System

Cumberland River Drainage. *Kentucky*: Cumberland River, Pulaski Co. (MZUM). *Tennessee*: Cumberland River (USNM); Bartons Creek, Lebanon, Wilson Co. (MCZ).

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INDEX

Plate 1.

The distribution of *Plagiola* (*Truncillopsis*) *triquetra* (Rafinesque).

This, the most primitive species of *Plagiola*, is the most widely distributed in the genus. It appears to have had refugia west of the Mississippi River beyond maximum Pleistocene glaciation (roughly to the Missouri River) on the Old Prairie and in the Meramec Basin, as well as in the upper White River system on the Ozark Plateau south of the Ozark Crest (record enclosed by large circle).

The occurrence of this species in the White River on the Ozark Plateau south of the Ozark Crest, as well as in the Tennessee and Cumberland river systems, including the Duck River drainage of the former, on the Cumberland Plateau, suggests that this species has persisted at least since the Cretaceous uplift. *P. triquetra* may also have had refugia in the Allegheny and Monongahela river drainages in the mountainous region of western Pennsylvania and West Virginia during the Pleistocene.

A. In post-glacial time *triquetra* spread into Wisconsin from a connection between the Fox and Wisconsin rivers in the vicinity of Portage, Columbia Co., Wisconsin.

B. The presence of *triquetra* in the Illinois River, Illinois and the Muskegon, Grand and St. Joseph rivers on the eastern side of Lake Michigan, suggests that before the formation of Lake Michigan the latter streams were tributaries of the Des Plaines River, which by way of the Chicago outlet drained into the Mississippi River, by way of the Illinois River.

C. The distribution of *triquetra* in the present rivers flowing into western and southern Lake Erie indicates they were part of the Greater Maumee River system, when the bed of Lake Erie was partially dry during the Trent outlet stage of the Great Lakes, and that there was a connection between the Wabash and Maumee rivers in the vicinity of Fort Wayne, Allen Co., Indiana.

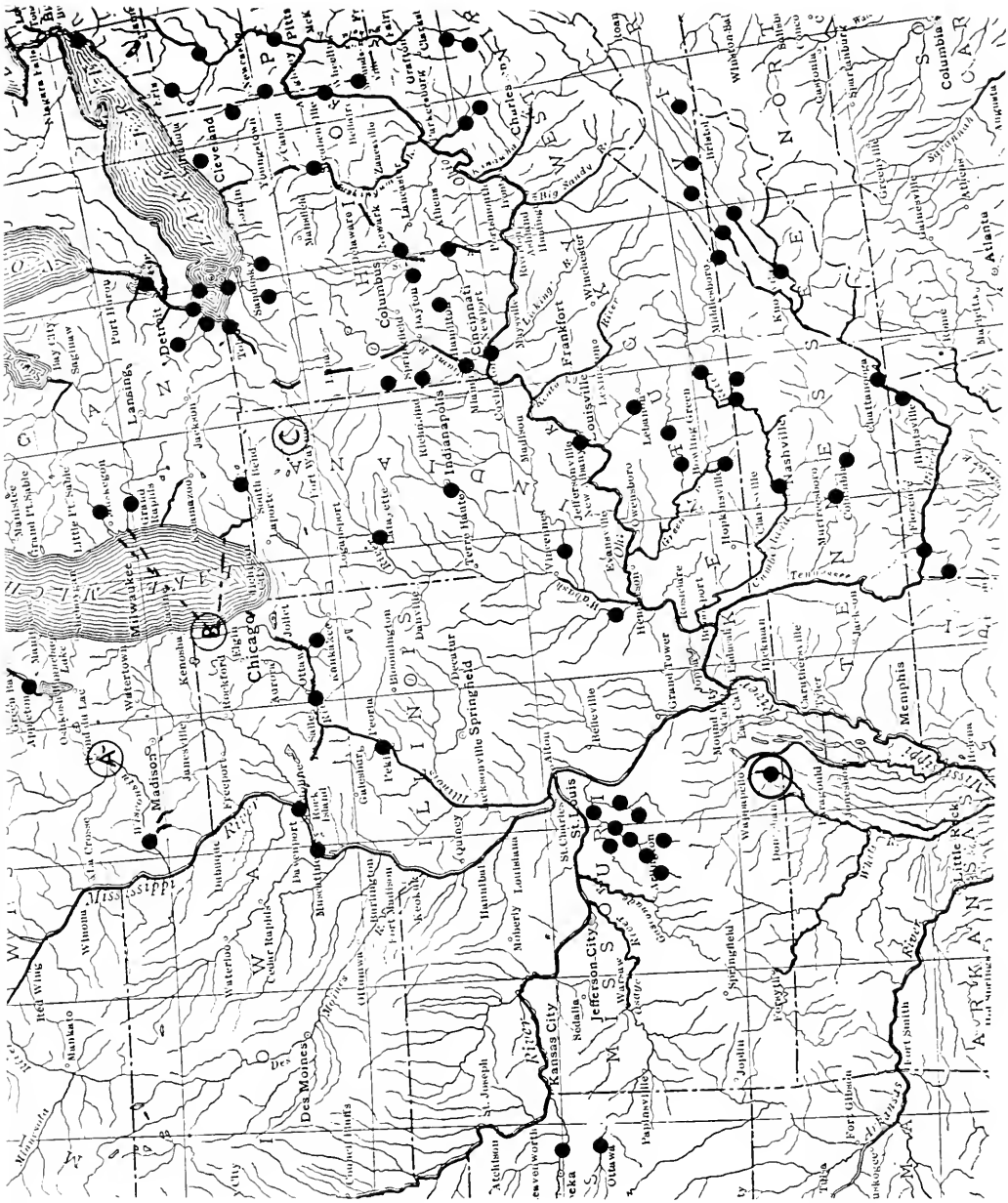
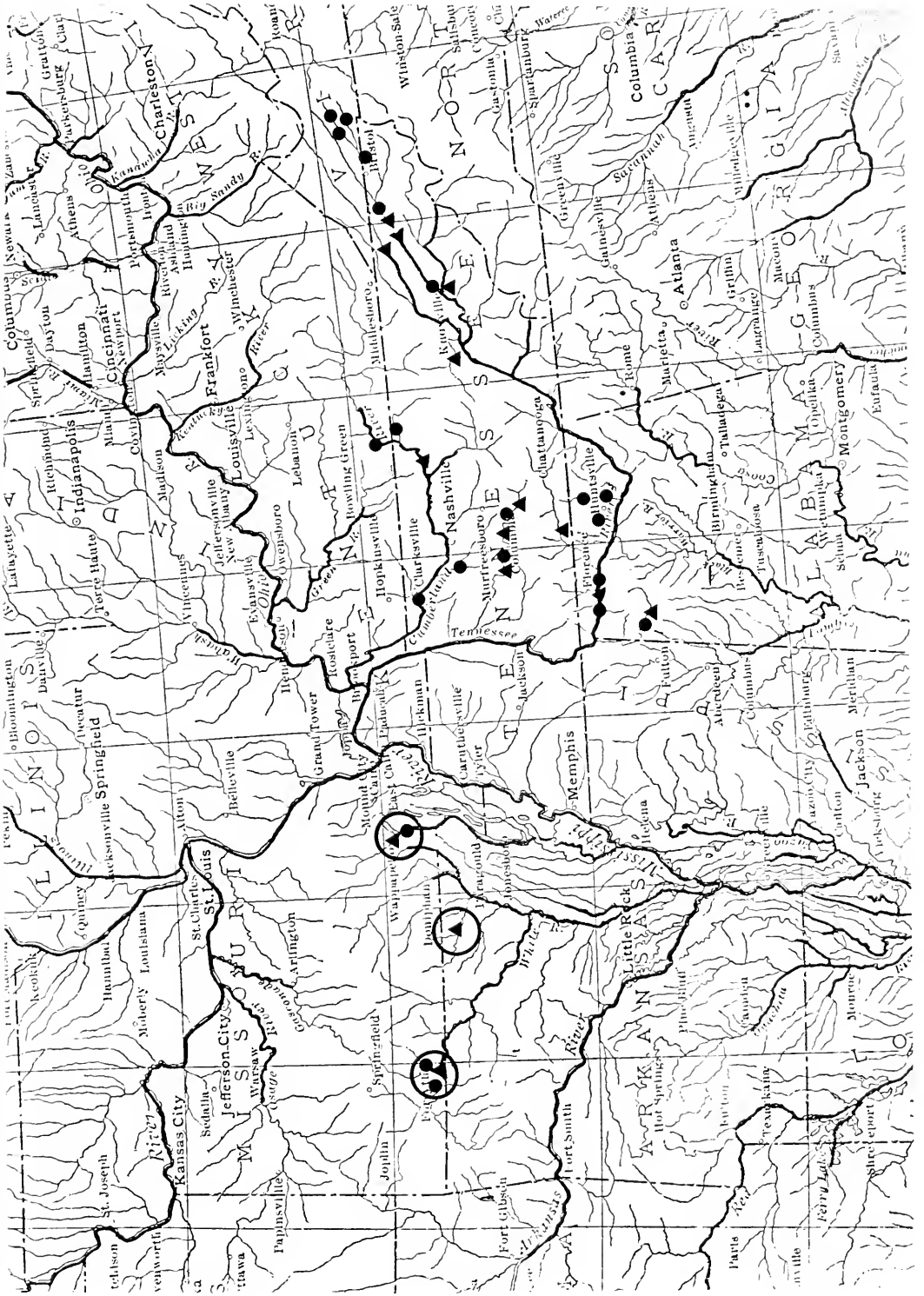

A
B
C

Plate 2.

The distribution of *Plagiola* (*Torulosa*) *turgidula* (Lea) (triangles), and *Plagiola* (*Torulosa*) *Ilorentina* (Lea) (dots).

The restricted distribution of *P. turgidula* and *Ilorentina* to the upper White River system on the Ozark Plateau (records south of the Ozark Crest enclosed by large circles) and to the Tennessee and Cumberland river systems (including the Duck River drainage of the former) on the Cumberland Plateau, suggests that these species have persisted at least since the Cretaceous uplift.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Wappapello
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Fort Smith
Texarkana
Shreveport
Monroe
Ohio
Mississippi
Tennessee
Cumberland
Kentucky
Green
Wabash
Missouri
Osage
Arkansas
White R.
Red
Big Sandy R.
Kanawha R.
Savannah
Coosa
Black Warrior R.

Plate 3.

The distribution of *Plagiola* (*Torulosa*) *torulosa* (Rafinesque).

This species has persisted in the Tennessee River system, and while it may have had refugia in the Green, Allegheny and Monongahela river drainages, it is assumed that it spread from the Tennessee River system in post-glacial time to form its present distribution.

Although not now found in any intervening rivers, it must have followed the same route as *triquetra* (Plate 1 B) in reaching the Grand River, Michigan.

Clearly it followed the same route as *triquetra* (Plate 1 C) in reaching lakes Huron and Erie.

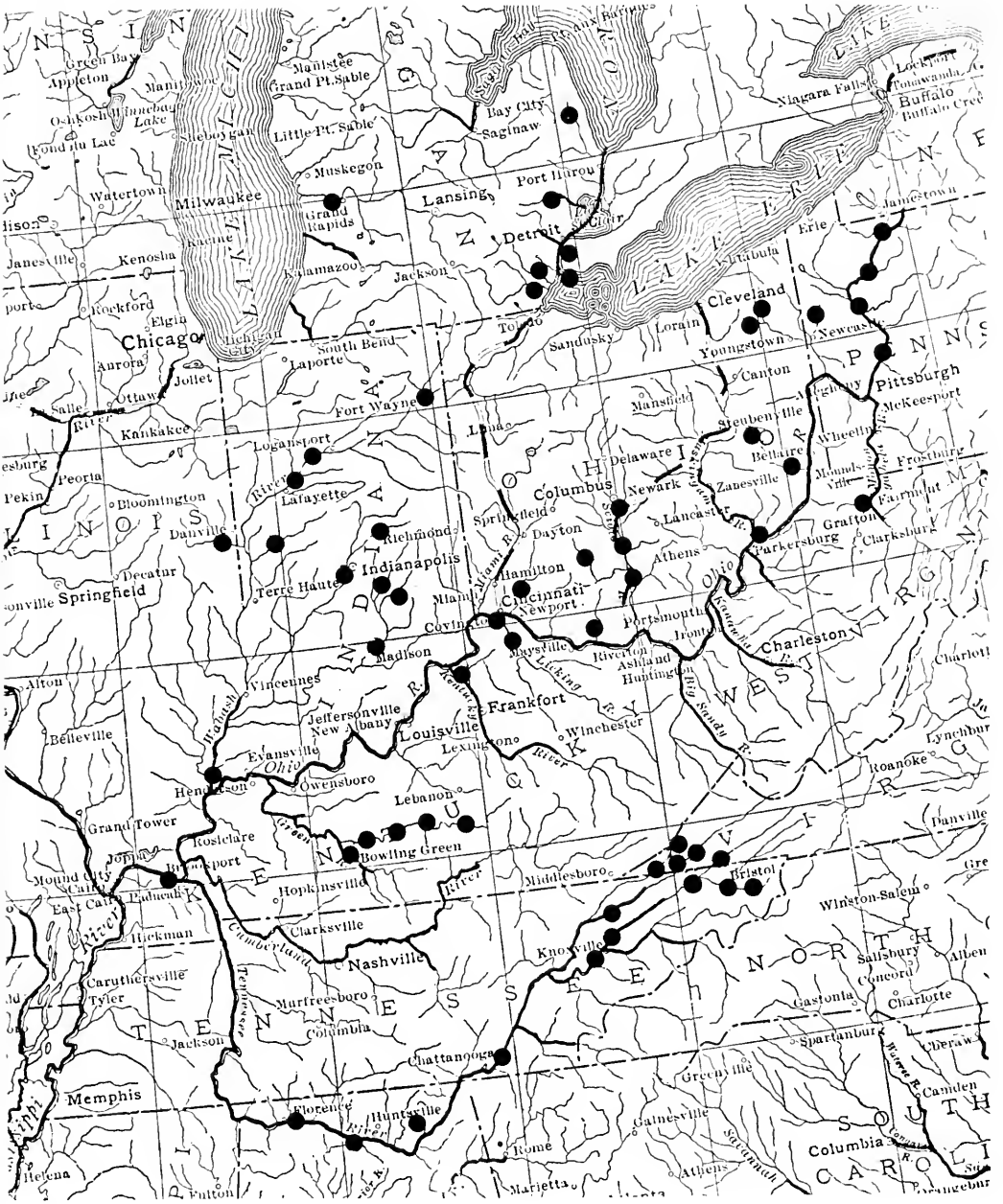
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Plate 4.

The distribution of *Plagiola* (*Pilea*) *obliquata* (Rafinesque).

This species has persisted in the Tennessee and Cumberland river systems, and while it may have had a refugia in the Green River drainage, it is assumed that it spread from the former systems in post-glacial time to form its present distribution.

Clearly it followed the same route as *triquetra* (Plate 1 C) and *torulosa* (Plate 3) in reaching Lake Erie. Unlike the latter two species, which occur in the Allegheny and Monongahela river drainages, it is not known to have ascended the Ohio River beyond Cincinnati, Hamilton Co., Ohio, though like *P. flexuosa* (Plate 5), it probably did.

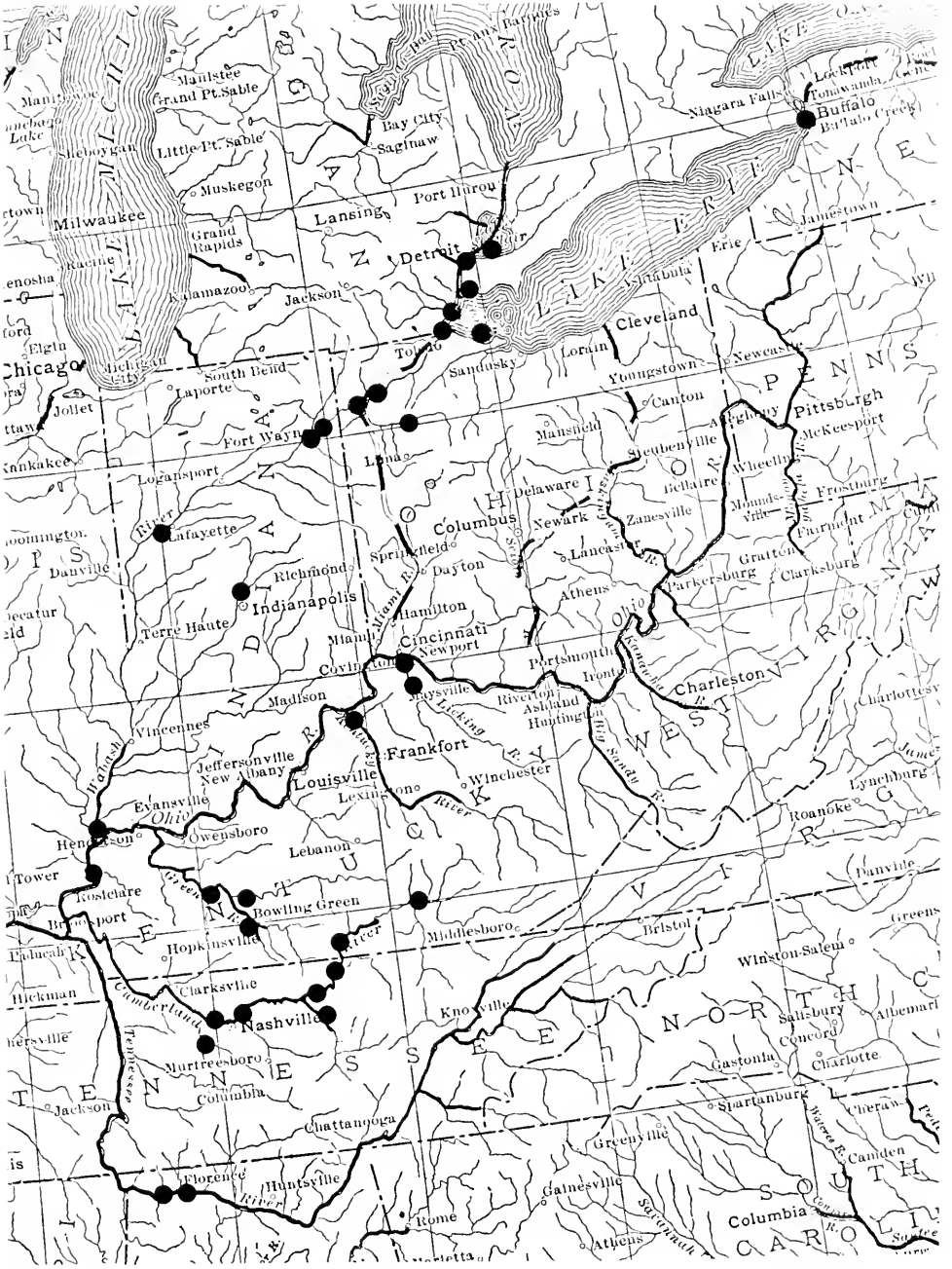
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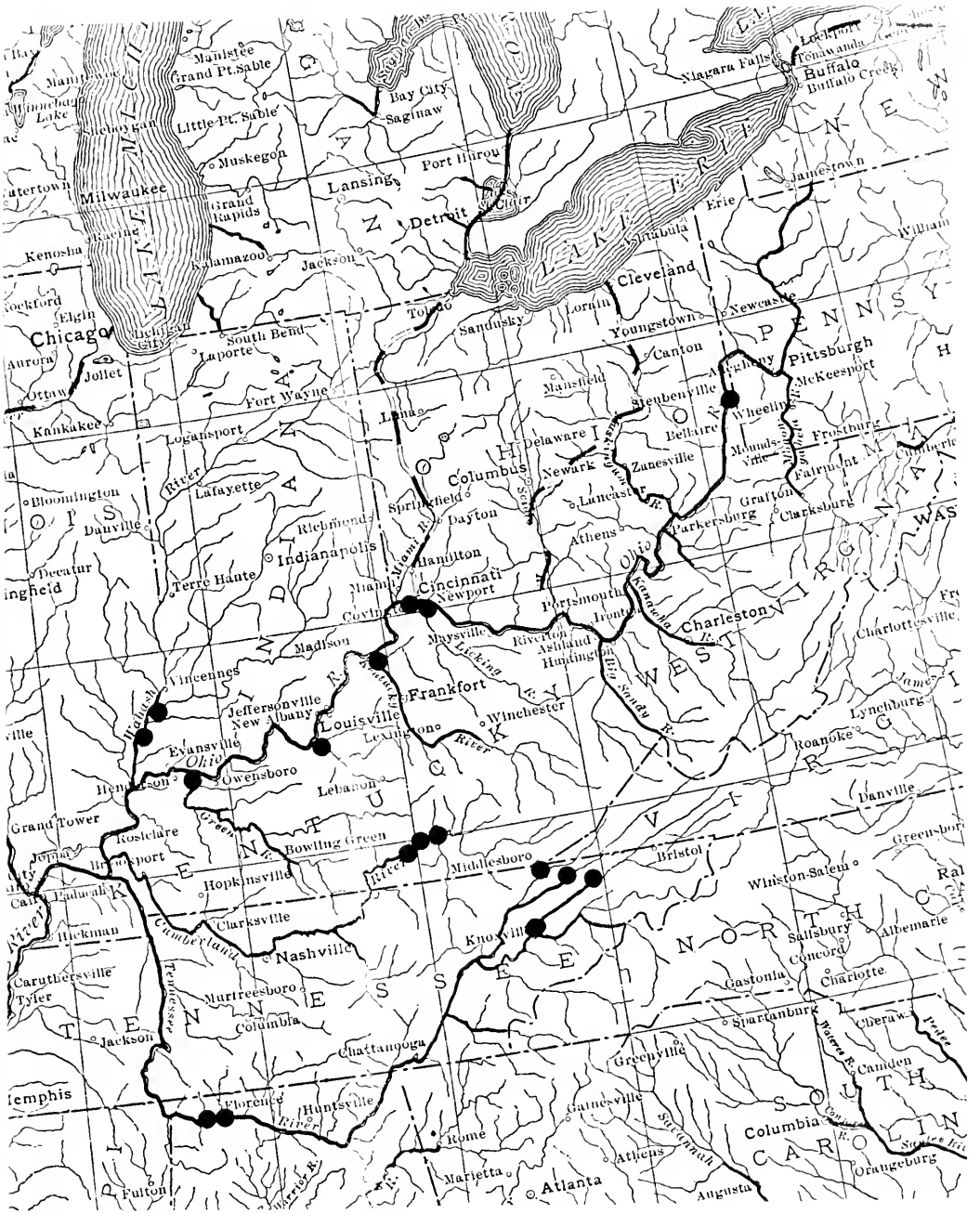
Plate 5.

The distribution of *Plagiola* (*Epioblasma*) *flexuosa* (Rafinesque).

This species has persisted in the Tennessee and Cumberland river systems; it is assumed that it spread from one or both of these systems in post-glacial time into the Ohio River system, where it occurs from the lower Wabash River drainage to the Ohio River, Steubenville, Jefferson Co., Ohio.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VIRGINIA
PENNSYLVANIA
NEW YORK
NORTH CAROLINA
SOUTH CAROLINA

Plate 6.

The distribution of *Plagiola* (*Pilea*) *personata* (Say), Fig. A, *Plagiola* (*Torulosa*) *propinqua* (Lea), Fig. B (dots), and *Plagiola* (*Torulosa*) *sampsoni* (Lea), Fig. B (triangles).

P. personata and *propinqua* have persisted in the Tennessee and Cumberland river systems, whereas *sampsoni* appears to be absent in the Cumberland. It is assumed that *sampsoni* spread from the Tennessee, while *personata* and *propinqua* spread from either or both the Tennessee and Cumberland river systems in post-glacial time, into the Ohio River system. They all occur in the lower Wabash River drainage, and extend in the Ohio drainage to Cincinnati, Hamilton Co., Ohio.

The location of *sampsoni* in the Tennessee River system is conjectural. An additional record, from the Ohio River at Cincinnati, is missing from the map.

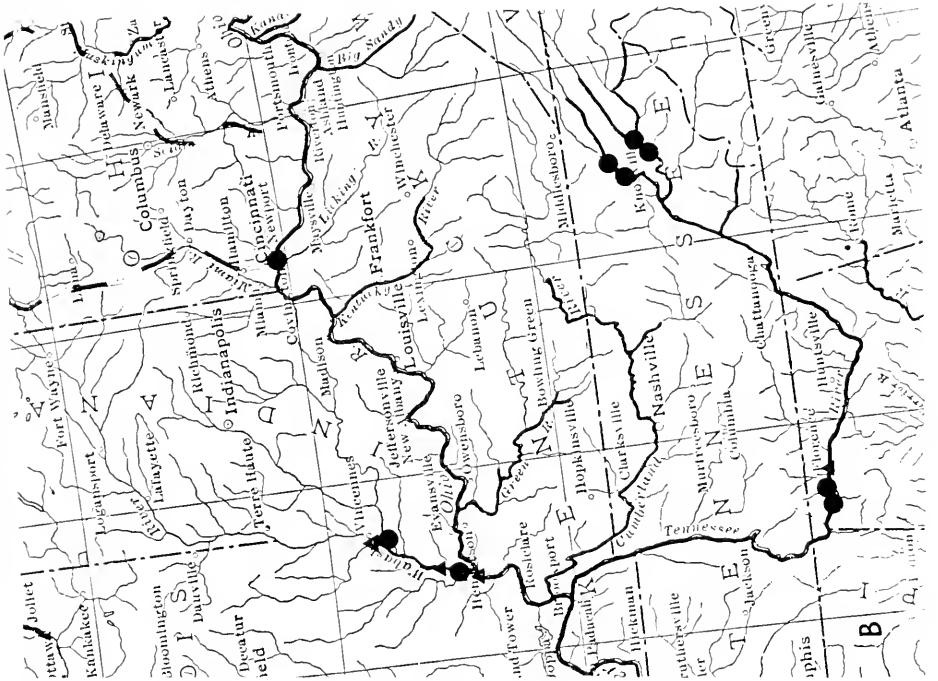
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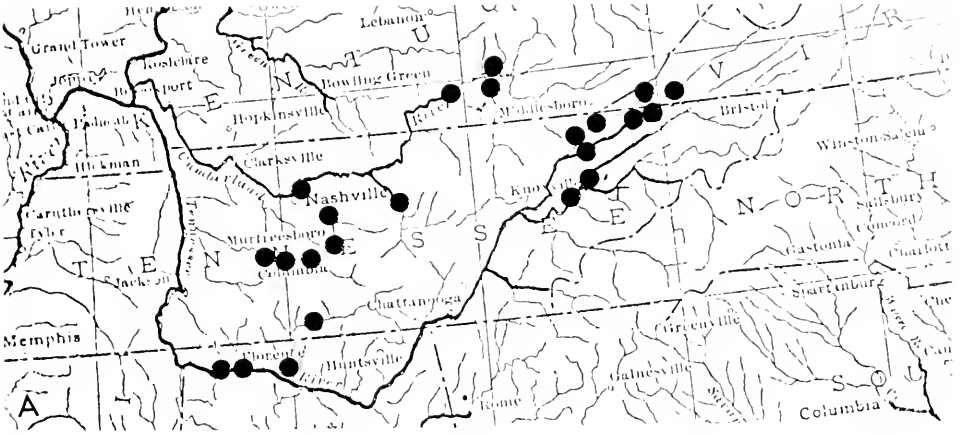
Plate 7.

The distribution of *Plagiola* (*Plagiola*) *interrupta* (Rafinesque), Fig. A, *Plagiola* (*Torulosa*) *capsaeformis* (Lea), Fig. B, and *Plagiola* (*Plagiola*) *lenior* (Lea), Fig. C.

These species have persisted in the Tennessee and Cumberland river systems, and the Duck River drainage of the former. According to Ortmann (1924: 46), Duck River was originally more directly connected with the Tennessee and Cumberland rivers.

They did not extend their distribution in post-glacial time.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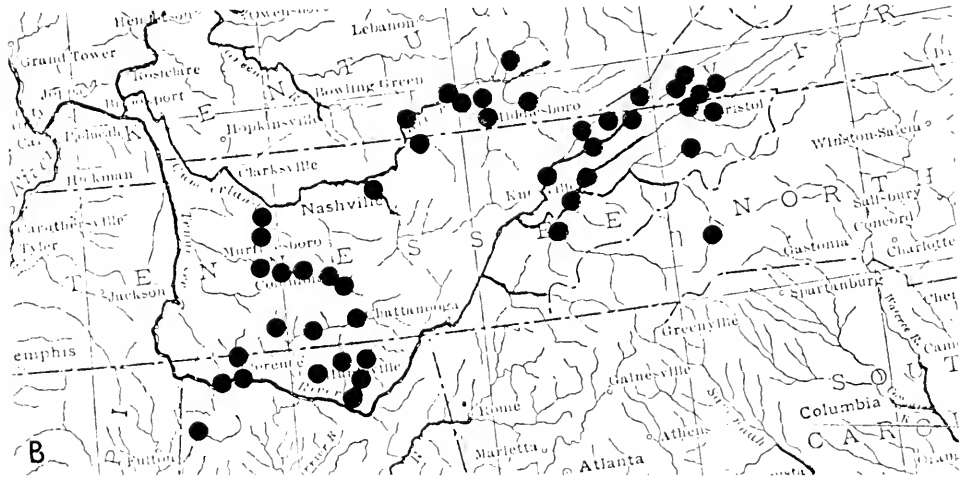
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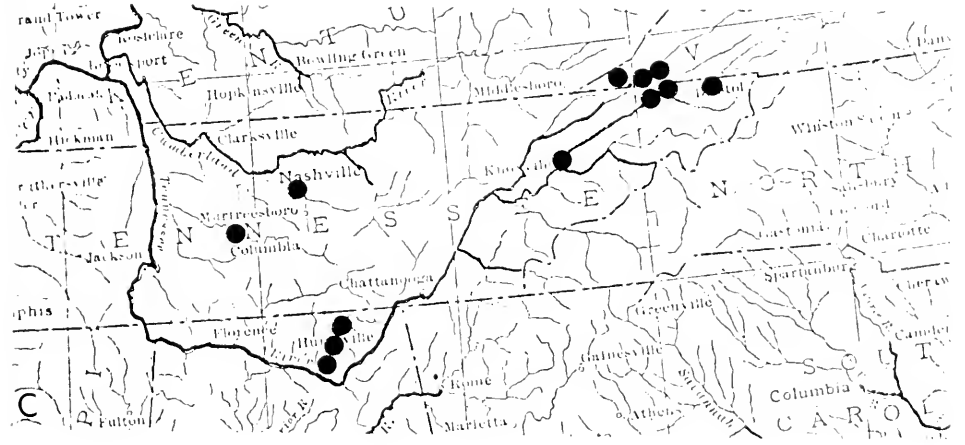
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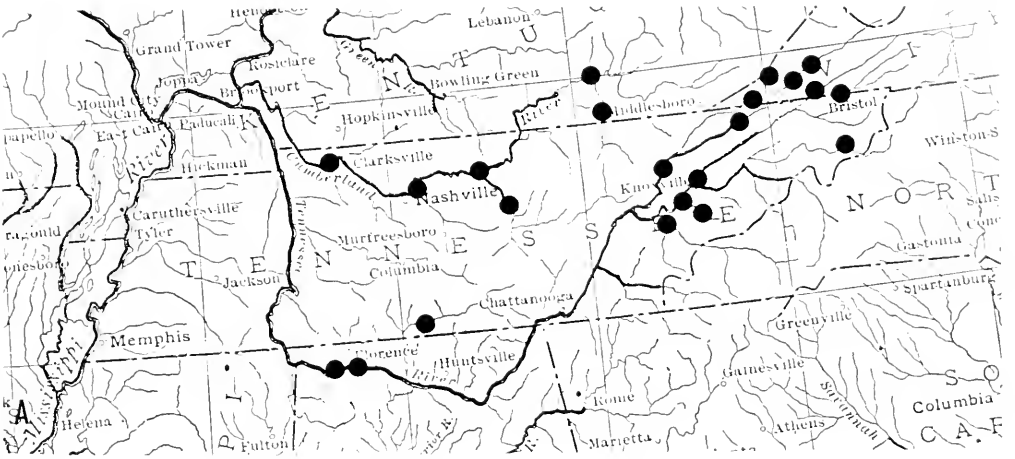
Plate 8.

The distribution of *Plagiola* (*Pilea*) *haysiana* (Lea), Fig. A, *Plagiola* (*Plagiola*) *arcaeformis* (Lea), Fig. B, and *Plagiola* (*Epioblasma*) *stewardsoni* (Lea), Fig. C.

These species have persisted in the upper and lower Tennessee River system as well as in the Cumberland River system. They did not extend their distribution in post-glacial time.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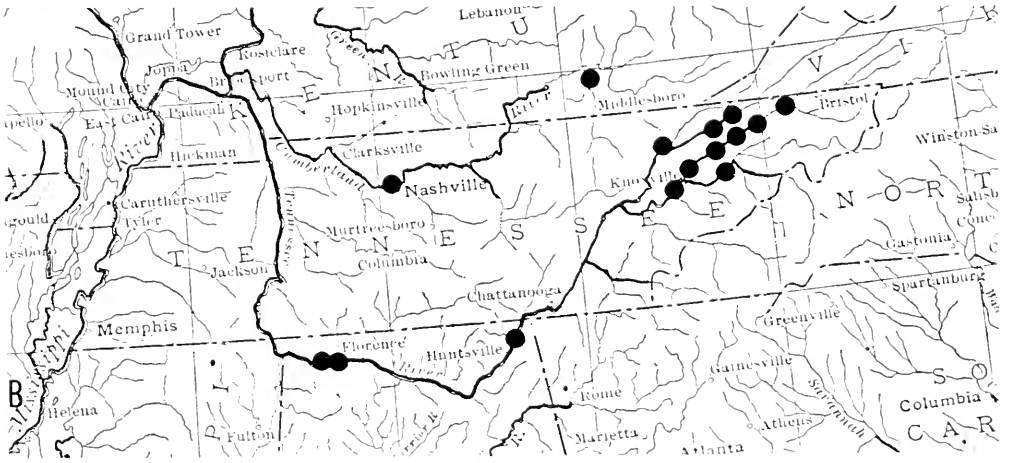
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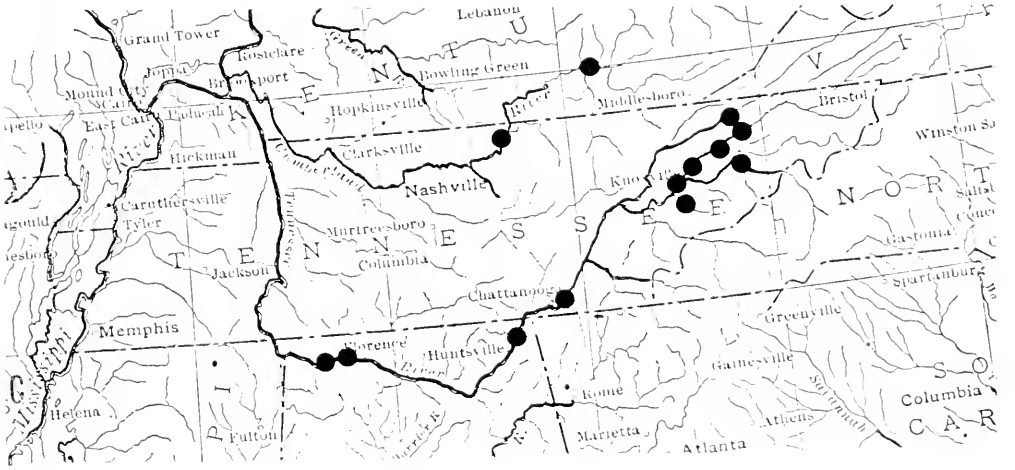
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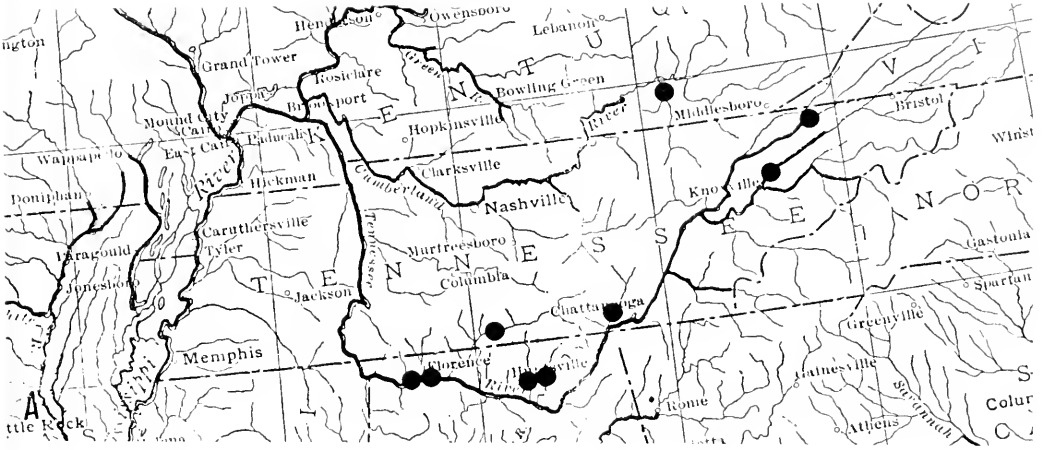
Plate 9.

The distribution of *Plagiola* (*Torulosa*) *biemarginata* (Lea), Fig. A, and *Plagiola* (*Plagiola*) *penita* (Conrad), Fig. B.

Figure A. *P.* (*T.*) *biemarginata* (Lea) has persisted in the upper and lower Tennessee River system and the Big South Fork of the Cumberland River. It, like the species shown on Plate 8, did not extend its distribution in post-glacial time.

Figure B. *P.* (*P.*) *penita* Conrad is restricted to the Alabama-Coosa River system and is clearly derived from *P.* (*P.*) *interrupta* (Rafinesque) of the Tennessee River system.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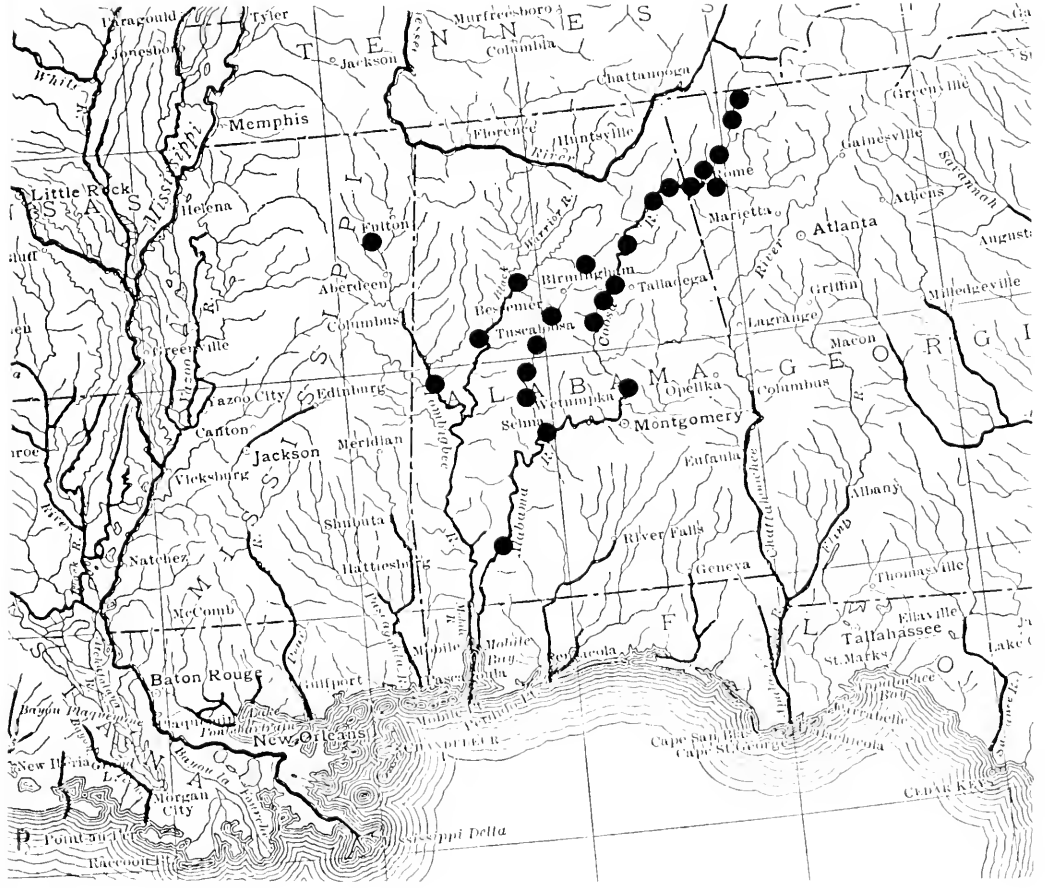
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New Orleans
Cape San Blas
Cape St. George
Apalachicola
Morgan City
CEDAR KEY
Pontchartrain
Raccoon
Mississippi Delta

Plate 10.

Plagiola (*Truncillopsis*) *triquetra* (Rafinesque)

Figure 1. *Truncilla triqueter* Rafinesque. Falls of the Ohio River, [near Louisville, Jefferson Co., Kentucky]. Lectotype ANSP 20231. Length 55, height 37, width 25 mm. Male.

Figure 2. Green River, 8 mi. S Campbellsville, Taylor Co., Kentucky. MCZ 220157. Length 44, height 31, width 24 mm. Male.

Figure 3. Ohio River, Cincinnati, Hamilton Co., Ohio. MCZ 6158. Length 39, height 24, width 24 mm. Female.

Figure 4. Green River, 8 mi. S Campbellsville, Taylor Co., Kentucky. MCZ 220157. Length 36, height 24, width 22 mm. Female.

Plagiola (*Plagiola*) *interrupta* (Rafinesque)

Figure 5. *Obliquaria* (*Plagiola*) *interrupta* Rafinesque. [Cumberland River, Tennessee]. Lectotype ANSP 20257. Length 55.5, height 43, width 26.5 mm. Male.

Figure 6. *Unio brevidens* Lea. [Cumberland River, Tennessee]. Specimen subsequently identified by Lea USNM 85349. Length 54, height 38, width 23.5 mm. Male.

Figure 7. *Unio brevidens* Lea. [Cumberland River, Tennessee]. Specimen subsequently identified by Lea USNM 85349. Length 68, height 53.5, width 43.5 mm. Female.

Plagiola (*Plagiola*) *penita* (Conrad)

Figure 8. Coosa River, Weduska Shoals, Shelby Co., Alabama. MCZ 29817. Length 52, height 40, width 26 mm. Male.

Figure 9. *Unio penitus* Conrad. Alabama River, near Claiborne, Munroe Co., Alabama. Holotype ANSP 59860. Length 51, height 35, width 26 mm. Female.

Figure 10. *Unio metastriatus* Conrad. Black Warrior River, near Blount's Springs, Blount Co., Alabama. Length 30, height 23, width 17 mm. Syntype [lost], from Conrad. Male.

Figure 11. *Unio metastriatus* Conrad. Black Warrior River, near Blount's Springs, Blount Co., Alabama. Length 28, height 21 mm, width unavailable. Syntype [lost], from Conrad. Female.

Figure 12. *Unio compactus* Lea. Etowah River, Georgia. Holotype USNM 84447. Length 32, height 27, width 19 mm. Male.

Figure 13. *Unio compactus* Lea. Etowah River, Georgia. Allotype USNM 84447a. Length 28, height 20, width 16 mm. Female.

Figure 14. *Unio modicellus* Lea. Connasauga River, Georgia. Holotype USNM 84841. Length 28, height 21, width 15 mm. Male.

Figure 15. *Unio othcaloogensis* Lea. Oothkalooga Creek, Gordon Co., Georgia. Holotype USNM 84615. Length 22, height 16, width 13 mm. Male.

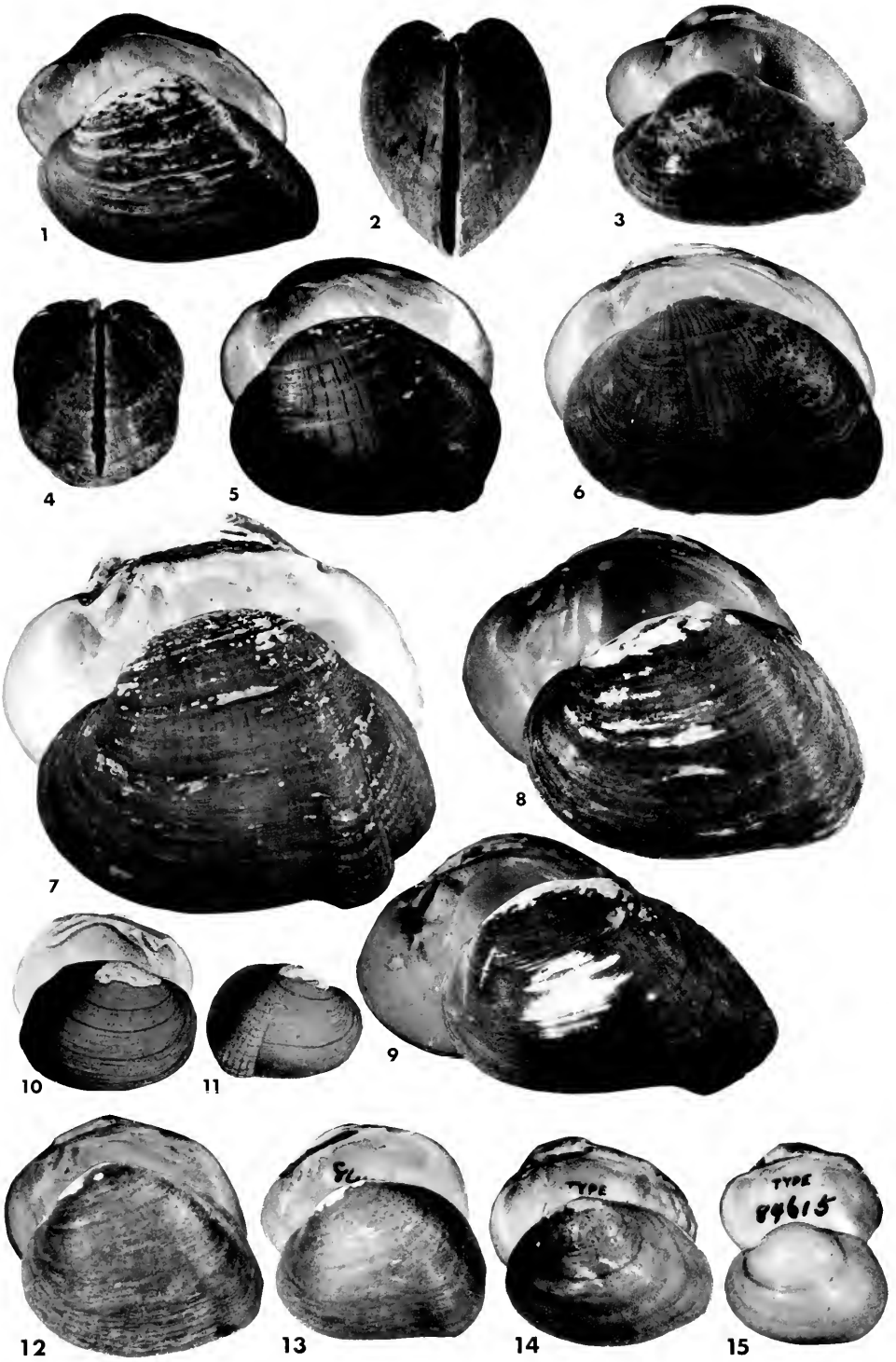
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Plate 11.

Plagiola (*Plagiola*) *arcaeformis* (Lea).

Figure 1. *Unio arcaeformis* Lea. Tennessee River, Florence, Lauderdale Co., Alabama. Specimen subsequently identified by Lea USNM 84422. Length 54.5, height 43.5, width 38 mm. Male.

Figure 2. Cumberland River, Tennessee. MCZ 5033. Length 42, height 34, width 27 mm. Male.

Figure 3. Cumberland River, Tennessee. MCZ 5033. Length 55, height 40, width 40 mm. Female.

Figure 4. *Unio arcaeformis* Lea. Tennessee River, Florence, Lauderdale Co., Alabama. Specimen subsequently identified by Lea USNM 84422. Length 56.5, height 39, width 39 mm. Female.

Plagiola (*Plagiola*) *lenior* (Lea)

Figure 5. Eastern Tennessee. MCZ 16387. Length 35, height 21, width 14 mm. Male.

Figure 6. *Unio lenior* Lea. Stones River, Tennessee. Holotype USNM 86130. Length 25, height 16, width 12.5 mm. Female.

Plagiola (*Torulosa*) *torulosa* (Rafinesque)

Figure 7. *Amblema gibbosa* Rafinesque. Ohio River. Lectotype ANSP 20232. Length 40, height 33, width 25 mm. Male.

Figure 8. *Unio perplexus* Lea. Ohio River, Cincinnati, Hamilton Co., Ohio. Holotype USNM 84324. Length 64, height 43, width 32.5 mm. Male.

Figure 9. *Unio cincinnatiensis* Lea. Ohio River, Cincinnati, Hamilton Co., Ohio. Holotype USNM 84199. Length 48, height 39, width 27.5 mm. Male.

Figure 10. *Unio rangianus* Lea. Mahoning River, near Poland, Mahoning Co., Ohio. Allotype USNM 84798. Length 51.5, height 36, width 26 mm. Male.

Figure 11. *Truncilla sulcata delicata* Simpson. Detroit River. Amherstburg, Essex Co., Ontario. Holotype USNM 160853. Length 44, height 31, width 24 mm. Male.

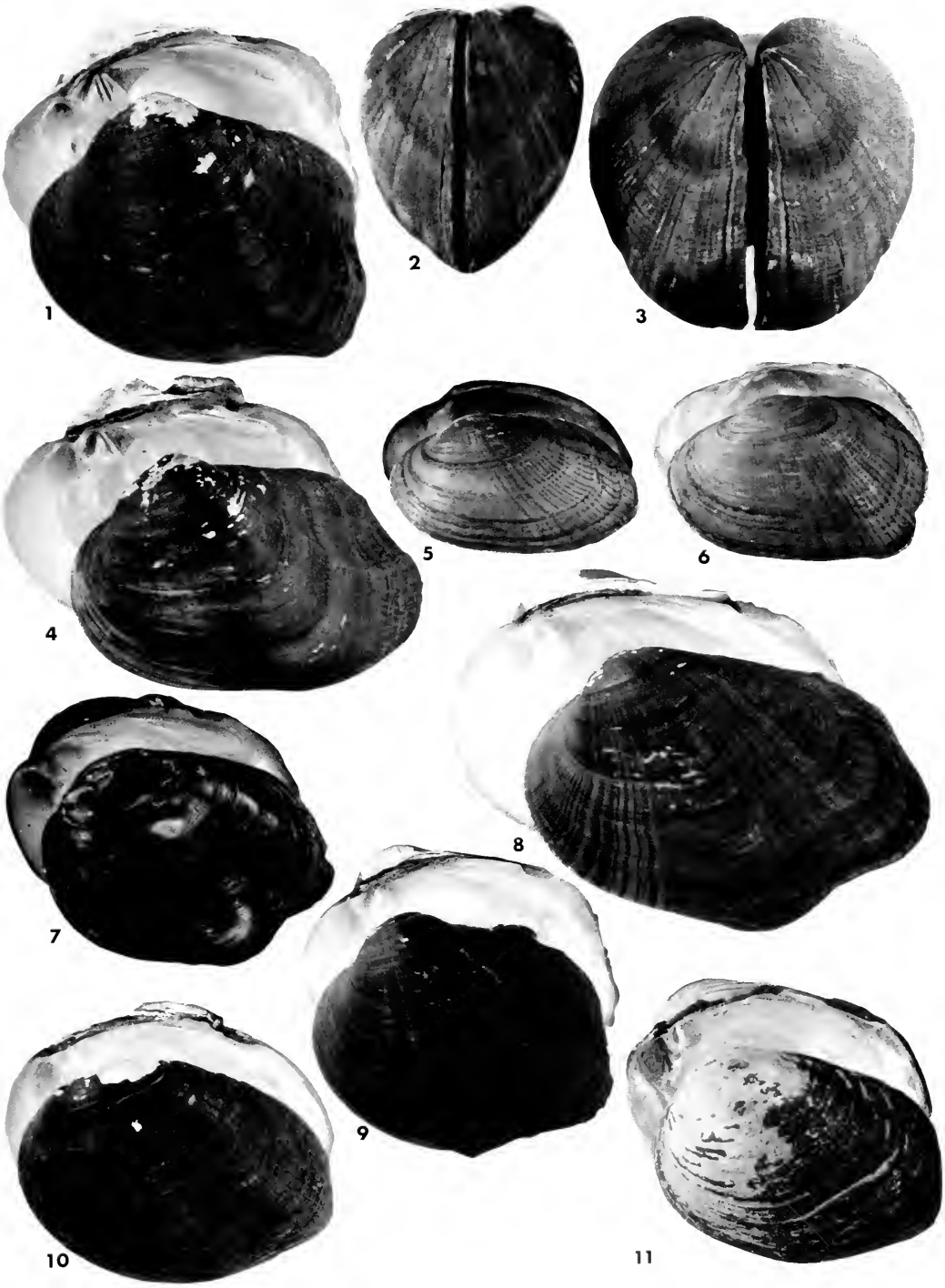
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Plate 12.

Plagiola (*Torulosa*) *torulosa* (Rafinesque)

Figure 1. *Amblema torulosa* Rafinesque. Kentucky River, Kentucky. Holotype ANSP 20218. Length 65, height 48, width 33.5 mm. Female.

Figure 2. *Unio rangianus* Lea. Mahoning River, near Poland, Mahoning Co., Ohio. Lectotype USNM 84798. Length 49, height 35.5, width 24 mm. Female. [Slightly larger than Lea's figured type].

Figure 3. *Unio gibbosus perobliquus* Conrad. Wabash River, Indiana. Figured type [lost] from Conrad. Length 56, height 48, width 32 mm. Male.

Figure 4. *Unio phillipsii* Reeve. North America. Length 54, height 45, width 30 mm. Holotype BMNH 196481. Female.

Figure 5. *Unio gubernaculum* Reeve. (Hab?). Holotype BMNH 1965203. Length 57, height 48, width 19 mm. Female.

Plagiola (*Torulosa*) *sampsoni* (Lea)

Figure 6. *Unio sampsonii* Lea. Wabash River, New Harmony, Posey Co., Indiana. Holotype USNM 84802. Length 42.5, height 33, width 25.5 mm. Male.

Figure 7. *Unio sampsonii* Lea. Wabash River, New Harmony, Posey Co., Indiana. Allotype USNM 84802. Length 45, height 38.5, width 29 mm. Female.

Plagiola (*Torulosa*) *propinqua* (Lea)

Figure 8. *Unio propinquus* Lea. Tennessee River, Florence, Lauderdale Co., Alabama. Holotype USNM 84332. Length 53, height 41, width 33 mm. Male.

Figure 9. Holston River, Knoxville, Knox Co., Tennessee. MCZ 5819. Length 44, height 46, width 31 mm. Female.


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Plate 13.

Plagiola (*Torulosa*) *biemarginata* (Lea)

Figure 1. *Unio biemarginatus* Lea. Tennessee River, Florence, Lauderdale Co., Alabama. Allotype USNM 84608a. Length 38.5, height 30, width 19 mm. Male.

Figure 2. *Unio biemarginatus* Lea. Tennessee River, Florence, Lauderdale Co., Alabama. Holotype USNM 84608. Length 36, height 31.5, width 18 mm. Female.

Plagiola (*Torulosa*) *capsaeformis* (Lea)

Figure 3. *Unio capsaeformis* Lea. Cumberland River, Tennessee. Holotype MCZ 178570. Length 45, height 33, width 24 mm. Male.

Figure 4. *Unio capsaeformis* Lea. Cumberland River, Tennessee. Specimen subsequently identified by Lea MCZ 178568. Length 43, height 30, width 18 mm. Female.

Plagiola (*Torulosa*) *florentina* (Lea)

Figure 5. *Unio florentinus* Lea. Tennessee River, Florence, Lauderdale Co., Alabama. Allotype USNM 84948. Length 36, width 27, height 20 mm. Male.

Figure 6. *Truncilla walkeri* Wilson and Clark. East Fork of Stones River, near Walterhill, Rutherford Co., Tennessee. Paralectotype MZUM 90729. Length 47, height 34, width 22 mm. Male.

Figure 7. *Truncilla curtisii* Frierson and Utterback. White River, Forsyth, Taney Co., Missouri. Paralectotype MZUM 90748. Length 35, height 26, width 19 mm. Male.

Figure 8. *Unio florentinus* Lea. Tennessee River, Florence, Lauderdale Co., Alabama. Holotype USNM 84948. Length 33, height 27, width 19 mm. Female.

Figure 9. *Truncilla walkeri* Wilson and Clark. East Fork of Stones River, Walterhill, Rutherford Co., Tennessee. Lectotype MZUM 90729. Length 42, height 30, width 17 mm. Female.

Figure 10. *Truncilla curtisii* Frierson and Utterback. White River, Forsyth, Taney Co., Missouri. Lectotype MZUM 90748. Length 32, height 27, width 17 mm. Female.

Figure 11. Black River, Hendrickson, Butler Co., Missouri. MCZ 260979. Length 26, height 21, width 13 mm. Female.

Figure 12. *Unio sacculus* Anthony. Tennessee. Holotype MCZ 161898. Length 33, height 24, width 16 mm. Female.

Figure 13. *Truncilla curtisii* Frierson and Utterback. White River, Hollister, Taney Co., Missouri. Figured syntype [lost] from Utterback. Length 33, height 23, width 15 mm. Female.

Figure 14. *Truncilla curtisii* Frierson and Utterback. White River, Hollister, Taney Co., Missouri. Figured syntype [lost] from Utterback. Length 22.5, height 19.5, width 13.5 mm. Male.

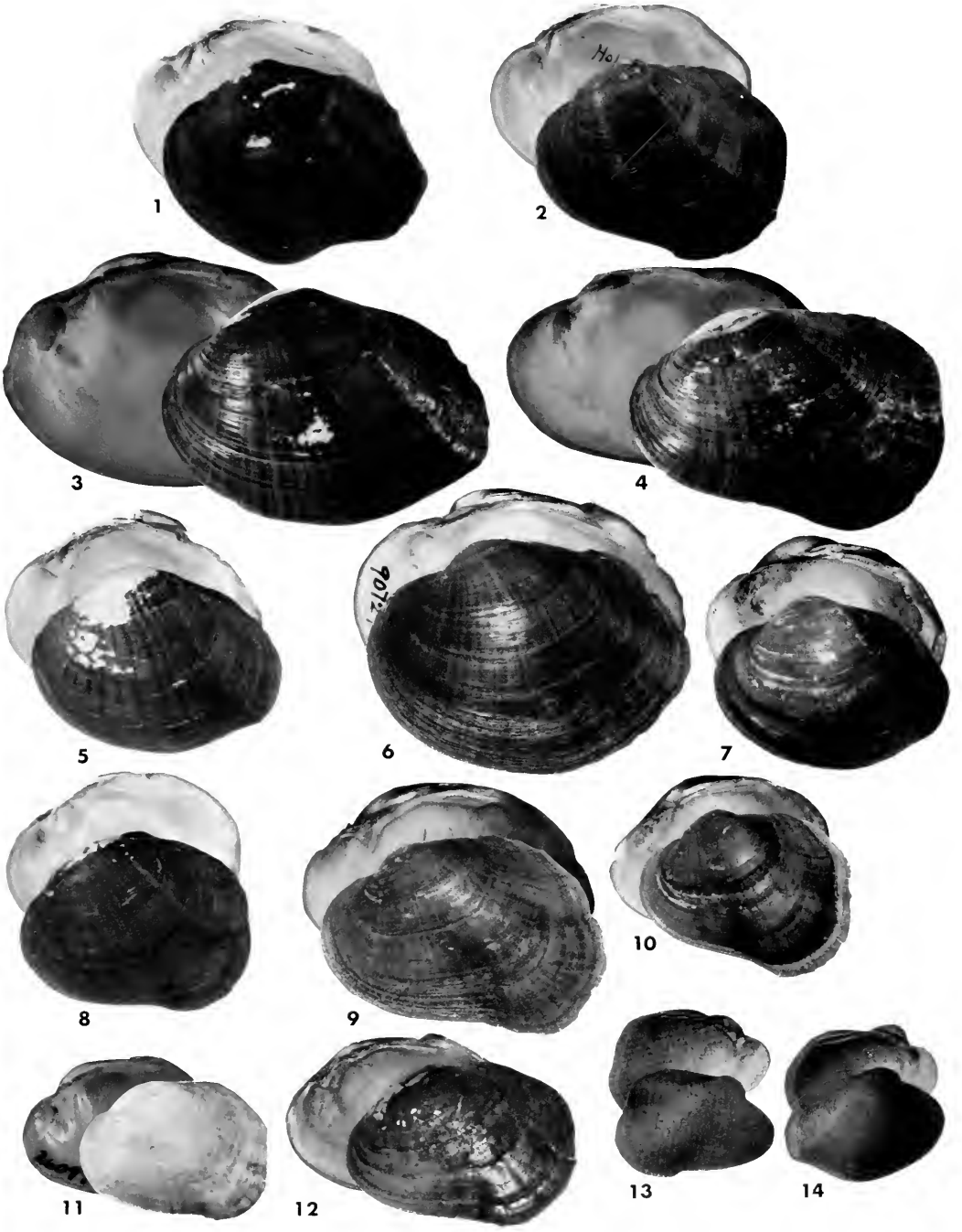
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Plate 14.

Plagiola (*Torulosa*) *turgidula* (Lea)

Figure 1. *Truncilla lefevrei* Utterback. Black River, Williamsville, Wayne Co., Missouri. Figured syntype [lost] from Utterback. Length 32, height 21, width 15 mm. Female.

Figure 2. *Truncilla lefeveri* Utterback. Black River, Williamsville, Wayne Co., Missouri. Figured syntype [lost] from Utterback. Length 26.5, height 18, width 14 mm. Male.

Figure 3. *Unio turgidulus* Lea. Cumberland River, Tennessee. Holotype USNM 84946. Length 41.5, height 30, width 23.5 mm. Male.

Figure 4. Spring Creek, Hardy, Sharp Co., Arkansas. MZUM 90742. Length 40, height 29, width 17 mm. Male.

Figure 5. *Unio deviatus* Anthony. Tennessee. Holotype MCZ 161895. Length 39, height 25, width 19 mm. Female.

Figure 6. Spring Creek, Hardy, Sharp Co., Arkansas. MZUM 90742. Length 33, height 24, width 15 mm. Female.

Plagiola (*Pilea*) *personata* (Say)

Figure 7. *Unio pileus* Lea. Ohio River, near Cincinnati, Hamilton Co., Ohio. Holotype USNM 84602a. Length 47, height 43, width 28 mm. Male.

Figure 8. *Unio capillaris* Lea. Ohio. Specimen subsequently identified by Lea USNM 84602. Length 54, height 46, width 33 mm. Female.

Figure 9. *Unio personatus* Say. Cumberland River, Tennessee. Neotype MCZ 5763. Length 54, height 48, width 31 mm. Female.

Plagiola (*Pilea*) *obliquata* (Rafinesque)

Figure 10. *Obliquaria obliquata* Rafinesque. Kentucky River. Lectotype ANSP 20226. Length 59, height 43, width 32.5 mm. Male.

Figure 11. *Unio sulcatus* Lea. Ohio. Holotype USNM 84803. Length 57, height 41, width 33 mm. Male.

Figure 12. *Unio sulcatus* Lea. Ohio. Allotype USNM 84803. Length 37, height 29.5, width 23 mm. Female.

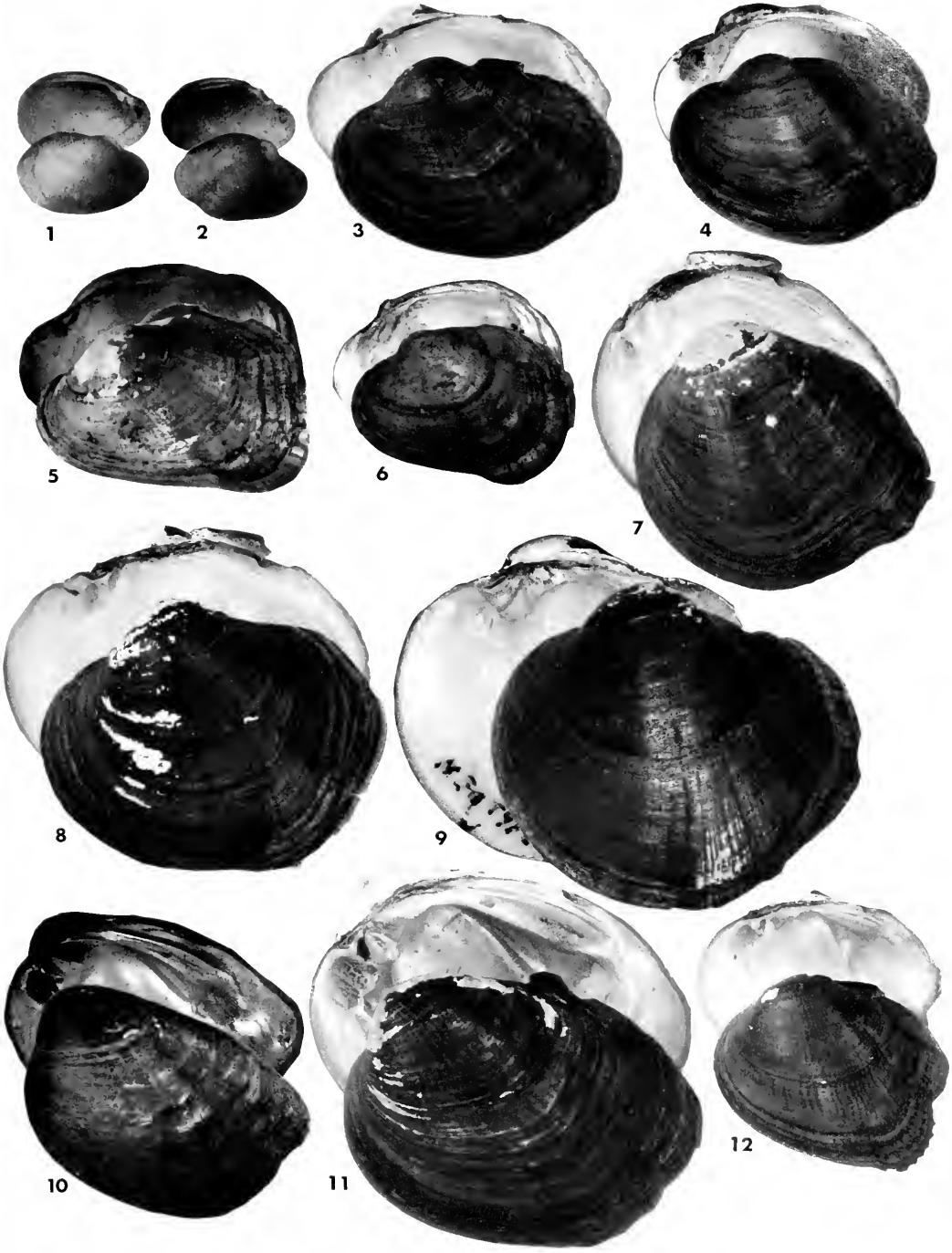
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Plate 15.

Plagiola (*Pilea*) *haysiana* (Lea)

Figure 1. *Unio haysianus* Lea. Cumberland River, Nashville, Davidson Co., Tennessee. Specimen subsequently identified by Lea USNM 84613. Length 51.5, height 49, width 36 mm. Male.

Figure 2. *Unio sowerbyanus* Lea. Caney Fork of the Cumberland River, Tennessee. Specimen subsequently identified by Lea MCZ 178886. Length 39, height 38, width 28 mm. Male.

Figure 3. Cumberland River, Tennessee. MCZ 5451. Length 32, height 30, width 28 mm. Female.

Figure 4. *Unio haysianus* Lea. Cumberland River, Nashville, Davidson Co., Tennessee. Specimen subsequently identified by Lea USNM 84613. Length 25.5, height 24.5, width 19 mm. Female.

Plagiola (*Epioblasma*) *flexuosa* (Rafinesque)

Figure 5. *Obliquaria flexuosa* Rafinesque. Kentucky River. Lectotype ANSP 20249. Length 57, height 47, width 33 mm. Male.

Figure 6. *Truncilla lewisi* Walker. Holston River, Tennessee. Paralectotype MZUM 91456. Length 43, height 37, width 22.5 mm. Male.

Figure 7. *Epioblasma biloba* Rafinesque. Ohio River, Cincinnati, Hamilton Co., Ohio. Neotype ANSP 56571. Length 65, height 59, width 40 mm. Female.

Figure 8. *Truncilla lewisi* Walker. Holston River, Tennessee. Lectotype MZUM 91456. Length 51, height 49.5, width 25 mm. Female.

Plagiola (*Epioblasma*) *stewardsoni* (Lea)

Figure 9. *Unio stewardsoni* Lea. Tennessee. Specimen subsequently identified by Lea MCZ 178817. Length 31, height 29, width 18 mm. Male.

Figure 10. *Unio stewardsoni* Lea. Tennessee River, Chattanooga [Hamilton Co.], Tennessee. Holotype ANSP 56572. Length 31, height 29, width 13 mm. Female.


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Biology and Evolution of the Avian Genus *Atlapetes* (Emberizinae)

RAYMOND A. PAYNTER, JR.

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 148 NUMBER 7
5 JULY 1976

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BIOLOGY AND EVOLUTION OF THE AVIAN GENUS *ATLAPETES* (EMBERIZINAE)*

RAYMOND A. PAYNTER, JR.[1]

CONTENTS

ABSTRACT. The 24 species of *Atlapetes* are furtive brush or forest inhabitors occurring mainly in subtropical or temperate zones in the highlands from Mexico to the southern Andes. They are grouped into four subunits: (1) *A. albinucha* superspecies, (2) *A. rufinucha* species-group with *A. rufinucha* superspecies, *A. tricolor* superspecies, *A. albofrenatus*, *A. leucopis*, *A. pileatus*, *A. fulviceps* superspecies, and probably *A. citrinellus*, (3) *A. schistaceus* species-group with *A. schistaceus*, *A. nationi*, *A. leucopterus*, *A. albiceps*, *A. pallidiceps*, and *A. rufigenis*, and (4) *A. torquatus* species-group with *A. brunneinucha* and *A. torquatus* superspecies. The *A. rufinucha* species-group, with 11 (or 12) species, and the *A. schistaceus* species-group, with six species, are the main evolu-

[1] Museum of Comparative Zoology.

* Published and supported in part by a grant from the Wetmore Coles Fund.

tionary lines. Their respective members are largely allopatric, suggesting a recent origin. Speciation within *Atlapetes* seems to have been greatly influenced by Pleistocene climatic ocellations and to have been most active in the northern Andes.

INTRODUCTION

Members of the genus *Atlapetes*, a moderately well-differentiated genus of emberizine sparrows, occur from the plateau of northern Mexico through the mountains of Central America and down the length of the Andes to northwestern Argentina (Fig. 1). There are 24 species, with the greatest number occurring in Colombia, where there are 14 species, and in Ecuador, where there are 11 species (Fig. 2). There is a general attenuation in the number of species north and south of the Colombia-Ecuador region. Several species have ranges that are restricted to a single valley system (*flaviceps*; *pallidiceps*) or massif (*melanocephalus*), while at the other extreme one species (*brunneinucha*) occurs from Mexico to Peru and has "a more extended range, . . . , than that of any other subtropical . . ." bird (Chapman, 1923a:245). However, for the most part, species of *Atlapetes* have ranges that are intermediate in length. The distribution of a number of species is discontinuous; at times the breaks appear to be unrelated to geography, vegetation, or collecting activities and offer clues to the evolutionary history of the genus.

All species are roughly the same size (ca. 130–180 mm long) and generally rather plainly marked. They are brown, brownish gray, or dark green dorsally and dull gray or bright yellow below. The majority have brown heads, the others are black with the exception of one which is white.

Members of the genus are characteristically furtive, seldom ascending more than a meter or two above the ground or emerging from the dense vegetation they prefer. They are solitary during the breeding season but may assemble in what appear to be family groups at other seasons. While many brush-inhabitors have loud, easily recognized vocalizations, the calls and songs of members of the genus *Atlapetes* are faint and undistinctive. In some localities these birds seem to make up a substantial portion of the avifauna, but this is apparent only to the most diligent observer.

Considerable information is available on the distribution of the genus. This has provided material for my primary objective, which is to reconstruct the evolutionary history of the species of *Atlapetes*. The secondary purpose of this paper is to assemble what information is available on all aspects of this little-known group. Knowledge of the living birds is so scant that the best that can be done is to establish a foundation for future studies.

The arrangement of species in Peters' *Check-list* (Paynter, 1970:190–206) was based on a preliminary study of the genus. The present treatment is essentially the same, except that two taxa (*virenticeps* and *atricapillus*) that were treated as races of *A. torquatus* are now considered to be allospecies of the *torquatus* superspecies. I have also somewhat revised the sequence of species to reflect my present concept of their relationship.

Information on the distribution and habits of the genus has been gathered from published material, from a limited amount of my own fieldwork (principally in Mexico, Colombia, and Ecuador) and from the examination of museum specimens (mainly the rarer species or those with limited ranges). The occurrences of all 24 species have been plotted on the accompanying distribution maps. Without doubt some existing records have not been found, particularly among the many specimens of the common species, but additional data from collections should not materially alter

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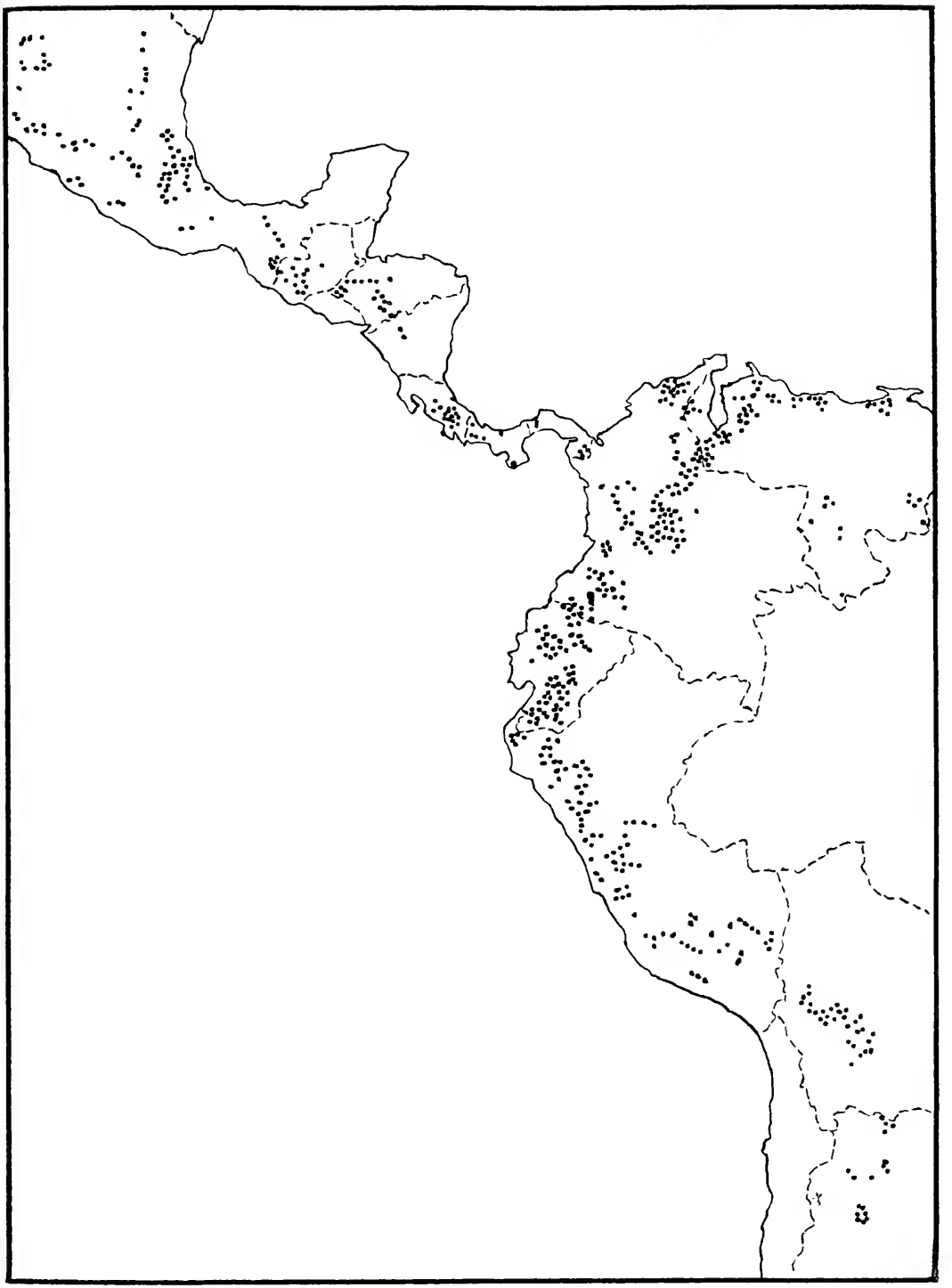
Figure 1. Distributional records for the genus *Atlapetes*.



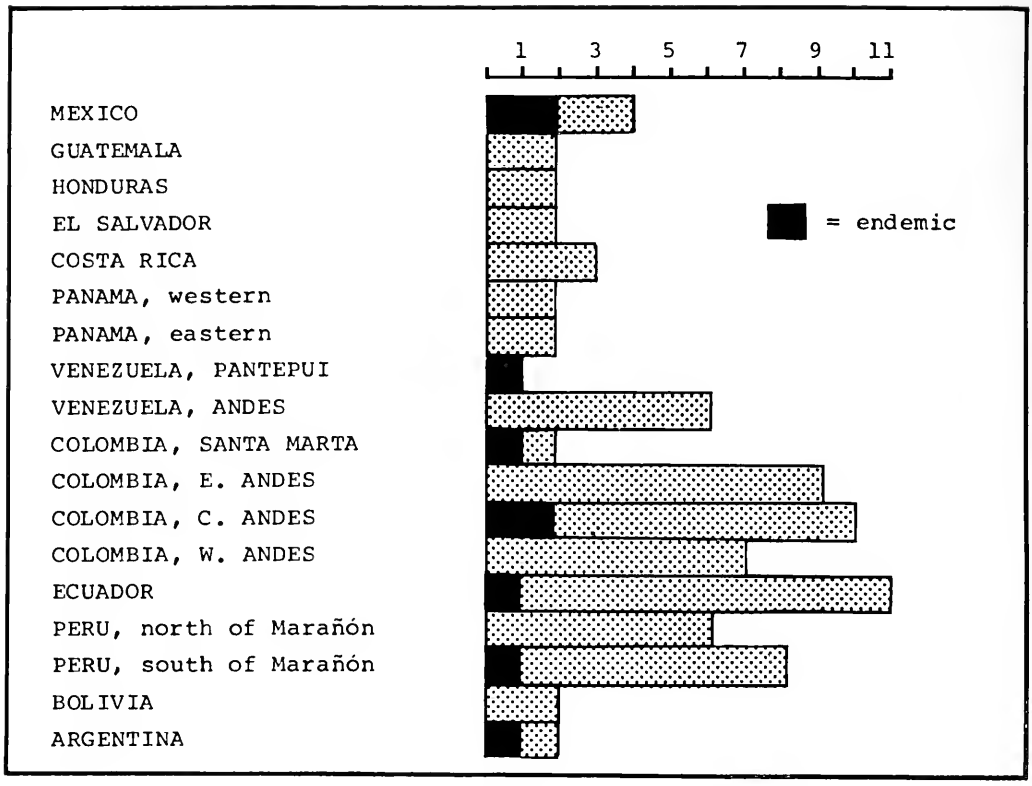


Figure 2. Geographical distribution of the 24 species of *Atlapetes*.

the depicted ranges of the more abundant forms. On the other hand, additional fieldwork should reveal more extensive ranges for at least some of the rarer species and for some of those whose distribution is now believed to be very restricted. Furthermore, one should not fail to appreciate that these maps show the distribution of each species from the time of its discovery until now. Therefore, the maps depict the maximum known ranges of the species. The enormous changes wrought on Neotropical vegetation during the past 100 years may have made the present-day ranges of some species more restricted than shown on the maps, while other forms may have flourished under these changes and occur outside the ranges as plotted.

To avoid repetition and cumbersome detail, I have not documented, by means of literature citations or reference to museum specimens, every locality plotted on the distribution maps or mentioned in the text. The compilation of Hellmayr (1938:384–423) was the primary source; records from more recent publications and from museum material are on file and available to future workers.

The *A. schistaceus* species-group, containing *A. schistaceus*, *nationi*, *leucopterus*, *albiceps*, *pallidiceps*, and *rufigenis*, was analysed in an earlier paper (Paynter, 1972) and will not be treated in detail again.

ACKNOWLEDGMENTS

I am grateful to the following institutions and individuals who have loaned specimens and answered queries regarding their collections: Dean Amadon of the American

Museum of Natural History; Melvin A. Traylor, Jr. and Emmet R. Blake of the Field Museum of Natural History; James Bond, Frank Gill, and R. M. de Schauensee of the Academy of Natural Sciences of Philadelphia; John W. Hardy, formerly of the Moore Collection at Occidental College; George H. Lowery, Jr. of the Museum of Zoology, Louisiana State University; Robert W. Storer of the Museum of Zoology, University of Michigan; Kenneth E. Stager of the Los Angeles County Museum; and Ernst Sutter of the Naturhistorisches Museum Basel.

For sharing with me their field experiences with a number of species of *Atlapetes* I thank Paul K. Donahue, John W. Fitzpatrick, John Terborgh, and Richard E. Webster.

The following have read drafts of the manuscript and offered me their comments, for which I thank them: J. W. Fitzpatrick, J. Haffer, E. Mayr, M. A. Traylor, Jr., and R. E. Webster.

Alison Pirie has prepared the maps, typed the manuscript, and done those innumerable but necessary chores that only the author can appreciate.

DISTRIBUTION, HABITS, AND MORPHOLOGY

Atlapetes albinucha superspecies

There are two allospecies in this superspecies, viz. *A. albinucha* and *A. pallidinucha*. Morphologically, they are only moderately similar, but it is their geographical and altitudinal distribution that leads me to believe that they share a common ancestor.

Atlapetes albinucha

Range.—*A. albinucha* is primarily a Middle American species of middle altitudes. It occurs from the Caribbean slope of central Mexico (Veracruz and Puebla), and the Pacific slope of southwestern Mexico (Chiapas), through the highlands of Central America to western Panama (Figs. 3, 4). It reappears in Colombia, where it occurs on all three ranges of the Andes except in the extreme south (Nariño) and in the Eastern Cordillera north of Cundinamarca.

This is a form principally of the humid subtropical and lower temperate zones. It has been found as low as 600 m in Mexico (Miller et al., 1957) and Costa Rica (Skutch, 1967) and up to 3,050 m in Guatemala (Land, 1970), but seems to occur most often from about 1,000 to 2,400 m. No latitudinal variation in altitudinal distribution is evident, in spite of Skutch's (1967) impression that the species occurs at higher elevations in southern Central America than in Mexico and Guatemala.

Habitat.—This atlapetes is found in thick vegetation near the edges of forests, in brushy woodland, and in dense second-growth, but not in the interior of heavy forest. It does not seem to occur regularly in pure stands of conifers, although Skutch (1967) once found it in low cypress. It is, however, common in mixed pine-broadleaf associations and in the low deciduous vegetation bordering pine forest (Dickey and van Rossem, 1938; Paynter, 1957; Skutch, 1967).

Habits.—*A. albinucha* is secretive and difficult to observe, as are all species of *Atlapetes*. Skutch (1967) reports that this species is even more shy than *A. brunneinucha* and *A. torquatus*. It generally occurs on or near the ground, but at times will go as high as 20 m (Slud, 1964); it roosts in trees (Skutch, 1967) and occasionally feeds there (Dickey and van Rossem, 1938; Skutch, 1967). Except when mated or accompanied by its young, the species is solitary (Skutch, 1967), sulking in the underbrush and seldom flying, and then only for short distances "in fluttering dips with [its] tail partially cocked" (Slud, 1964:282).

While in Honduras in April 1976, I saw this species for the first time in many years, and my attention was immediately drawn to the loud noise of the flapping wings, a characteristic I had first noticed in *A. nationi* (Paynter, 1972:303). One wonders whether the sound of the wingbeats, in-

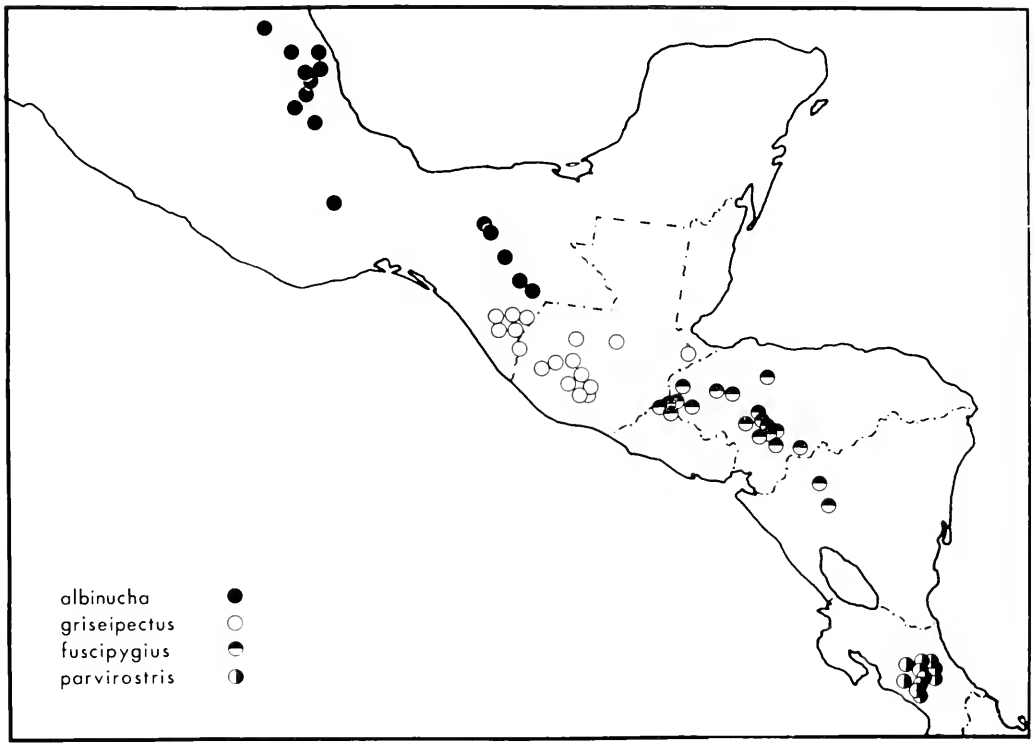


Figure 3. Northern races of *A. albinucha*.

stead of voice signals, is a means of keeping members of a family group together, or whether the noise is merely an aerodynamic byproduct with no special significance.

Skutch (1967) saw the species feeding on berries of *Fuchsia arborescens*. This seems to be the only specific record of its diet but because the bird is often heard foraging in the forest litter, it may be assumed to be omnivorous. Skutch (1967) surmises that the bird turns the litter with its bill, although apparently no one has yet seen this behavior.

A. albinucha builds a bulky, open nest in weeds close to or on the ground or in dense tangles a meter or two above it (Cherrie, 1892; Blake, 1956; Skutch, 1967). Two or three white or pale blue eggs are laid, and at least some white eggs turn pale blue when their contents are removed (Cherrie, 1892). The nests are frequently parasitized by *Molothrus aeneus* (Cherrie, 1892; Slud, 1964).

The breeding season is poorly known. In Middle America, it appears to be from April through June or even late July (Cherrie, 1892; Blake, 1958; Paynter, 1957; Skutch, 1967); in Colombia, March and April dates are recorded (Miller, 1963).

The call is said to be a faint high-pitched *tseep-tsee-eep* (Edwards, 1972) or *sst*, *sr*, or *tsr* (Slud, 1964), and its song is described as a weak "squeaky pully" sound with descending churrs (Slud, 1964) on a thin slow "O see me, O see, I'm weary, pity me" (Skutch, 1967).

Morphological variation.—There is minor sexual dimorphism in size, with the male's wing and tail averaging slightly longer and the bill minutely longer. No geographical variation in these characters is apparent.

There is very little variation in the color

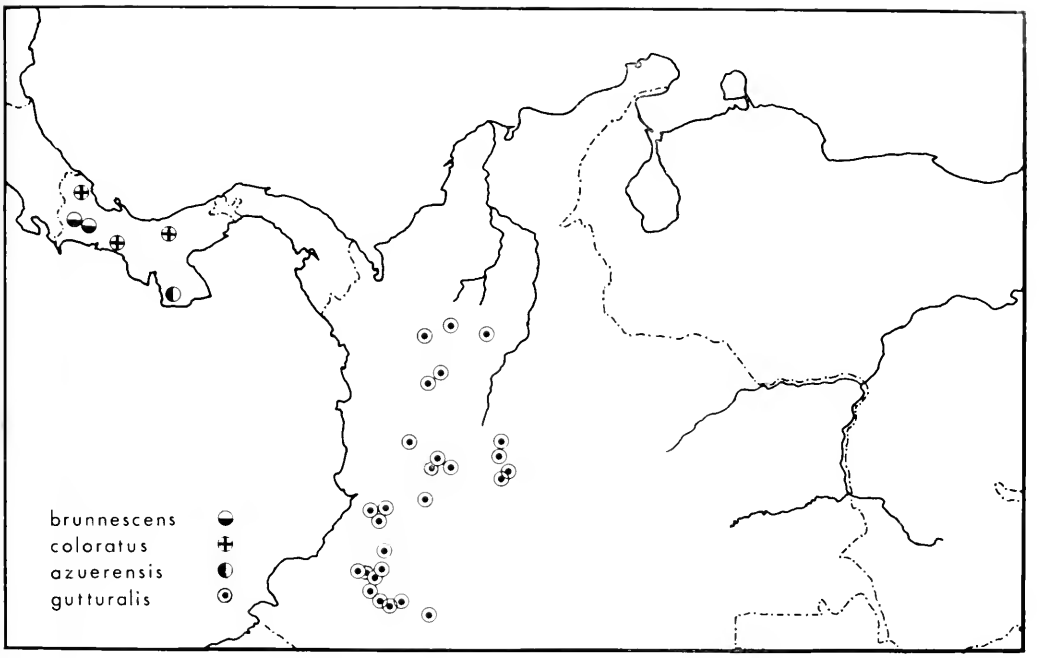


Figure 4. Southern races of *A. albinucha*.

of the populations from southernmost Mexico southward. The differences that do exist are clinal changes in the intensity of the yellow of the throat (and possibly in its extent), in the degree of brownish or blackish cast on the back, and in the grayness of the flanks. The variation in back color, however, may merely be a function of the age of museum skins. From southwestern Mexico to Colombia seven races have been recognized (Paynter, 1970) on the basis of color, but these are very weak races and at least two (*coloratus* and *azuerensis*) are almost certainly invalid. On the other hand, an eighth race, the population of eastern Mexico (nominate *albinucha*) is conspicuously different in that the entire underparts, rather than merely the throat, are yellow. There are no other differences.

A. a. albinucha was long treated as a distinct species. This is doubtless because it was originally described from Cartagena on the coast of Colombia (a most improbable locality for any form of *Atlapetes*), and, consequently it was thought to occur only in Mexico and Colombia. Paynter (1964) pointed out that the collector of the holotype had visited both Colombia and eastern Mexico on the same voyage, and because there has never been another specimen of the taxon collected in Colombia, it is logical to assume the provenance of the type was wrongly recorded. The type locality was, therefore, amended to the Caribbean slope of Mexico, and Colombia was deleted from the range of *albinucha*.

A. a. albinucha does not intergrade with *A. a. griseipectus* of southwestern Mexico, Guatemala, and El Salvador, although the two forms are known to occur less than 100 kilometers apart in southwestern Chiapas. It is possible that the valley of the Río Grijalva (= Río Grande) is sufficiently low here to act as a barrier. The river is at approximately 1,000 m in this region while the bird has been taken on both sides of the valley at 1,500 m or higher. It could be

argued that since the two taxa are so nearly parapatric they should be treated as allospecies. Nevertheless, although the entirely yellow underparts of *A. a. albinucha* are conspicuously different from the gray abdomen and yellow throat of *A. a. griseipectus* and the remaining races, this dissimilarity almost certainly is not indicative of great genetic difference. Furthermore, it would appear that intergradation is prevented by a geographical barrier (low valley) and is not the result of ecological exclusion. I find it difficult to conceive that interbreeding would not occur if the taxa were in contact and believe that racial treatment of *A. a. albinucha* best reflects its status.

Atlapetes pallidinucha

Range.—Occurs in the Eastern Andes of Colombia, barely extending into Venezuela, and through the Central Andes southward to central Ecuador (Fig. 5). In Ecuador this species seems to be almost absent on the western slope although there are many records from the eastern slope.

A. pallidinucha is principally a temperate region species, although on occasions it descends to the upper subtropical zone and ascends into the páramo zone. No other atlapetes is found in the páramo. It ranges from about 1,700 to 3,800 m, but most commonly from 2,000 to 3,100 m.

Habitat.—Olivares (1969) says the species is found in scrub and the remnants of forest. R. Webster (in litt.) noted the species sympatric with *A. rufinucha* in moist shrubbery and in forest edges in Ecuador. It is also sympatric with *A. torquatus* in similar habitats around Bogotá (Webster, in litt.; Donahue, verb. comm.).

Habits.—Although Olivares (1969) found *A. pallidinucha* to be the most abundant "fringillid" in Cundinamarca, and the number of records from elsewhere also suggest it is a common species, nothing seems to have been recorded of its habits or voice.

Morphological variation.—Females have slightly shorter wings and tails than the males.

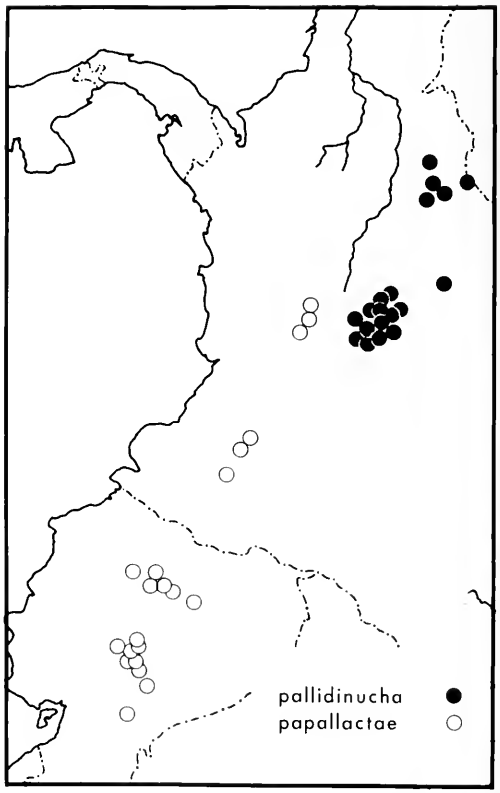


Figure 5. Distribution of *A. pallidinucha*.

Two races are recognized, the nominate form from the Eastern Cordillera of Colombia and adjacent Venezuela, and *A. p. papallactae*, a somewhat darker race, from the remainder of the range.

Atlapetes rufinucha superspecies

A. melanocephalus, which is endemic to the Sierra Nevada de Santa Marta, Colombia, seems to have been derived recently from nearby *A. rufinucha*. The two taxa are, therefore, treated as allospecies.

Atlapetes rufinucha

Range.—*A. rufinucha* has a wide but disjunct distribution in the Andes (Figs. 6, 7). It reaches its northernmost point in the

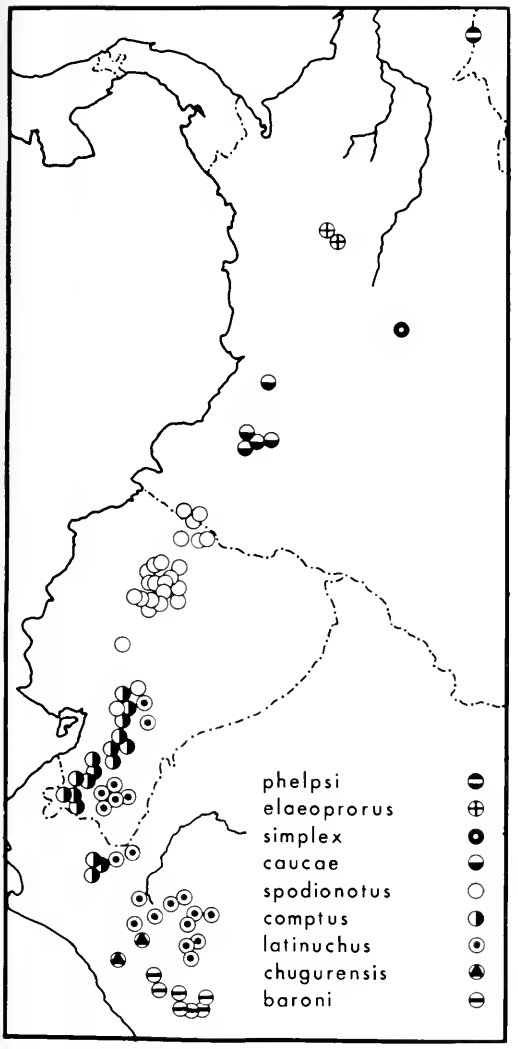


Figure 6. Northern races of *A. rufinucha*. *A. r. simplex* is recorded from "Bogotá" but probably comes from farther south in the Eastern Andes.

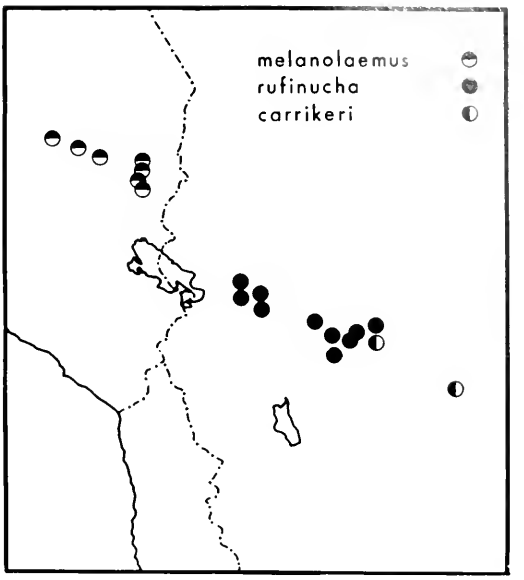


Figure 7. Southern races of *A. rufinucha*.

Sierra de Perijá along the Colombia-Venezuela border (*A. r. phelpsi*). It next occurs in three widely separated localities in central Colombia, viz., near the northern end of the Central Andes (*A. r. elaeoprorus*), possibly in the central or southern portion of the Eastern Cordillera although it is known only from native "Bogotá" specimens (*A. r. simplex*), and in south-central Colombia on the western slope of the Central Andes and on the eastern slope of the Western Andes (*A. r. caucae*).

The species then occurs, more or less continuously, from Nariño, southern Colombia, south on the Pacific slope and interandean plateau through Ecuador to northwestern Peru (*A. r. spodionotus* south to central Ecuador where it intergrades with *A. r. comptus* of farther south). On the Amazonian slope of Ecuador there are records from the north in the vicinity of Papallata, but for the next 250 kilometers the species is absent; it reappears in Azuay, as the race *latinuchus*, and is common from here southward well into Peru. It is almost certain that the distributional gap is real and not a collecting artifact; several areas within the gap have been well-collected (see Paynter and Traylor, 1977:138).

In northern Peru *A. r. comptus* occurs on the western slope in Piura and is replaced farther south by *A. r. chugurensis*. On the eastern slope *A. r. latinuchus* reaches Amazonas and *A. r. baroni* is in southern Cajamarca and Libertad, just entering the Pacific drainage west of the upper reaches of

the tributaries of the Marañón west of Cajamarca. The species is found no farther south on the western slope but recurs on the Amazonian slope in southern Peru (Fig. 7) in Cuzco and Puno (*A. r. melanolaemus*) continuing through eastern Bolivia (nominate *rufinucha*) to Santa Cruz (*A. r. carrikeri*). While the gap in distribution in eastern Ecuador seems genuine, the gap in eastern Peru is less certain, owing to the paucity of collections from that region.

It is a species of subtropical and, less often, temperate regions. It has a notably wide altitudinal distribution, ranging from as low as 600 m in Bolivia (nominate *rufinucha*; range 600–3,350 m) to as high as 3,700 m in southernmost Colombia (*A. r. spodionotus*; range 1,760–3,700 m). While there seems to be a tendency for the species to occur at generally higher elevations near the equator, the data are too scanty to confirm this. It is probable that the equatorial population will be found to average only a few hundred meters higher than those populations at the ends of the range.

Habitat.—Mainly in thick mesophytic scrub of moderate height, but also found in drier or wetter situations. It seems to be most common in moderately wet habitats, although near Gonzanamá, Loja, in southern Ecuador, I once observed it in small numbers in a rather dry subtropical area which was also occupied by *A. nationi simonsi* (Paynter, 1972:303) and there are numerous records of the species in the dry interandean region of northern Ecuador.

Habits.—I observed the species on several occasions in southern Ecuador and noted it to be somewhat less shy and more arboreal than most species of *Atlapetes*. At each observation, the species was from half a meter above the ground to as high as six meters. In the latter instance a small flock was feeding in bromeliads and other epiphytes. The species is notably active for an atlapetes. It moves about in flocks of up to five or six individuals, at least when not breeding. These observations confirm those of Taczanowski (1884) made in Peru.

Little is known of the breeding season. No breeding was noted in a long series of specimens collected from late July through October in southern Ecuador (MCZ collection). Chapman (1927) reported a male with much enlarged testes in Cajamarca, Peru on 20 April.

I have heard *A. rufinucha* give two calls. One is a single high-pitched thin *zeep*, which seems feeble for a bird of its size. This call appears to be given when a bird is concealed and relatively inactive. Presumably it is used to communicate with other members of the flock when they are scattered and out of sight. The second call is a series of louder, lower-pitched notes resembling the calls of squabbling flycatchers, such as *Myiozetetes similis*, although not nearly so loud. This call has been heard when a flock is actively moving about; several birds may call at once. No song has yet been noted.

Morphological variation.—Twelve races have been described. Most of them are extremely well-differentiated from one another. *A. rufinucha* is, morphologically, one of the most variable species within the genus, even exceeding highly variable *A. torquatus*.

No clear difference in size is evident between the various subspecies although the few measurements that are available for the southernmost race (*A. r. carrikeri*) suggest that its wing and tail may be slightly shorter than those of other subspecies. In contrast to size, however, some of the variations in color are striking.

In addition to more subtle or gradual differences in the color of the tail, venter, etc., there are six characters that vary markedly within the species (Table 1). No pattern of variation of a single character or correlation of one character with another appears to exist. For example, a sizable alar speculum is present in *elaeoprorus*, *caucae*, and *latinuchus*, but all three forms are widely separated from one another and not bridged by either *chugurensis* or *simplex*, the two forms with small (or inconsistently present)

TABLE 1. MAJOR MORPHOLOGICAL VARIATIONS IN *A. rufinucha*.

	Alar speculum	Yellow loral spot	Throat pattern	Forehead	Crown	Back
phelpsi	lacking	lacking	chin black, broad malar streaks	broad black	chestnut	gray; slight olivaceous tinge
elaeoprorus	large	small	faint malar streaks	as crown	chestnut	gray; strong olivaceous tinge
simplex	lacking or small	small to very small	faint malar streaks	as crown	dark chestnut	gray; olivaceous tinge
caucae	large	small	faint malar streaks	as crown	dark chestnut	slate
spodionotus	lacking	lacking	moderate malar streaks	as crown	chestnut	very dark gray
comptus	lacking	large	large malar streaks	as crown	rufous	dark gray
latinuchus	medium	lacking or very small	very faint malar streaks	as crown	chestnut	very dark slate
chugurensis	small	small	very faint malar streaks	as crown	light chestnut; paler on nape	dark slate
baroni	lacking	large	moderate malar streaks	as crown but with encroaching yellow	rufous; very pale nape	dark gray
melanolaemus	lacking	lacking	nearly all black	narrow black	chestnut	black
rufinucha	lacking	large	moderate malar streaks	narrow black	chestnut	black
carrikeri	lacking	lacking	moderate malar streaks	narrow black	chestnut	dark gray; olivaceous tinge

patches. Another example is the yellow loral spot that is present in *elaeoprorus*, *simplex*, *caucae*, *comptus*, *chugurensis*, *baroni*, and nominate *rufinucha*, all of which, with exception of *chugurensis* and *baroni*, are well separated from one another, either by distributional gaps or by the presence of taxa lacking the character. Even *melanolaemus* and *carrikeri*, which resemble one another more than they do any other races are not contiguous or even proximate, but are separated by nominate *rufinucha* which is more similar to the northern races.

Noteworthy, because it might appear to be a clue to evolutionary relationships, is the fact that *A. r. baroni* bears a very strong resemblance to *A. pallidinucha papallacta*. However, I do not think the two are related. The latter is larger and greener, ventrally, with the white of the nape more restricted, and its white feathers edged with black.

Atlapetes melanocephalus

Range.—Endemic to the Sierra Nevada de Santa Marta, Colombia (Fig. 8) where it occurs in the upper tropical and the subtropical zones at altitudes from 600 to 2,400 m.

Habitat.—Reported by Todd and Carriker (1922:525) to occur in "almost all kinds of conditions throughout its range—in the forest, scrub-growth, and even in low bushes in the open."

Habits.—In contrast to other members of the genus, *A. melanocephalus* is stated by Todd and Carriker (1922:525) to be "not at all shy"; they also note that it keeps near to the ground, moves about in pairs, and lays two white eggs in a domed nest low in a bush. No other atlapetes is yet known to build a domed nest and for that reason the observation is suspect.

Atlapetes tricolor superspecies

The three species comprising this superspecies are little-known but they are, morphologically, quite similar, except for the color of the pileum. I have no hesitancy in postulating a monophyletic origin for them.

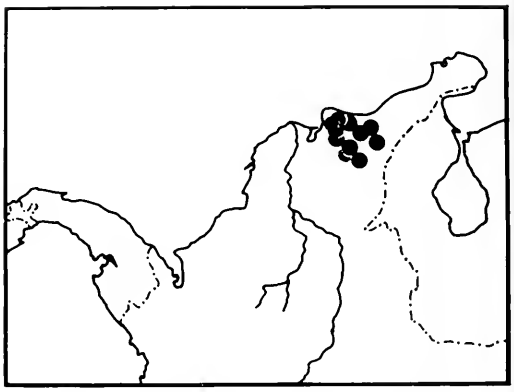


Figure 8. Distribution of *A. melanocephalus*.

Atlapetes flaviceps

Range.—Known from only two specimens collected over 65 years ago in the subtropical zone (2,050–2,160 m) at Toche and Río Toche in a deep valley on the Nevada de Tolima on the eastern slope of the Central Andes of Tolima, north-central Colombia (Fig. 9).

Habits.—Nothing is known of the living bird.

Atlapetes fuscoolivaceus

Range.—Most of the few known specimens were collected at least 50 years ago. These specimens and more recent observations indicate that the species occurs only in the subtropical zone, at altitudes from 1,500 to 2,400 m on the eastern side of the Central Andes in the upper Magdalena Valley, Huila, Colombia (Fig. 9).

Habitat.—The four localities from which the species is known (San Agustín, La Palma, La Candela, and Moscopán) are (were?) in the region of dense, tall, subtropical forest. I have seen one specimen bearing on its label the notation "forest."

Between 3–5 April 1977, I saw the species three times at San Agustín. I observed one bird in very thick, 2-meter high second-

growth; the second was in a hedgerow with dense brush and small trees up to 5 meters in height, and the third was in a row of 15-meter trees whose tops were only slightly above the level of a road cut into the side of the hill. Although in a region of high rainfall, the sites where the birds were noted were not particularly lush. There remain patches of fairly high forest around the archaeological sites of San Agustín, but no atlapetes were seen within the forest.

Habits.—Only single birds were seen at San Agustín. No calls were given, but once the beat of the wings, a characteristic noted in several other forms of *Atlapetes*, was heard as the bird flew off.

Two of the three birds seen were surprisingly high in the vegetation. One was two meters above the ground and easily seen against the horizon, but it quickly dropped down when approached. The other was in the crown of a 15-meter tree, where it was leisurely feeding on dark purple or black fruit about 5 mm in diameter in company with various tanagers, warblers, and a Swainson's thrush (*Catharus ustulatus*). The bird was watched for five minutes until it dropped down into shrubs and disappeared. The rich yellow underparts, and even the streaked throats, were conspicuous on these two birds whose behavior was in such contrast to the usual furtive demeanor of other atlapetes.

Chapman (1914) reported the type specimen, a male from San Agustín, had much enlarged gonads. The specimen probably was collected in April or May (see Chapman, 1917:45).

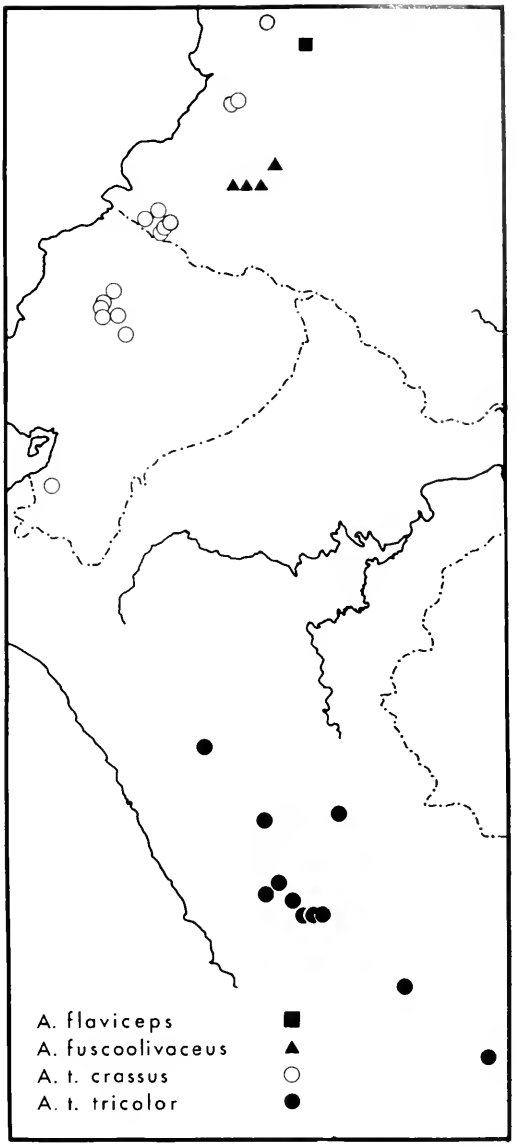


Figure 9. Distribution of *A. tricolor* superspecies.

Atlapetes tricolor

Range.—The species is known in Colombia on the eastern slope of the Western Andes from a single specimen (San Antonio, Valle) and on the western slope of the same range from several specimens taken from Caldas south to Nariño, with the majority of reports from the latter department. Although San Antonio is the type locality for the species (specimen taken by M. G. Palmer, 11 Dec. 1907, according to Bangs, 1908:61), the absence of any other record from the eastern slope of the Western Andes makes the record suspect. Furthermore, in a year spent at San Antonio in 1958–59, Miller (1963) failed to find this species. There is a cluster of records from

adjacent northwestern Ecuador and a single specimen, far to the south, from La Chonta, El Oro, in southwestern Ecuador, again on the western slope. The species is absent in northern Peru but reappears in central Peru on the eastern slope in San Martín and ranges south to Cuzco (Fig. 9).

The species seems to have a particularly wide altitudinal range in the northern portion of its distribution, occurring from somewhat below 300 m up to 2,000 m and from the moist upper tropical zone to the subtropics. In Peru, however, it seems not to occur much below 1,700 m and ranges up to at least 2,400 m which means that in this region it is a species of the subtropical and lower temperate zones.

Habitat.—Taczanowski (1884) quoted Jelski's observation that the bird frequented dense thickets. Terborgh (in litt.) has seen it in Peru in elfin forest which was barely shoulder high and in undergrowth bordering small clearings. R. Webster (in litt.) saw the species around Tandapi [= Manuel Cornejo Astorga; 00°25′S/78°48′W], Ecuador in dense thickets within the forest and on its edges.

Habits.—This atlapetes seems to be rare. It is little-known; Jelski observed it in Peru nearly a century ago (Taczanowski, 1884) and reported it to be a shy bird that moves about in small bands, but becomes more bold and more visible when courtship and song begin in February.

Richard Webster (in litt.) saw the species in June and September 1975 at three places on the slopes between Tandapi and above Santo Domingo de los Colorados, Ecuador. On 19 June at Tandapi he saw three pairs in an hour and a half; one pair was feeding a fledgling. Webster describes the species as being noisy, with a call of "a squeak followed by two chirps," many single squeaks, and a song of "*sweet* [slight pause], *churr.*" In early September, he noted the species in a mixed flock of *Synallaxis azara*, *Myiodynastes miniatus* and *M. chrysocephalus*, *Pipraeidea melanonota*, and *Tangara nigroviridis*. Jelski (Taczanowski, 1884) reported that flocks of *A. tricolor* are sometimes accompanied by one or two individuals of *A. schistaceus*.

Morphological variation.—The northern and southern populations, which are widely separated, have been recognized as racially distinct. The northern race (*crassus*) has a noticeably thicker and longer bill and is generally darker and more richly colored.

de Schauensee (1951) thought that there might be sufficient variation in the northern taxon to warrant naming additional races. This led Miller (1960) to believe *crassus* might even be a distinct species, but de Schauensee had based his speculations on the mistaken belief that the type of *crassus* has a brown crown, when it is instead merely a rich, tawny gold, not differing appreciably from other specimens from Colombia and Ecuador.

Atlapetes albofrenatus

Range.—Occurs in the Eastern Andes of Colombia from about Bogotá northward to Santander and in the Andes of Venezuela in Táchira and Mérida (Fig. 10). Its altitudinal range is from about 1,000 to 2,500 m, but it seems mainly to occur above 1,600 m, and thus most often inhabits the subtropical zone and less frequently the upper tropical zone.

Habitat.—I saw the species on two occasions, 1–2 April 1975, in thick subtropical cloud forest, as well as in more open scrub, a short distance north of Bucamaranga, Colombia, at altitudes of 2,000–2,400 m. The birds moved into somewhat exposed situations for brief periods but preferred dense tangles such as the masses of ferns and bamboo that cascade over road cuts. Phelps and Phelps, Jr. (1963) imply that in Venezuela it is a species of forests. Webster (in litt.) informs me that he saw this atlapetes at altitudes ranging from 2,100 to 2,300 m, in dry, thorny, low scrub, on the mountains above Villa de Leiva, Boyacá, Colombia. The species' tolerance of a wide range of vegetation is confirmed by Olivares who wrote (in litt.) that the bird "occurs in low

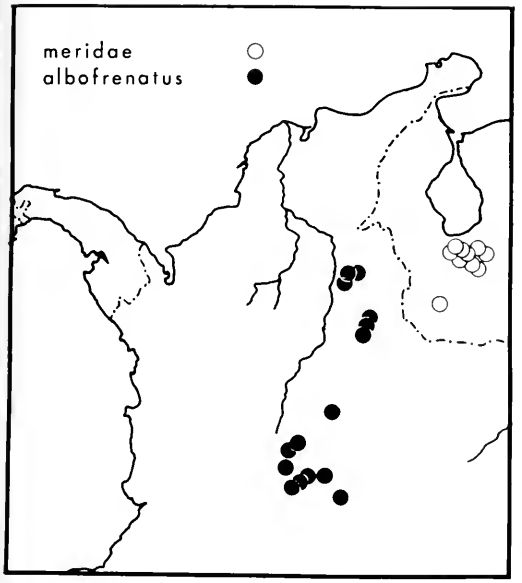


Figure 10. Distribution of *A. albofrenatus*.

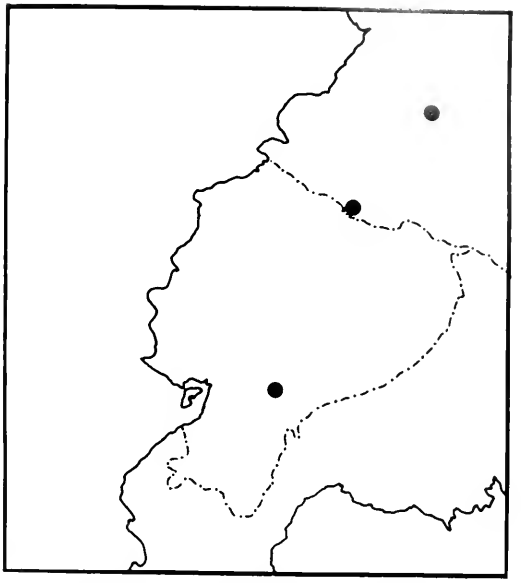


Figure 11. Distribution of *A. leucopis*.

forest which ranges from dry to moist, as well as in very humid subtropical forest."

Habits.—North of Bucamaranga the species was seen singly, paired, and in what appeared to be small family groups. They were mainly close to the ground but at times 10 m high in trees. In general their movements were, conspicuously, more rapid than those of *A. schistaceus*, which was also noted in the same area. The only call heard was a thin "zeep," characteristic of the genus. Webster (in litt.) also noted the species' propensity to range high in trees in the scrubby oaks bordering streams on the dry slopes above Villa de Leiva. Olivares (in litt.) has found the species in the lower branches of trees in the interior of the forest and says that an examination of several stomachs revealed mainly insects in some, while others contained more seeds. I observed a bird catch a small white moth.

Morphological variation.—Two well-differentiated races are recognized. The race *meridae*, of the Mérida Andes, which is separated from nominate *albofrenatus* of the Eastern Andes of northern Colombia by the valley of the Río Torbes, is markedly different in having reduced malar stripes, a forehead that is concolor with the crown instead of being black, and underparts that are entirely yellow rather than white on the throat and upper breast. No difference in size is apparent.

Atlapetes leucopis

Range.—Known with certainty from only three localities, apparently all in the subtropical zone (Fig. 11). The first is at La Plata (2,350 m) which is in a deep valley on the eastern slope at the southern end of the Central Andes and at the head of the Magdalena Valley in Huila, Colombia. The second is on Cerro Pax (alt. ?), which is on the eastern slope in Nariño, also in southern Colombia. The third is at Palmas (ca. 2,500 m), Azuay, on the eastern slope of southeastern Ecuador. The species was described from "Yanayaca" [= ? Yanayacu, *fide* Paynter and Traylor, 1977], a locality somewhere on the east slope of Ecuador.

Habitat.—Unknown.

Habits.—Only eight specimens are be-

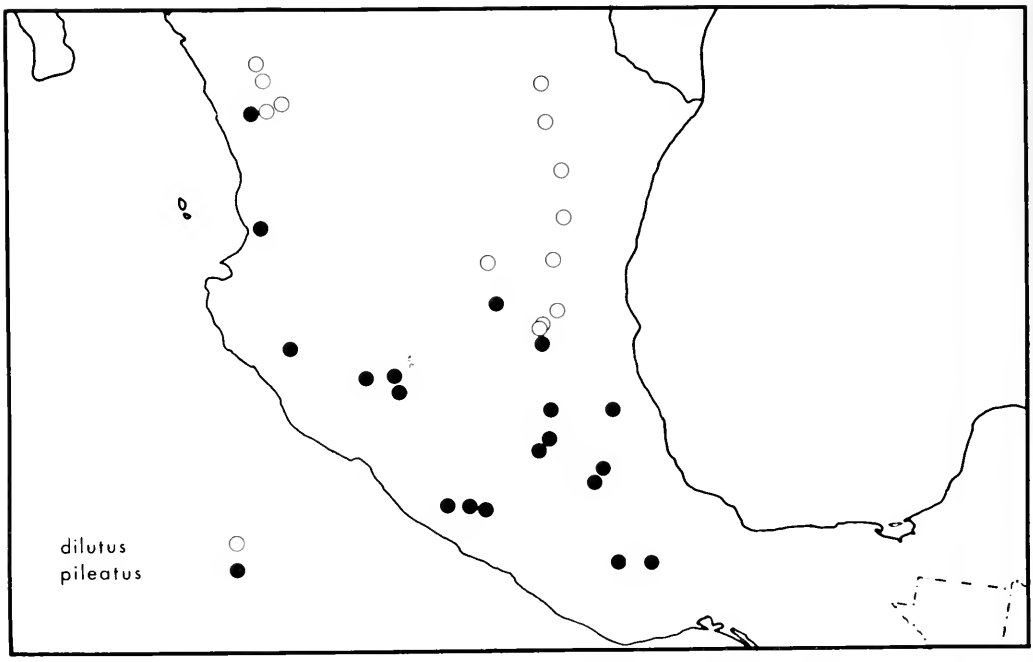


Figure 12. Distribution of *A. pileatus*.

lieved to exist (de Schauensee, 1951). It is among the least known of all atlapetes. There are no accounts of the living bird.

Morphological variation.—de Schauensee (1951) noted that a single bird from La Plata differed in color from four specimens from Cerro Pax, but there is no way to appraise the significance of this single observation.

Atlapetes pileatus

Range.—Distributed on the Mexican Plateau from Chihuahua and Tamaulipas south to Oaxaca (Fig. 12). Occurs from 900 to 3,500 m, but most commonly from 1,500 to 2,800 m, in the temperate zone.

Habitat.—Moderately moist undergrowth, usually at edges of pine, oak, or pine-oak forest.

Habits.—Little is known of the habits of this secretive bird, which does not seem to be particularly common anywhere.

It has been described as remaining within a few feet of the ground, moving rapidly, being "nervous," and jerking its tail (Edwards, 1972). Cody and Brown (1970) report that 90 percent of the bird's foraging is done on the outer branches of small trees and bushes and that, at least during the breeding season in Oaxaca (late March–early April), the species seems to be insectivorous. There is no further information on feeding habits.

The breeding season is prolonged, extending from late April in Oaxaca (Cody and Brown, 1970) to the end of August in San Luis Potosí (Miller et al., 1957).

The voice, which is "thin" and delicate, has been described by Edwards (1972:257) as "a high-pitched *wees*, a metallic *chip*, a *chip-chip-chip* chatter; and several song variations of a series of notes, such as *chip-ee-wee-wee-wee* or *chip-ee-r-r—r-r-r*, ascending in pitch to the first *wee* or *r-r* note."

Morphological variation.—The northern population (*A. p. dilutus*) is slightly smaller and generally paler than the nominate form.

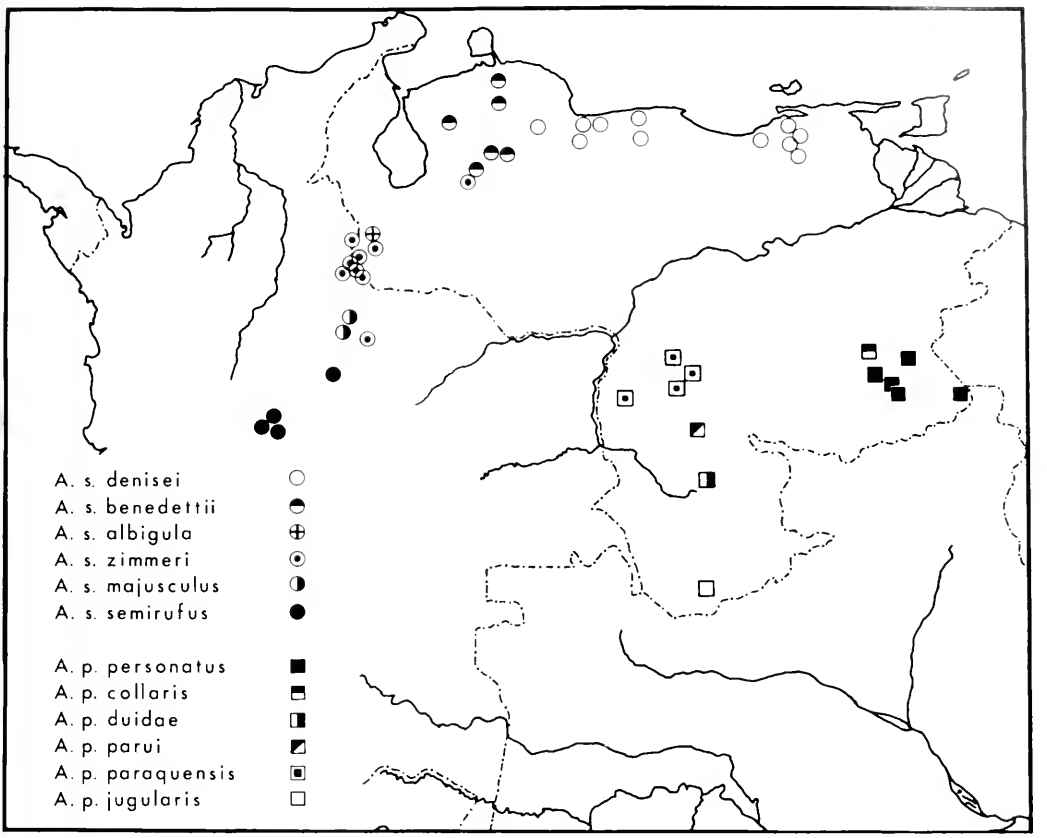


Figure 13. Distribution of *A. semirufus* and *A. personatus*.

These differences are easily distinguished but of no great magnitude. It is noteworthy that this is one of the few atlapetes exhibiting intraspecific variation in size.

Atlapetes fulviceps superspecies

This superspecies consists of three allospecies, viz. *semirufus*, *personatus*, and *fulviceps*. Although widely separated geographically (Figs. 13, 14), the three are morphologically very similar, with chestnut heads, yellow underparts, and green backs. Chapman, as long ago as 1931, postulated that *personatus* and *fulviceps* might be conspecific; this may be the eventual disposition of all three taxa, but I should like to know more of the living birds before taking this step.

Atlapetes semirufus

Range.—Occurs from the coastal cordillera of northern Venezuela southward through the mountains to Cundinamarca in the Eastern Andes of Colombia (Fig. 13). At the northeastern extremity of its range the species (*A. s. denisei*) descends to as low as 600 m in the upper tropical zone and ascends as high as 2,100 m in the subtropical zone. Elsewhere the species does not occur below 1,200 m and is in the subtropical zone, exclusively, except at its southernmost limits where in the vicinity of Choachi,

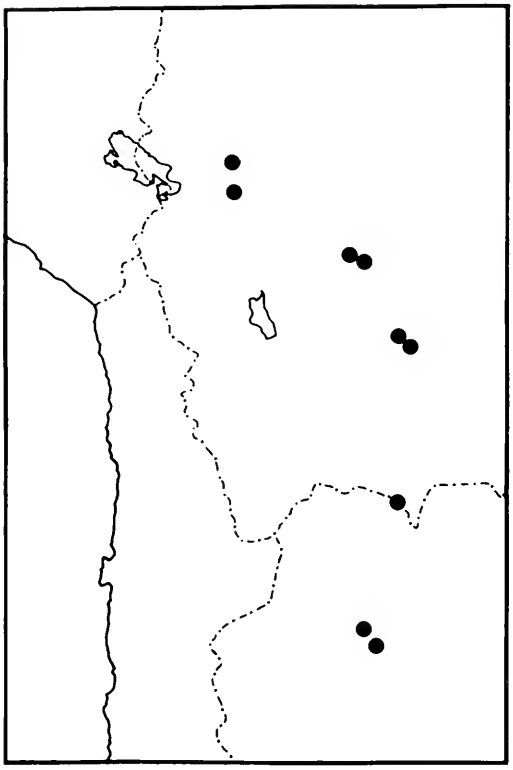


Figure 14. Distribution of *A. fulviceps*.

Cundinamarca it ranges between 3,000 and 3,500 m and is in the temperate/subpáramo zone (Olivares, 1969).

Habitat.—Schäfer and Phelps (1954) reported that *A. s. denisei* has a wide ecological range, occurring in moderately moist to somewhat xerophytic second-growth and in the weeds of low forest. Nothing seems to have been published concerning the habitat requirements of the other races. Because they appear to be confined to the subtropical zone (or temperate zone in the case of nominate *semirufus*), they probably have more restricted habitat preferences.

Habits.—Again, all we know about this species is contained in the brief account by Schäfer and Phelps (1954). They found that at Rancho Grande, Aragua, Venezuela the bird is of limited abundance, sedentary, and occurs in pairs or in groups of up to eight individuals. Breeding is from May to July.

Schäfer and Phelps' observations suggest that this species might benefit by the creation of second-growth through human activity; one might even imagine the bird becoming more abundant than it was in the past. However, Olivares (1969) observes that in Cundinamarca, it was common early in this century, and he implies that thereafter it was exceedingly rare until a number of birds were discovered at Une in 1967. Whether this is an indication of a recovery of the species as a whole or merely the fortuitous discovery of a restricted population is unknown.

Morphological variation.—Morphological variation is not great, although six races have been recognized. Geographical variation in the shade of green on the back and of the brownish rufous and yellow on the venter are the obvious differences. There may be variations in size, but if so, they are of no great magnitude as they are not detectable in the limited material available for study.

Atlapetes personatus

Range.—Found in scattered and isolated populations in the moist subtropical zone, between 1,000 and 2,500 m, on the table mountains ("tepuis") of southern Venezuela and adjacent Brazil (Fig. 13).

Habitat.—From the descriptions of Chapman (1931) it appears that the species occurs in the brushy wet forests on the summits of the tepuis.

Habits.—Nothing recorded.

Morphological variation.—The species has been divided into six subspecies, most of which are well-differentiated by color, pattern, or both. There are two basic color patterns, viz., that in which the bird's entire head, chin, throat, and chest are chestnut and that in which the chestnut does not extend to the throat and chest. Nominate *personatus* and *A. p. collaris* occur in southwestern Bolívar in relatively close proximity. They are of the latter type and the re-

maining four races, which lie to the west, have the former pattern. The two color patterns correspond to the two zoogeographical subdivisions of the "pantepui" region which lie on either side of the Río Caura (Mayr and Phelps, 1967). Variation within these two groupings is in the extent of the chestnut color or in the general intensity or shade of the colors. No significant differences in size have been noted.

Atlapetes fulviceps

Range.—This little-known species has been recorded from the eastern slopes of Bolivia (La Paz to Chuquisaca) and in northwestern Argentina, apparently from about 400 m to as high as 2,700 m (Fig. 14). Hellmayr (1938) states that this is a form of the subtropical zone, but if the altitudinal range is as wide as the collecting records seem to indicate, the species must reach the temperate, or at least subtemperate, zone. Apparently this is a very rare bird in Argentina.

Habitat and habits.—Nothing recorded.

Morphological variation.—No geographical variation in morphology has been detected.

Atlapetes citrinellus

Range.—The species, which is the southernmost representative of the genus, is restricted to the subtropical slopes of the Andes in Salta, Jujuy, and Tucumán, northwestern Argentina, from about 1,000 to 3,100 m (Fig. 15). I can find no substantiation for Olrog's (1963) inclusion of Catamarca within the range. There is one suspect record from northern Paraguay (Bertoni, 1924).

Habitat.—Dinelli (1918) reported that the species occurs in dense ferns in shady, humid ravines; Wetmore (1926) found it in thick weeds at the edge of a grove.

Habits.—Dinelli (1918) noted this bird on the ground in small groups and reported it is not timid and is readily lured into sight when its call is imitated (described as a faint "*tsip*" by Wetmore, 1926). This is a

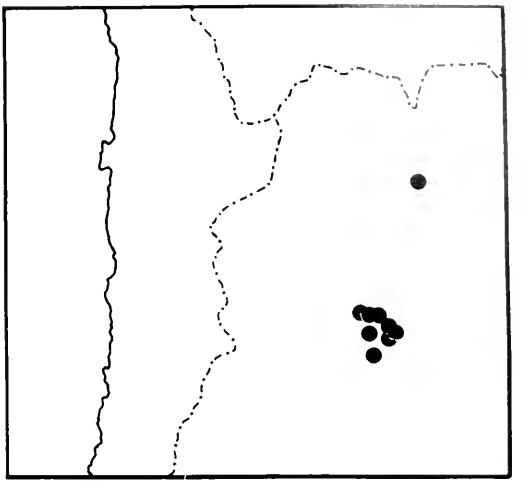


Figure 15. Distribution of *A. citrinellus*.

remarkably different type of behavior for an atlapetes. Dinelli (1918) describes the nest as being about 1½ m above the ground in a shrub. The egg is rosy-pink or white with dark brown or maroon spots and blotches, principally at the large end (Dinelli, 1918; Smyth, 1928). Smyth (1928) implies that a clutch consists of three eggs, and Pereyra (1951) also mentions a nest with three eggs; the latter was collected on 21 November, which is the only breeding date available for this little-known bird. Unfortunately, there appears to be no description of the nest itself.

Morphological variation.—There is no indication of either sexual or geographical differences in morphology.

Atlapetes brunneinucha

Range.—*A. brunneinucha* ranges from northwestern Mexico to southeastern Peru (Figs. 16, 17) and thus has the most extensive distribution of any atlapetes. It is a species of humid regions, generally occurring in the subtropical zone although at times it ranges well down into the tropical zone or up to the lower temperate zone, but only where the vegetation is lush and dense, such as in cloud forest.

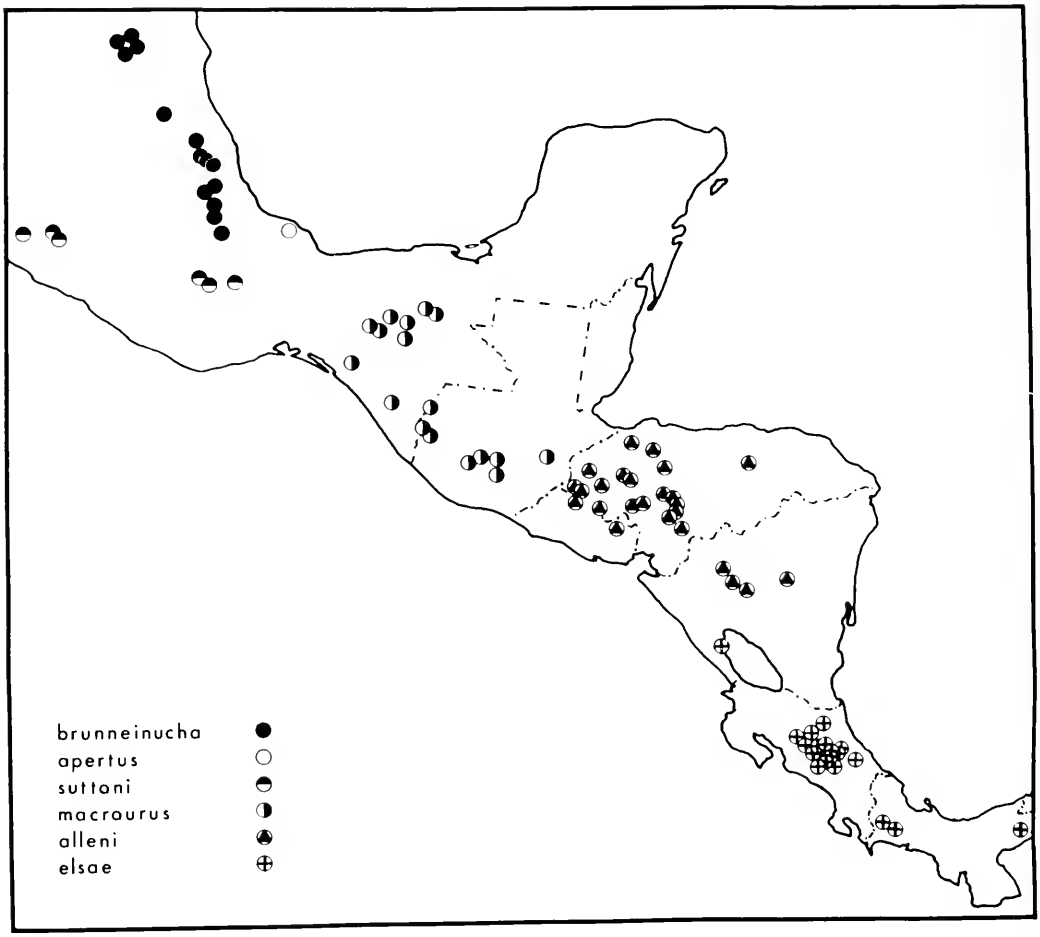


Figure 16. Northern races of *A. brunneinucha.*

At the northern end of its range, the species occurs as low as 200 m (nominate *brunneinucha* of eastern Mexico) and 350 m (*A. b. apertus* of the Sierra de Tuxtla, southern Veracruz) but on the other hand in the same area it also reaches an extreme altitude of 3,500 m (*A. b. suttoni* of Guerrero and Oaxaca).

This is doubtless the maximum altitudinal range for any species of atlapetes within a reasonably circumscribed area. In Central America, the species ranges from 550 to 3,400 m and in South America from 900 to 3,400 m. Throughout, however, it seems most abundant between roughly 1,000 and 2,000 m.

Because of the abundance of moist subtropical forest, the species is widely distributed with few major discontinuities. As with birds of similar requirements, the species is absent in most of Panama, but it occurs throughout the Andes south to northern Peru where, owing to the absence of moist forests, it drops out on the western slope but continues southward on the eastern side.

In the coastal range of northern Venezuela there is an interesting transposition of

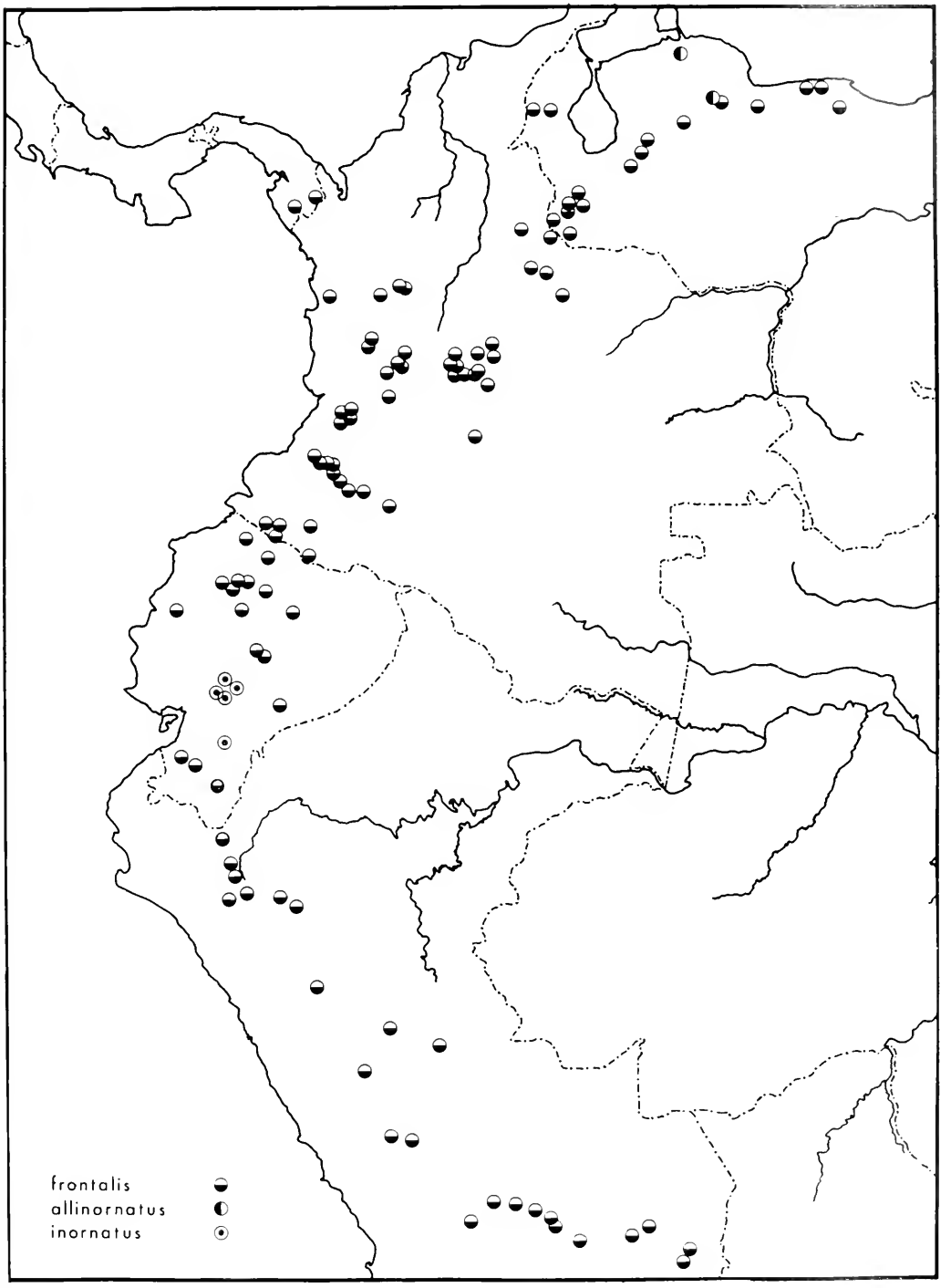


Figure 17. Southern races of *A. brunneinucha.*

relative altitudes between *A. b. frontalis* and *A. torquatus phaeopleurus*. Throughout their joint ranges, *A. torquatus* occupies the higher altitude and *A. brunneinucha* the lower, but at Rancho Grande, Aragua, *A. torquatus* ranges from 700 to 900 m while *A. brunneinucha* occurs from 900 to 2,400 m but its optimum range is between 1,600 and 2,000 m (Schäfer and Phelps, 1954).

Habitat.—The bird is an inhabitant of the interior of humid forest or of the thick undergrowth at the edges of the forest, but is still under taller trees. This propensity for the cover of forests has been remarked upon by Miller (1963) and Slud (1964). The latter also pointed out that in Costa Rica *A. gutturalis* [= *albinucha*] and *A. brunneinucha* have ranges in common but *A. albinucha* is a nonforest species. This dichotomy in habitats seems to hold throughout the ranges but no broadening of the habitat of *A. brunneinucha* seems to occur south of Colombia where *A. albinucha* is absent.

Habits.—The ecology of *A. brunneinucha* is fairly well known considering the difficulty in obtaining this information for other members of the genus. This is perhaps because, although a quiet species, it does not seem to be so shy as some other atlapetes.

As was noted long ago by Taczanowski (1884), and later by Carriker (1910), *A. brunneinucha* is usually found in pairs or in family groups. Schäfer and Phelps (1954) reported a maximum flock size of six.

A. brunneinucha is a bird of the dark forest floor, although Miller (1963) once found it 20 feet up in second-growth where it was feeding on seeds in company with tanagers. This, however, is probably an infrequent practice. Miller also comments on the bird's habit of kicking dry leaves in search of food, although Taczanowski (1884) reported that the species tossed the leaves with its beak. While in Venezuela and Peru, Fitzpatrick (in litt.) has seen the bird stir the litter with its feet but has never seen it use its bill for this purpose.

Miller (1963) believed that, in Colombia, breeding probably occurs throughout the year. Farther north, in Mexico and Central America, breeding seems to begin in March or as early as late February and extends to April or May or even June (Miller et al., 1957; Blake, 1958; Carriker, 1910). Breeding in Venezuela has been recorded from April to June (Schäfer and Phelps, 1954); in Peru the only breeding record known to me is that of a nest found in January (Taczanowski, 1884).

The nest, which is placed in shrubs or ferns close to the ground, is made of coarse leaves and lined with finer material (Taczanowski, 1884; Carriker, 1910). The clutch seems to consist of but one or two greenish or bluish white eggs (Sclater and Salvin, 1879; Carriker, 1910).

A. brunneinucha appears to be omnivorous (Olivares, 1969), although Taczanowski (1884) examined one specimen that had eaten only invertebrates.

As with all forms of *Atlapetes*, this species has an inconspicuous voice. Taczanowski (1884) described its call note as a series of rapid *tsit-tsit* notes and its song as reminiscent of the "voice" produced by a rubber doll; presumably this refers to "a series of high-pitched notes" (Peterson, 1973). Miller (1963), in spite of long-term observations in Colombia, never heard a song but described the infrequently produced alarm calls as chattering *tsip*'s and noted a mewing note suggesting that of *Pipilo chlorurus*.

Morphological variation.—Chapman (1923a) in his review of the genus *Buarremon* [= *Atlapetes*] pointed out that *A. brunneinucha* probably has a more extensive range than any other species of the subtropics and believed it exhibited no geographical morphological variation in spite of its wide distribution. Chapman did, however, recognize the taxon *inornatus* as being close to *brunneinucha* but, as was customary at that time, treated it as a full species rather than as a race of *A. brunneinucha*. Parkes (1954) in his review of the species detected more variation and rec-

ognized nine races, five of which he described. Subsequently two more races were named (Phillips, 1966; Rowley, 1968) bringing the total to 11 subspecies. There is no doubt that there is geographical variation within the species, but most of this variation is extremely subtle and probably not worth nomenclatural recognition.

There is some geographical variation in size (see Parkes, 1954, p. 134 for details). *A. b. frontalis*, the most widespread race of South America, has a slightly longer bill than all other populations, possibly excepting the races *inornatus* and *allinornatus* which are restricted to west-central Ecuador and central Venezuela, respectively. *A. b. suttoni* of Guerrero and Oaxaca and particularly *A. b. macrourus* of Chiapas and Guatemala have generally longer tails than the remaining populations. No geographical trend in these variations is evident.

Variations in color and patterns are also not pronounced. The extent of yellow bordering the chestnut crown varies somewhat, as does the amount of black on the forehead and what portion of the venter is occupied by either gray or white. Presumably these variations are of no biological significance. There is one characteristic, however, that does have a pattern, although its significance is also not apparent. This is the absence of a black breast band in three small, isolated or relatively isolated populations. One of the characteristic and striking markings of most taxa of *A. brunneinucha* is a black band that separates the white throat from the gray, or gray and white, chest and abdomen. In *A. b. apertus*, which is isolated in the Sierra de Tuxtla of Veracruz, Mexico, in *A. b. allinornatus* of the Sierra de San Luis and Sierra de Aroa in northwestern Venezuela, and in *A. b. inornatus* which occurs in a pocket on the western slopes of the Andes of central Ecuador, the black pectoral band is absent or rudimentary. The significance of this is unknown. The isolation of the three taxa leads one to suspect that the breast band is a species recognition character which might be unnecessary in small or isolated populations. *A. b. apertus* lacks congeners nearby but both *A. b. allinornatus* and *A. b. inornatus* do have congeners in the vicinity. Some relationship between the lack of a breast band and the presence of closely allied *A. torquatus* also suggests itself, but *A. torquatus*, while near *A. b. inornatus*, is absent from the range of *A. b. apertus* and *A. b. allinornatus*. Furthermore, in Mexico and most of Central America, where *A. torquatus* is absent, *A. brunneinucha* has a breast band. Especially baffling is the fact that the width of the band does not vary appreciably between the populations that do possess it, which is contrary to what one might expect if this is especially important in inter- or intraspecific recognition in large populations. Parkes (1954) has pointed out that there is no way to resolve whether the banded or unbanded condition is ancestral to the other.

Atlapetes torquatus superspecies

There are 15 allopatric taxa that are very similar morphologically, that certainly are closely related, and that doubtless are best treated as members of a superspecies, viz., *A. torquatus*. The *torquatus* superspecies seems to be comprised of the allospecies *virenticeps*, *atricapillus*, and *torquatus*, but to which allospecies certain of the 15 taxa belong is a vexing problem, a circumstance not met with elsewhere in the genus. The root of the problem is the rather major morphological variation between a number of the 15 taxa, further complicated by the fact that variation occurs within several characters, and these variations are seldom concordant.

Except for the absence of a chestnut pileum, most forms of *A. torquatus* superspecies are notably similar to *A. brunneinucha*, a species which has about as extensive a range but which exhibits little geographic variation.

Within the *A. torquatus* superspecies there is some minor geographical variation in overall size and in the relative lengths of the wing and tail, and somewhat greater

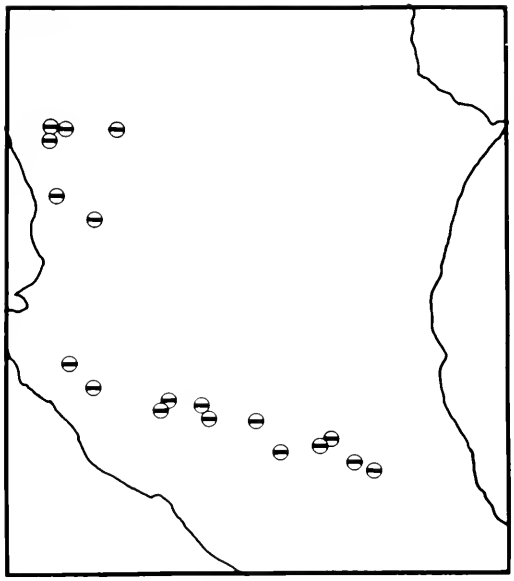


Figure 18. Distribution of *A. virenticeps*, of the Mexican plateau.

variation in the color of the venter, but larger differences occur in the pattern and color of the head, in the presence or absence of a pectoral band, and in the color and extent of the superciliary stripe. Two forms, *tacarcunae* and *atricapillus*, have markedly more robust bills.

There are three basic head types, viz. all black (*tacarcunae* and *atricapillus*), black with a medial stripe and superciliaries that are yellowish green (*virenticeps*), and black with a medial stripe and superciliaries that are either gray or white (the remaining 12 taxa). The geographical distribution of these three patterns is relatively simple (Fig. 20); *virenticeps* is in Mexico, *tacarcunae* and *atricapillus* are in eastern Panama and north-central Colombia, respectively, and the other forms occur, some in isolation and others contiguously, from Costa Rica to Argentina.

The distribution of taxa with or without breast bands is more complex (Fig. 20). The forms *virenticeps*, *costaricensis*, *tacarcunae*, *atricapillus*, *assimilis*, *nigrifrons*, and *borelli* lack the band; the remaining eight taxa have it. In geographical terms this means that forms without breast bands occur in the northern part of the range, except for the Sierra Nevada de Santa Marta and the Venezuelan Andes, and in the extreme south, while forms with pectoral bands occur in the southern range, with the exception of southern Bolivia and northwestern Argentina which are occupied by *borelli*, a taxon without a band.

The color of the superciliaries (ignoring minor departures from these generalizations, such as white lores with gray stripes) is either (a) black (= absent), which is the case in black-headed *tacarcunae* and *atricapillus*, or (b) yellowish-green, as in *virenticeps*, or (c) gray, as in *costaricensis*, *basilicus*, *perijanus*, *larensis*, *assimilis*, *nigrifrons* and *poliophrys*, or (d) white, which is the condition in the five taxa remaining. The geographical pattern (Fig. 20) is even more complex than that which exists for pectoral bands. Agreeing with the pattern of distribution found for head color are *virenticeps* and also *tacarcunae* and *atricapillus*. White eye stripes occur in the outliers at both ends of the Andes, viz. *phaeopleurus* and *phygas* in north and northeastern Venezuela and *torquatus*, *fimbriatus*, and *borelli* in Bolivia and northwestern Argentina. The remaining taxa have gray stripes. From this distribution one might suspect the existence of some sort of relationship between outlying populations and white superciliaries, but this is dispelled upon recalling that *basilicus* of the Sierra Nevada de Santa Marta and *costaricensis* of Costa Rica and westernmost Panama are both completely isolated but have gray eye stripes. There exists no correlation between breast band and the color of the superciliaries; all five forms with white superciliaries have breast bands but of the seven with gray eye stripes, four have pectoral bands and three do not.

Chapman (1923b) was the first to attempt to determine the interrelationships of this perplexing complex of birds. However, this work was done when "mutations" had attracted the fancy of biologists and when

many phenomena were attributed to "mutations." We now know, however, that these phenomena have been brought about by a variety of less radical causes. Chapman, dealing with 13 taxa (*perijanus* and *larensis* had not been named at that time), treated the thick-billed, black-headed forms *atricapillus* and *tacarcunae* as conspecific, placed into one species the three taxa with no pectoral bands and gray superciliaries (*assimilis*, *nigrifrons*, and *costaricensis*), and treated each of the remaining forms as a full species. The later action was doubtless because of the prevailing belief that even obviously related taxa were to be considered distinct species unless morphological intergradation could be demonstrated.

Hellmayr (1938) maintained the two black-headed forms as one species (*A. atricapillus*) but lumped all other taxa into a single species, *A. torquatus*. He even included *virenticeps* of Mexico and pointed out that it was a distinctive form that closely resembled the immature of the more southern taxa.

The next to deal with the problem were de Schauensee and Eisenmann (de Schauensee, 1966) who proposed a quite different treatment. This made Mexican *virenticeps* a full species and *costaricensis* a race of *A. atricapillus* on the premise that *tacarcunae* of eastern Panama is morphologically intermediate between *costaricensis* and nominate *atricapillus*. All other forms were placed in *A. torquatus*. On geographical grounds this treatment is appealing, because it avoids the problem of explaining the distant isolation of *costaricensis* from other members of its species. Nevertheless, I cannot appreciate how *tacarcunae* can be considered to be morphologically intermediate between *costaricensis* and *atricapillus*. On the contrary, I find *tacarcunae* difficult to distinguish from *atricapillus* and to be well-differentiated from *costaricensis*.

The last attempt to resolve the problem (Paynter, 1970) resulted in the lumping of all taxa into a single species (*torquatus*). The reasoning behind this was based partially on an uncritical acceptance of de Schauensee and Eisenmann's claim that *tacarcunae* was intermediate between *costaricensis* and *atricapillus* and partly on the belief that *atricapillus* and *assimilis* were geographically well separated. As explained above, *costaricensis* does not appear particularly close to *tacarcunae*. Also, since my earlier analysis, *atricapillus* and *assimilis* have been found (Olivares, 1969) within about 25 kilometers of one another, which is so close that it now seems a definite possibility that they may be parapatric.

I think that the best treatment is to recognize three allospecies within the superspecies *A. torquatus*. *A. virenticeps* is the first species. It appears to be a relict form which in its isolation has reverted to or (less likely) has retained some juvenile characteristics.

The second allospecies is *A. atricapillus*, with *tacarcunae* as a subspecies. Its completely dark head and thick bill, its relatively restricted range, its lower altitude (see below), and its apparent parapatry with *assimilis* suggest that this is an offshoot of the third allospecies, *A. torquatus*. *A. atricapillus* seems to have differentiated from its stem stock but has not progressed far enough to allow it to be ecologically compatible with *A. torquatus* or possibly to be reproductively isolated from it.

Into the third allospecies, *A. torquatus*, I place all the remaining taxa. The presence or absence of a breast band and the color of the superciliaries are probably characters that readily respond to isolation. They may have no adaptive significance, or they may be important in interspecific recognition. I am inclined to believe they are of little significance since, for example, one can see in the geographical continuum of *torquatus*, *fimbriatus*, and *borelli* successive stages in the loss of the pectoral band.

Atlapetes virenticeps

Range.—Occurs in the temperate zone of the southwestern portion of the Mexican Plateau and Pacific slope from Sinaloa south to Michoacán (Fig. 18). In the north

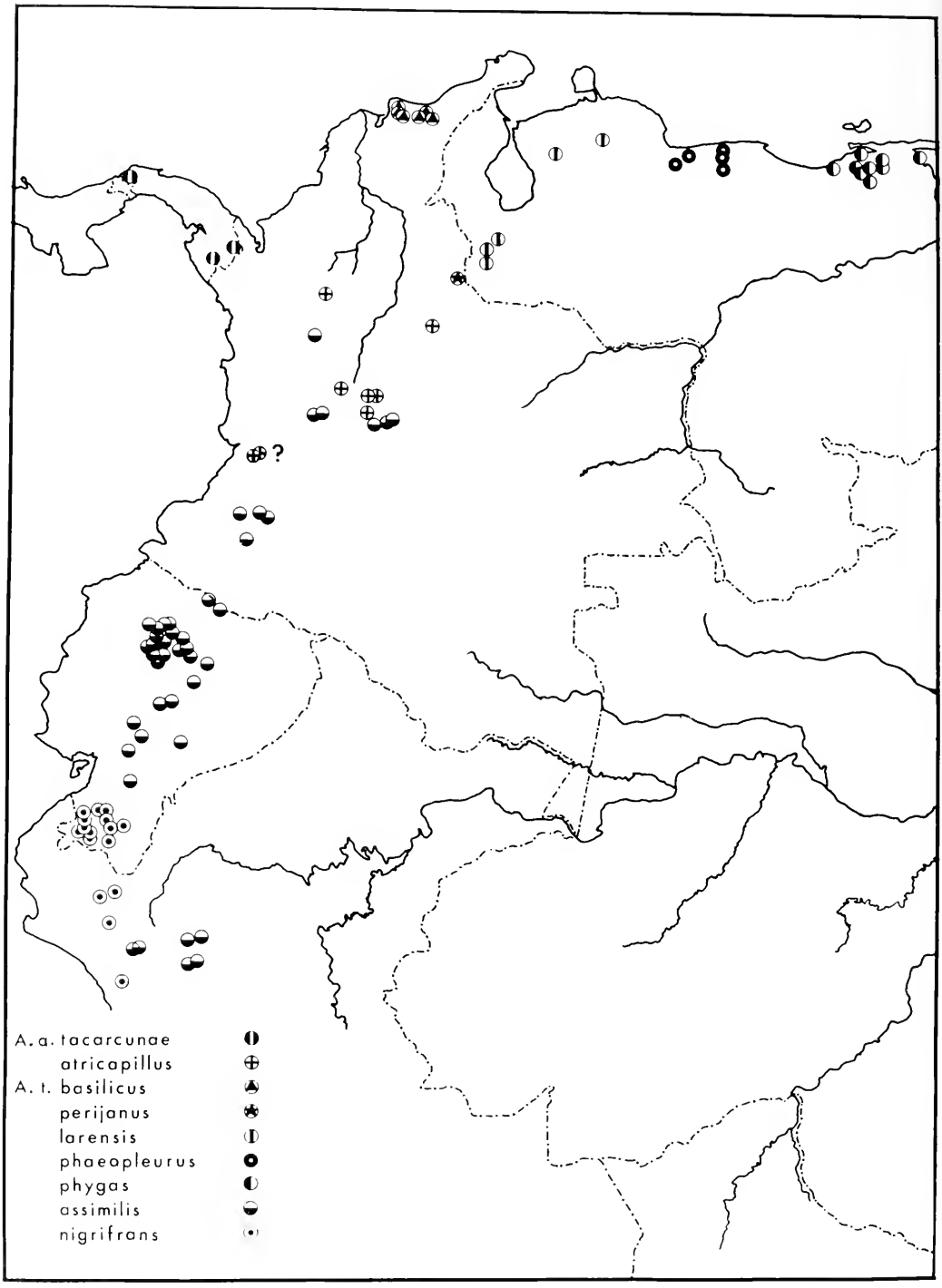


Figure 19. Distribution of *A. atricapillus* and the centrally located races of *A. torquatus*. Birds from the Western Andes have not been examined but are presumed to be referable to nominate *atricapillus*.

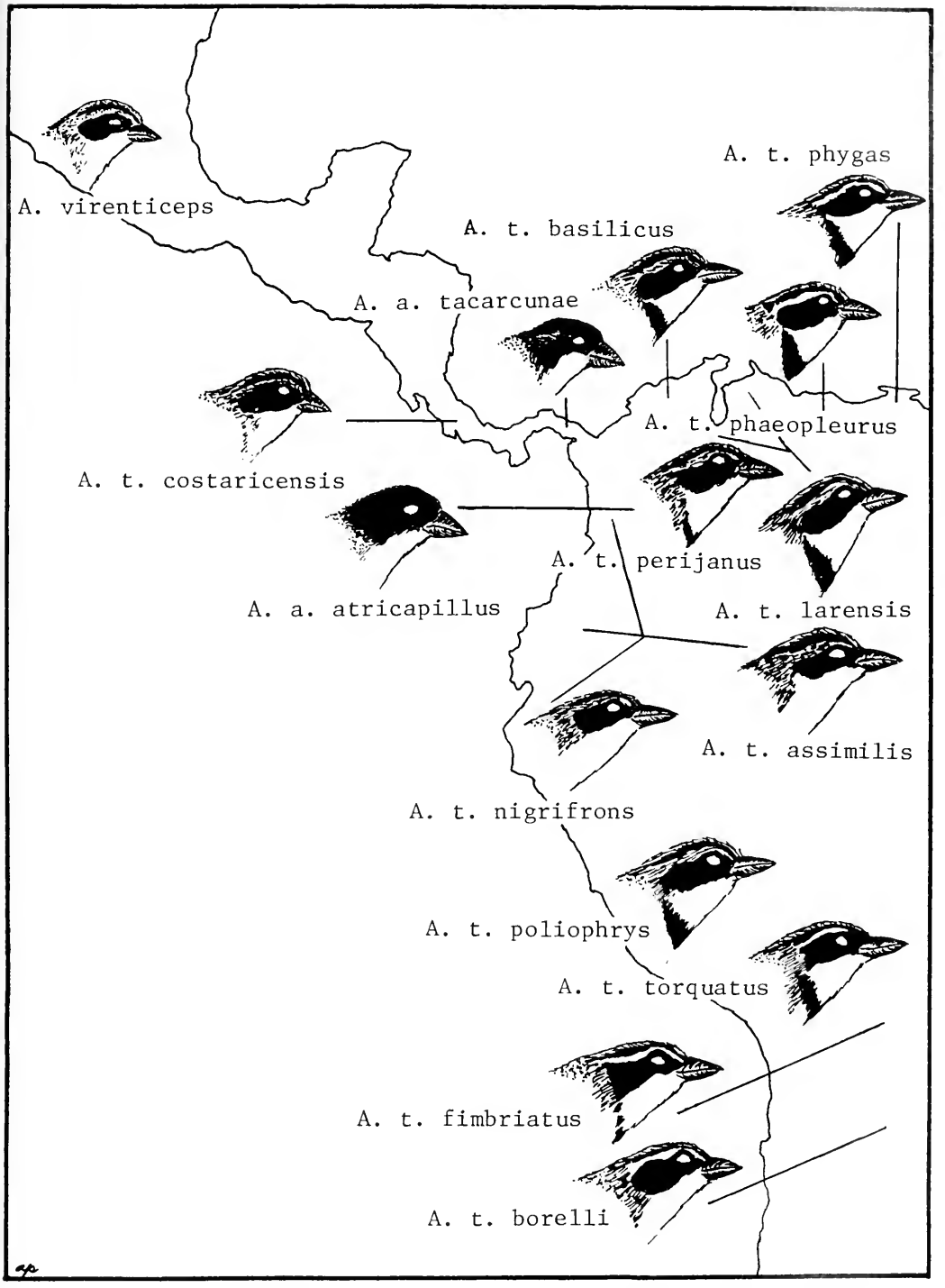


Figure 20. Color and pattern in the head and breast of the *A. torquatus* superspecies.

it ranges from about 1,100 to 1,900 m while farther south it occurs from about 2,000 to 3,600 m.

Habitat.—Thick undergrowth of oak or coniferous forests and at their edges (Edwards, 1972).

Habits.—Very little is known of the species. Schaldach (1963) reported behavior similar to that of towhees (*Pipilo*) in that the bird feeds in litter, turning over leaves in its search for food. Unfortunately, he was unable to determine whether the bill or feet were used for this activity.

Nesting and laying have been noticed in June and July (Miller et al., 1957; Schaldach, 1963). Schaldach (1963) believed the species to be doubled-brooded.

Morphological variation.—Some slight variation in color and size, perhaps not concordant with geography, seems to exist, but the pattern described by Moore (1938) and leading to his description of a northern race (*verecundus*) cannot be confirmed (Hardy and Webber, 1975).

Atlapetes atricapillus

Range.—The species has been found on a few of the higher mountains of eastern Panama (east of the Canal Zone) and in Colombia in the middle Magdalena Valley on the eastern slope of the Central Andes and western slope of the Eastern Andes, once at the northern end of the Central Andes (above Puerto Valdivia, Antioquia) and, recently (Hilty, 1977) on the Pacific slope of the Western Andes between Cali and Buenaventura (Fig. 19). In all there are records from only about a dozen specific localities, all of which are at an altitude from about 700 to 1,500 m. Although various authors (e.g., Chapman, 1923b; Hellmayr, 1938) have said this is a species of the subtropical zone, its altitudinal range would seem to indicate it is a form of the upper tropical zone, to which the species was also ascribed by de Schauensee (1951).

Habitat.—Dense undergrowth in wet forest and edges (Ridgely, 1976).

Habits.—A breeding pair was collected at La Vega, Cundinamarca (Olivares, 1969) but the date was not recorded. Nothing else has been published.

Morphological variation.—The birds of Panama were separated by Chapman (1923b) from the Colombian population on the basis of slight differences in color patterns and supposedly a longer, thicker bill. The only character I am able to recognize is a tendency for the western birds (*tacarcunae*) to have a barely distinguishable gray postocular line, in contrast to the solid black head of the nominate race.

The records of Hilty (1977) from the Western Andes have been tentatively assigned to the nominate form, although I have not examined the birds.

Atlapetes torquatus

Range.—The range of allospecies *A. torquatus* is the most extensive of the three taxa within the superspecies. *A. t. costaricensis*, an isolate (Fig. 21), is found in southwestern Costa Rica and presumably in adjacent Chiriquí, Panama (Ridgely, 1976), but I can find no specific record for the latter. It ranges from about 1,100 m down to 300 m in the subtropical zone and upper reaches of the tropical zone. The species next appears in the Sierra Nevada de Santa Marta, Colombia, again as an isolate (*A. t. basilicus*), where it occurs from the upper tropical zone to the temperate zone (600 to 2,800 m) (Fig. 19).

A. t. assimilis has a wide but curiously disjunct range (Fig. 19). In Colombia it occurs on both slopes of the Eastern Andes, but only in the vicinity of Bogotá. (The species seems to be absent south of here, but this may be because of the lack of observations and north of Bogotá it is absent for about 300 km, until it recurs, as other races near the Venezuelan border.) *A. t. assimilis* is found on both slopes of the mid-portion of the Central Andes from near Medellín to about the Quindío Pass and then reappears on the west slopes in the vicinity of Popayán. The race also occurs near Popayán on the eastern slopes of the

Western Andes. From the Colombia-Ecuador border south to south-central Ecuador, *A. t. assimilis* is found on both sides of the Andes but in southwestern Ecuador and northwestern Peru the race is replaced by another (*nigrifrons*). In southeastern Ecuador the species seems to be totally absent, only to appear again (as *assimilis*) on the eastern slope of northern Peru. Some of the patchiness of the distribution is doubtless because of spotty collecting, but the broad pattern is probably as outlined. *A. t. assimilis* has an altitudinal range from about 1,500 to 3,600 m and is typically found in the temperate zone.

The outlying Andes of northeastern Colombia and of Venezuela are occupied, from south to north, by four races (*perijanus*, *larensis*, *phaeopleurus*, and *phygas*). They occur at altitudes from about 700 to 1,800 m in the subtropical zone and, apparently on occasion (at least in *phaeopleurus*), in the upper tropical zone (Schäfer and Phelps, 1954; also see discussion under *A. brunneinucha*, p. 344).

On the slopes of southwestern Ecuador and northwestern Peru there occurs *A. t. nigrifrons* with an altitudinal range from 600 to 2,700 m, which is considerably wider than that of *A. t. assimilis*. It is found from the upper tropical zone up to the beginning of the temperate zone.

The species seems to be absent from northern (except the extreme north) to central Peru. It reappears on the eastern slopes of central Peru and ranges from here through eastern Bolivia to northwestern Argentina in a series of four subspecies (*poliophrys*, *torquatus*, *fimbriatus*, and *borelli*). These generally occur in the temperate and subtropical zones in the north but are restricted to the subtropical zone in the south (Fig. 22). There is, of course, a corresponding drop in altitudinal ranges from north to south (*poliophrys*, ca. 1,800–3,650 m; *torquatus*, ca. 2,000–3,100 m; *fimbriatus*, ca. 700–3,050 m; *borelli*, ca. 400–1,200 m).

From this survey, it is evident that the

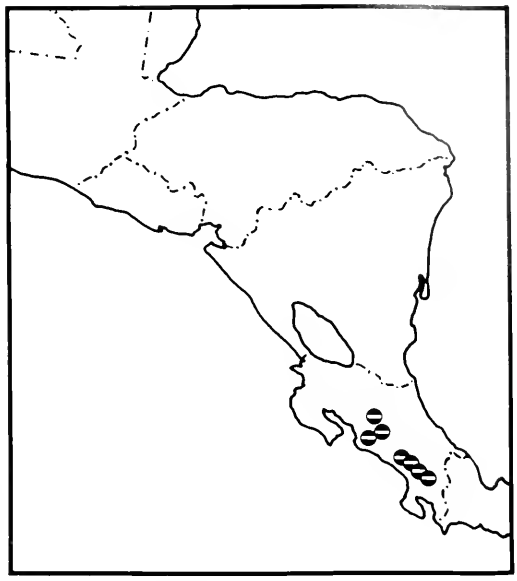


Figure 21. Distribution of *A. torquatus costaricensis*.

subspecies of *A. torquatus* generally frequent the subtropical zone and quite regularly reach the tropical zone. The one exception to this is *A. t. assimilis* which is strictly a temperate zone form.

Habitat.—*A. torquatus* is a species of thick second-growth and other dense vegetation in fairly humid areas. Slud (1964) pointed out that in Costa Rica *A. brunneinucha* prefers heavy growth within tall forest, and *A. gutturalis* [= *albinucha*] selects brush in the open, while *A. torquatus* occupies the bushy borders of forests, an intermediate habitat. My observations of these species in Mexico and Ecuador confirm this.

Habits.—Skutch (1954) has written a brief life history account of this species in Costa Rica.

A. torquatus frequently occurs alone or in pairs, in contrast to the somewhat more gregarious species such as *A. rufinucha*, *brunneinucha*, or *schistaceus*, although at times it does occur in moderate-size groups.

In Ecuador on several occasions, I have observed the species foraging on the ground and turning leaves with its bill. I have never

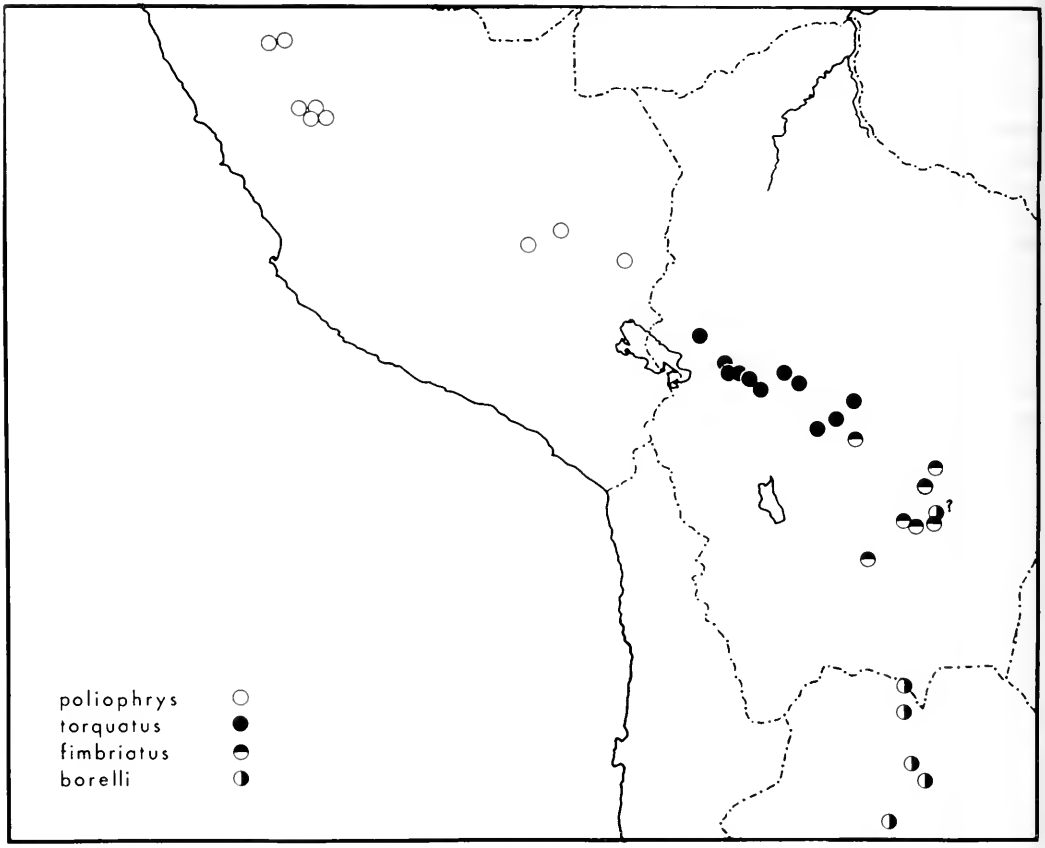


Figure 22. Southern races of *A. torquatus*.

seen it use its feet for this purpose. Skutch (1954) also commented on this use of the bill and noted that the bird feeds on small invertebrates and at times eats decaying leaves.

Its voice is thin and weak. In Ecuador, I noted a song as *zeep, which-a-whee*, with the tone dropping on the *a* and rising on the *whee*. Skutch (1954) notes that the song is given from, or close to, the ground and describes the male's song as being squealy, high-pitched, tuneless, and rapid; the female's song is similar but even weaker. I noted two calls in Ecuador, a high, metallic, *zeep* and a soft throaty *chuck*. Skutch (1954) described the call as similar to that given by a Cardinal (*Cardinalis cardinalis*). Slud (1964:383) described the voice as an insect-like trill or as the "tinkling of a fine silver chain"; he also noted a *cherrr* which must be what I described as *chuck*.

Breeding in Costa Rica is from February to September (Skutch, 1954), in northern Venezuela it is from May to July (Schäfer and Phelps, 1954). There is no information from farther south. Skutch (1954) noted that the species builds a bulky nest in dense tangles from one to six meters above the ground; two white or very pale blue eggs are laid and incubated only by the female.

Morphological variation.—As has been discussed above, morphological variation is extensive within *A. torquatus*. The pectoral band appears in *basilicus, perijanus, phaeopleurus, phygas, larensis, poliophrys, torquatus*, and *fimbriatus* (faint) and is absent

in *costaricensis*, *assimilis*, *nigrifrons*, and *borelli* (Fig. 20). Because of the irregular distribution of this character, one is led to suspect that the absence of the pectoral band might be related to sympatry or parapatry with *A. brunneinucha*, the species that *A. torquatus* so closely resembles morphologically, as well as in behavior and altitudinal distribution. However, no correlation can be found.

The color of the superciliary is about equally divided between races with gray stripes and races with white stripes (Fig. 20). The northeastern and southern Andean forms have white superciliaries; *nigrifrons* of southwestern Ecuador and northwestern Peru has a gray superciliary with white lores; the remaining taxa have gray superciliaries. This pattern does not seem to be related to the presence or absence of a pectoral band, or to be correlated with contact with other species of *Atlapetes*.

There is considerable, but not extreme, variation in the color of the flanks and undertail coverts (gray-green, brownish, etc.) and the extent to which this color suffuses the white belly. There are also minor variations in the width and length of the medial head stripe and in the color of the back and tail. No patterns in these variations are recognizable.

Males are slightly larger than females, but I am unable to detect any significant difference in size (wing, tail, culmen) between like sexes of the various races for which I have adequate series of specimens (*costaricensis*, *basilicus*, *assimilis*, and *nigrifrons*); measurements of specimens in the remaining races all fall within the ranges noted in the four large series. I conclude that if there are racial differences in size they are doubtless very small and certainly of no biological significance.

ORIGIN AND INTERRELATIONSHIPS OF THE TAXA

Introduction

It is now generally believed that the exceptional abundance of Neotropical avian species, as well as that of other animals and plants, is mainly the result of Pleistocene fluctuations in both temperature and precipitation. These climatic changes resulted in the expansion and contraction of forests and grasslands in the lowlands, as well as in vertical shifts in biomes in the mountains. These changes, in turn, led to the shrinkage and even disappearance of some populations during one phase of the cycle while during the alternate phase the populations expanded their ranges. Species differentiated to various degrees, disappeared, or remained unaltered during the restrictive phases while in the expansive stages they kept their identity, were absorbed by other populations, disappeared altogether, or even further differentiated. Over the course of several cycles of varying duration and intensity, the opportunities for permutations were enormous so that now, at best, only broad patterns of speciation or those of recent occurrence can be discerned.

This theory has been developed principally by Haffer (for a summary see Haffer, 1974), who has applied it mainly to the tropical lowland forest avifauna. He has postulated 16 major areas in Central and South America that served as forested refugia for birds during the most arid periods of the Pleistocene. Because climatic fluctuations affected the mountains as well as the lowlands, it was not surprising when in a study of the *Atlapetes schistaceus* species-group (Paynter, 1972) it became evident that some subtropical/temperate zone taxa seemed to have had their origin in close proximity to the lowland refugia postulated by Haffer. Furthermore, it was also apparent that the origin of certain other taxa could be explained only if there had existed additional refugia in pockets on the slopes of the mountains.

The present study completes the review of the genus *Atlapetes* and refines and expands some of the zoogeographic concepts developed earlier.

The 24 species that constitute *Atlapetes* fall into four natural subunits that reflect

the evolutionary history of the genus. The order in which these four subunits are treated below is intended to show a general trend from the most "typical" atlapetes to those that approach other emberizine genera. However, because a linear arrangement sometimes does not permit all related taxa to be near one another, and because even the limits of emberizine genera are fuzzy, only the grouping of the species within the units should be considered as significant.

Atlapetes albinucha superspecies

Two allospecies comprise this superspecies, *A. albinucha* of Mexico, Central America, and Colombia and *A. pallidinucha* of Colombia and Ecuador.

Atlapetes albinucha

A. albinucha has eight races (Figs. 3, 4). Two (*coloratus* and *azuerensis*) have been described from Chiriquí and Veraguas, western Panama, and are almost certainly inseparable from *brunnescens*, also from western Panama. Five of the remaining races (*griseipectus*, *fuscipygius*, *parvirostris*, *brunnescens*, and *gutturalis*), ranging from southwestern Mexico to Colombia, differ only slightly from one another, while nominate *albinucha* of eastern Mexico is distinctly different, having a completely yellow venter rather than only a yellow throat. Although distinctive, this is believed to represent a small genetic difference (see p. 330).

The sharp, albeit relatively minor, discontinuity in phenotype displayed by *A. a. albinucha*, in contrast to the very minor and intergrading morphological variation in the remaining races, even including *A. a. gutturalis* of Colombia which is isolated from the Middle American populations by a sizable gap in eastern Panama, is provocative. This suggests that *A. a. albinucha* may have been isolated from the southwestern Mexico and Central American populations for considerable time, or at least more completely. And, conversely, it could indicate that the isolation of *A. a. gutturalis* may have been more recent, or less complete.

Climatic changes in the Pleistocene might account for this pattern. During the height of a glacial period, when the vegetation zones were lower, a population may have been isolated in the lowlands of eastern Mexico, possibly only north of the Isthmus of Tehuantepec but more probably spanning the Isthmus of Tehuantepec to northeastern Chiapas as well; the latter distribution would explain the present occurrence of morphologically similar populations on either side of the Tehuantepec lowlands (see Fig. 3). In isolation the northern population either differentiated into distinctive nominate *A. albinucha* or, more probably, simply did not change appreciably, thereby retaining its similarity to *A. pallidinucha*, its South American allospecies (see p. 335).

On the other hand, during the Pleistocene glaciations the low mountains of eastern Panama, which now lack subtropical vegetation, except for a limited area on Cerro Tacarcuna, and which are not now occupied by this species, probably had a suitable habitat. The presence of subtropical vegetation provide a series of stepping stones facilitating exchange between the Central America and Colombian populations. The populations of Central America proper were at lower elevations than today and probably were more nearly continguous with one another than they are now. This would account for their morphological similarity which also suggests that their present isolation is fairly recent. In addition, the Colombian population doubtless was farther west than now, owing to its presence on the "discontinuous mountain bridge" (Haffer, 1974:15) which connected the Western Andes and the mountains of Darién, across what is now the lower Río Atrato valley.

With the amelioration of the climate, the low mountains of eastern Panama lost their

subtropical vegetation and became unsuitable for the species. The Atrato "mountain bridge" also disappeared and the species retreated to the Andes. These events resulted in a wide distributional breach. Meanwhile, the subtropical zone moved higher in the mountains of Chiapas. This shift allowed the eastern and western populations to move closer together. This teeter-totter effect would, therefore, bring the northern isolate closer to the main body of the species while at the same time it would progressively increase the isolation of the southernmost population. This seems to be a reasonable explanation for the unusual pattern of morphological variation now seen.

ATLAPETES PALLIDINUCHA

A. pallidinucha generally resembles *A. a. albinucha.* The principal difference is the presence in *A. pallidinucha* of yellow lores, an orange wash on the anterior part of the central crown stripe, and, ventrally, faint green striations, suggesting the plumage of immature birds. The more southern forms of *A. albinucha* differ more markedly in that the yellow of the venter is confined to the throat.

A. pallidinucha occurs in the Eastern and Central Andes of Colombia and south to central Ecuador, and just reaches Venezuela (Fig. 5). In South America *A. albinucha* is found on all three ranges of the Colombian Andes, but in the Eastern Andes it is not north of Cundinamarca (Fig. 4). (Neither species has been recorded in the Eastern Andes south of the vicinity of Bogotá, but this seems merely to be because of the absence of collectors; the southern portion of the Eastern Andes are very poorly known; see Fig. 1.) The two species have, therefore, overlapping ranges in the Central Andes and in the midportion of the Eastern Andes. They are, however, altitudinally segregated with *A. pallidinucha* in the temperate zone, or higher, and *A. albinucha* in the subtropics.

There are approximately 50 sites within the zone of overlap where either one or the other of the species has been recorded. At only one site have both been reported. This is at La Aguadita, Cundinamarca, at an altitude of about 2,000 m (Olivares, 1969). This location is on the steep western slope of the Eastern Andes. Altitudes exceeding 3,400 m are only a short distance from La Aguadita. Presumably the two species are segregated altitudinally within the region but were imprecisely cited as having come from the same place.

INTERRELATIONSHIPS

The morphological similarity and altitudinal segregation of these two species suggests that they are related but ecologically incompatible. I consider them, therefore, to be members of a superspecies. The resemblance of the Mexican race of *A. albinucha* to *A. pallidinucha* of South America, or conversely the greater dissimilarity between the two species where they are altitudinally parapatric is suggestive. It may indicate that nominate *A. albinucha*, the Mexican race, is a little-changed offshoot from the same stem giving rise to *A. pallidinucha.* The other races of *A. albinucha*, or at least the stock for these, may have arisen while in proximity to *A. pallidinucha* and, therefore, diverged more than did nominate *A. albinucha* which was far to the north.

I have postulated above (p. 354) that the race of *A. albinucha* in Colombia (*A. a. gutturalis*), although well-isolated from the Central American populations of the species, is morphologically similar to these populations because this isolation is relatively recent. On the other hand, the Mexican race, *A. a. albinucha*, which is narrowly isolated from another population, is morphologically distinct because it is an older isolate that only recently has come in near contact with another population.

The postulated origin of the races of *A.*

albinucha and the origin of the allospecies *A. albinucha* and *A. pallidinucha* can be reconciled as follows. Presumably the species had their origin during a dry period in the Quaternary when an ancestral population became divided between two (or more) forest refugia. Probably *A. pallidinucha* formed in a refuge at the head of the Central and Western Andes (the Caribbean Colombian or Nechí Refuge of Haffer, 1974). The other allospecies, *A. albinucha*, may have been formed in isolation in a refuge on the Pacific side of the Western Andes (Pacific Colombian, or Chocó, Refuge) or, even more probable, in Central America in the Caribbean Central American or in the Caribbean Costa Rican Refuge (all refuge names from Haffer, 1974), or possibly in a refuge in Mexico north of the Isthmus of Tehuantepec. Later with the amelioration of the climate the two forms moved out from their centers of origin and came into contact. They had not diverged much from one another, either morphologically or ecologically, but they were sufficiently differentiated so that they were reproductively isolated and retained their identity. There may have been parapatry, or partial sympatry, or, more likely, some altitudinal overlap with *A. pallidinucha* the higher taxon. In any case this may have resulted in further divergence between the two similar species. *A. pallidinucha* may have been prevented from ranging into Central America because of the lack of temperate forest on the low mountains. During the next phase of the climate cycle *A. pallidinucha* may have withdrawn to the Nechí Refuge, or even to the Napo Refuge of eastern Ecuador, and another population was isolated in the Eastern Cordillera of Colombia; here the two existing races differentiated. Meanwhile, *A. albinucha* pulled back to two or more refugia, the northern one (probably in Mexico) holding the population which had been farthest from the zone of contact with *A. pallidinucha* and a southern refuge in Central America or northwestern Colombia, with a population which had been in contact with *A. pallidinucha*. This isolation allowed *A. albinucha* in its southern refuge to consolidate morphological and ecological divergencies brought about because of competition with *A. pallidinucha*, while the population in the northern refuge remained relatively stable in appearance, having been far away from the zone of contact with *A. pallidinucha*. During the next warm-moist period (the current one?) the population in the northern refuge (*A. a. albinucha*) moved higher in the mountains of southeastern Mexico, but was unable to cross the low Río Grijalva valley in Chiapas. The population in the Central American refuge spread throughout much of Central America and across into Colombia, later abandoning eastern Panama as the climate warmed and subtropical vegetation disappeared. Because of its attenuated range, clinal morphological changes have developed, resulting in the weakly differentiated races now recognized.

Although *A. pallidinucha papallacta* is remarkably similar to *A. rufinucha baroni* (see p. 334), I do not believe they are particularly closely related.

Atlapetes rufinucha species-group

The 11 species within this group are presumed to have had a common origin, although all do not seem to have split off at the same time. With only one or two exceptions, and these are based on doubtful records, none of the species is sympatric with any other member of the species-group, which, of course, lends credence to the belief that this is a natural assemblage of closely related taxa.

Atlapetes rufinucha superspecies

This superspecies is composed of *A. rufinucha*, a widespread polytypic species, and *A. melanocephalus*, a monotypic endemic of the Sierra Nevada de Santa Marta, the isolated massif in northern Colombia.

ATLAPETES RUFINUCHA

A. rufinucha is the most widespread of the 11 species within the species-group, occurring from westernmost Venezuela to Bolivia. There are a number of gaps in its range (Figs. 6, 7). While it is present in the Sierra de Perijá, a northward extension of the Eastern Andes on the Venezuela-Colombia border, it has not been found in the Eastern Andes except for a few dubious records from "Bogotá" (*A. r. simplex*, known only from native "Bogotá" specimens). It does not occur on the eastern slope of the Central Andes, but is found at the northern tip of this range, as well as on its western slope at the head of the Cauca valley. In the Western Andes, it is found only on the eastern slope, also far up the Cauca valley.

In Ecuador it is distributed on both slopes, but is absent for about 250 km in the central portion of the eastern slope. The species ranges a short distance down the western slope of northern Peru and in the east reaches central Peru. There is then a gap before the species recurs in southern Peru and eastern Bolivia.

Its ecological requirements are broad. It occurs in the subtropics, sometimes in the temperate zone, and in dry to moderately moist vegetation. Its altitudinal range is also notably extensive, covering about 3,000 m. In general this is a common and abundant bird, as one would expect from its tolerance of a wide range of ecological conditions. Unfortunately, the versatility of the species makes it impossible to speculate on its place of origin. The gaps in its distribution, however, are valuable clues in reconstructing the history of other species in this species-group (see *A. tricolor* superspecies, *A. albofrenatus*, and *A. leucopis*).

ATLAPETES MELANOCEPHALUS

A. melanocephalus is the second allospecies of the *rufinucha* superspecies. It is one of the two atlapetes in the isolated Sierra Nevada de Santa Marta (Fig. 8) and is closely allied to *A. rufinucha* and might even be considered a particularly well-marked race of that species. It differs from *A. rufinucha* in having a fully black head (not chestnut), a black chin and upper throat, and silvery ear coverts. These characters are found in varying degrees in some races of *A. rufinucha* (see Table 1). For example, the black of the chin and throat occurs in *A. r. melanolaemus*. Also, in *A. r. phelpsi*, the race nearest to Santa Marta, there is a broad black band on the forehead and along the sides of the head which seems to be a step toward a fully black head; its ear coverts are nearly as silvery as in *A. melanocephalus*.

INTERRELATIONSHIPS

There seems little doubt that *A. melanocephalus* had its origin in *A. rufinucha*, and probably from stock from which arose *A. r. phelpsi*. It is probably the youngest species within the *A. rufinucha* species-group.

A. melanocephalus occurs from the upper tropical zone (600 m) through the subtropical zone (2,400 m). It is the only member of the species-group to occur so low. Although this altitudinal range coincides with that of *A. torquatus* on Santa Marta, *A. melanocephalus*, if it is like *A. rufinucha*, is probably more arboreal and, therefore, is not ecologically competitive with it. There are no additional atlapetes on Santa Marta and presumably this allows *A. melanocephalus* a wider range in altitude than is usual in the genus.

Atlapetes tricolor superspecies

The three allospecies of this superspecies are morphologically very similar, the principal difference being in the color of the crown, which in *A. tricolor* is gold, in *A. flaviceps* is yellow, and in *A. fuscoolivaceus* is blackish. Immature *A. tricolor* has a dull crown, resembling that of adult *A. fuscoolivaceus*; no immature examples of *A. flaviceps* are known. Interestingly, immature *A. rufinucha* bears a strong resemblance to *A.*

tricolor, suggesting a relationship between the two taxa. The distribution of the two species (see below) further strengthens this belief.

Atlapetes tricolor

A. tricolor has an extended range (Fig. 9), beginning on the western slope (and one doubtful record for the eastern slope) of the Western Andes of Colombia and extending down the western slope of Ecuador, but becoming very sparse in the south, presumably because of increasing aridity. It reappears on the eastern slope in central Peru, after a gap of about 1,000 km. It occurs from the humid upper tropical zone to the upper subtropical zone in the north and in the subtropical and temperate zone in Peru.

Atlapetes fuscoolivaceus and *A. flaviceps*

Both *A. fuscoolivaceus* and *A. flaviceps* have very restricted ranges on the eastern slope of the Central Andes (Fig. 9). *A. flaviceps* occurs in a deep valley on the south slope of Nevada de Tolima and *A. fuscoolivaceus* at the headwaters of the Río Magdalena in a cul de sac where the Eastern Andes swing abruptly west to join the Central Andes. Both species are known only from the subtropical zone. There has been little ornithological work on the east side of the Central Andes; it is possible that the ranges of these two species may be more extensive than now known.

Interrelationships

A. flaviceps and *A. fuscoolivaceus* appear to be remanent offshoots of the stock that produced *A. tricolor*. Presumably ancestral *A. tricolor* was once confined to the Pacific Colombian (or Chocó) Refuge, as defined by Haffer (1974), and later expanded its range down the western slope of Ecuador, crossing over to the east at the low passes in southern Ecuador and northern Peru. A subunit of the same ancestral stock seems also to have been restricted to the eastern side of the Central Andes, perhaps in the Caribbean Colombian (Nechí) Refuge. During a warm-moist period, it may have spread up the Magdalena valley along the eastern slopes of the Central Andes, only to retreat later to one area at the head of the valley, where *A. fuscoolivaceus* is now found, and to another restricted region 300 kilometers to the north, where *A. flaviceps* occurs.

The reason why *A. fuscoolivaceus* and *A. flaviceps* are restricted to two small areas doubtless is related to the wetness of the subtropical habitat at these points. Both places are at the head of valleys which are cut deep into the Andes. Presumably these regions receive much more precipitation than points that are farther east, away from the mountains, and nearer the arid upper Magdalena valley. Thus both species are probably unable to move down the valleys or up over their sides because of unsuitable habitats. These two places are certainly not the only sites with moist subtropical vegetation along the entire eastern slope of the range. Future work may reveal additional populations in pockets at the heads of other deep valleys.

Geographical Displacement

The wide geographical breach between the subspecies of *A. tricolor* is puzzling, as is the absence of the species on the eastern slope of Ecuador. Displacement by another species would seem an explanation. *A. rufinucha*, which in immature plumage is similar to *A. tricolor*, appears a likely species. The races *A. r. baroni* and *latinuchus* more or less fill the breach on the eastern slope from southeastern Ecuador to central western Peru (Fig. 6). *A. t. tricolor* then occurs from central to southern Peru, and this is followed by two races of *A. rufinucha* ranging from southern Peru to southeastern Bolivia (Figs. 7, 23). Although this would appear to be a classical example of a geographical replacement, there are some

flaws, the most important being that in general the species are found at different altitudes. In western Colombia and Ecuador, the two species have generally overlapping ranges, but *A. tricolor* is invariably at lower elevations. If the two species are competitors, one would expect that in the absence of one, the other might expand its altitudinal range. However, *A. rufinucha* in eastern Ecuador, where *A. tricolor* is absent, has the same vertical range as it does in western Ecuador, where *A. tricolor* is found. In Peru *A. t. tricolor* is at moderately higher elevations than is *A. t. crassus* in Colombia and Ecuador and, therefore, it occupies the lower part of the altitudinal range of *A. rufinucha*. In other words, *A. tricolor* seems to have expanded slightly upward in the absence of *A. rufinucha*. I can find no evidence that *A. rufinucha* drops to lower altitudes in Peru where *A. tricolor* is lacking; it does, however, occur as low as 600 m in Bolivia. Unfortunately, there are available only about 100 records for both species in a range covering over half the length of the Andes. While broad outlines of altitudinal preferences are obtained, it is hardly likely that more subtle differences in altitude between species and races will be revealed by these few data.

The manner in which *A. tricolor* replaces *A. rufinucha* and the resemblance of immature *A. rufinucha* to *A. tricolor* lead to the conclusion that the two are members of the same species-group. It follows that if *A. tricolor* is a member of the species-group then its allospecies, *A. flaviceps* and *A. fuscoolivaceus*, must also be in the group. The presence of these two species on the eastern slope of the Central Andes, occupying a gap in the range of *A. rufinucha*, further reinforces the belief that these are indeed members of a closely related assemblage.

Atlapetes albofrenatus

A. a. albofrenatus is one of the most distinctive taxa of the *A. rufinucha* species-group by virtue of its white throat, heavy malar streaks, and green back; however, in the race *A. a. meridae*, the white throat and heavy streaks are reduced, and the bird is much less distinctly different from *A. rufinucha*. In any case, these characters are minor. The placement of *A. albofrenatus* in association with *A. rufinucha* is reinforced by two points. First, this is an active bird whose behavior is similar to that of *A. rufinucha* in contrast to the slower, more secretive movements of most atlapetes. Second, and more important, the species occurs within a breach in the range of *A. rufinucha* in the Eastern Andes from Bogotá north to southwestern Venezuela (Fig. 23). Of particular note is the fact that it does not occur in the Sierra de Perijá, the northward projecting spur of the Andes which is occupied by isolated *A. r. phelpsi*, but it does cross the barrier created by the depression formed by the Río Torbes, which separates the Eastern Andes from the Andes of Mérida. The only possible instance of sympatry is in the vicinity of Bogotá where *A. r. simplex* is said to occur, but this race is known only from several native "Bogotá" specimens and certainly comes from elsewhere, probably in the little-known Eastern Andes south of Bogotá. The altitudinal range of *A. albofrenatus* is somewhat more restricted than that of *A. rufinucha*, but the species displays the same versatility in habitat preference.

Thus there is no doubt that *A. albofrenatus* is related to the *A. rufinucha* species-group. Its relative distinctiveness indicates it is not part of the *A. rufinucha* species branch, but was derived from the same stock that produced *A. rufinucha*. It would seem to have originated in the Eastern Andes, simply because that is where it is now found. No Pleistocene refuge for subtropical forest forms has been proposed in the area now occupied by *A. albofrenatus*, although Haffer (1974) believes one existed farther north (the "Catatumbo Refuge"). The western slopes of the Sierra Nevada del Cocuy, the highest peak in the Eastern Andes, may have served as refugium. The

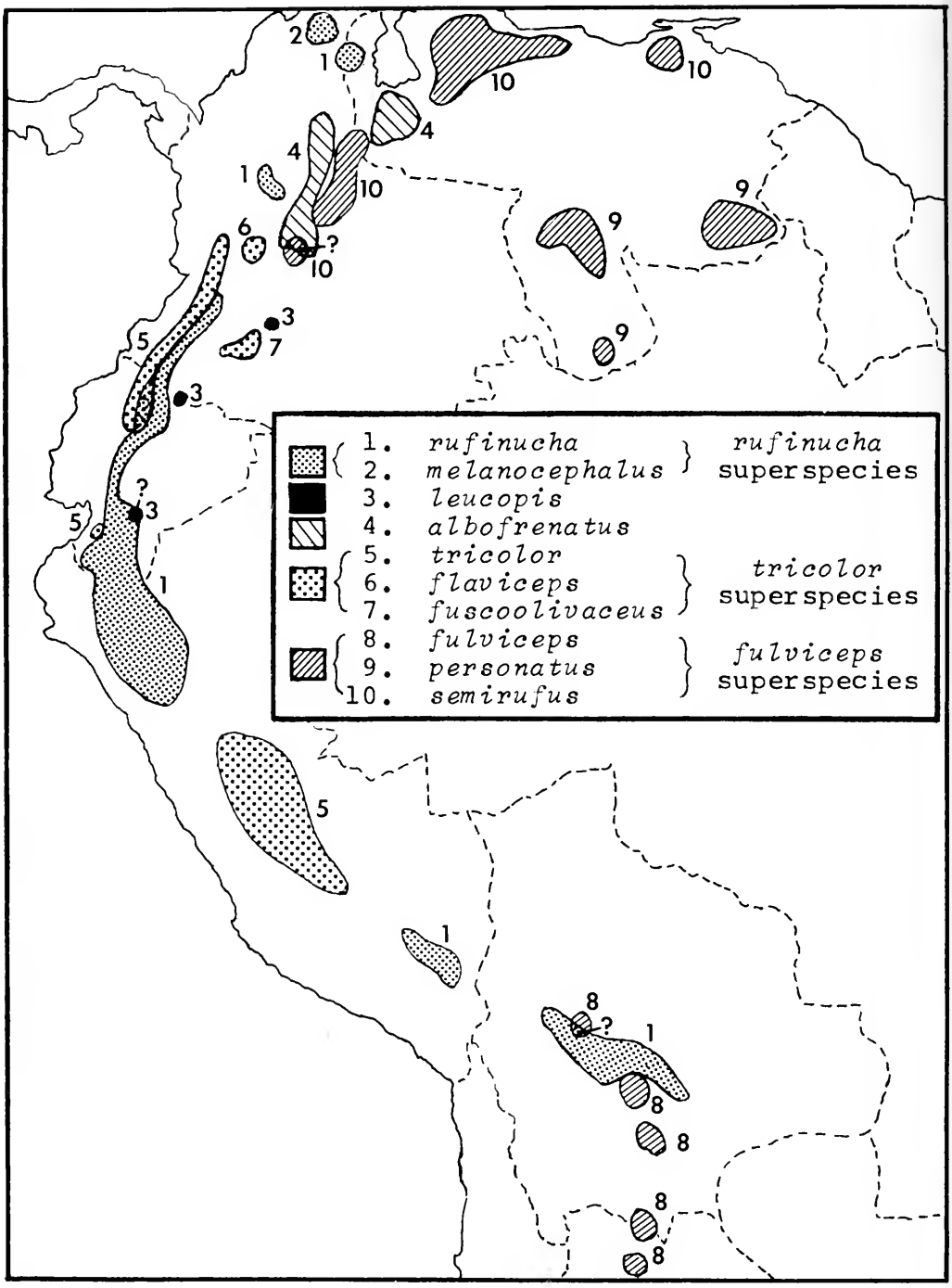


Figure 23. Geographic replacement within the *A. rufinucha* species-group in South America. Areas of doubtful sympatry are marked "?".

mountain is at the head of the long and arid Chicamocha valley running west to the Magdalena and may have caught moisture during dry periods and served as a refuge for forest inhabitants, even if the valley itself was arid. This is the region occupied by nominate *A. albofrenatus*. On the other hand, the fact that *A. albofrenatus meridae*, the race of the Mérida Andes, is less distinct from *A. rufinucha* than is *A. a. albofrenatus*, suggests that the Mérida Andes may have served as the initial isolation area and that the species later crossed the Río Torbes barrier where it further differentiated. Both hypotheses could be embellished, but there seems no way to establish which area could have served as a speciation center. Indeed, *A. albofrenatus* may be a relict and not autochthonous to either place.

Atlapetes leucopis

As I have observed before (Paynter, 1970), *A. leucopis* resembles *A. rufinucha melanolaemus* of Peru, the most distinctive race of *A. rufinucha*, except for its much larger size, white eye ring and eye stripe, and green underparts.

It seems to be sympatric with *A. rufinucha* at Palmas, Azuay, on the eastern slope of Ecuador, but does not coexist at the other two localities from which it is known, viz. La Plata, Colombia, which is on the east side of the Central Andes and Cerro Pax, on the east slope in southern Colombia (Fig. 23). The Palmas locality is suspect, however. The single bird from there was obtained by M. Olalla (Berlioz, 1932), a member of the family of professional collectors that is noted for inaccurately labeled specimens. From a few hours spent at Palmas, I know, that *A. rufinucha*, which Olalla also records from here, does indeed occur at this locality; I believe that *A. leucopis* may be somewhere in the general region but not sympatric with *A. rufinucha*.

The two Colombian sites for *A. leucopis* are to the east of the range of *A. rufinucha* and the Ecuadorian locality is at the northern edge of the range of *A. rufinucha*, which reappears again about 250 kilometers farther north in Ecuador. Thus it seems that *A. leucopis* is a geographical replacement for *A. rufinucha*, although it is possible that allopatry may break down in Azuay at the southern end of the range of *A. leucopis* and the northern end of the range of *A. rufinucha*.

A. leucopis is not known to be sympatric with any other member of *A. rufinucha* species-group, but it should be noted that *A. fuscoolivaceus* occurs in Colombia at Moscopán (alt. 2,400 m), Huila, which is only 32 km west of La Plata (alt. 2,350 m), and in the same valley.

It would seem that *A. leucopis* bears a relationship to *A. rufinucha* similar to that existing between *A. rufinucha* and *A. albofrenatus*, i.e., *A. leucopis* appears to have arisen from the same ancestral stock as *A. rufinucha*, but it is not a derivative of *A. rufinucha*. It is not possible to speculate on its place of origin.

Atlapetes pileatus

A. pileatus, the Mexican endemic (Fig. 12) is a small pallid version of *A. rufinucha*. It is isolated from the remainder of the species-group by all of Central America. It appears to be a relict that originated in Mexico or Central America, but it is not possible to speculate further.

Atlapetes fulviceps superspecies

There are three allospecies within the *A. fulviceps* superspecies, viz. *A. fulviceps*, *A. personatus*, and *A. semirufus*. All are morphologically very similar inhabitants of the subtropical zone, and all have a marked resemblance to *A. rufinucha*, but differ from *A. rufinucha* in that the black of the sides of the head is replaced by chestnut and, in some taxa, the chestnut extends to the throat and breast. *A. fulviceps*, which is monotypic, is found in Bolivia and northwestern Argentina (Fig. 14). *A. personatus*, with six well-

marked races, occurs in the "pantepuis" of southwestern Venezuela (Fig. 13). Both species are at or near the outer edges of the distribution of the genus. *A. personatus* is the sole atlapetes in its region; *A. rufinucha* occurs in the general area with *A. fulviceps*, in the latter's northern range, but has been recorded as sympatric with it only at Tilotila (alt. 2,150 m), La Paz, Bolivia. The Tilotila records are those of Buckley, whose collections were made from 900 to 3,700 m (Sclater and Salvin, 1879). The absence of further evidence of sympatry suggests that Buckley's specimens were altitudinally separated, but which were at the higher elevation is unknown because the altitudinal records from elsewhere overlap.

Highly polytypic *A. semirufus* is the species of the Eastern Andes of Colombia and the coastal mountains of Venezuela (Fig. 13). It may be sympatric with *A. albofrenatus* near Bogotá, but the data suggest that *A. semirufus* occurs at higher altitudes.

Presumably *A. personatus* was derived from early *A. semirufus*. Mayr and Phelps (1967), apparently following Chapman (1931), state that *A. personatus* is most closely related to far-distant *A. fulviceps*. However, morphological evidence is inconclusive and derivation of *A. personatus* from *A. semirufus* seems more logical, simply because they are geographically closer.

The long gap between *A. semirufus* of the northern Andes and *A. fulviceps* of the southern Andes is provocative and suggests that the two allospecies are separated by another species or group. The *A. rufinucha* species-group fills the breach without any indication of sympatry, except for the very dubious record of *A. rufinucha simplex* from native "Bogotá" specimens (Fig. 23). This close fit does not seem to be an artifact. *A. fulviceps* superspecies not only is phenotypically similar to the *A. rufinucha* species-group but must also be very closely related and, hence, unable to coexist with it.

Although one could argue well for the inclusion of *A. personatus*, *A. semirufus*, and *A. fulviceps* within the *A. rufinucha* species-group, there is a morphological cohesiveness among the three species which probably indicates that this group branched from the ancestral stem stock earlier than the individual species making up the *A. rufinucha* species-group.

Atlapetes citrinellus

A. citrinellus, of Argentina, is the southernmost representative of the genus (Fig. 15). It stands apart from other members of the genus and obviously is an aberrant representative. It does bear some resemblance to *A. fulviceps* without the chestnut crown and cheeks. The two may have had an ancestral branch in common.

Atlapetes schistaceus species-group

This group of six closely-related species is distributed through the Andes from western Venezuela to southern Peru (Fig. 24). The species replace one another geographically in a manner reminiscent of the mosaic pattern of the *A. rufinucha* species-group. The group was analyzed earlier (Paynter, 1972) and only brief outlines are given here.

Atlapetes schistaceus

This species has the widest distribution of any species within the *A. schistaceus* species-group, ranging disjunctly from the Cordillera de Mérida, Venezuela through the three ranges of the Colombian Andes and thence on the eastern slope to central Ecuador. The species reappears in central eastern Peru and then again in southeastern Peru (Fig. 24). It is mainly a humid temperate region form but does reach the subtropical zone on occasion. Its total range is from 1,850 to 3,750 m. Color and pattern vary geographically; 12 races have been described. It is, therefore, morphologically the most variable of all atlapetes.

Altapetes nationi

A. nationi (Fig. 24) is the southern Andes western slope counterpart of *A. schista-*

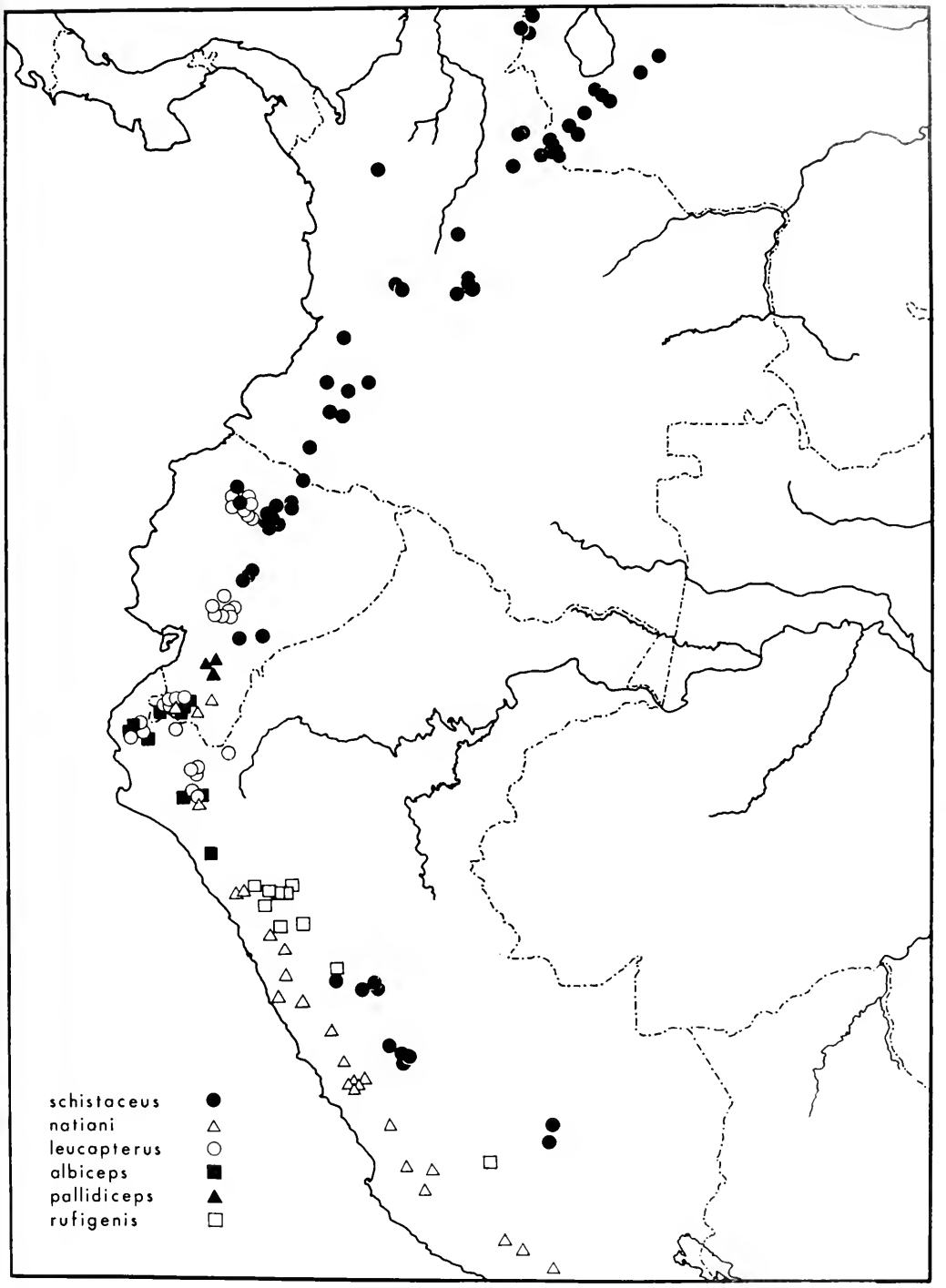


Figure 24. Distribution of the *A. schistaceus* species-group.

ceus, occurring from southwestern Ecuador south to Arequipa, Peru, with almost the same altitudinal range as *A. schistaceus* but apparently with a greater tolerance for drier habitats. It is the only *Atlapetes* to range so far south on the western side of the Peruvian Andes. It also has a fragmented distribution and is morphologically varied, with eight races being recognized.

Atlapetes leucopterus

This, the smallest bird in the genus, is found on the western slopes from northwestern Ecuador to northern Peru, and recently was collected by J. W. Fitzpatrick on the eastern side of the Andes in the Cordillera del Condor, Cajamarca, Peru (Fig. 24). It has a notably wide altitudinal range, having been found from 600 to 2,900 m, and appears to be common in rather xerophytic areas, but it also occurs in moist regions.

Distributional records show three clusters, viz. northern Ecuador, central Ecuador, and southern Ecuador and northwestern Peru (Fig. 24). The northern and central Ecuador populations represent one subspecies and the southern Ecuador and northwestern Peru populations another race. The recently discovered population in brushy edges of cloud forest in the Cordillera del Condor, to the east of the previously known Peruvian range, represents a very distinctive form that has not yet been named.

A. leucopterus is sympatric with *A. nationi* and *A. albiceps* in the dry, low mountains of southern Ecuador/northern Peru. These are the only known instances of sympatry within the species-group. The area of sympatry is in a region that probably has been particularly sensitive to variations in climate, owing to its low mountains and proximity to the arid Pacific coast. The vegetation has doubtless varied greatly. The instability would have made the region unsuitable for the long-term presence of any species of *Atlapetes*. The species, now meeting there and overlapping, seem to have had their origins elsewhere—*nationi*, and probably *albiceps*, to the south and *leucopterus* to the north (see Paynter, 1972: 317–318).

Atlapetes albiceps

A. albiceps, a monotypic taxon, is another western slope form. It is found from southernmost Ecuador to Cajamarca, northern Peru (Fig. 24). It is an arid zone species with an altitudinal range from 250 to 1,500 m.

Atlapetes pallidiceps

This is another arid area form, ranging from about 1,500 to 2,100 m. It is endemic to the valley of the upper Río Jubones and its tributaries, southwestern Ecuador (Fig. 24).

Atlapetes rufigenis

A. rufigenis is a large species with a population in the drainage system of the Río Marañón, northern Peru and another, racially distinct, population far to the south in the Río Apurimac region (Fig. 24). It occurs from 2,750 to 4,000 m and seems to frequent mesic underbrush.

Atlapetes torquatus species-group

There are four species within this species-group. The presence of a chestnut pileum in *A. brunneinucha* sharply distinguishes it from *A. torquatus* superspecies, but except for this one character, there is little morphological difference. All four species are surely derived from a common stem. However, because *A. brunneinucha* is frequently sympatric with *A. torquatus*, the two must be old, well-established, species, in contrast to the species comprising the *A. rufinucha* species-group which, because they seem unable to coexist and therefore form a complex geographical mosaic, are presumably actively speciating.

Atlapetes brunneinucha

A. brunneinucha has the most extensive range of any atlapetes (Figs. 16, 17) but

shows remarkably few morphological variations, except for the absence of a breast band in the races *apterus*, *allinornatus*, and *inornatus*, three very small populations. This is a notable contrast to the variability within *A. torquatus* superspecies, which is almost as widely distributed.

The lack of morphological variability is probably because *A. brunneinucha* inhabits the interior of moist subtropical forest. This habitat doubtless continued to exist in abundance and with few discontinuities even during the peak of climatic deterioration when lowland forests withdrew to isolated or semi-isolated refugia. Indeed, with the lowering of vegetation zones on the mountains, subtropical forest may have become more abundant than at any period, owing to its presence on the vast shoulders of the mountains.

The morphological differentiation that has occurred in the races *apterus*, *allinornatus*, and *inornatus* is doubtless the result of isolation, but why the breast band is the variable character is unknown. *A. b. apterus* is on an isolated mountain standing in lowland forest in Veracruz; *A. b. allinornatus* is on a northward-projecting spur off the main range of the Venezuelan Andes. There is no geographical feature associated with the range of *A. b. inornatus*, but its origin may be attributed to isolation brought about by climatic changes. Note that the arid coastal belt of western South America reaches northern limits at about the same latitude as the range of *inornatus*. During a warm-dry period the arid zone must have extended higher on the western slopes of the Andes. *A. b. inornatus* may have originated in a surviving pocket of wet, semitropical forest high on these slopes. A refugium in the same area has already been proposed to explain the origin of *A. leucopterus* (Paynter, 1972:317).

Atlapetes torquatus superspecies

A. virenticeps, the northernmost representative of this superspecies (Fig. 18), is a relict population. Its plumage is reminiscent of immature *A. torquatus*, but whether this indicates that the plumage of *virenticeps* represents the ancestral pattern of the superspecies, or is a case of reversion from a more "adult" plumage, or is an entirely "new" plumage is unanswerable.

The origin of *A. atricapillus* (Fig. 19) is perhaps one of the most intriguing but baffling problems of this nature in the genus. If, as it seems now, *A. atricapillus* and *A. torquatus* are parapatric, the former is probably a fairly recent offshoot. The fact that it is a lower altitude species than *A. torquatus*, and also occurs mainly in the northern extremities of the Andes suggests that it may have originated on outliers of the main Andean ranges, but more specific speculation is not possible until we have a better knowledge of the range of the species.

The morphological variability of *A. torquatus* (Figs. 19–22) stands in contrast to the uniformity of its sister species *A. brunneinucha*. The difference may lie in their habitats. While both are subtropical forms, although *A. torquatus* also ranges higher, *A. torquatus* is an edge dweller, often frequenting second-growth. Under natural conditions, edges and second-growth are generally uncommon and scattered, which means that populations of *A. torquatus* probably never have been as large or as contiguous as those of *A. brunneinucha*, and presumably this would have resulted in increased polymorphism.

A. torquatus seems to be somewhat less restricted to a given biome than many atlapetes, which may be indicative of its nature as a generalist and exploiter of temporary changes in habitats. However, of particular interest is the race *A. t. assimilis* which is strictly a temperate zone form. It is also the only race within the range of the allospecies *A. atricapillus*. This is strongly suggestive of altitudinal displacement, with *A. t. assimilis* moving higher to accommodate *A. a. atricapillus* in the upper tropical zone. However, it should be borne in mind that *assimilis* has an extensive range, only a small part of which is known to be near that

of *A. atricapillus*, and that its restriction to the temperate zone may be for other reasons.

CONCLUSIONS

The species of *Atlapetes* are most abundant at middle elevations in the northern Andes, and it is assumed that the genus had its origin in that region. This would mean that the genus can be no older than the uppermost Pliocene/lowermost Pleistocene, because this was when the main uplift of the Andes took place (Haffer, 1974: 130). It could, of course, be considerably younger.

The majority of the species seem to have arisen in the northern Andes, but five of the 24 species (*pileatus*, *fulviceps*, *personatus*, *citrinellus*, and *virenticeps*) must have originated well outside of this area and four species (*nationi*, *albiceps*, *rufigenis*, and *pallidiceps*) may have arisen in the midportion of the Andes.

The present pattern of distribution, as well as the pattern of speciation, show many indications of having been greatly influenced by climatic changes. The connection between climate and speciation is sometimes seen directly, as when the birds have ranges that coincide with patches of vegetation and the patchines could only have developed through the disappearance of suitable intervening areas. The fragmentation of belts of vegetation must have been caused by climatic changes. For example, *A. flaviceps* and *A. fuscoolivaceus* seem to have arisen when populations of ancestral *A. tricolor* were stranded in isolated pockets of moist subtropical forest on the eastern slopes of the Central Andes of Colombia, above the arid upper Magdalena valley. Another example may be found in *A. pallidiceps*, a distinctive form isolated in the arid valley of the upper Río Jubones, eastern Ecuador. *A. pallidiceps* is a derivative of *A. leucopterus*, a species of generally wetter areas. In this case the population was left behind by a shrinking belt of moist forest but instead of finding refuge in a wetter pocket (there are none in the region) adapted to a drier situation.

Other indications of the effect of climatic changes on speciation may be seen in the patterns of distribution. For example, the failure of *A. albinucha gutturalis* of Colombia to diverge appreciably from Central American populations, although well-isolated, while nominate *A. albinucha* of Mexico is markedly different from a series of Central American populations, even though less than 100 kilometers apart (see p. 329), can only be explained by a shifting of biomes through climatic changes. Another illustration is found in the intricate distributional mosaic of the *A. rufinucha* species-group (Fig. 23) which certainly must have arisen through a series of climatic oscillations that caused a series of contractions and expansions in several different populations. There seems no other explanation, for example, for the leap-frog pattern displayed by *A. tricolor* and *A. rufinucha* or for the appearance of populations of *A. albofrenatus* between those of *A. semirufus*.

The 24 species of *Atlapetes* cluster into four main groups which seem to represent four multi-branched evolutionary lines. These pathways and the interrelations of the component species are shown diagrammatically in Figure 25. Starting at the bottom of the diagram and reading clockwise, the following information is indicated.

A. brunneinucha and *A. torquatus* (with the three allospecies, *atricapillus*, *torquatus*, and *virenticeps*) share a common origin and form one evolutionary line, the *A. torquatus* species-group. Superspecies *A. albinucha* (with allospecies *albinucha* and *pallidinucha*) is a second main branch. The third, and largest, branch is made up of 12 species. *A. pileatus*, *A. leucopis*, *A. albofrenatus*, *A. rufinucha* superspecies (with allospecies *rufinucha* and *melanocephalus*), and *A. tricolor* superspecies (with allospecies *flaviceps*, *tricolor*, and *fuscoolivaceus*) form the core of this branch while *A. fulviceps* superspecies (with allospecies *fulviceps*, *semirufus*, and *personatus*) is an off-

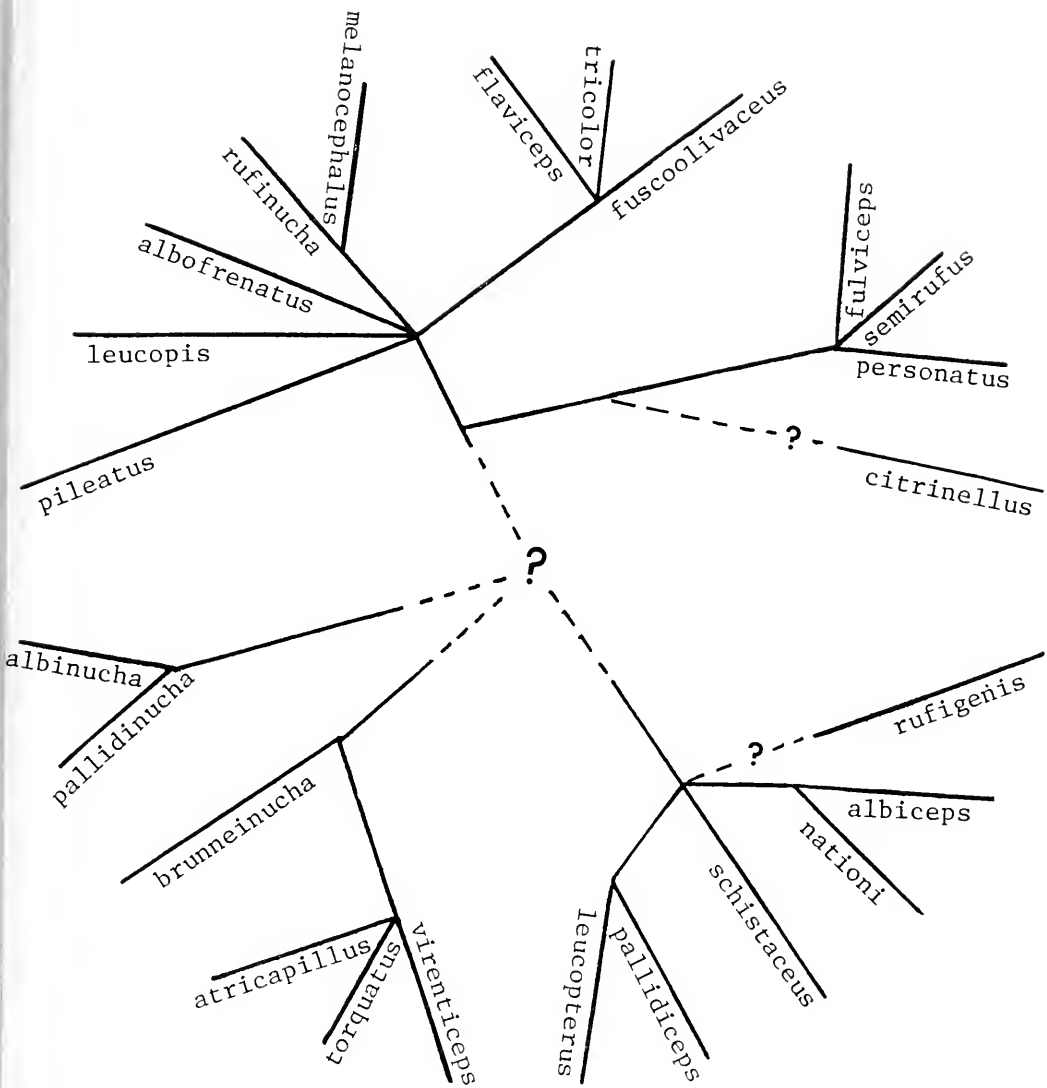


Figure 25. Interrelationships within the four main evolutionary paths in the genus *Atlapetes*. The relative lengths of the lines and their angles are of no significance. See text (p. 366) for details.

shoot of the main branch, and *A. citrinellus* is presumed to be a derivative of this offshoot. The fourth line of descent is the *A. schistaceus* species-group. *A. rufigenis* seems to have been an early offshoot, or it may merely be distinctive because of its distance from the center of the species' distribution. *A. albiceps* and *nationi*, while sharing a common origin from the main branch, are too distinct to be considered allospecies. *A. schistaceus* seems to represent the main line of evolution for this unit. *A. pallidiceps* and *A. leucopterus* are another pair of species that come off a common point but also are too divergent to be treated as members of a superspecies.

Of particular interest are the *A. rufinucha* species-group and *A. schistaceus* species-

group, which form the two main evolutionary lines within the genus. The former has 11 species (12 if *citrinellus* is included) falling into three superspecies, plus three (or four) separate species, while the *A. schistaceus* species-group is composed of six species, none of which is a member of a superspecies. The species within each species-group are distributed in an intricate checkerboard pattern. Sometimes the species are geographically separated, at other times they are contiguous, and only very rarely are they partially sympatric. In other words, the species within each species-group, even those which are not allospecies, almost invariably do not have overlapping ranges. This general allopatry implies that the species are incompatible and seems to indicate that they have only recently speciated.

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Natural History of Carion VIII: Little Bahama Bank—A Revision Based on Genetics, Morphometrics, and Geographic Distribution

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NATURAL HISTORY OF *CERION* VIII: LITTLE BAHAMA BANK—A REVISION BASED ON GENETICS, MORPHOMETRICS, AND GEOGRAPHIC DISTRIBUTION*

STEPHEN JAY GOULD[1]

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ABSTRACT. Close to a dozen names are now available to describe variation in *Cerion* on the islands of Little Bahama Bank. These names, plotted in the supposed areas of their occurrence, form the "crazy-quilt" distribution pattern, traditionally, associated with *Cerion* and ascribed to haphazard transport by hurricanes. We, on the other hand, find remarkably stable patterns in *Cerion* throughout the northern Bahamas. More than 200 "species" can be reduced to a single, unerringly predictable distribution and interaction of two imperfectly separated entities: a ribby morphotype associated with coasts that abut the edges of the Pleistocene banks, and a mottled morphotype from interior areas and coasts adjacent to bank interiors. We find the same distribution throughout Little Bahama Bank and reduce the current taxonomy to two semispecies: *C. bendalli* Pilsbry and Vanatta (the mottled morphotype) and *C. abacoense* Pilsbry and Vanatta (the ribby morphotype). The distribution of these semispecies maps the edges and interiors of Pleistocene banks, as described above; the morphological differences make sense in adaptive terms; wherever the taxa meet (at the junction of bank-edge and bank-interior coasts), they hybridize in narrow zones that exhibit characteristic morphometric and genetic patterns. We intend to use this combined morphometric and genetic study as a model for our biological revision of the entire genus.

We measured 20 characters in samples of 20 shells (when available) in each of 52 samples spanning the range of phenotypes and their geographic distribution in Little Bahama Bank cerions. Three factor axes encompass nearly all information (96.3 per cent) in the matrix of mean sample vectors; two axes account for 88 per cent. Ribby and mottled samples from Abaco sort unambiguously on the first two axes; the third axis distinguishes mottled samples from Grand Bahama by their characteristic covariance (high narrow shells with small and numerous whorls). All samples, defined as hybrids by their geographic position in zones of interaction (not by their morphology), have intermediate projections on the first two axes and plot in the intermediate phenetic field between them on a triangular diagram; samples of the hybrid zone at Rocky Point plot in perfect geographical order. Patterns within morphotypes are equally smooth and simple. Trend surface analysis displays the even variation in size (a multivariate compound of all measures) for mottled samples throughout Grand Bahama, the previous basis for three discrete "species"; minor, but consistent, differences characterize slightly isolated regions on Abaco—samples at Treasure Cay, for example. Samples from areas of interaction are intermediate in phenotype between ribby and mottled "parental" populations. At Rocky Point, the very narrow (less than 1 km.) hybrid zone displays continuous transition in mean phenotype with no increase in variability within samples.

A study of allozyme variation at 28 loci (6 variable and scorable) for the same samples yields very little concordance between biochemical data and patterns of variation in shell phenotypes. *Cerion*, though facultatively hermaphroditic, are outcrossing and moderately variable for structural genes surveyed (polymorphic loci per population, 20–36 percent; average heterozygosity per individual, 5–12 percent). All samples are markedly similar. Nei's I for 820 pairwise comparisons ranges only from 0.9451 to 0.9999 (average of 0.9849); no "marker" gene characterizes any region or morphotype—though characteristic frequencies of variable alleles clearly separate Grand Bahamian from Abaconian populations in a statisti-

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* Published and supported in part by a grant from the Wetmore Coles Fund.

cal manner. The genetic analysis of hybrid samples affirms our decision to treat the Little Bahama Bank cerions as two semispecies, rather than as geographic variation in a single entity. Although we find no increased variation in shell phenotypes, hybrid *Cerion* are significantly more variable genically (both within and among samples) than animals collected elsewhere. They are also polymorphic for alleles not found in either adjacent "parental" population.

I. INTRODUCTION

The current taxonomy of the Little Bahama Bank cerions is a microcosm of the problems that beset this entire fascinating genus, with its 600-odd named taxa (Clench, 1957; Mayr and Rosen, 1956). Little Bahama Bank was spared from visits by the most exuberant conchological splitters, but even its conservative monographers (Clench, 1938, for example) followed the hallowed tradition of naming every distinctive allopatric morphology. Seven species are now recognized for the islands of Little Bahama Bank.

A taxonomic scheme is not merely a neutral description of diversity; it is, as Mayr (1976) has emphasized, a theory of resemblances. And, like all theory, it channels thought along prescribed lines. In *Cerion*, the geographic mapping of described taxa yields a "crazy-quilt" (Mayr and Rosen, 1956) of disordered distribution. Published reports and museum specimens show this pattern for the seven taxa of the Little Bahama Bank (Fig. 1). All leading students of *Cerion* have invoked the vagaries of hurricane transport as an explanation for this incoherence (Maynard, 1919; Bartsch, 1920, p. 53; Clench, 1957; Mayr and Rosen, 1956). Yet if the taxonomy is incorrect—if these "species" are only local demes of persistent and widespread biological species—then this biogeographic postulate falls.

The few scientists who approached *Cerion* with the integrative goals of modern evolutionary biology have realized that something in the state of its systematics must be very rotten (Clench, 1957; Mayr, 1963; see also Plate, 1906 and 1907 for similar insights from a non-Darwinian evolutionary perspective). As a primary though generally unrecorded fact, no unambiguous case of sympatry has ever been reported among *Cerion*'s 600-odd taxa. The two most probable cases are both in doubt. Mayr (1963, p. 398) reported two species from one of his Cuban localities, but his specimens (S. J. Gould, personal observations) include a few clear intermediates. Bartsch (1920) reported no hybridization between two "species" from Andros Island transplanted to the same locality in the Florida Keys. But he later came to question his own observation (Bartsch, 1931, p. 373). In our own field work, extending over five years and as many major islands, morphotypes ("species" of previous authors) hybridize freely at their zones of contact, no matter how distinct their morphologies—and some of the zones on Long Island mark the smooth mixture of the most distinctly different morphologies within the genus (e.g., smooth, squat "*C. malonei*," with a long, triangular member of the peculiar subgenus *C.* (*Umbonis*); see Gould, Woodruff, and Martin, 1974, Fig. 1, upper row, specimens 3 and 4). Moreover, we have detected very little genetic difference among animals of divergent shell morphology (Gould, et al., 1974, Woodruff, 1975a,b). *Cerion* seems to possess a remarkable capacity (among animals) for developing localized, highly distinct morphologies without attendant reproductive isolation from other demes.

We wish to emphasize that our quest for a revised taxonomy is not motivated by any abstract desire for tidiness or simplification. Rather, a more adequate nomenclature both arises from and potentially leads to a better evolutionary understanding of *Cerion*'s unusual biology. A well-revised taxonomy is both a precondition and a promise.

We began our work in 1972 in the basic tradition of evolutionary natural history. We wished, first of all, to study selected islands in detail and, to map the distribution of morphological variation, hoping to find

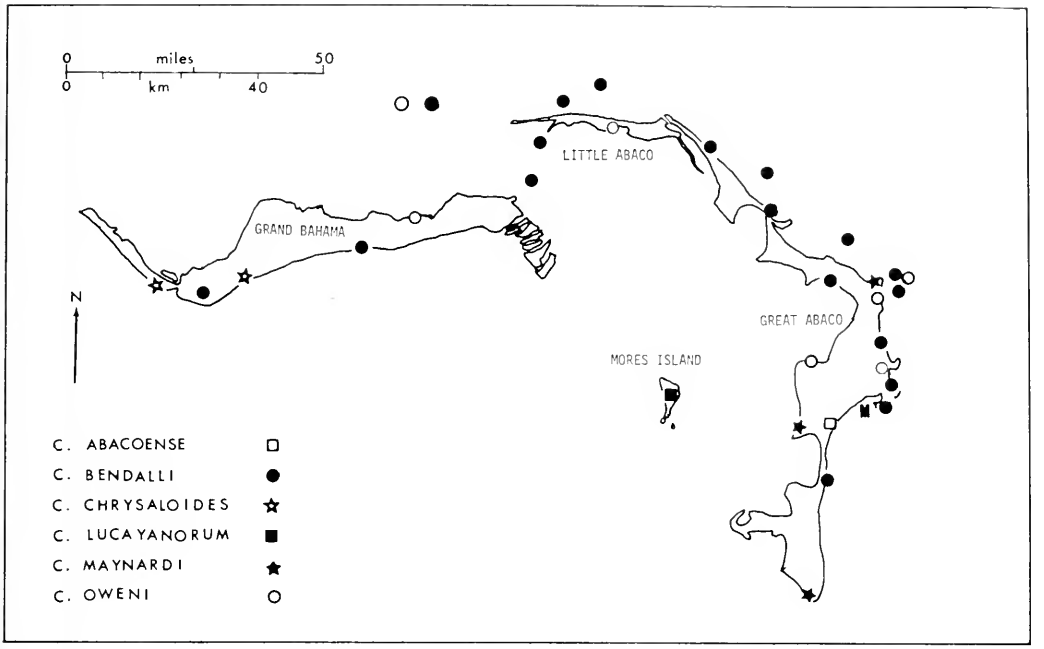

Figure 1. Distribution of *Cerion* on Little Bahama Bank as recognized taxonomically at the time this study was initiated. M marks Duck Cay, suspected by Clench as being the type locality of *C. milleri*. Pilsbry and Vanatta did not specify a locality for *C. abacoense* (beyond simply "Abaco" itself); we have placed it on the only part of Abaco where shells of its morphology occur.

some correlation with local environment. We also wanted to record everything we could observe about the virtually unknown basic biology of these snails (feeding habits, predators, etc.). Beyond this, we decided to apply a dual strategy of genetic and morphometric study of the same animals (as fruitfully applied, for example, by Soulé, 1976 and Johnston, 1975). Consequently, we collected large samples at many localities—either by gathering all the adult specimens we could find in about 30 minutes, or, in areas of high abundance, by recovering 100–200 specimens within an area of less than 100 m^2. Our genetic methods are described in Woodruff, 1975b; our morphometric approaches in Gould et al., 1974.

In our first report (Gould, Woodruff, and Martin, 1974), we showed that a local set of populations on Abaco Island, clearly distinct enough morphologically to win specific designation by all previous criteria, could only be ranked as a well-marked geographic variant within the only taxon inhabiting its general area. We now extend this approach to consider the entire *Cerion* fauna of Little Bahama Bank (Fig. 2).

II. GEOGRAPHIC DISTRIBUTION AND TAXONOMIC SIMPLIFICATION

Of the two major platforms that include most of the Bahama Islands, Little Bahama Bank is the smaller and more northerly. It includes (Fig. 3) the two major land masses of Abaco and associated islands on the northeast and eastern part of the bank, and Grand Bahama on the southwest and south. In contrast with Great Bahama Bank (6 major islands, hundreds of minor ones and about 250 recorded species of *Cerion*), it represents a tractable area for the study of *Cerion* over a broad and distinct portion of its range.

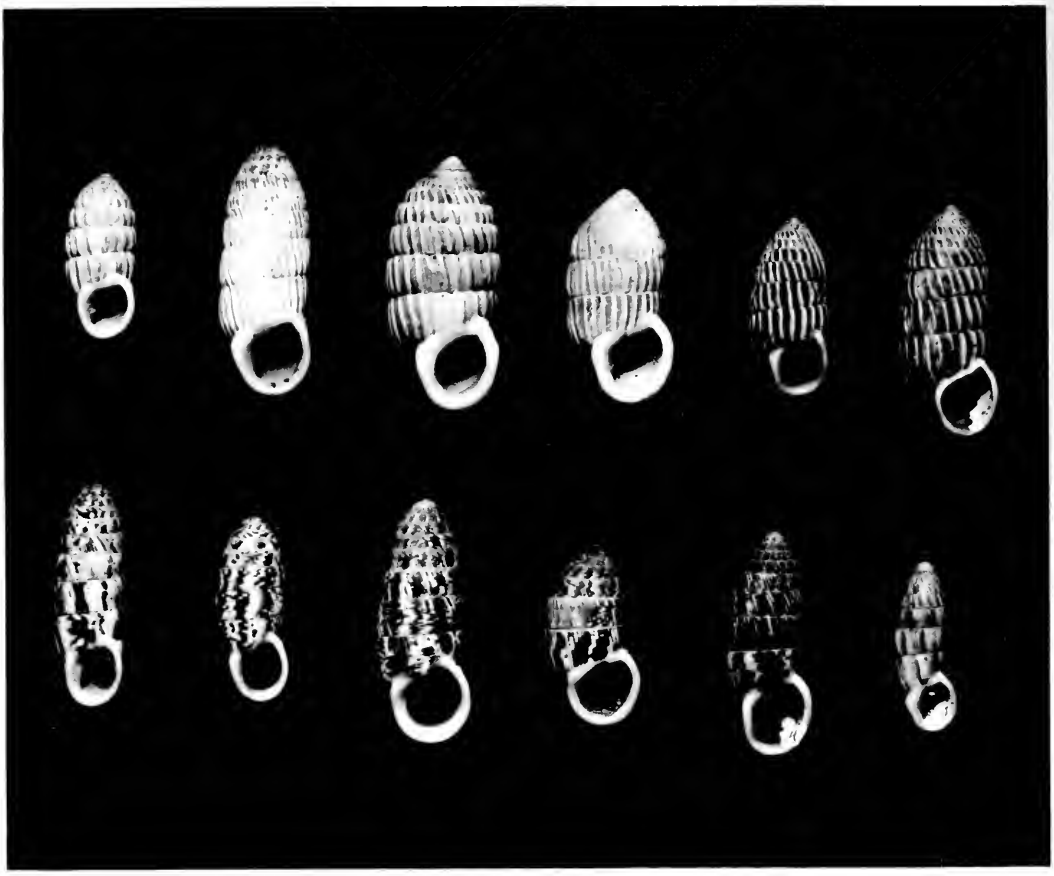

Figure 2. Representative specimens displaying the range of variation within the two morphotypes of the Northern Bahamas. Top: ribby morphotype. Bottom: mottled morphotype. Conventional taxonomy as follows: Top row, left to right: *C. chrysaloides*, Grand Bahama; *C. lucayanorum*, Mores Island (holotype); *C. maynardi*, southern end of Abaco, locality 250; *C. abacoense*, southeastern shore, Abaco, locality 254; *C. glans coryi* from western end of New Providence Island; *C. salinaria*, Salt Cay north of New Providence (holotype). Bottom row, from left to right: *C. bendalli*, Grand Bahama, locality 200; *C. bendalli*, Abaco locality 228; *C. bendalli*, western tip of Great Abaco, locality 217; shell that could be assigned to any one of 10–15 species, Culbert's Point, New Providence Island, locality 267; shell that could be assigned to any one of 10–15 species, central New Providence, locality 275; holotype of *C. degeneri* from New Providence.

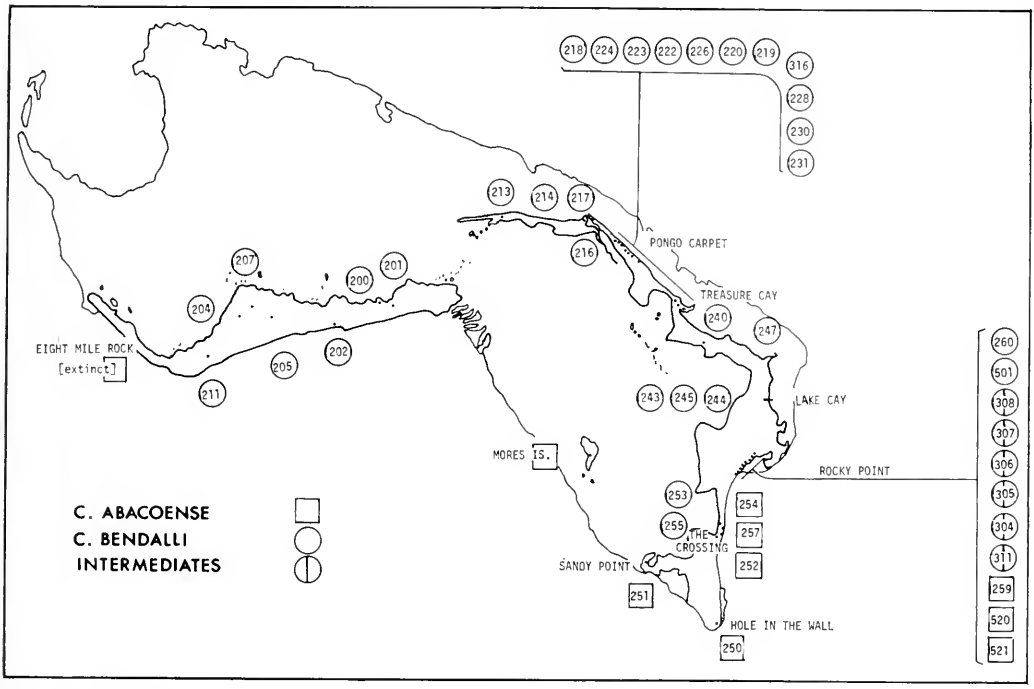

Figure 3. Distribution of *Cerion* on Little Bahama Bank revised in accordance with this study. Numbers refer to the authors' field localities and samples (see appendix). The edge of the bank is indicated. For details of the area of interaction on Great Abaco, see Figure 5.

Both previous monographers of Little Bahama Bank *Cerion* recognized that its several species could be allocated to two groups within the subgenus *C.* (*Strophiops*) (Pilsbry, 1902; Clench, 1938). Beyond this basic statement, the literature contains nothing of an explanatory or integrative nature. We have only a list of localities and taxa.

The two groups are distinct in morphology. Shells of the "ribby" morphotype are white or weakly mottled, relatively wide, and cylindrical with a fairly sharp break between a triangular apex and parallel-sided later whorls, strongly recurved aperture with thick lip, and a complete covering of strong, often widely spaced ribs (Fig. 2)—in short, a lightly colored, heavy and ribby shell. Shells of the "mottled" morphotype are strongly colored with irregular, brownish mottling, generally narrow with a more rounded apex passing smoothly to more barrel-shaped later whorls, apertures either thickly or thinly lipped depending upon the habitat (though never so thickly lipped as the ribby morphotype), with a shell surface either smooth or covered with fine ribs (Fig. 2)—in short, a mottled, light and relatively smooth shell.

We use the archaic term "morphotype" to describe these basic features because we find the same contrast—and the same correlation with geographic position and habitat—on island after island in the northern Bahamas. We have no reason to assert homology and transport among islands, though this has been the unstated assumption of all previous work. It is just as likely, we believe, that these basic morphologies are developed in situ, again and again, as adaptive responses to recurring habitats. On each island, the ribby and mottled

morphotypes interbreed in zones of contact; yet all the zones display features (varying from island to island) suggesting that at least a minor amount of genetic differentiation has occurred. They are imperfectly separated forms, perhaps best designated as semispecies, if conventional categories must be applied. (The biological species concept breaks down for an animal like *Cerion* with such amazing morphological diversity accompanied by, at best, imperfect reproductive isolation. We can scarcely recognize but a single species for a pattern of discrete and coherent morphological variation unexcelled among genera of land snails. Yet we cannot identify taxa by lack of interbreeding in sympatry.) We envisage a basic genetic system, common to all *Cerion* and including the potential to develop any one of a set of basic morphotypes. The morphotypes are alternative pathways of development that can be evoked from a common genotype by mechanisms of regulation utterly unknown to us. Once evoked, however, these morphotypes can become relatively stable within local areas. The basic features of any morphotype do not form a labile ecophenotype, easily altered by rearing in different conditions (Bartsch's transplants of Bahamian, Cuban, Puerto Rican, and Curaçao cerions all bred true to type for at least two generations on the Florida Keys and Dry Tortugas —Bartsch, 1920).

We believe that a modern taxonomy of the Little Bahama Bank cerions can do no more than recognize the two morphotypes as imperfectly separated semispecies. We base this conclusion on three sets of observations: consistent geographic distribution of the morphotypes, adaptive correlations with habitat, and patterns of interaction in zones of contact.

1. Geographic distribution. Among the myths that surround Cerion, none has been more persistent than the claim that it is a halophilic species restricted to coastal areas. All previously reported records for both ribby and mottled morphotypes are from localities within about 100 m of the sea. Yet we have found that the mottled morphotype ranges right across these low islands, penetrating the middle of the Grand Bahamian pine forest and the middle of the once forested area of Abaco. At locality 204 (see Fig. 3), 10 km from the nearest coast we found mottled *Cerion* at very low densities ($< 0.1/m^2$) in the shrubs and grass on the forest floor. Beneath one slab of aeolianite, however, we discovered an aggregation of more than 50 adults. Only in open, disturbed areas in the forest (locs. 205, 207) did we find *Cerion* in abundance (approx. $1/m^2$), and, even then, not in numbers typical of coastal populations where densities greater than $10/m^2$ are common. These sparse and patchy interior populations undoubtedly escaped the notice of early collectors, whose activities were usually restricted to a few minutes walk from the point where they beached their dinghies. W. J. Clench (1938), the most careful collector of *Cerion* found some interior specimens, but did not appreciate the generality of their occurrence.

In contrast to our discovery that the mottled morphotype ranges far from present day coasts, the ribby morphotype is restricted to within 200 m of the coast. Furthermore, and most importantly, it is restricted to coastal areas adjacent to the edge of the island bank (Fig. 3, for example). In contrast, the mottled morphotype occurs along coasts that do not border the island bank. If we designate the ribby morphotype as having a "bank edge" distribution, then the mottled morphotypes are found in "bank interior" situations. The mottled shells may represent an inland or bank interior morphotype evolved for geographic or ecological conditions prevailing during Pleistocene hypothermal periods when the sea level was much lower than it is today. If this hypothesis is correct, then the mottled morphotype has been living in coastal situations (along the northern coast of Grand Bahama and the western coast of Abaco) for less than 6,000 years. In contrast to the

traditions of *Cerion* study, and for reasons presented herein, we believe that current distributions may be highly persistent. The preference for fluid, haphazard distributions proposed by earlier workers (illustrated in Fig. 1) arises from a taxonomy that we will show to be fundamentally incorrect.

Distribution patterns based on the revisions in this paper are shown in Figure 3. The generally coherent pattern of bank edge vs. bank interior distribution found in these two taxa is one of our most important findings: it permits us to predict the distribution of analogous morphotypes on the various islands of the Great Bahama Bank. On Andros, New Providence, Great Exuma, and Long Island, we have found that the mottled morphotype invariably lives on bank interior coasts and inland areas, while the ribby morphotype is restricted to bank-edge coasts. We expect eventually to show that more than 200 "species" of Bahamian *Cerion* only represent the distribution of these two morphotypes and their interaction.

The consistent differences in distribution provide, in themselves, a strong argument for regarding the two morphotypes as partly distinct, biological taxa. They live on different kinds of coasts and react differently to inland conditions. Were it not for their patterns of interaction (see below), we might regard this strong correlation of form with habitat and geography as an aspect of normal geographic variation within a single taxon (perhaps purely phenotypic), rather than as the adaptations of imperfectly separated entities.

2. Adaptation of form to habitat. For all the effort devoted to taxonomy (more than 2,000 printed pages), no previous workers have directly studied the adaptive nature of form in *Cerion*. Nonetheless, the persistent correlation of form and habitat suggests that the morphotypes have been selected for survival value. Accordingly, we have initiated a series of experiments designed to establish some of the physical correlates of the various morphologies. Looking first for the possible adaptive significance of shell pigmentation, we contrasted the white shells of the ribby morphotype with those of the mottled morphotype. John Quensen, working in Woodruff's laboratory, found that in direct sunlight the interior of a mottled shell averages 1°C warmer than the interior of an unpigmented shell. It may well be that the ribby shells, characteristic of exposed bank-edge situations, are protected from overheating by the lack of shell pigmentation. Such an ecological correlation between shell color and body temperature has been found in other land snails (Rensch, 1932; Schmidt-Nielson et al., 1971; Yom-Tov, 1971; Heath, 1975). It is also possible that shell pigmentation plays a role in predator avoidance. The mottled shells are initially hard to find, as they hang from bush stems and on blades of grass in the dabbled sunlight and shadow (a clear case of disruptive coloration to our eyes) (Fig. 4). In contrast, the white shells of the ribby morphotype are fairly conspicuous on the stems and leaves of bushes and other plants. Only when they descend to the ground in rocky areas is their coloration at all cryptic. In a second investigation, Quensen has examined Vermeij's (1975) suggestion that sculpturing (ribbing) is a defensive adaptation in snails since it confines the predator's crushing force to the thickest part of the shell. Quensen's preliminary results indicate that, in *Cerion*, overall shell size is more important than ribbing in determining the strength of the shell. Approximately 80 percent of a shell's ability to resist fracture is attributable to shell weight and shell height; interrib shell thickness is more significant than shell thickness at a rib or ribbing density. This does not mean that ribs are unimportant in *Cerion*'s defense, but only that they do not protect the animal from compression applied generally along the sides of the shell. While the identity of *Cerion*'s key predators remains unknown, Woodruff's detailed population studies on Abaco and elsewhere implicate land crabs,

Figure 4. Cryptic nature of mottled coloration. When sunlight is filtering through bushes, the mottled shells are very hard to see (at least for us). Photo taken by J. Martin on northeast coast of Great Abaco.

rats, and possibly a bird. The results of these studies will be reported elsewhere (Woodruff and Quensen, in prep.).

3. Patterns of interaction. Populations of the ribby morphotype once inhabited the bank edge at Eight Mile Rock on the southwest Coast of Grand Bahama (Plate, 1907). In 1936, Clench and Greenway searched extensively for this form in the area where Millspaugh originally collected it. After two weeks they found only a single dead shell on the eastern side of Hawksbill Creek. Clench (1938) concluded that the hurricane of 1935 may have destroyed this colony, as it did a great deal of damage along the entire south coast of the island. In 1963 and 1964, small samples of ribby shells were again found at Freeport and Smith's Point (specimens in the Museum of Comparative Zoology). In September 1972, we spent several days searching the south coast of the island, from Freeport to West End; no *Cerion* were found. This is the only case we know in which a morphotype has apparently become extinct on an entire island.

On Abaco, however, we need only a map of bank edges to predict exactly where the contacts between ribby and mottled morphotypes should occur. The village of Sandy Point (Fig. 5) marks the coastal transition from bank edge to bank interior; here we collected a sample of intermediate morphology. The ribby morphotype inhabits the coast south of Sandy Point, around the southern tip of the island, up to the narrow area known as The Crossing (Fig. 5). Here, the second contact occurs as the interior, mottled populations are squeezed into close contact with ribby animals on the eastern shore. We observed no interactions; a narrow hill, running parallel to the coast, seems to separate the morphotypes com-

pletely. Yet there must be some "leakage" across the hill, for morphometric analysis (see below) demonstrates the intermediate nature of apparently mottled shells at this locality. According to the map, we must predict an interaction around Cherokee Harbor (Fig. 5), for here the coast again switches from bank edge to bank interior. Here, indeed, is the third and by far the most interesting interaction. Ribby populations, extending from the south, encounter mottled populations from the north in an apparently smooth, but local hybrid zone. We shall analyze this zone in detail in the following sections on morphometrics and genetics (see also Woodruff and Gould, in press) since it holds the key to our interpretation of these two taxa.

The current taxonomy of Abaco cerions recognizes seven taxa within these two morphotypes. Ribby populations have been allocated to four species:

1. *Cerion abacoense* Pilsbry and Vanatta, 1895, p. 209. The type specimen (Acad. Nat. Sci. Phila. No. 25337) and all associated museum material (M.C.Z., Harvard University, and Acad. Nat. Sci. Phila.) clearly indicate that this name applies to ribby populations from The Crossing, north to the hybrid zone. These shells are somewhat smaller, lighter with more though weaker ribs than southern samples. Pilsbry and Vanatta list their locality simply as "Abaco Island."

2. *Cerion maynardi* Pilsbry and Vanatta, 1895, p. 210. Again, listed only as "Abaco Island," but we have found this morphology only near Hole-in-the-Wall Light near South Point (southern tip of the island) where ribby shells are larger with very strong and sparse ribs.

3. *Cerion chrysaloides* Plate, 1907, p. 597. The extinct, bank-edge population collected by Millspaugh at Eight Mile Rock on the southwestern coast of Grand Bahama. Shells are considerably smaller than those of other ribby populations, but differ from them in no other evident way.

4. *Cerion lucayanorum* Clench, 1938. A longer and more slender shell with more numerous and finer ribs. From Mores Island (Fig. 3).

These populations are distinct in morphology one from the other. Indeed, all students of *Cerion* (including ourselves) agree that virtually every local population in this peculiar genus has its own recognizable form. (Disagreement centers only on appropriate taxonomic definition.) In this case, we cannot possibly justify any separation into species. We can barely distinguish the far more different ribby and smooth populations on the basis of their patterns of interaction. It is not likely that any reproductive barriers exist among local populations of the same morphotype. (Gould and Paull, 1977, have lumped within-morphotype variation for all cerions from Hispaniola to the Virgin Islands into a single species.) We therefore reject *C. maynardi*, *C. chrysaloides*, and *C. lucayanorum* as synonyms of the first-named form, *Cerion abacoense*. The ribby morphotype of Little Bahama Bank should bear this name, at least until we can determine whether it is homologous with populations of the ribby morphotype on islands of Great Bahama Bank.

At least two, and possibly three, names are available for populations of the mottled morphotype.* The rejected names for the ribby morphotype apply to geographically distinct subpopulations meriting subspecific rank, if we were inclined—as we decisively are not, lest *Cerion* maintain its burden of hundreds of names—to use this category. The "species" of the mottled morphotype, on the other hand, have no geographic definition; they are names

* Things could have been worse. Specimen labels in the Department of Mollusks, United States National Museum, include two additional names, apparently never published by Bartsch. These anagrams of the island—*C. mahaba* (U.S.N.M. No. 179439) and *C. hamaba* (U.S.N.M. No. 369715)—both apply to dwarfed forms of *C. bendalli* inhabiting the northern coast of Grand Bahama Island.

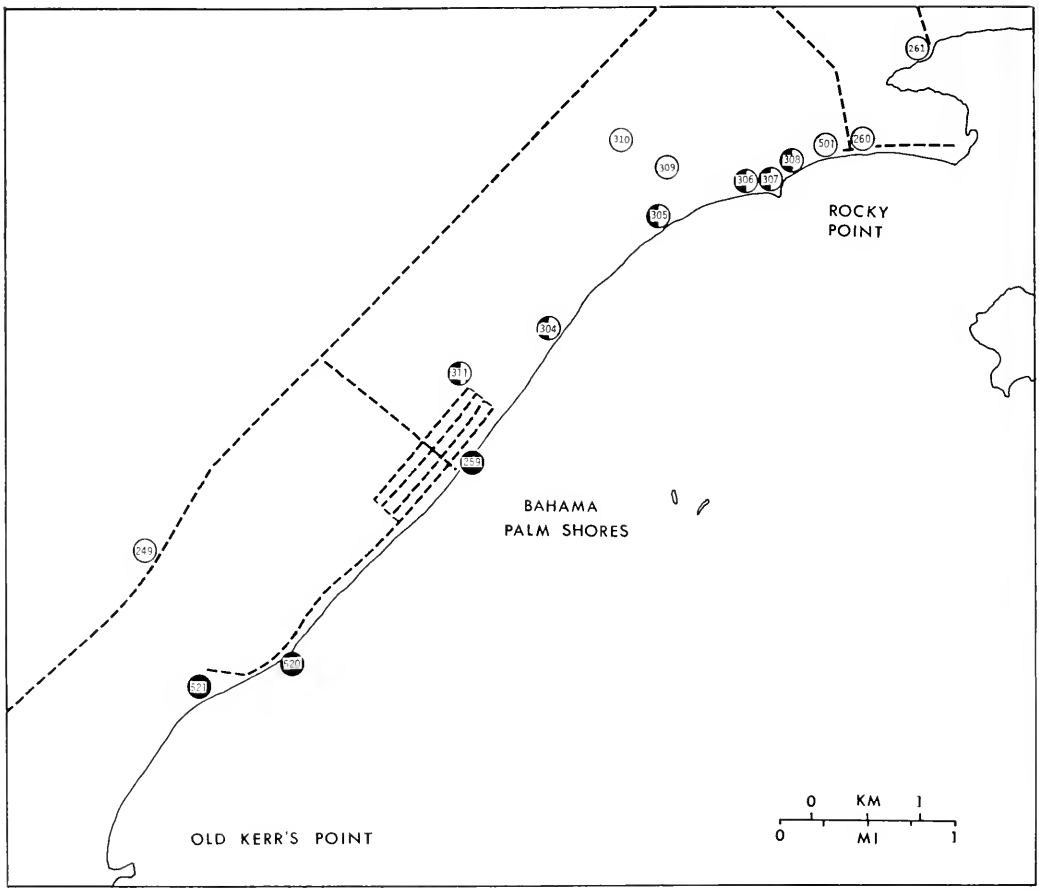

Figure 5a. Area of interaction between *C. bendalli* and *C. abacoense* on southern Great Abaco. Modal morphotype at each locality is indicated: *C. bendalli*, open circle; *C. abacoense*, closed circle; intermediates, half-closed circle.

for minor, recurrent differences in form throughout the range of mottled demes:

1. *Cerion bendalli* Pilsbry and Vanatta, 1896, p. 332. In an uncharacteristic act of lumping (overlumping, in our judgment!) Pilsbry and Vanatta originally defined *C. bendalli* as a subspecies of the ribby *C. abacoense*—though they wrote (1896, p. 333): "This form at first sight looks extremely different from *C. abacoense*, and as we have seen no intermediate examples, it may well prove to be a distinct species." In 1902, Pilsbry returned to his former consistency and elevated *C. bendalli* to specific rank. Pilsbry and Vanatta applied this name to samples of the mottled morphotype with fine ribs.

2. *Cerion oweni* Dall, 1905, p. 443. A name for smooth or very finely ribbed samples of the mottled morphotype; no other characters distinguish it from *C. bendalli*. Dall (1905) recognized three subspecies within *C. oweni* (*C. oweni incisum*, *C.o. vermiculum*, and *C.o. veticulatum*), but these have already been rejected by Clench (1938, p. 328).

3. *Cerion milleri* (Pfeiffer), 1867, p. 129. Pfeiffer applied this name to a small sample

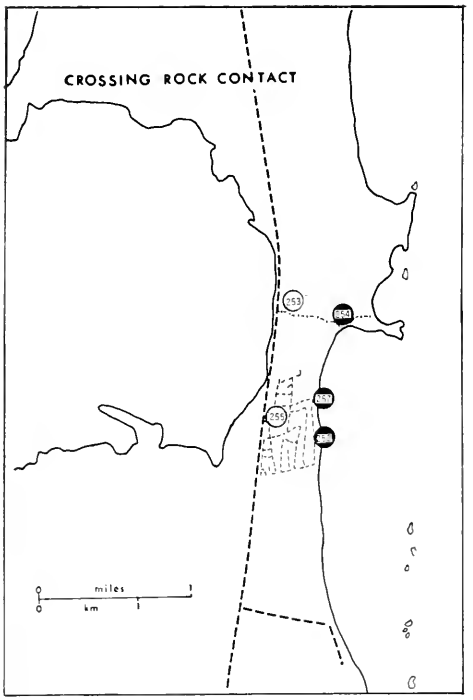

Figure 5b. Area of interaction between *C. bendalli* and *C. abacoense* on southern Great Abaco. Modal morphotype at each locality is indicated: *C. bendalli*, open circle; *C. abacoense*, closed circle; intermediates, half-closed circle.

of mottled shells from "Duck Cay, Exuma Group, Bahama Islands." But Clench (1935, p. 50) noted that the Exumas contain no Duck Cay, while an appropriate islet of this name sits in Cherokee Harbor, Abaco. He therefore supposed that *C. milleri* might be an Abaconian species. If Clench is correct, then *C. milleri*, as the oldest available name, should designate the mottled cerions of Little Bahama Bank. Yet we prefer to leave it in limbo, for we do not know how to verify Pfeiffer's locality; mottled shells are much of a muchness throughout the Bahamas, and occur throughout the Exumas.

We therefore reject *C. oweni* Dall (with its three subspecies) and *C. milleri* (Pfeiffer) and designate the mottled morphotype on Little Bahama Bank as *Cerion bendalli* Pilsbry and Vanatta, 1896.

III. MORPHOMETRICS OF CERION ON LITTLE BAHAMA BANK

A) *Introduction*

We were originally attracted to Cerion because it is such an ideal animal for morphometric study. Like most mollusks, it preserves a complete record of its ontogeny in an accretionary shell. Its particular advantages arise from two properties of growth: 1) The transition between embryonic shell and later accretionary growth is precisely marked by a discontinuity in ribbing and rate of expansion; we therefore obtain an unambiguous, biological criterion for numbering whorls; we take this discontinuity as the beginning of the 0'th whorl. This numbering permits us to define morphometric properties at a variety of standardized stages throughout growth. 2) As it reaches maturity, *Cerion* changes its direction of coiling and, finally, secretes a terminal adult aperture with an expanded and reflexed lip. We can therefore measure the traits of its definitive adult size. (Most mollusks have no stage of terminal growth; we can define neither the mean nor variance of adult characters because we cannot sort ontogenetic from static adult variation.) In *Cerion*, we can compare adult characters with corresponding traits at any stage of growth; in most mollusks, we can define neither set of measures unambiguously.

We have chosen a suite of variables that should measure all of the traits (except color) commonly used to erect taxa within *Cerion*. Our set also defines the major aspects of growth and covariation: size and shape of the embryonic shell, patterns of ribbing, size and shape of juvenile and preadult whorls, number of whorls, measures of final size, and characters of the adult umbilicus and aperture. Although our measures contain some inevitable redundancy, our previous studies clearly demonstrate at least five independent patterns of covariation among them (Gould et al., 1974; Gould and Paull, 1977).

Our measures follow the definition and

protocol of Gould et al. (1974, pp. 522–524) with the exception of 6 and the addition of 20 (used only as the numerator of ratio measure 18 in Gould et al., 1974; we have since determined that it includes interesting, independent information of its own):

1. width of the protoconch
2. width at the end of the fourth whorl
3. total number of whorls (with the termination of the protoconch taken as the 0'th whorl)
4. number of ribs on the fourth whorl
5. number of ribs on the sixth whorl
6. number of ribs in 50 micrometer units at the termination of the first whorl
7. length of the adult shell, apex to lower apertural tip
8. maximum width of the adult shell
9. height of the protoconch
10. total height of the shell at the end of the fourth whorl
11. height from the end of whorl 4 to the end of whorl 6
12. width of the umbilicus
13. width of the apertural lip at its widest point (measured parallel to the plane of the aperture
14. thickness of the apertural lip at its thickest point (measured perpendicular to the plane of the aperture)
15. height of the aperture
16. width of the aperture
17. protrusion of the aperture
18. tilt of the aperture
19. weight of the shell
20. distance from aperture to preceding suture: line EC of Gould et al., 1974, fig. 5, p. 523.

B) *The Basic Pattern*

We chose 52 samples, representing all taxa and habitats, and measured 20 shells from each sample when available—14 samples contain fewer shells, but only 5 of these have fewer than 15 specimens. Localities are listed in the appendix. Forty-eight samples are from our own field collections, 4 from the collection of the Department of Mollusks, Museum of Comparative Zoology, Harvard University [3 of the extinct ribby morphotype ("*C. chrysaloides*") from Grand Bahama, 1 of "*C. lucayanorum*" from Mores Island]. We are more than conventionally grateful to John Hevelin for spending half a year compiling one of the most scrupulously accurate data sets ever assembled in molluscan biometrics.

Many strategies are available for reducing a data set of 20 measurements on nearly 1000 specimens from 52 samples. We decided to treat each sample as a potentially random extract from a single statistical universe, rather than as a definite entity to be separated, if possible, from other groups. This decision—a methodological correlate of our belief that *Cerion* is a single entity with local inhomogeneities led to a factor-analytic model. We computed the mean vector for each sample (Table 1) and performed a Q-mode factor analysis of the 52 items using program CABFAC (Klovan and Imbrie, 1971). We included the following data transformations:

1. percent-range method of equalizing weights. The highest value of each variable receives a value of 100, the lowest becomes 0; others are scaled as a percentage of this range. This is not always (or even often) a desirable method for achieving equality of weights. Suppose, for example, that a trait varies narrowly and randomly among specimens. We would not want such variation to count as much as the wider range of another measure clearly adapted to variation in habitat. But, in this case, our values are well-determined means of samples, not the random error of individual specimens. A stable narrow range may be just as important as a wider one.

2. normalization of vectors. Each vector is rescaled to unit length before the extraction of eigenvalues. This transformation removes the explicit influence of variation in average shell size among samples. (However, the allometric correlates of size may still be expressed as shape.) We preferred to eliminate this explicit variation in size

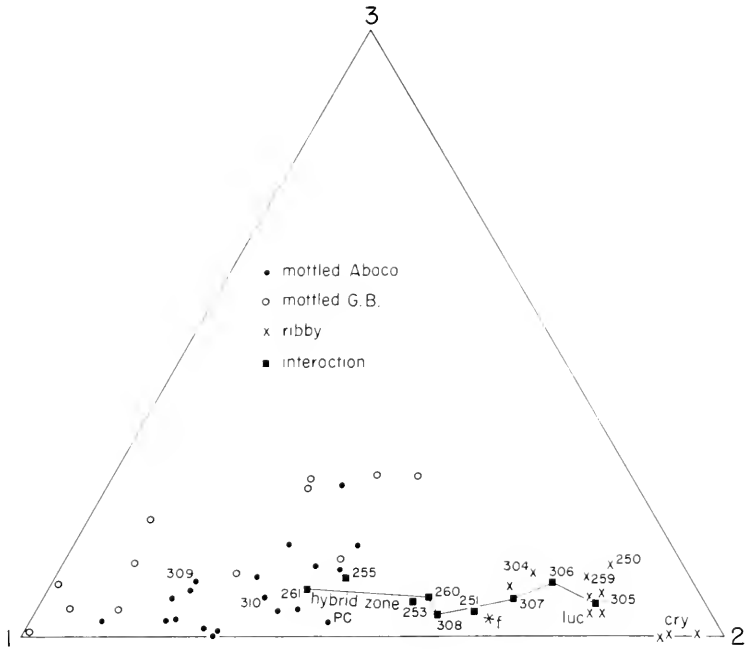

Figure 6. Position of mean vectors for all samples of Little Bahama Bank cerions. This is a triaxial plot of normalized factor loadings for a 3-axis, varimax solution in the Q-mode. These three axes explain 96.3 per cent of all information; the first two axes explain 88 per cent. Ribby and mottled morphotypes are well separated by the first two axes. Mottled samples from Grand Bahama Island have higher projections on the third axis. Closed circles are mottled samples from Abaco; open circles are mottled samples from Grand Bahama; crosses are ribby samples; squares represent samples defined by geography and ecology (not morphology) as inhabitants of zones of interaction between ribby and mottled populations (note their intermediate position in morphology as well); the star represents the single fossil sample from Abaco. The line connects samples of the hybrid zone at Rocky Point in geographical order. pc is the Pongo Carpet sample (mottled, partly convergent upon ribby); f is the fossil sample; cry are "*C. chrysaloides*" (the name applied to ribby samples on Grand Bahama); luc is "*C. lucayanorum*" (ribby sample from Mores Island). Other numbers refer to localities discussed in text.

because it can control so much covariance in a matrix (large shells have high values of almost all variables), and because all morphotypes and areas contain both large and small-shelled samples. We eliminate this pervasive control of size in order to see smaller but more stable influences more clearly. However, we also performed an analysis without normalization and obtained nearly identical results (see below).

Three axes encompass 96.3 per cent of the information in 52 samples; no subsequent axis reaches one per cent. We performed a varimax rotation and computed the factor loadings of all samples upon the three axes (in Q-mode analysis, samples are loadings). CABFAC normalizes the triaxial loadings to permit a plot as a triangular graph.

Figures 6–7 display a remarkable result. All the variation in Little Bahama Bank cerions, the basis of 7 species and a host of subsidiary distinctions, reduces to a matrix not far from rank 2! (Two varimax axes explain 88 per cent of all information.) And the foci of these axes are our two old friends—the ribby and mottled morphotypes in their "pure" form. All intermediate samples from zones of contact—and only these samples—plot in between. Moreover, the minor third axis has its own coherence, for all samples that load strongly upon it (with one excep-

TABLE 1. MATRIX OF MEANS (IN MM, G, OR COUNTS) FOR ALL SAMPLES TREATED BIOMETRICALLY IN THIS WORK. (CONVERTED FROM ORIGINAL DATA IN MICROMETER UNITS—VARIABLES 1, 9, 13, 14 MULTIPLY BY 18.0; VARIABLES 2, 10, 11, 12, 15, 16, 17, 20 MULTIPLY BY 8.0 FOR MICROMETER UNITS. ALL BIOMETRICAL WORK DONE IN MICROMETER UNITS. DATA IN THIS FORM AVAILABLE FROM AUTHORS.)

Sample Number	Location	Proto-conch width	4th whorl width	total whorls	4th ribs	6th ribs	1st ribs	height	width	Proto-conch height
92367	Grand Bahama:	2.74	7.79	7.50	21.33	19.67	6.83	22.77	9.57	1.26
247236	ribby	2.84	8.16	7.41	22.85	20.80	7.08	23.90	10.11	1.38
250620		2.78	8.23	7.33	23.47	21.67	7.63	23.21	9.96	1.39
212	Grand Bahama:	2.93	8.20	8.30	79.83	57.60	17.00	23.99	9.05	1.19
211	mottled	2.94	8.50	8.71	48.00	44.00	11.45	26.96	10.44	1.30
208		3.03	8.81	8.29	60.60	52.20	12.53	25.13	9.81	1.26
204A		3.29	9.65	9.20	53.83	47.78	12.58	32.09	11.86	1.39
204B		3.15	9.41	8.63	48.75	44.05	12.05	27.86	11.28	1.27
207		3.09	8.22	9.28	86.00	77.95	16.13	28.91	10.79	1.35
209		2.79	7.52	8.99	100.00	81.00	13.58	23.05	9.17	1.27
205		3.11	9.25	8.80	73.10	68.80	12.42	29.86	11.53	1.25
202		3.19	9.47	8.51	71.30	65.65	13.65	29.74	11.61	1.39
199		2.71	7.27	7.20	94.88	73.31	16.83	20.07	8.08	1.32
200		3.15	8.37	8.71	99.25	78.50	18.10	27.11	9.93	1.32
201		3.03	8.33	8.93	93.90	83.35	15.60	27.68	10.18	1.27
213	Little Abaco	3.22	9.36	8.70	85.55	75.55	15.78	31.27	11.06	1.32
214		3.13	9.14	8.38	100.85	86.65	17.93	28.05	10.58	1.22
216		3.04	8.81	8.17	93.70	73.05	17.85	26.15	10.08	1.29
217	Great Abaco	3.17	9.18	8.21	95.56	71.28	16.09	28.83	11.00	1.35
218		3.00	8.98	9.04	80.25	60.40	14.85	32.61	11.37	1.28
316		2.85	8.03	7.93	58.45	41.15	13.85	24.68	9.63	1.34
228		3.02	8.31	7.89	81.45	63.10	14.43	24.27	9.61	1.50
229		3.05	8.39	8.02	79.21	67.33	15.97	25.31	9.87	1.47
230		3.00	8.08	8.43	95.95	85.21	18.23	26.08	9.82	1.41
231		3.05	8.74	8.85	78.80	61.10	14.82	30.49	11.47	1.48
233		3.42	9.06	9.25	96.00	76.00	16.50	31.10	11.20	1.54
240		3.10	8.89	8.71	80.65	62.65	15.72	29.56	10.83	1.27
247		3.18	8.81	7.88	103.20	75.35	17.30	25.26	10.15	1.26
246		3.02	8.38	8.42	47.68	40.00	10.58	25.92	9.93	1.55
243		3.29	8.97	8.53	100.00	84.06	17.91	27.08	10.61	1.31
245		3.38	9.66	8.23	95.70	79.35	17.05	28.14	11.00	1.37
244		3.25	9.17	7.79	97.80	74.85	14.90	25.23	10.24	1.24
261		3.21	9.73	8.55	94.71	78.57	15.36	30.26	10.99	1.33
260		3.13	9.40	7.84	58.85	49.45	12.63	26.73	11.13	1.31
308		3.08	9.23	7.68	53.50	45.65	12.90	25.76	10.96	1.31
307		3.02	9.38	7.84	46.65	41.10	11.40	26.97	11.39	1.35
306		3.17	9.95	7.93	44.10	38.90	10.95	28.68	12.18	1.35
310		3.39	10.53	8.13	95.82	74.90	15.78	27.60	11.82	1.39
309		3.38	9.78	8.12	98.33	89.56	16.70	28.88	11.38	1.37
305		3.12	9.95	7.76	39.80	34.65	10.53	28.83	12.15	1.37
304		3.11	9.82	8.08	44.40	39.90	11.43	29.52	12.30	1.33
311		3.04	9.51	7.94	44.20	39.15	10.95	27.52	11.45	1.35
259		3.08	9.68	8.22	38.80	34.45	9.95	31.37	12.83	1.36
249		3.63	10.35	9.46	82.05	74.95	14.27	34.40	12.71	1.44
254		3.29	10.49	7.87	38.55	33.05	9.18	29.97	12.70	1.44
303		3.29	10.38	7.88	43.40	37.47	9.85	29.40	12.58	1.35
253		3.34	9.51	8.05	67.50	44.45	13.20	27.49	10.91	1.30
255		3.18	9.10	8.31	73.50	48.60	14.40	28.14	10.53	1.25
257		3.11	10.12	8.04	38.55	32.65	9.15	30.10	12.72	1.35
251		3.01	9.07	8.05	53.55	41.65	12.55	26.98	11.20	1.36
250		3.37	10.90	8.79	26.20	24.85	8.53	34.35	13.76	1.52
LUC	Mores Island	3.09	9.42	8.10	42.02	32.10	10.40	30.26	11.62	1.43

TABLE 1 [CONTINUED]

4th whorl height	4th–6th height	umbilical width	lip width	lip thickness	aperture height	aperture width	protrusion	tilt	weight	aperture-suture
6.65	10.92	4.63	1.22	1.09	8.83	7.25	2.50	1.64	.79	4.42
6.88	11.64	4.55	1.23	1.09	9.31	7.73	2.47	1.82	.73	5.13
6.84	11.52	4.52	1.22	.88	9.05	7.42	2.10	1.82	.68	4.83
6.15	9.71	4.30	.98	.65	8.81	7.15	2.62	2.15	.49	4.51
6.08	9.87	4.64	.91	.63	9.38	8.01	2.43	1.98	.71	5.51
6.25	10.01	4.38	1.13	.73	9.12	7.41	2.54	2.05	.62	5.01
6.26	10.17	5.48	1.21	1.14	11.10	8.99	3.15	1.95	1.49	6.30
6.03	10.28	4.93	1.11	.84	10.19	8.50	2.81	2.06	.96	5.73
6.10	8.79	4.94	.95	.62	9.76	8.10	2.31	1.87	.82	5.42
5.38	7.49	4.12	.85	.44	7.86	6.63	2.13	2.21	.37	3.79
6.22	10.59	5.19	.98	.69	10.73	9.07	2.78	2.04	1.12	6.18
6.57	11.06	5.14	.99	.75	10.65	8.96	2.64	2.11	1.36	6.23
6.60	10.03	3.13	.71	.52	7.51	6.49	1.93	2.15	.41	5.05
6.68	9.53	4.49	.96	.63	9.49	7.68	2.76	2.30	.81	5.49
6.24	9.42	4.74	.99	.74	9.72	7.87	2.75	2.20	.83	5.39
6.59	11.10	5.59	1.38	1.47	11.94	9.29	3.35	2.19	1.48	6.01
6.42	10.70	5.19	1.14	.91	10.77	8.61	3.06	2.40	1.21	5.41
6.65	10.49	4.68	1.06	.85	10.18	8.21	2.86	2.28	.89	4.91
6.74	11.57	4.96	1.18	1.20	11.42	9.18	3.23	2.40	1.11	5.85
6.50	10.73	5.91	1.46	1.32	12.61	10.13	4.01	2.81	1.34	5.96
6.44	10.63	4.23	1.13	1.04	9.41	7.94	2.64	2.00	.84	5.24
6.72	10.44	4.49	1.06	.84	9.38	8.11	2.93	2.65	.62	4.82
6.69	10.63	4.81	.99	.83	9.51	8.24	2.69	2.19	.69	5.12
6.35	9.88	4.73	.90	.74	9.44	7.76	2.62	1.99	.69	5.14
6.64	10.08	6.03	.96	.83	11.16	9.08	2.74	1.86	.98	5.69
6.66	9.43	5.25	1.47	.92	11.50	9.34	2.78	2.26	1.12	5.63
6.34	10.11	5.95	1.13	1.21	11.18	9.05	3.88	2.49	1.15	5.26
6.58	10.96	3.83	1.02	1.06	9.93	8.37	2.67	2.19	1.00	5.99
7.38	10.45	4.43	.98	1.38	9.95	8.08	3.29	2.39	1.12	5.89
6.48	10.06	4.93	.96	1.11	9.93	8.31	3.14	2.31	1.13	5.28
6.83	11.58	5.13	1.06	1.17	10.58	9.11	3.15	2.15	1.15	5.88
6.89	11.18	4.43	.85	.87	9.78	8.24	2.95	2.40	.87	5.35
6.81	11.30	5.63	1.12	1.09	11.25	9.08	3.06	2.09	1.39	5.85
6.73	11.63	5.63	1.09	.84	10.73	8.71	3.00	2.03	1.06	5.44
6.77	12.08	5.16	.95	.79	10.23	8.40	2.71	2.05	.95	5.82
6.74	12.04	5.31	1.17	.89	10.59	8.97	2.82	1.95	1.13	6.20
6.84	12.42	5.98	1.20	1.07	11.28	9.23	2.98	1.85	1.58	6.27
6.47	11.73	5.56	1.14	.67	10.53	8.84	2.89	2.27	.76	5.41
6.26	10.40	5.34	1.01	.72	10.50	8.74	2.67	2.20	.86	5.58
7.04	13.28	6.18	1.15	1.04	11.76	9.31	3.18	1.83	1.71	6.15
6.76	12.16	5.81	1.32	1.25	11.95	9.72	3.22	2.37	1.70	6.53
6.62	11.73	5.60	1.21	1.01	11.21	8.95	3.11	2.20	1.08	5.84
6.84	12.73	6.71	1.54	1.61	12.91	10.29	3.51	2.41	2.13	6.24
6.27	10.30	6.19	1.15	.88	12.39	10.19	3.41	2.21	1.36	6.73
7.54	13.26	5.95	1.40	1.38	12.23	10.29	3.36	2.50	1.83	6.15
7.15	13.35	6.33	1.53	1.55	12.37	10.23	3.40	2.12	1.48	6.29
6.98	11.49	5.37	.99	1.08	10.89	9.07	3.07	2.21	1.01	5.48
6.80	10.98	5.18	.98	.98	10.72	8.75	3.15	1.99	.98	5.59
7.20	12.87	6.23	1.61	1.15	12.53	10.43	3.24	2.14	1.80	5.89
6.80	11.41	4.79	1.15	1.43	10.66	8.93	2.95	2.31	1.34	5.82
7.20	12.11	6.62	1.93	1.84	13.14	11.23	3.73	2.12	2.07	6.41
7.36	12.48	5.89	1.55	1.60	11.71	9.77	3.49	2.19	1.54	5.99

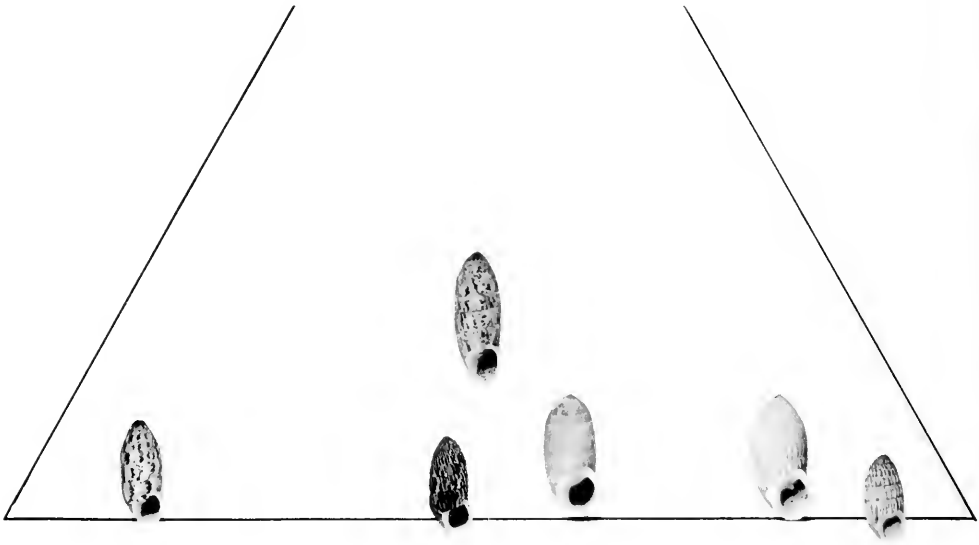

Figure 7. Representative shells for samples depicted in same positions on Fig. 6. At bottom line, left to right: locality 230 (typical *C. bendalli*); locality 316 (convergent *C. bendalli* from Pongo Carpet); locality 253 (intermediate shell from The Crossing); locality 254 (*C. abacoense*); "*C. chrysaloides*" from Grand Bahama. Above: locality 204 (*C. bendalli* from Grand Bahama).

tion) are *C. bendalli* from Grand Bahama. The third axis divides samples of *C. bendalli* (the mottled morphotype) into its two isolated areas.

The matrix of factor scores (Table 2) permits us to infer the basis of separations in Figure 6 (consult the matrix of mean values—Table 1—for the raw information). Only three variables score highly on the first axis. (This axis serves as a dimension of reference for the mottled morphotype, *C. bendalli*. Samples of *C. bendalli* load strongly upon it, and weakly upon the second axis—see Figs. 6–7.) Not surprisingly, these three variables are the ribbing measures 4–6. (Mottled samples always have much weaker ribs than ribby samples, but the ribs are always far more numerous in mottled samples; all our ribbing measures are counts.) No other variable so consistently separates *C. bendalli* from *C. abacoense*. The second axis, with it high loadings for *C. abacoense* (the ribby morphotype), contains high scores for most measures of final size and whorl size. (The scores are negative in this case. The sign is of no particular importance, since it only indicates the direction of the reference vector. The pattern of scores and loadings would not change if the vector pointed 180° in the opposite direction, thus reversing all the signs.) To some extent, this suite of high scores only mirrors the distinction by ribbing made on the first axis. Since reference vectors are normalized, a small number of ribs must lead to a greater contribution to the vector from other measures. But the ordering of intensity within this group of high scores clearly distinguishes the primary characteristics of *C. abacoense*. Shells of *C. abacoense* do not have more whorls than *C. bendalli* (note small positive score for whorl number—primarily due to low whorl numbers of small "*C. chrysaloides*"), and they are not generally taller (modest score for shell height). The highest scores belong to measures of size that best distinguish the two taxa by higher mean values

TABLE 2. FACTOR SCORES OF ORIGINAL VARIABLES UPON THE THREE FACTOR AXES USED TO DEPICT SAMPLES IN FIGURE 6.

1. protoconch width	0.155	−0.102	−0.206
2. 4th whorl width	0.070	−0.228	−0.191
3. total whorls	0.280	−0.007	−0.387
4. 4th ribs	0.536	0.162	0.122
5. 6th ribs	0.491	0.149	0.030
6. 1st ribs	0.492	0.108	0.153
7. height	0.129	−0.187	−0.292
8. width	0.053	−0.247	−0.182
9. protoconch height	0.078	−0.204	0.283
10. 4th-height	0.072	−0.341	0.514
11. 4th–6th height	0.025	−0.362	0.344
12. umbilical width	0.071	−0.273	−0.149
13. lip width	−0.018	−0.236	0.041
14. lip thickness	−0.025	−0.272	0.122
15. aperture height	0.062	−0.258	−0.182
16. aperture width	0.047	−0.226	−0.175
17. protrusion	0.087	−0.200	−0.106
18. tilt	0.239	−0.040	0.102
19. weight	−0.003	−0.242	−0.158
20. aperture-suture	0.119	−0.265	−0.036

for *C. abacoense*. Shells of *C. abacoense* are heavier (measure 19), and wider both in spire (8) and umbilicus (12); they have a larger aperture (15–16) with a more strongly developed lip (13–14); finally, they are taller at standardized whorl numbers during middle portions of ontogeny (10–11). Thus, most of the information in this large matrix reduces to a single contrast between mottled (*C. bendalli*) and ribby (*C. abacoense*) morphotypes.

The third axis contains only 8.2 per cent of the total information, but it also displays a significant separation *within* the mottled morphotype, *C. bendalli*. With a single exception (sample 249, a peculiar, very large and many-whorled, interior sample of Abaconian *C. bendalli*), all samples with strong loadings are from Grand Bahama. Factor scores for this axis display a pattern of covariation found throughout the genus (Gould *et al.*, 1974; Gould and Paull, in press): whorl number (3) and shell height (7) are in negative association with measures of size at standardized whorl numbers. Shells become large either by growing large whorls (2, 10–11) or many whorls (3 and 7). Shell height reflects whorl number because shells add height but not width during later growth; maximum width is reached early in ontogeny in this genus named for a beehive. If final size can vary only within narrow limits, then these two alternate pathways to a given size must covary negatively. The primary geographic differentiation within *C. bendalli* on Little Bahama Bank has apparently followed this common pattern of covariance. Populations on Grand Bahama have taken the route of small whorls leading to high shells and many whorls (high scores for whorl number and shell height are matched by high loadings of the same sign for Grand Bahamian samples—Table 2 and Figs. 6–7). Abaconian samples reach the same sizes with fewer, larger whorls.

C) *Coherence of Regional and Local Patterns of Variation Within Morphotypes*

Our consistent discovery of coherent, broadly regional patterns of variation provides the primary datum for our rejection of the traditional view about *Cerion*—that its geographic variation is a "crazy-quilt" formed by haphazard shifting about of hundreds of species via hurricanes. We have never failed to detect a hierarchy of geographic coherence:

i) broad contiguous regions including several islands have distinctive morphologies. *C. striatellum*, the only *Cerion* throughout the eastern regions of its range (Hispaniola to the Virgin Islands), exhibits a clinal pattern of variation with increasing departure from "normal" morphology away from major centers of distribution in Cuba and the Bahamas (Gould and Paull, 1977). *Cerion uva*, the only species on the outlying islands of Aruba, Bonaire, and Curaçao, is sufficiently distinct to warrant its own subgenus in the traditional classification (Pilsbry, 1902).

ii) islands within broad regions are unambiguously, if subtly, distinct. The most important discriminator of eastern cerions, the first canonical axis of 23 samples, un-

covers the clinal pattern reported above (Gould and Paull, 1977), but subsequent axes clearly sort each island from all others with no overlap. *Cerions* of Aruba, Bonaire, and Curaçao also cluster by island (Baker, 1924; Gould, 1969).

iii) contiguous geographic subregions within islands can also be identified by very minor, but thoroughly consistent, patterns of character means and covariation; the more isolated the subregion, the more distinct the morphology. The narrow "waist" of Curaçao, for example, separates populations of *C. uva* into two distinct groups (Gould, 1969).

We will not venture any speculation about adaptive values, importance of founders, etc., but it does seem clear that geographic isolation is the primary correlate of morphological variation within taxa of *Cerion*. These patterns of geographic variation, by their stability and coherence, also indicate that episodes of transport and colonization have been rather less frequent than tradition dictates.

The geographic variation of Little Bahama Bank cerions conforms fully with these new expectations of coherence. We confine our comments to the mottled morphotype, *C. bendalli* since regional patterns have never been demonstrated within it before. We do not have enough samples of *C. abacoense*, and we have not seen two of its three major populations in the field—Mores Island and the apparently extinct population of Grand Bahama. Nonetheless, traditional taxonomy has already recognized the geographic coherence of four areas—Grand Bahama, Mores Island, southern tip of Abaco, and southeastern coast of Abaco. We reject the names, but confirm the distinction in our morphometric analysis.

1. Separation of *C. bendalli* from Grand Bahama and Abaco. Figure 6 demonstrates the morphological distinction of the two islands (see discussion above). We are particularly pleased to note that the basis of separation is not a few static adult features of unknown significance, but alternate pathways of a major pattern in covariance found throughout the genus.

TABLE 3. FACTOR SCORES OF ORIGINAL VARIABLES UPON THE FIRST Q-MODE AXIS FOR *C. bendalli* FROM GRAND BAHAMA.

1. protoconch width	0.249
2. 4th whorl width	0.289
3. total whorls	0.188
4. 4th ribs	–0.129
5. 6th ribs	–0.077
6. 1st ribs	–0.075
7. height	0.259
8. width	0.295
9. protoconch height	0.189
10. 4th height	0.178
11. 4th–6th height	0.245
12. umbilical width	0.255
13. lip width	0.212
14. lip thickness	0.181
15. aperture height	0.282
16. aperture width	0.311
17. protrusion	0.201
18. tilt	–0.051
19. weight	0.240
20. aperture-suture	0.301

2. The regional pattern on Grand Bahama. As we collected on Grand Bahama, it seemed to us that patterns of morphology followed general trends throughout the island. Shells of northern samples were small, particularly in coastal populations near mangrove areas. (This is another consistent pattern within the mottled morphotype. Mottled shells are also dwarfed on the low, bank-interior western coasts of Andros, Eleuthera and Great Exuma).

We used trend surface analysis to test a hypothesis of simple regional patterns. This technique widely employed by geologists but little known among biologists (Marcus and Vandermeer, 1966), performs a multiple regression analysis of a morphological feature (dependent variable) against independent variables expressed as geographic coordinates. Increasingly more complex surfaces are obtained by adding terms in a polynomial expansion of the X and Y coordinates. Predictions from the best fit surface are compared with actual values to generate a vector of residuals that defines

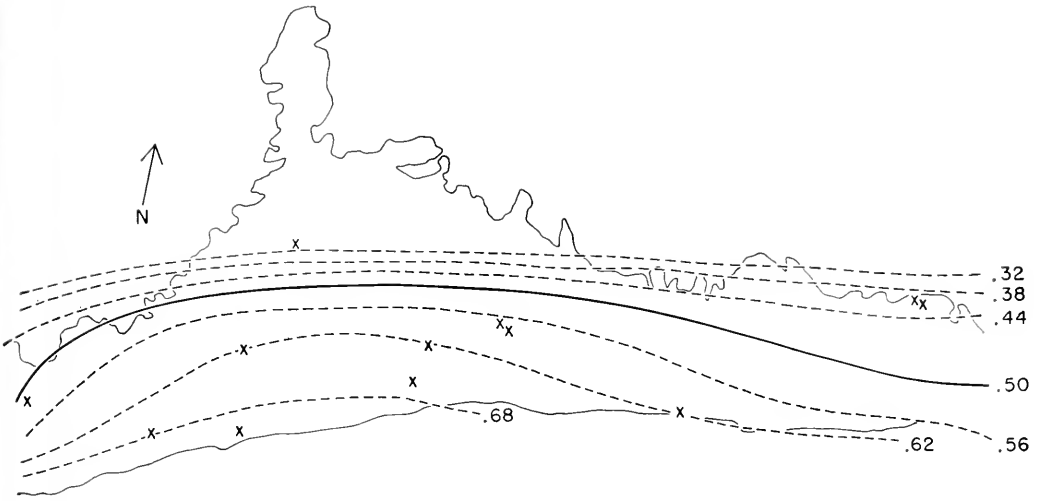

Figure 8. Third order trend surface analysis (with interaction terms suppressed) for projection of Grand Bahamian samples on the first varimax axis of a Q-mode analysis; this is a "size" axis based on all variables. Note simple pattern of increasing size from north to south, with more rapid transition near the northern coast, where dwarfed samples pass rapidly to interior samples of modest size. Actual localities indicated by crosses. This smooth variability has, in the past, been parcelled among three separate species defined only by differences in size.

"goodness of fit." The "art" of trend surface analysis involves the selection of a fit that explains enough information, yet remains sufficiently simple to represent a truly regional pattern. Points can be fit exactly with polynomial surfaces of sufficiently high order. We used the program of Lee (1969).

We decided not to use the mean of individual characters as dependent variables, but a value expressing major determinants of covariance among samples. Consequently, we performed a Q-mode factor analysis of all *C. bendalli* samples from Grand Bahama and used loadings on the first varimax axis (for a three-axis solution) as the dependent variable. This single axis encompasses 57.2 per cent of the variance among 20 characters for the 12 samples. Factor scores of variables upon it (Table 3) show that it represents a fairly "pure" size axis, with high and similar loadings for measures of final size and whorl size. (We do not detect the common negative interaction here, because we do not consider alternate pathways to a similar final size. We have, instead, the opposite situation—a wide range of mean shell size from very small on the north coast to quite large elsewhere. The dwarfed shells have both few whorls and small whorls.)

The first order fit alone has a multiple correlation of .82 for a coefficient of determination, $r^2 = .67$. A simple sloping plane encompasses ⅔ of all geographic variation expressed by the most important single dimension based on all 20 measured characters. As expected, the axis runs almost due E-W with smaller values to the north. Figure 8 represents our highest surface, a third order fit with interaction terms suppressed (X_1X_2, $X_1^2 X_2$, and $X_1X_2^2$—we did not have enough sample points for the degrees of freedom needed to fit them). This surface yields a multiple correlation of .934, for a coefficient of determination, $r^2 = .87$. Even at this level of potential complexity, the surface represents a surprisingly smooth cline from small northern shells to larger southern shells. Contour lines follow the

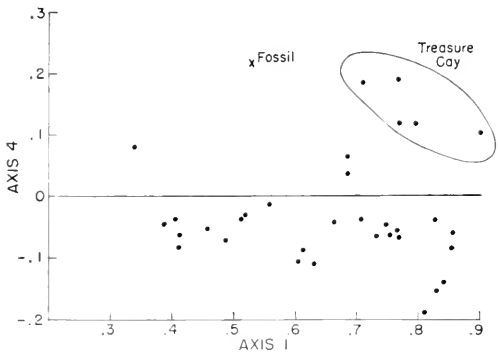

Figure 9. Factor loadings on the first and fourth axis for all samples of Little Bahama Bank cerions. Although the fourth axis explains less than 1 per cent of the total variance among samples, it separates both the Treasure Cay populations and the single fossil sample from all others.

island itself, while bunching of lines at the northern coast indicates the rapid transition from coastal dwarfs to interior shells of modest size that we observed in the field. (Though we had noticed the coastal phenomenon, we did not expect the regional pattern to be so simple.) We detected no geographic pattern in the vector of residuals.

3. Distinction of subareas on Abaco. With more than 30 samples of *C. bendalli* from Abaco, we could detect more local patterns of distinction, also correlated with geographic isolation.

i) small, ribby shells of Pongo Carpet. We have already reported in detail on a semi-isolated coastal area well within the range of *C. bendalli* (Gould, Woodruff, and Martin, 1974). Here, along nearly 7 km of eastern coast, we find a small, heavy, fairly ribby morphology partly convergent on *C. abacoense*. (We included only one Pongo Carpet sample in this study; it has the highest loading of any pure *C. bendalli* sample upon the *C. abacoense* axis—Fig. 6.) This Pongo Carpet morphology is most distinct in its southern area of greatest isolation, and varies in a clinal fashion towards "normal" morphology as it approaches the northern zone of contact. It cannot be distinguished genetically from surrounding populations of standard morphology. In fact, it shares *with* these surrounding normal populations the only distinctive genetic marker (the rare Mdh-2^a allele) of its area—Mdh-2^b is fixed in all other populations of *C. bendalli*. Although these Pongo Carpet shells clearly merit specific distinction on all previous criteria, we cannot regard them as any more than a local variant within a coherent taxon.

ii) populations on Treasure Cay. The difference between statistical and biological significance is rarely appreciated. Morphometricians routinely ignore axes of variation that encompass too little variation to win statistically significant distinction from zero. Yet minor patterns can be very real in a biological sense. Suppose that we have a large matrix with many samples and variables, and that a few samples from a geographically isolated region gain distinction from all others by consistent differences in just a few covarying characters. Suppose also that this distinction is not evident in qualitative observation. The information recorded by this distinction may include far less than 1 per cent of the total matrix; yet it is highly significant from a biological point of view, especially since it is so easily missed in raw data or qualitative observation. The criterion for importance must be correlation with geography, not per cent of information.

We offer such a case in the semi-isolated samples of Treasure Cay (Fig. 3). The fourth axis of our Q-mode analysis for all samples encompasses only 0.95 per cent of all information. Yet a plot of loadings upon the fourth axis clearly separates all Treasure Cay samples from all others with no overlap (Fig. 9). Loadings for the Treasure Cay samples never exceed 0.2, so the distinction arises from less than 4 per cent of the information (squared loading) in these populations. Factor scores for this axis (Table 4) indicate that the separation of these samples arises from their high values for protoconch height and, to a lesser extent, whorl number.

iii) temporal variation. The carbonates of Little Bahama Bank islands are largely marine, and we do not find the soil zones with abundant fossil cerions so common on other islands. But we did collect one fossil sample from an aeolianite in a cut on the road leading to Snake Cay. We are especially pleased to report that this sample can be distinguished clearly from all modern populations, though its general appearance links it unambiguously with living forms of its area. As a strongly and fairly sparsely ribbed sample of general *C. bendalli* shape, its mean morphology gives it an intermediate position in the essential distinction of the two morphotypes (Fig. 6). Its uniqueness is apparent in Fig. 8. It shares, with Treasure Cay samples, the joint high values of protoconch height and whorl number (in fact, its loading on the fourth axis is maximal among all samples), but it differs from them in its weaker loading on the first axis (i.e., its greater affinity with the ribby morphotype).

The study of fossil cerions is yielding important information on the stability of modern patterns of geographic variation within taxa. In all three cases studied so far, fossil samples share the same basic morphology of modern populations, but the fossils occupy presently unrealized portions of the morphological spectrum (*C. rude* of St. Croix vs. all living eastern cerions, Gould and Paull, 1977; *C. uva* from Indian shell middens on Curaçao, Gould, 1971; and this Snake Cay Road sample).

A note on technique: A potentially valid objection has been raised against much work in multivariate morphometrics: available techniques for separation are now so numerous and varied that proper selection may be able to affirm nearly any a priori preference. Robust conclusions may require the joint confirmation of several techniques. Readers may criticize our distinctions by pointing to unusual features of our factor analytic model; we use a Q-technique in I-space while most workers prefer more conventional R-mode analysis in A-space

TABLE 4. FACTOR SCORES FOR THE 4TH Q-MODE AXIS TO ILLUSTRATE THE BASIS OF DISTINCTION (IN COVARIANCE) FOR THE TREASURE CAY SAMPLES.

1. protoconch width	−0.131
2. 4th whorl width	−0.243
3. total whorls	0.477
4. 4th ribs	−0.097
5. 6th ribs	−0.012
6. 1st ribs	−0.131
7. height	0.118
8. width	0.015
9. protoconch height	0.735
10. 4th height	0.036
11. 4th–6th height	−0.212
12. umbilical width	0.044
13. lip width	0.089
14. lip thickness	−0.011
15. aperture height	−0.084
16. aperture width	−0.068
17. protrusion	−0.159
18. tilt	−0.090
19. weight	−0.114
20. aperture-suture	−0.026

(Sneath and Sokal, 1973, p. 116). We normalize vectors to eliminate size explicitly, while most studies include these differences. Finally, we equalize weights of variables with an uncommon transformation, while most studies use raw data or transform with different techniques. Consequently, we redid the analysis in the R-mode with no normalization or character weighting (using BMD program P4M).

The factor loadings (Table 5) display the same pattern as the factor scores of our Q-mode analysis with two interesting exceptions, one expected. The first axis of the R-mode analysis reflects shell size, the variation explicitly eliminated in our Q-mode analysis. The fourth axis displays a pattern of covariance often seen in *Cerion* (Gould *et al.*, 1974), but not encountered in our Q-mode analysis. We find joint high loadings for four variables: apertural protrusion and tilt (17–18) and lip width and thickness (13–14). When we specified our measures before beginning this study, we selected these as potentially correlated traits expressing the intensity of changes in

TABLE 5. FACTOR LOADINGS OF ORIGINAL VARIABLES FOR AN R-MODE ANALYSIS OF ALL LITTLE BAHAMA BANK SAMPLES.

	1	2	3	4	5
1. protoconch width	0.789	0.441	0.016	–0.021	0.190
2. 4th whorl width	0.931	–0.037	0.226	0.013	0.018
3. total whorls	0.329	0.288	–0.864	0.074	0.108
4. 4th ribs	–0.150	0.943	–0.195	0.083	–0.071
5. 6th ribs	–0.085	0.927	–0.268	–0.006	–0.048
6. 1st ribs	–0.144	0.918	–0.172	0.087	–0.078
7. height	0.900	0.000	–0.332	0.189	0.136
8. width	0.941	–0.251	0.015	0.033	0.099
9. protoconch height	0.200	–0.120	0.017	0.043	0.955
10. 4th height	0.305	–0.302	0.698	0.272	0.388
11. 4th–6th height	0.541	–0.412	0.709	0.102	–0.018
12. umbilical width	0.876	–0.269	–0.051	0.150	0.038
13. lip width	0.565	–0.536	0.001	0.407	0.164
14. lip thickness	0.485	–0.437	0.202	0.593	0.166
15. aperture height	0.909	–0.167	0.021	0.328	0.076
16. aperture width	0.910	–0.162	0.062	0.300	0.138
17. protrusion	0.689	–0.071	0.020	0.648	–0.018
18. tilt	0.090	0.407	0.019	0.809	0.017
19. weight	0.822	–0.318	0.113	0.299	0.072
20. aperture-suture	0.849	–0.070	0.135	0.023	0.147

growth that mark secretion of the adult aperture (intense change in coiling direction should be associated with a stronger lip). We are gratified to see their joint association on an axis mathematically independent of shell size. It would be less enlightening to find that intense development correlated only with large shell size. The association of size and adult development exists to be sure (13, 14, and 17 also load highly on the size axis), but the fourth axis displays the partial independence of adult development.

The other axes are essentially identical with the factor scores of our Q-mode analysis. Axis 2 reflects the differences in ribbing that produced the basic separation of mottled and smooth morphotypes in our Q-mode analysis (axis 1); axis 3 records the negative association of whorl number and shell height with measures of whorl size that separated Grand Bahamian and Abaconian *C. bendalli* in our Q-mode analysis (axis 3); finally, axis 5 makes the same separation of the Treasure Cay and Snake Cay Road fossil samples from all others, primarily on the basis of protoconch height.

When we consider factor scores to see how these R-mode axes sort samples, we find virtual identity with our loadings of Q-mode analysis. The first axis is different, since we eliminate its effects by normalization of sample vectors in our Q-mode analysis. The R-mode first axis merely sorts samples by shell size—a biologically unenlightening distinction in this case. But axes 2, 3, and 5 make the same separations as corresponding axes in the Q-mode analysis. The correlation coefficients (at N = 52) for R-mode scores with Q-mode loadings for corresponding axes are .87 for R-mode 2 with Q-mode 1 (ribbing) to separate the morphotypes; .60 for R-mode 3 with Q-mode 3 (negative interaction of whorl number and whorl size to separate Grand Bahama and Abaco *C. bendalli*); .72 for R-mode 5 with Q-mode 4 (to separate Treasure Cay and Snake Cay Road fossil samples from all others). We are therefore confident that our Q-mode patterns identify real and important distinctions in nature, robust with respect to techniques used to identify them, and not artifacts of unusual multivariate procedures.

TABLE 6. UNIVARIATE ANOVA FOR DISCRIMINATORY POWER OF ORIGINAL VARIABLES IN SAMPLES OF THE HYBRID ZONE AT ROCKY POINT. UNIVARIATE F-RATIOS WITH 4 AND 89 DEGREES OF FREEDOM.

Variable	among mean sq.	within mean sq.	F-ratio	Probability
1. protoconch width	23.33	9.59	2.43	0.5242E–01
2. 4th whorl width	136.52	20.35	6.71	0.2163E–03
3. total whorls	0.25	0.14	1.83	0.1299E+00
4. 4th ribs	1046.82	32.45	32.26	0.1014E–07
5. 6th ribs	608.14	18.56	32.77	0.9304E–08
6. 1st ribs	18.53	2.76	6.72	0.2131E–03
7. height	36.94	2.80	13.22	0.2309E–05
8. width	5.87	0.32	18.27	0.2895E–06
9. protoconch height	5.64	6.46	0.87	0.5149E+00
10. 4th height	16.83	13.50	1.25	0.2963E+00
11. 4th–6th height	3.84	0.99	3.89	0.6083E–02
12. umbilical width	265.17	29.25	9.07	0.2865E–04
13. lip width	59.04	18.88	3.13	0.1843E–01
14. lip thickness	85.70	19.15	4.47	0.2774E–02
15. aperture height	465.77	28.87	16.13	0.6345E–06
16. aperture width	166.91	20.18	8.27	0.5324E–04
17. protrusion	32.23	10.79	2.99	0.2271E–01
18. tilt	14.48	8.33	1.74	0.1474E+00
19. weight	2.04	0.05	40.03	0.3185E–08
20. aperture-suture	169.07	27.66	6.11	0.3978E–03

D) *Interaction Between Morphotypes*

We recorded the areas of interaction between ribby (*C. abacoense*) and mottled (*C. bendalli*) morphotypes in our discussion of geographic distribution (pp. 376–377). We identified these areas before performing any multivariate analysis upon the shells. Thus, the intermediate position of all these samples in the contrast between ribby and mottled morphotypes (axes 1 and 2 of our Q-mode analysis) serves as a strong confirmation of interaction. The intermediate field of Figure 6 is shared by only two other samples: the convergent Pongo Carpet sample (No. 316) lies on the border of mottled and intermediate samples; secondly, the fossil sample (No. 246) occupies an intermediate position.

All other points in the intermediate zone belong to samples in areas of geographic contact between the morphotypes. These include:

1. the sample from Sandy Point Village (Fig. 6) marking the transition from exterior to interior coast (sample 251).

2. samples from the main road at The Crossing (Fig. 6—samples 253 and 255) where interior *C. bendalli* is separated by 500 m and a narrow hill from coastal *C. abacoense*. We did not record these in the field as intermediate in morphology; they appeared to us at the time as somewhat peculiar *C. bendalli*. Their intermediate position on Figure 6 indicates that some leakage occurs in this area of closest geographic contact between morphologies apparently separate in the field.

3. the hybrid zone at Rocky Point. We noted in the field that the transition from southern ribby to northern mottled seems to occur in the narrow area between samples 305–260. We are therefore pleased to demonstrate a smooth transition in morphology, spanning the entire range from pure ribby to pure mottled, along the geographic sequence in this area: 305-306-307-308-260 (Fig. 6). Our impression that the effects of hybridization do not spread far south of 305 seems to be affirmed by the non-clinal positions of the next two southern samples, 304 and 259. Finally, the interior samples of *C. bendalli* collected in the area of coastal hy-

TABLE 7. MATRIX OF MAHALANOBIS D^2 DISTANCES FOR SAMPLES OF THE HYBRID ZONE AT ROCKY POINT.

	305	306	307	308	260
305	0.0				
306	8.81493	0.0			
307	19.71928	6.93176	0.0		
308	27.42574	14.81611	5.17647	0.0	
260	36.26627	19.43301	10.82527	4.94755	0.0

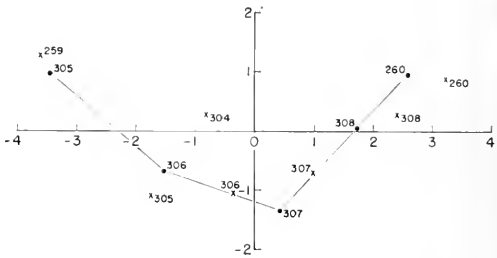

Figure 10. Samples from the hybrid zone at Rocky Point projected on the first two axes of a discriminant analysis. Points represent an analysis based only on samples that, from our field impressions, constitute the zone of transition (numbers 305-306-307-308-260 from south to north). Note the smooth transition along the first axis (74.3 per cent of all information). Crosses represent a separate analysis (shown here on the same scales) for these samples plus two more southern samples in the same area (304 and 259). Sample 304 breaks the morphological cline, thus confirming our impression that it is beyond the localized zone of interaction.

bridization confirm the localization of interaction. Sample 310, collected 400 m from the coast between sample 305 (the pure ribby beginning of the hybrid zone) and sample 306 lies among mottled samples, but near the periphery of mottled and intermediate forms. Sample 309, about 600 m inland from 310, is well within the *C. bendalli* cluster and shows no signs of intermediacy.

We then performed a discriminant analysis on samples of the hybrid zone, using D/DA, a program written by John Rhoads, Dept. of Anthropology, Yale University (see Gould et al., 1974 for more details). In the field, we had concluded that the morphological effects of hybridization are confined to a small, coastal area at Rocky Point (Fig. 5). We therefore performed our analysis on the five samples collected along this mile of coast (from south to north, 305, 306, 307, 308, and 260).

The table of univariate ANOVA's (Table 6) shows that the best discriminators are measures of ribbing and shell size—scarcely surprising since shells of *C. bendalli* are characteristically smaller and more copiously (though more weakly) ribbed than those of *C. abacoense*.

As a first indication of evenly clinal patterns, the matrix of Mahalanobis D^2 distances (an overall measure of similarity based on all characters with variance and covariance adjustments) exhibits a smooth morphological transition along the geographic axis of collections (Table 7). Figure 10 represents a plot of all samples against the first two discriminant axes. The first axis, which encompasses fully ¾ (74.3 per cent) of all information, arrays the samples in a smooth and gradual transition. The second axis (only 13.2 per cent) produces the "horseshoe pattern" so commonly seen when two axes exhaust nearly all information (Reyment, 1975). (If end-member samples have high values on the main discriminator and intermediate samples lie close to zero, then the second axis must emphasize these intermediate samples.)

The table of discriminant loadings displays the patterns of covariance that separate samples (Table 8—these loadings are correlations of original variables with new axes, not coefficients of the discriminant axes themselves). Ribbing (positive loadings) and adult size (negative loadings) dominate the first axis. Northern (*C. bendalli*) samples with their numerous ribs and small shells have high positive projections upon this axis. Moving southward through the hybrid zone, shells gradually become larger as ribs become sparser and stronger. (Measures of ribbing and size are invariably independent as patterns of covariance within samples—see Gould et al., 1974. They are united as joint discriminators of the morphotypes in this study of among sample covariance.) Loadings on the mi-

TABLE 8. DISCRIMINANT LOADINGS OF ORIGINAL VARIABLES UPON AXES USED TO SEPARATE SAMPLES OF THE HYBRID ZONE AT ROCKY POINT.

	1	2
1. protoconch width	−0.0377	0.1390
2. 4th whorl width	−0.2121	0.0888
3. total whorls	−0.0300	−0.1247
4. 4th ribs	0.5185	0.3257
5. 6th ribs	0.5322	0.2315
6. 1st ribs	0.2313	0.1053
7. height	−0.3043	0.0137
8. width	−0.3785	−0.0351
9. protoconch height	−0.0767	−0.0508
10. 4th height	−0.0965	0.0967
11. 4th–6th height	−0.1753	0.0695
12. umbilical width	−0.2312	0.2911
13. lip width	−0.1008	−0.1465
14. lip thickness	−0.1716	−0.0549
15. aperture height	−0.3355	0.2920
16. aperture width	−0.2413	−0.0571
17. protrusion	−0.1074	0.2179
18. tilt	0.1210	0.0371
19. weight	−0.5706	0.1420
20. aperture-suture	−0.1840	−0.3474

nor, second axis make little biological sense to us; they seem to represent a concatenation of those variables that distinguish, in a minor way, the intermediate samples from both endpoints. Thus, any measure that distinguishes *either* endpoint has a relatively high loading (ribs and size now have joint positive loadings), while three disparate measures with generally higher values in the intermediate samples (variables 3, 13, and 20) have negative loadings.

As a final example of smooth transition, Table 9 presents a matrix of classification. Seventy-nine of 94 specimens lie nearest to their own sample centroids (84 per cent). Every misclassified individual groups with a geographically adjacent sample.

This smooth transition is matched by a total lack of evidence for any increased variability in intermediate samples (as we might expect in a "classic" hybrid zone—Mayr, 1963). Table 10 presents C.V.'s for all 5 samples and for typical samples of "pure" mottled and ribby shells in the central areas of their distribution.

In an attempt to learn whether the

TABLE 9. CLASSIFICATION (HITS AND MISSES) TABLE FOR DISCRIMINANT ANALYSIS OF SAMPLES FROM THE HYBRID ZONE AT ROCKY POINT. TOTAL HITS = 79 OUT OF 94 POSSIBLE. RATE = .8404.

	305	306	307	308	260
305	18.	0.	0.	0.	0.
306	2.	15.	2.	0.	0.
307	0.	1.	17.	1.	0.
308	0.	0.	3.	11.	4.
260	0.	0.	0.	2.	18.

smooth morphological transition continues southward beyond our perception of it in the field, we performed a similar analysis on 7 samples—the 5 used before plus 304 and 259, the next southern coastal samples (Fig. 10). The first axis is virtually unchanged in both loadings and discriminatory power. As the previous factor analysis indicated (Fig. 6), the next southern sample (304) breaks the smooth transition by plotting closer to the *C. bendalli* axis than sample 305 directly to the north.

This morphometric analysis cannot resolve the key question of appropriate biological status for populations of the two morphotypes. Are they imperfectly separated entities meriting taxonomic recognition as semispecies or simple geographic variants with uneventful and unrestricted mixture at points of contact? The habitat preferences and coherence in areas of near contact (The Crossing) might argue for separation, and the very localized nature of the hybrid zone would support such an assertion. But rapid transitions and step clines occur within coherent taxa (Endler, 1977). We must turn to genetic analysis for further enlightenment.

IV. ALLOZYME VARIATION OF *CERION* ON THE LITTLE BAHAMA BANK

A. Introduction

The practice of combining electrophoresis with histochemical staining methods to study variation of enzymes is now well established. The applicability of this meth-

TABLE 10. COEFFICIENTS OF VARIATION FOR HYBRID ZONE SAMPLES AND FOR REPRESENTATIVE SAMPLES OF *C. bendalli* AND *C. abacoense* FROM THE CENTER OF THEIR RANGES

	central *bendalli*	b		hybrid zone		a	central *abacoense*
	214	260	308	307	306	305	250
1. protoconch width	6.3	4.7	5.7	5.9	6.2	4.8	5.2
2. width of 4th whorl	5.4	5.2	4.6	7.3	7.1	4.8	6.1
3. total whorls	4.9	4.7	5.1	5.0	5.2	4.7	5.6
4. ribs fourth whorl	19.5	10.8	12.9	11.2	11.6	12.0	11.0
5. ribs sixth whorl	20.1	10.4	11.9	10.4	8.6	6.7	11.3
6. first ribs	22.3	12.0	11.8	13.8	16.6	18.4	19.4
7. shell length	8.0	6.2	6.9	4.5	6.3	6.8	6.8
8. shell width	4.1	3.6	4.9	5.0	5.8	4.4	4.3
9. protoconch height	14.0	9.4	9.5	10.5	12.3	10.5	8.8
10. height 4th whorl	5.4	5.2	6.3	9.0	6.9	6.3	8.0
11. height 4–6	7.6	9.3	9.4	9.8	11.3	10.3	8.3
12. umbilical width	8.0	12.3	12.3	13.1	11.6	12.0	9.9
13. lip width	15.3	14.9	27.0	19.3	22.2	23.0	14.4
14. lip thickness	31.1	32.5	18.8	24.7	26.0	26.6	24.1
15. aperture height	7.4	7.2	5.0	5.7	7.1	5.3	3.9
16. aperture width	6.5	5.8	4.9	6.9	6.9	6.4	5.5
17. protrusion	16.7	14.2	12.9	16.5	13.0	12.7	12.3
18. tilt	16.4	16.5	20.0	10.7	13.3	12.9	17.9
19. weight	27.0	25.8	14.2	15.3	14.1	15.3	13.9
20. aperture to suture	9.2	8.5	17.5	7.9	12.7	9.0	11.6

odology to current problems of evolutionary biology is well reviewed by Avise (1974), Lewontin (1974), and various authors in the volume edited by Ayala (1976). We originally applied this approach to *Cerion* in the hope that genic variability might be more conservative than shell form in these morphologically variable animals. In the following account, we will report our findings as they apply to the systematic problem of the relationship between ribby and mottled morphotypes. For convenience, these contrasting shell types will be referred to *C. abacoense* and *C. bendalli* respectively as suggested above. In subsequent papers, we will describe the genetic aspects of the interaction between these taxa in more detail (Woodruff and Gould, in press), and the relation between genic and phenic variation at the level of the individual, population, and species (Woodruff, in prep.).

Variation in the electrophoretic pattern of structural gene products was surveyed in 1,575 individual adult snails from 47 populations from the islands of the Little Bahama Bank. Localities are indicated in Figure 3. In most cases, these are the same localities described in the morphometric analyses presented above. Furthermore, whenever possible, we have examined the same individual snails. Sample preparation, biochemical specifics, and other technical aspects of the starch gel electrophoresis apparatus employed are described elsewhere (Woodruff, 1975b). In the context of this survey, we have examined 16 enzyme systems and some general proteins and interpreted the observed banding patterns in terms of at least 28 loci. Here we will describe the variation in 20 of these structural gene products: ones that we found to give reproducible and genetically interpretable patterns. Variation of these enzymes among the Little Bahama Bank *Cerion* is outlined in Table 11. While 14 of these proteins are monomorphic and are fixed for the same allele in both taxa, polymorphisms were detected in the remaining six. (Est-3 and Pgi are also variable allozymes but are excluded from this

discussion.) Variation in each case is due to a simple Mendelian system involving codominant alleles. In the absence of formal genetic crosses, our genetic interpretations are based on two criteria. First, phenotypic ratios (and presumed genotypic ratios) agree closely with Hardy-Weinberg expectations. Second, patterns of banding of particular enzymes correspond to simple models of molecular structure. In most cases, the inferred structures are similar to those of functionally analogous enzymes in other animals whose structures have been established by other techniques. The six polymorphic loci segregate independently of one another; this is quite reasonable as one species of *Cerion* is known to have 27 pairs of chromosomes (Burch and Kim, 1962).

Before proceeding with the results of this genetic survey, we wish to outline the general nature of population structure in *Cerion*. Beginning in 1973, Woodruff has been studying two large marked populations of *C. bendalli* and *C. abacoense* on Abaco (3 years' experience with over 1,500 individually marked snails). Generation time for *Cerion* is not well defined. Juveniles grow slowly and erratically and probably do not lay down the shell's adult lip until they are 3 years old. The duration of the adult phase is also poorly defined; multiple-recapture studies suggest that some adults live at least another 10 years. Snail distribution at the coastal study sites is patchy but averages 8–13 adults per square meter. Dispersal data are now being used to estimate various evolutionarily important parameters. Effective neighborhood size or effective population size (N of Wright, 1946) is about 1,000 snails. Neighborhood area is 50–100 m^2. Our preliminary estimate for gene flow (l of May et al., 1975) suggests that this variable will be shown to have a value of about 3 meters. This estimate is, however, based on the formula $l = x\sqrt{g}$ where x is the mean distance travelled in a generation and g is the probability of leaving a deme or neighborhood. While these parameters can be estimated fairly accurately in *Cerion*, the ultimate determinant of effective gene flow, reproductive success outside the deme of birth, will be very difficult to assess.

TABLE 11. ELECTROPHORETICALLY DEMONSTRABLE ALLOZYMIC VARIATION IN *Cerion* FROM THE LITTLE BAHAMA BANK.

Enzyme	No. of alleles
Variable Enzymes:	
Esterase-2 (Est-2)	7
Esterase-3 (Est-3)	*
Malate dehydrogenase-1 (Mdh-1)	2
Malate dehydrogenase-2 (Mdh-2)	2
6-Phosphogluconate dehydrogenase-1 (6-Pgdh)	2
Phosphoglucose isomerase (Pgi)	*
Glutamic oxalacetic transaminase (Got-1)	3
Leucine aminopeptidase (Lap)	3
Invariable enzymes: alcohol dehydrogenase (Adh), Est-1, Est-6, Est-7, isocitrate dehydrogenase-1 (Idh-1), Idh-2, α-glycerophosphate dehydrogenase (α-Gpdh), indophenol oxidase (Ipo), phosphoglucomutase (Pgm-1), Pgm-2, Got-2, acid phosphatase-1 (Acp-1), Acp-2, alkaline phosphatase-1 (Ap-1)	

* At least two alleles segregating; variation not yet interpretable.

One of the first things we were able to establish was that *Cerion*, a facultative hermaphrodite (Richter, 1926; Jaenicke, 1933), is apparently outbreeding. This conclusion is based on the close agreement between observed and expected genotype frequencies in all the larger ($N > 30$) samples. This concordance is particularly impressive in the samples where four and five alleles are segregating at the Est-2 locus. In addition, estimates of inbreeding (F of Wright, 1965) and outcrossing (λ, where $F = (1 - \lambda/1 + \lambda)$, Nei and Syakudo, 1958) were also calculated for the four largest samples. In each case, lambda was greater than 0.96 thus confirming our conclusion regarding panmixia with respect to the allozymes studied.

The second important finding about *Cerion* was that like most other organisms

TABLE 12. VARIATION IN MALATE DEHYDROGENASES AND 6-PHOSPHOGLUCONATE DEHYDROGENASE.

Locality	Number of snails	Allele frequency					
		Mdh-1[a]	Mdh-1[b]	Mdh-2[a]	Mdh-2[b]	6-Pgdh[a]	6-Pgdh[b]
Grand Bahama—*C. bendalli*							
211	70	0.40	0.60	------	1.00	0.64	0.36
208	1	1.00	----	------	1.00	1.00	------
204B	64	0.65	0.35	------	1.00	0.54	0.46
205	38	0.49	0.51	------	1.00	0.67	0.33
207	6	0.50	0.50	------	1.00	0.83	0.17
202	38	0.51	0.49	------	1.00	0.64	0.36
200	6	0.42	0.58	------	1.00	0.67	0.33
201	11	0.50	0.50	------	1.00	0.68	0.32
Little Abaco—*C. bendalli*							
213	35	0.20	0.80	------	1.00	1.00	------
214	37	0.27	0.73	------	1.00	1.00	------
216	36	0.18	0.82	0.14	0.86	0.90	0.10
Great Abaco—*C. bendalli*							
217	18	0.28	0.72	0.08	0.92	1.00	------
218	38	0.26	0.74	0.13	0.87	1.00	------
224	45	0.32	0.68	0.01	0.99	1.00	------
223	25	0.36	0.64	0.02	0.98	1.00	------
222	39	0.35	0.65	0.03	0.97	1.00	------
226	53	0.26	0.74	0.01	0.99	1.00	------
220	56	0.25	0.75	------	1.00	1.00	------
219	77	0.36	0.64	------	1.00	1.00	------
316	14	0.43	0.57	------	1.00	1.00	------
228	21	0.36	0.64	0.05	0.95	1.00	------
230	7	0.29	0.71	------	1.00	1.00	------
231	15	0.27	0.73	0.03	0.97	1.00	------
240	37	0.28	0.72	------	1.00	1.00	------
247	37	0.34	0.66	------	1.00	1.00	------
243	102	0.29	0.71	------	1.00	1.00	------
245	42	0.31	0.69	------	1.00	1.00	------
244	41	0.37	0.63	------	1.00	1.00	------
Great Abaco—area of interaction between *C. bendalli* and *C. abacoense*							
260	36	0.28	0.72	------	1.00	1.00	------
501	12	0.33	0.67	------	1.00	1.00	------
308	24	0.21	0.79	------	1.00	0.81	0.19
307	24	0.25	0.75	------	1.00	0.69	0.31
306	36	0.31	0.69	------	1.00	0.57	0.43
305	29	0.34	0.66	------	1.00	0.53	0.47
304	36	0.29	0.71	------	1.00	0.60	0.40
311	24	0.27	0.73	------	1.00	0.56	0.44
253	36	0.39	0.61	------	1.00	1.00	------
255	30	0.35	0.65	------	1.00	1.00	------
251	84	0.43	0.57	------	1.00	1.00	------
Great Abaco—*C. abacoense*							
259	13	0.25	0.75	------	1.00	0.62	0.38
520	7	0.36	0.64	------	1.00	0.93	0.07
521	36	0.28	0.72	------	1.00	0.40	0.60
254	34	0.29	0.71	------	1.00	0.78	0.22
257	12	0.42	0.58	------	1.00	0.75	0.25
252	24	0.25	0.75	------	1.00	0.79	0.21
250	70	0.36	0.64	------	1.00	1.00	------

TABLE 13. VARIATION IN GLUTAMIC OXALACETIC TRANSAMINASE AND LEUCINE AMINOPEPTIDASE.

Locality	Number of Snails	Allele frequency					
		Got-1[a]	Got-1[b]	Got-1[c]	Lap-1[a]	Lap-1[b]	Lap-1[c]
Grand Bahama—*C. bendalli*							
211	70	0.67	0.33	.....	0.73	0.14	0.13
208	1	1.00	.....	.....	.....	1.00	.....
204B	64	0.77	0.23	.....	0.74	0.24	0.02
205	38	0.84	0.16	.....	0.78	0.17	0.05
207	6	0.33	0.67	.....	0.92	0.08	.....
202	38	0.55	0.45	.....	0.89	.....	0.11
200	6	0.58	0.42	.....	0.92	.....	0.08
201	11	0.47	0.53	.....	0.77	.....	0.23
Little Abaco—*C. bendalli*							
213	35	0.60	0.40	.....	0.81	.....	0.19
214	37	0.66	0.34	.....	0.86	.....	0.14
216	36	0.43	0.57	.....	0.96	.....	0.04
Great Abaco—*C. bendalli*							
217	18	0.56	0.44	.....	0.97	.....	0.03
218	38	0.54	0.46	.....	0.95	.....	0.05
224	45	0.51	0.49	.....	0.96	.....	0.04
223	25	0.56	0.44	.....	0.96	.....	0.04
222	39	0.59	0.41	.....	0.95	.....	0.05
226	53	0.48	0.52	.....	0.96	.....	0.04
220	56	0.46	0.54	.....	0.95	.....	0.05
219	77	0.51	0.49	.....	0.99	.....	0.01
316	14	0.54	0.46	.....	0.89	.....	0.11
228	21	0.50	0.50	.....	1.00	.....	.....
230	7	0.57	0.43	.....	1.00	.....	.....
231	15	0.53	0.47	.....	0.97	.....	0.03
240	37	0.55	0.45	.....	0.96	.....	0.04
247	37	0.58	0.42	.....	0.93	.....	0.07
243	102	0.47	0.53	.....	0.87	.....	0.13
245	42	0.54	0.46	.....	0.90	.....	0.10
244	41	0.52	0.48	.....	0.95	.....	0.05
Great Abaco—area of interaction between *C. bendalli* and *C. abacoense*							
260	36	0.58	0.42	.....	0.90	.....	0.10
501	12	0.54	0.46	.....	0.88	.....	0.12
308	24	0.50	0.42	.08	0.94	.....	0.06
307	24	0.69	0.31	.....	0.81	.....	0.19
306	36	0.56	0.44	.....	0.78	.....	0.22
305	29	0.57	0.43	.....	0.90	.....	0.10
304	36	0.60	0.40	.....	0.86	.....	0.14
311	24	0.44	0.54	0.02	0.90	.....	0.10
253	36	0.53	0.47	.....	0.67	0.14	0.19
255	30	0.48	0.50	0.02	0.72	0.13	0.15
251	84	0.51	0.47	0.02	0.83	0.04	0.13
Great Abaco—*C. abacoense*							
259	13	0.62	0.38	.....	0.81	.....	0.19
520	7	0.36	0.64	.....	0.50	.....	0.50
521	36	0.32	0.68	.....	0.82	.....	0.18
254	34	0.28	0.72	.....	0.73	0.09	0.18
257	12	0.58	0.42	.....	0.79	0.13	0.08
252	24	0.38	0.62	.....	0.77	.....	0.23
250	70	0.61	0.38	0.01	0.71	0.22	0.06

TABLE 14. VARIATION IN ESTERASE-2.

Locality	Number of Snails	Allele frequency						
		Est-2[a]	Est-2[b]	Est-2[c]	Est-2[d]	Est-2[e]	Est-2[f]	Est-2[g]
Grand Bahama—*C. bendalli*								
211	70	------	------	0.04	0.18	0.24	0.54	<0.01
208	1	------	------	------	------	1.00	------	------
204B	64	------	------	0.05	0.14	0.46	0.32	0.03
205	38	------	------	0.03	0.07	0.54	0.33	0.03
207	6	------	------	0.08	------	0.42	0.42	0.08
202	38	------	------	0.01	0.20	0.14	0.58	0.07
200	6	------	------	------	0.17	------	0.83	------
201	11	------	------	------	0.23	0.09	0.68	------
Little Abaco—*C. bendalli*								
213	35	------	------	------	0.10	------	0.90	------
214	37	0.01	0.01	------	0.22	------	0.76	------
216	36	------	------	------	------	------	1.00	------
Great Abaco—*C. bendalli*								
217	18	------	------	------	0.22	------	0.78	------
218	38	------	------	------	0.04	------	0.96	------
224	45	------	------	------	0.06	------	0.94	------
223	25	------	------	------	0.10	------	0.90	------
222	39	------	------	------	0.03	------	0.97	------
226	53	------	------	------	0.07	------	0.93	------
220	56	------	------	------	0.02	------	0.98	------
219	77	------	------	------	0.05	------	0.95	------
316	14	------	------	------	0.04	------	0.96	------
228	21	------	------	------	0.02	------	0.98	------
230	7	------	------	------	0.14	------	9.86	------
231	15	------	0.03	------	0.10	------	0.87	------
240	37	------	------	------	------	------	1.00	------
247	37	------	------	------	------	------	1.00	------
243	102	------	------	------	0.03	------	0.97	------
245	42	------	------	------	------	------	1.00	------
244	41	------	------	------	------	------	1.00	------
Great Abaco—area of interaction between *C. bendalli* and *C. abacoense*								
260	36	------	0.03	------	0.64	------	0.33	------
501	12	------	0.04	------	0.58	------	0.38	------
308	24	------	0.02	------	0.52	------	0.46	------
307	24	------	0.08	------	0.40	------	0.52	------
306	36	------	------	------	0.29	------	0.71	------
305	29	------	0.02	------	0.26	------	0.72	------
304	36	------	0.03	------	0.57	------	0.40	------
311	24	------	0.08	------	0.54	------	0.31	0.06
253	36	------	0.09	------	0.85	------	0.06	------
255	30	------	0.10	------	0.85	------	0.05	------
251	84	------	------	------	------	------	1.00	------
Great Abaco—*C. abacoense*								
259	13	------	------	------	0.50	------	0.50	------
520	7	------	------	------	------	------	1.00	------
521	36	------	------	------	0.19	------	0.81	------
254	34	------	------	------	0.28	------	0.72	------
257	12	------	0.04	------	0.50	------	0.46	------
252	24	------	------	------	0.25	------	0.75	------
250	70	------	------	------	0.04	------	0.96	------

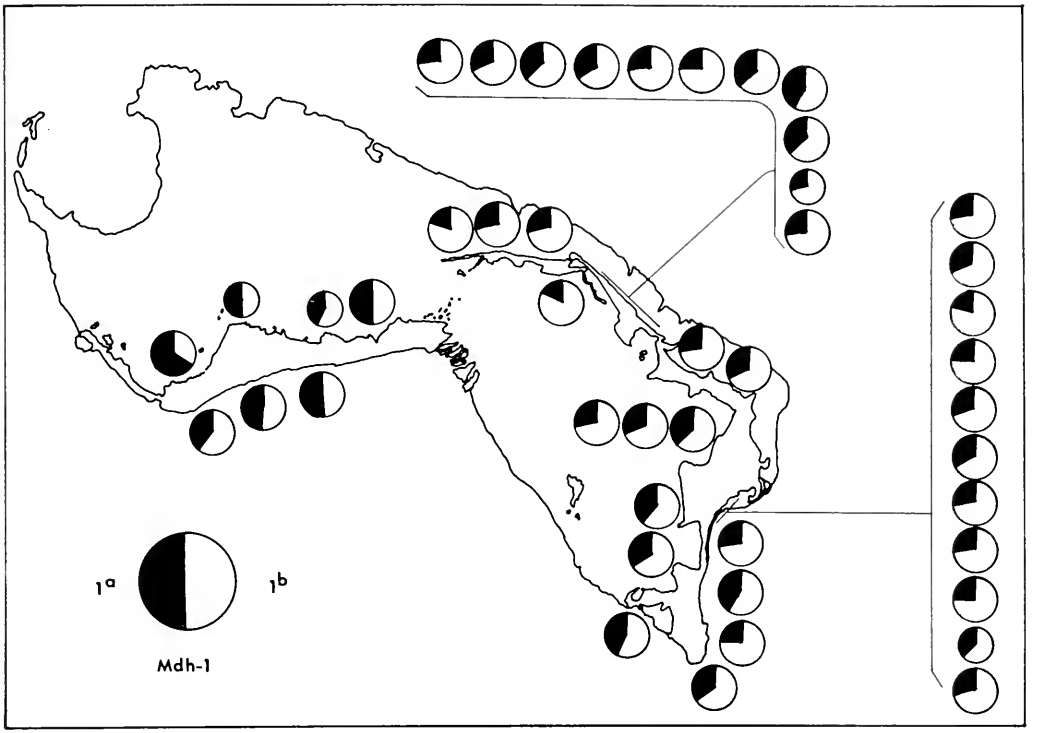

Figure 11. Geographic variation in malate dehydrogenase-1. Sample locality numbers may be discerned from Figure 3.

with open population structures, it has a rich endowment of genetic variability. The proportion of loci that are polymorphic per population (*P*) was in the range of 20–30 per cent (20–36 per cent if the variable but uninterpretable Est-3 and Pgi loci are included). Average heterozygosity per individual (*H*) was in the range of 5–12 per cent. Interpretation of variation in *P* and *H* will be discussed below after the geographic variation in the polymorphic allozymes has been described.

B. Geographic Variation in Polymorphic Loci

Having established that *C. bendalli* and *C. abacoense* were identical with respect to 14 genetic loci, we turned our attention to variation at the six polymorphic loci. We will present these data in two ways. In Tables 12–14, the allele frequencies are shown with the localities grouped according to geographic and taxonomic constraints. The decision as to whether a sample was placed in category 4 (transition zone) in the tables or in category 5 (*C. abacoense*) was based on shell morphology as outlined in the previous section. In Figures 11–16, the presentations are not biased by any a priori taxonomic constraints. Note that the smallest samples are not shown in the figures. We have initially resisted the temptation to group our samples according to island or sample region in any more formal sense, because the population structure of these animals suggests that such data pooling could seriously distort our conclusions.

Malate dehydrogenase-1. Two NAD dependent alleles have been demonstrated at this locus in *C. bendalli* from Abaco (Gould

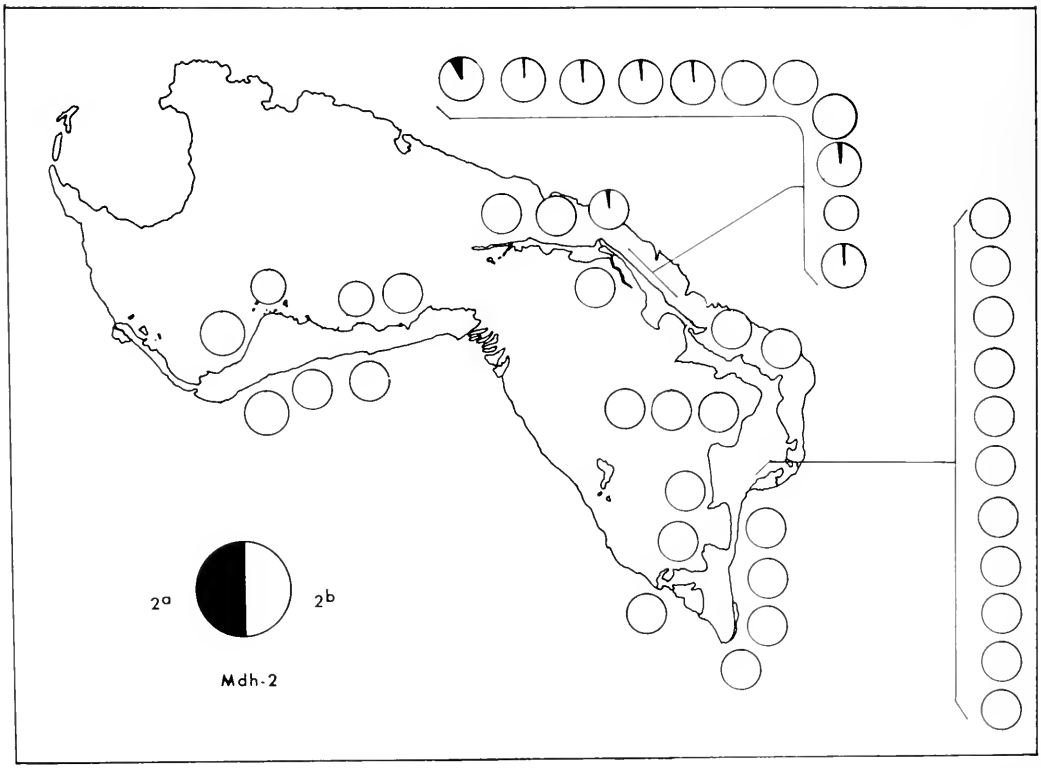

Figure 12. Geographic variation in malate dehydrogenase-2. Sample locality numbers may be discerned from Figure 3.

et al., 1974; Woodruff, 1975). Data in Table 12 and Fig. 11 indicate that there is no consistent difference in allele frequency between *C. bendalli* and *C. abacoense* morphotypes on Great Abaco where Mdh-1[a] varies in frequency between 0.21–0.43 in both taxa. Elsewhere, frequencies of Mdh-1[a] are slightly different: being lower on Little Abaco (0.18–0.27), and higher on Grand Bahama (0.40–0.65). Allele frequencies in adjacent populations are similar, and no dramatic shifts or clines in allele frequency were noted. There is no marked change in this allozyme in the area of interaction between *C. bendalli* and *C. abacoense* on Great Abaco.

Malate dehydrogenase-2. Gould et al. (1974) found two alleles at this locus in populations of *C. bendalli* from northern Great Abaco. NAD–Mdh-2[a] is a rare allele (0.01–0.04) that occurs in standard *C. bendalli* and in some samples of the aberrant Pongo Carpet morphotype found in this area. This allele was detected in populations extending from the eastern end of Little Abaco (Loc. 216) south to Treasure Cay, a distance of about 30 km. (It was not found in the three most isolated (and morphometrically differentiated) of the Pongo Carpet samples.) Subsequently, Woodruff (1975) reported Mdh-2[a] was absent in 3 samples of *C. bendalli* from localities about 50 km. south of this area. We now report that the Mdh-2[a] allele has not been detected in over 1,000 snails from elsewhere on the Little Bahama Bank (Table 12, Fig. 12). We conclude that *C. bendalli* and *C. abacoense* are not differentiated at

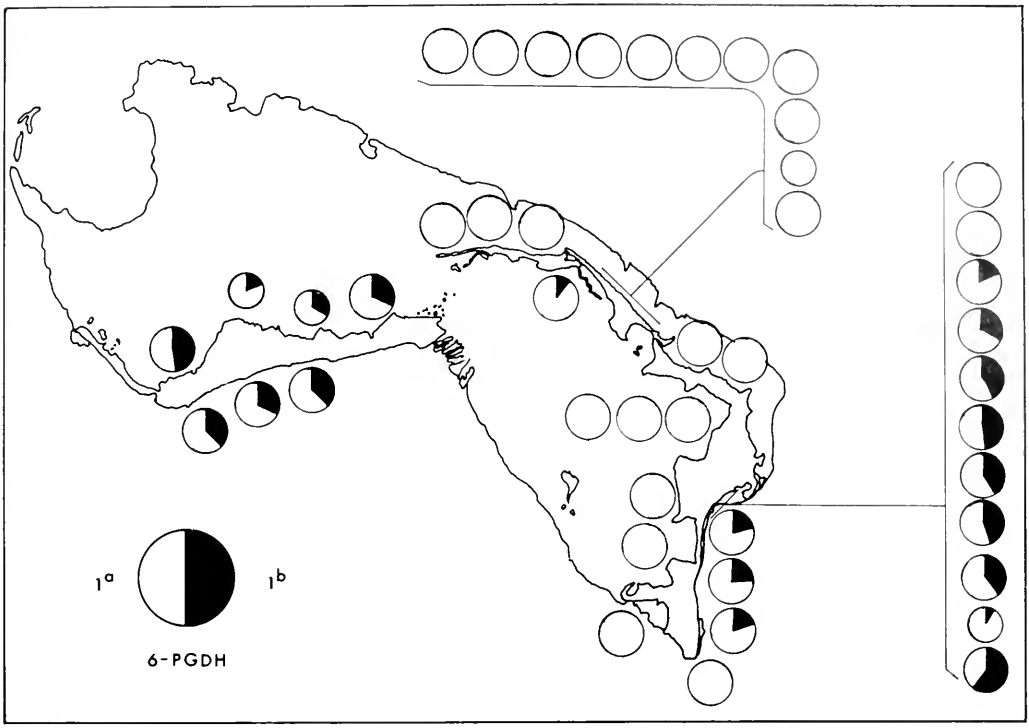

Figure 13. Geographic variation in 6-phosphogluconate dehydrogenase. Sample locality numbers may be discerned from Figure 3.

this locus and that the presence of the rare allele in northern Great Abaco is a biochemical area effect. Until more is known about the variation of this gene elsewhere in the Bahamas, we are inclined to invoke mutation and the spread of a locally advantageous allele as the most likely explanation for this phenomenon. An alternative hypothesis—that Mdh-2^a was introduced into the area with the aberrant Pongo Carpet morphotype by hurricane transport from elsewhere—is rejected at present because the allele was not detected in the three most differentiated populations of the Pongo Carpet snails.

6-Phosphogluconate dehydrogenase. While populations of *C. bendalli* from near Pongo Carpet (Gould et al., 1974) and Snake Cay, Great Abaco (Woodruff, 1975) are monomorphic for 6-Pgdh^a, a second codominant allele (6-Pgdh-1^b) has been found elsewhere on the Little Bahama Bank (Fig. 13). This allozyme stains as a single, sharp band of slightly reduced mobility relative to 6-Pgdh-1^a; heterozygotes are 3-banded. As shown in Table 11 and Fig. 13, all samples from Grand Bahama are polymorphic with 6-Pgdh-1^a varying in frequency between 0.54–0.83. On Little and Great Abaco, the 6-Pgdh-1^b allele has been found in two separate areas. First, at the eastern end of Little Abaco (Loc. 216), 7 heterozygotes were noted among 36 snails examined. No trace of this allele was found in the sample from Loc. 217 which was collected 100 m away on Great Abaco at the other end of the causeway connecting the two islands. Sixty kilometers further south, the 6-Pgdh-1^b allele was found again in samples from the area of interaction between *C. bendalli* and *C. abacoense*. It was detected in 6 of 11 samples between Rocky

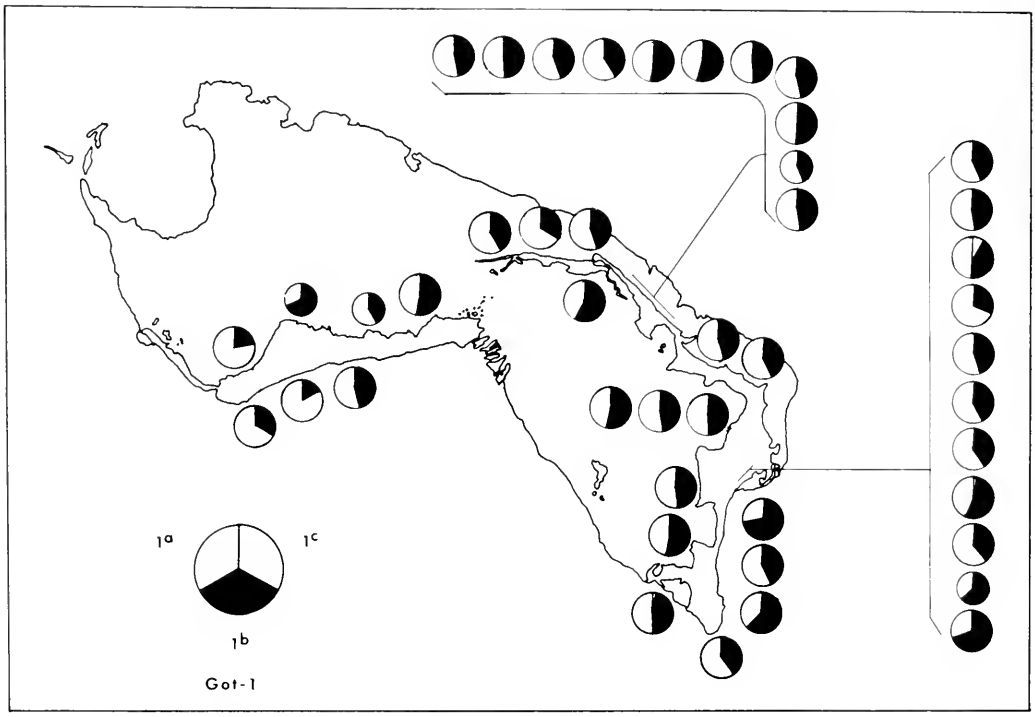

Figure 14. Geographic variation in glutamic oxalacetic transaminase. Sample locality numbers may be discerned from Figure 3.

Point and The Crossing and in 5 of 6 samples of *C. abacoense* morphotype. Its frequency in this area ranged up to 0.60 in the populations where it was detected. It was, however, conspicuously absent in samples of intermediate morphotype from the west side of The Crossing (Locs. 253, 255) and Sandy Point (Loc. 251) and in the "pure" *C. abacoense* from Hole-in-the-Wall (Loc. 250). The isolated occurrence of 6-Pgdh-1^b on Little Abaco is tentatively interpreted as being due to mutation and drift. The occurrence of this allele at higher frequencies on Grand Bahama and in the transition zone between the morphotypes on Great Abaco must be due to other forces.

Glutamic oxalacetic transaminase. In *C. bendalli*, two equally common alleles were found in 12 populations from northern and central Great Abaco (Gould et al., 1974; Woodruff, 1975). As seen in Table 13 and Fig. 14, Got-1^a occurs at a slightly higher frequency than Got-1^b throughout the range of this taxon. Got-1^a reaches its greatest frequencies (0.77–0.84) in western and interior samples from Grand Bahama. Seven samples of the ribby morphotype, *C. abacoense*, were also examined and found to have Got-1^a frequencies of 0.28–0.62. Frequencies of 0.44–0.69 were found to characterize samples from the area of interaction between these taxa. A third allele, Got-1^c is now reported from southern Great Abaco where it occurs at low frequency (0.01–0.08). It has been detected in "pure" *C. abacoense* (Loc. 250) and 4 samples of intermediate morphotype from Sandy Point (Loc. 251), The Crossing (Loc. 255) and near Rocky Point (Locs. 308, 311). This rare allele has yet to be found in "pure" *C. bendalli* from Abaco or Grand Bahama. In mobility, Got-1^c is slower than Got-1^b;

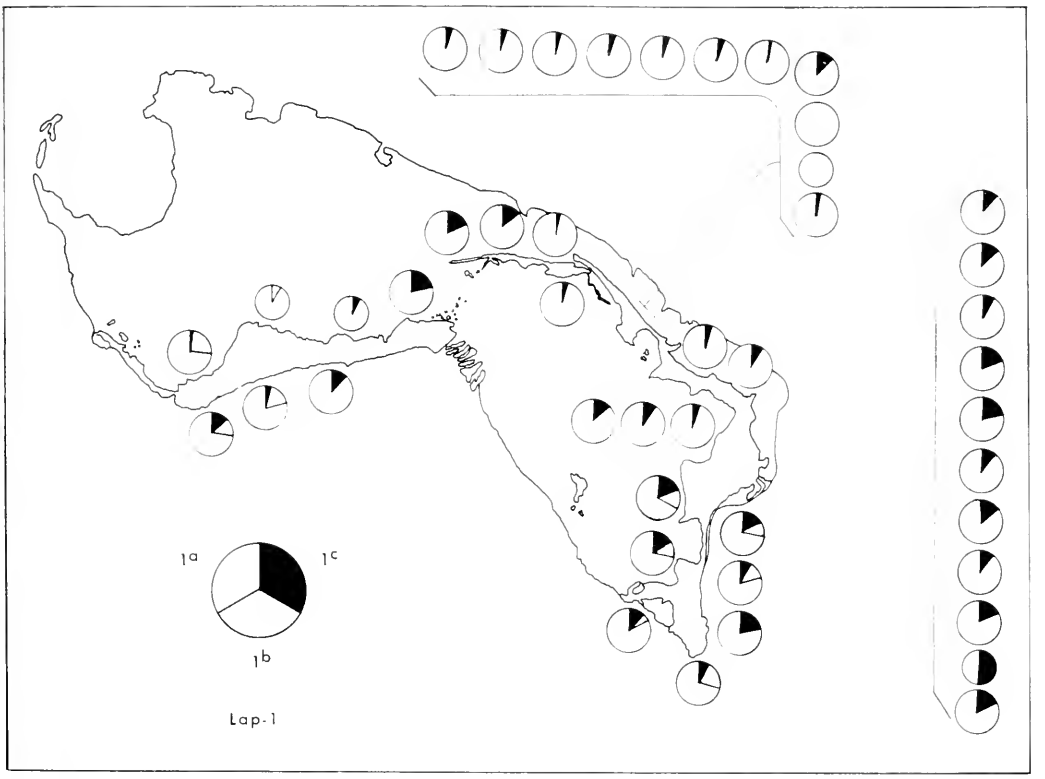

Figure 15. Geographic variation in leucine aminopeptidase. Sample locality numbers may be discerned from Figure 3.

like the latter the former stains a well-defined doublet, the heterozygotes having four bands.

Leucine aminopeptidase. We have previously shown that Lap-1^a is the predominant allele in *C. bendalli* near Pongo Carpet and Snake Cay (Gould et al., 1974; Woodruff, 1975). In these populations a slower allele (previously designated Lap-1^b) occurred at a frequency of up to 0.13. Now we report finding a third allele of intermediate mobility in *Cerion* from Grand Bahama and southern Great Abaco (Table 13, Fig. 15). For consistency, the newly discovered allele is now designated Lap-1^b; the designation of the slowest allele is accordingly changed to Lap-1^c.

Lap-1^a is the common allele throughout the Little Bahama Bank: it varies in frequency and is typically over 0.85 (range: 0.67–1.00). Lap-1^c is also widespread. Its absence in a few samples is presumably due to sampling error. No particular biological significance is attached to the minor interpopulation variation in frequency of this allele. The third allele, Lap-1^b, is known from 5 localities in western Grand Bahama and from 6 localities at the southern end of Great Abaco. It reaches its highest frequency in the interior of the pine forest on Grand Bahama and in "pure" *C. abacoense* from Hole-in-the-Wall on Great Abaco. Lap-1^b was detected from 4 to 5 localities at The Crossing where it has a frequency of about 0.10.

Esterase-2. Woodruff (1975) first detected variation at this non-specific esterase locus in *C. bendalli* from Loc. 243 near

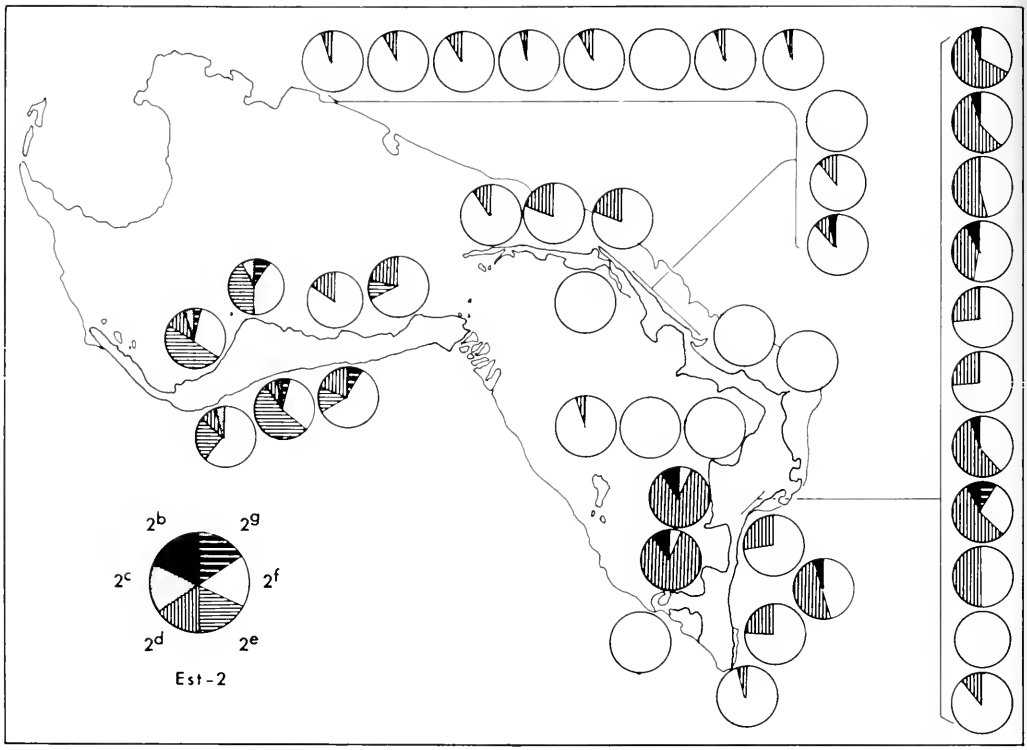

Figure 16. Geographic variation in esterase-2. Sample locality numbers may be discerned from Figure 3.

Snake Cay, Great Abaco. At that time, the codominant alleles were designated Est-2^b and Est-2^c. Now, as a result of this far more extensive survey, we report that at least 7 alleles occur at this locus among the *Cerion* of the Little Bahama Bank. The various alleles are all codominant and are designated Est-2^a, Est-2^b . . . Est-2^g in order of decreasing mobility. The alleles reported by Woodruff (1975) are now redesignated Est-2^d and Est-2^f respectively. Allele frequencies and the overall pattern of allele distribution are shown in Table 14 and Fig. 16. Est-2^a, a very rare allele found in only one sample, is omitted from Fig. 16. The distribution of each allele may now be considered in turn.

Est-2^a. A rare allele whose presence is based on a single specimen of *C. bendalli* from Little Abaco with a two-banded phenotype interpreted as Est-2^a/Est-2^f.

Est-2^b. Another rare allele found in 12 samples of *C. bendalli* from Great and Little Abaco. Its isolated occurrence on Little Abaco and near Treasure Cay may be due to recurrent mutation. Its occurrence at frequencies of up to 0.10 in ten samples from the area of interaction between *C. bendalli* and *C. abacoense* is probably due to other forces. We note that nine of these samples were of *C. bendalli* or intermediate morphotype; only one (Loc. 257 at The Crossing) was referable to *C. abacoense*. In this same area, the Est-2^b allele was not detected at Locs. 259, 520, 521, 254, and 252 where snails are judged to be typical *C. abacoense*.

Est-2^c. A rare allele (frequency: 0.01–0.8) detected in heterozygous form in four populations of *C. bendalli* from western Grand Bahama.

Est-2^d. A common allele detected in most populations of *Cerion* from the Little Ba-

hama Bank. It occurs at moderate frequencies (0.02–0.23) throughout most of the range of the *C. bendalli* morphotype. The notable feature about the distribution of this allele is that it reaches higher frequencies in the area of interaction between the two morphotypes on Great Abaco than elsewhere. In fact, it is the commonest allele at eight localities in this area. Intersample variation in this area is also marked and is probably too great to be due to sampling error alone. For example, Est-2^d occurs at the three localities on the eastern side of The Crossing at frequencies of 0.25–0.50 while on the western side of The Crossing, only 500 m away, the allele is present at a frequency of 0.85 in two localities. The absence of Est-2^d at Sandy Point (Loc. 251) is probably not due to sampling error.

Est-2^d is also present throughout northern Great Abaco although its presence in some populations was not detected by Gould et al. (1974). We have subsequently rerun all the Pongo Carpet specimens and now report the occurrence of this allele at low frequency. This correction does not alter any of the conclusions we reached in that paper about the systematic status of the Pongo Carpet morphotype.

Est-2^e. This allele was detected on Grand Bahama where it occurs in all populations sampled (its absence at Loc. 200 is almost surely due to sampling error) and is the commonest allele in the three interior samples.

Est-2^f. This is the commonest allele in the majority of the *Cerion* populations on the Little Bahama Bank. It varies in frequency between 0.76–1.00 in samples of *C. bendalli* from Little Abaco and Great Abaco. It is less common in *C. bendalli* from Grand Bahama where it falls to frequencies as low as 0.32–0.42 in the interior populations dominated by Est-2^e. Lower frequencies were also noted in the area of interaction between *C. bendalli* and *C. abacoense* where Est-2^d was the commonest allele in 7 of 11 samples. This area and the adjacent populations of *C. abacoense* is also characterized by considerable interpopulation variation in the frequency of Est-2^f. This is particularly marked at The Crossing where the frequency of Est-2^f increases from 0.05–0.06 in the mottled western samples to 0.46–0.75 in the ribby eastern samples.

Est-2^g. A rare allele occurring at low frequency in five samples of *C. bendalli* from Grand Bahama and one sample of intermediate morphotype from Great Abaco.

C. Genetic Differentiation of *Cerion* on the Little Bahama Bank

The patterns of geographic variation in the six polymorphic enzymes bear little relation to the distribution of the two taxa recognized on the basis of shell morphology. There is not a single case of fixation, or even near fixation, for alternative alleles in the two taxa. In only 5 out of the 19 polymorphic cases is an allele restricted to one or the other morphotype: Est-2^a, Est-2^c, Est-2^e, Est-2^g, and Mdh-2^a. With the exception of Est-2^c, which is common in the interior of Grand Bahama, these alleles are all rare in most or all of the samples in which they were detected. The overall impression emerging from these data is that *C. bendalli* and *C. abacoense* are very similar to one another genically. This conclusion was confirmed by calculating the normalized identity of genes (*I* of Nei, 1972) between all 41 samples where $N > 11$. The values of *I* obtained for the 820 pairwise combinations of samples were in the range 0.9451–0.9999. The average similarity was 0.9849. Values of Nei's (1972) genetic distance, *D*, were accordingly very small and do not exceed 0.0564.

This overall lack of pronounced genetic differentiation does not mean that local patterns of variation cannot be discerned. On the contrary we find sporadic occurrences of alleles that are unique to one group of populations or another. There is also a moderate amount of interpopulation variation that does not appear to be either obviously clinal or closely correlated with simple environ-

TABLE 15. VALUES OR MEAN VALUES FOR NEI'S GENETIC DISTANCE (D) BETWEEN VARIOUS SAMPLES OR GROUPS OF SAMPLES (N) OF *Cerion bendalli* FROM GRAND BAHAMA (G.B.) AND *Cerion* FROM ELSEWHERE ON THE LITTLE BAHAMA BANK. MORPHOTYPES ARE B (*C. bendalli*), Ab (*C. abacoense*) AND I (INTERMEDIATE). NOTE PARTICULARLY THE ACROSS-TABLE LOW VALUES FOR COMPARISONS INVOLVING ROCKY POINT AND THE CROSSING—EAST, AND HIGH VALUES FOR COMPARISONS INVOLVING THE CROSSING—WEST.

			Grand Bahama Sample				
Sample(s)	Morph	N	211	204	205	202	201
Loc. 211, G.B.	B	1	—	—	—	—	—
Loc. 204, G.B.	B	1	.0082	—	—	—	—
Loc. 205, G.B.	B	1	.0066	.0032	—	—	—
Loc. 202, G.B.	B	1	.0033	.0120	.0129	—	—
Loc. 201, G.B.	B	1	.0051	.0184	.0195	.0018	—
Little Abaco	B	3	.0161	.0422	.0329	.0157	.0134
Pongo Carpet	B	9	.0170	.0411	.0332	.0142	.0124
Treasure Cay	B	2	.0176	.0414	.0336	.0143	.0128
Snake Cay	B	3	.0180	.0428	.0350	.0151	.0123
Rocky Point	I	6	.0082	.0250	.0233	.0076	.0083
The Crossing—east	Ab	3	.0101	.0304	.0285	.0083	.0056
The Crossing—west	B	2	.0301	.0440	.0417	.0308	.0299
Sandy Point	I	1	.0170	.0389	.0332	.0141	.0107
Hole-in-the-Wall	Ab	1	.0146	.0356	.0292	.0162	.0154

mental parameters. Regional differentiation is most marked for the Grand Bahama populations. These are distinguishable from Abaconian populations on the basis of their higher frequencies of Mdh-1^a and Lap-1^b and lower frequency of 6-Pgdh-1^a. This differentiation does not, however, permit the characterization of individual specimens. Only in Est-2 has any regional differentiation of diagnostic genotypes occurred: Est-2^c and Est-2^e are restricted to Grand Bahama, while Est-2^a and Est-2^b have been detected only on Abaco. A second potentially diagnostic allele may be Got-1^c found in *C. abacoense* and populations of intermediate morphotype on southern Great Abaco. It is regrettable that we do not know, at this time, whether Got-1^c characterizes *C. abacoense* from Mores Island or whether it was present in the presumed extinct *C. abacoense* from Grand Bahama. Indeed *C. abacoense* cannot be considered properly characterized until more samples away from the area of interaction with *C. bendalli* have been analyzed.

We are struck by the similarity between populations of *C. bendalli* on Grand Bahama and populations of *Cerion* from the area of interaction on Great Abaco. This pattern emerged repeatedly in the distribution of individual alleles: 6-Pgdh-1^b, Lap-1^b, and Est-2^g (Figures 13, 15, 16). It is also apparent from a comparison of interpopulation genetic distances (Table 15). In each set of interpopulation distance comparisons, we see that Grand Bahamian populations are more similar to Abaconian populations from the eastern side of the area of interaction between *C. bendalli* and *C. abacoense* than they are to Abaconian *Cerion* of either taxon collected away from this area. This pattern is consistent and not obscured by the slight regional differentiation on Grand Bahama itself. Note also that D values between the populations on either side of The Crossing are greater than those between various isolated populations of *C. bendalli* and greater than those between the "parental" taxa themselves.

This similarity between *Cerion* from Grand Bahama and the area of interaction on Abaco was noted again in the pattern of variation for individual heterozygosity (H). Table 16 shows that significantly higher levels of heterozygosity prevail in these two areas than elsewhere on the Little Bahama

Bank. In this case, however, populations on both sides of The Crossing are characterized by higher values of *H*.

Although we treat the determinants of these patterns more fully elsewhere (Woodruff and Gould, in prep.), we can make some general comments about their relationship to ecology and genetics of *Cerion*. *Cerion* populations are very variable in size. While Woodruff's study demes are moderate (N = approx. 1,000) in size and contiguous with adjacent demes, this is not always the case. *Cerion*'s distribution is typically patchy, and dramatic declines in abundance occur over a distance of a few meters. Stochastic processes are undoubtedly important in small, isolated populations. Gene flow is restricted by the low vagility of the snails themselves but is nevertheless demonstrable in nature. Recurrent mutation is probably responsible for some aspects of genic variation in Little Bahama Bank *Cerion*. Finally, selection may play an important role in regulating the frequency of certain alleles, either directly or through its action on coadapted, linked gene complexes.

It is likely that these various stochastic and deterministic agents act differentially on the various populations which differ in size and degree of isolation or exposure to gene flow. In this context it may be recalled that we found moderate amounts of genic variability in *Cerion*: mean number of alleles per locus lies in the range 1.65–1.70, frequency of loci polymorphic per population ranged from 0.15–0.30, and the frequency of heterozygous loci per individual ranged from 0.054–0.128. The occurrence of more variable populations in some areas may indicate greater environmental heterogeneity or perhaps increased levels of gene flow between partially differentiated populations. Alternatively, lower levels of genic variation elsewhere may indicate environmental homogeneity and reduced levels of gene flow. It must be remembered, however, that higher (or lower) levels of variability in different areas (as in the case of *Cerion* from Grand Bahama and The Crossing on Great Abaco) may have quite different determinants. Thus, while the overall pattern of genic variation in these *Cerion* may appear relatively simple, we should be alert for the selective development of slightly different coadapted gene complexes in different areas. As in the case of an area effect in *Cepaea nemoralis* recently restudied by Johnson (1976), we expect much synergism between history, environmental selection, and coadaptation.

TABLE 16. GENIC HETEROZYGOSITY (H) PER INDIVIDUAL FOR VARIOUS SAMPLES AND GROUPS OF SAMPLES (N) OF *Cerion* FROM THE LITTLE BAHAMA BANK.

Sample(s)	N	$\bar{H}$	(range)
Grand Bahama	7	10.43	(9.17–12.27)
Little Abaco	3	6.25	(6.22–6.28)
Pongo Carpet	9	6.01	(5.67–6.67)
Treasure Cay	3	5.30	(4.52–5.71)
Snake Cay	3	5.37	(5.00–5.74)
Rocky Point	7	10.46	(8.95–11.50)
The Crossing—east	3	9.63	(8.30–10.60)
The Crossing—west	2	9.35	(9.03–9.67)
Sandy Point	1	6.40	—
Hole-in-the-Wall	1	7.00	—

Finally, we note that the overall genic similarity of *Cerion* on Little Bahama Bank indicates that these populations were not founded by dozens of independently derived hurricane-borne propagules. While we cannot exclude the possibility of hurricane transport of alleles from elsewhere, we cannot properly assess the significance of such occurrence until we have completed our survey of genic variation elsewhere in the Bahamas and Cuba. Until this information is gathered, we prefer to interpret the pattern of genic variation as a product of evolution *in situ*, probably during Pleistocene hypothermals when the Little Bahama Bank was a single large island. The differentiation between Grand Bahama and Abaco could easily have occurred since the flooding of the bank, when the various island populations became isolated from each other. Using Nei's (1975) crude but useful method of relating electrophoretic

data to time of evolutionary divergence, where $t = 5 \times 10^5 D$ (and taking 0.0150 for D), we find that the Grand Bahamian and Abaconian populations diverged about 7,500 years ago if rates of genetic change have been constant. This is very close to the estimated time of submergence for the bank.

V. DISCUSSION

The preceding genic analysis has considerable bearing on the taxonomic status of ribby and mottled morphotypes. We have shown that patterns of allozyme variation bear little relation to distribution of the shell morphotypes. In fact, these taxa are so similar to one another that if we had never seen samples from the area of interaction, we would probably have concluded that the two morphotypes are genically identical. Recall that the highest value of D calculated among 820 comparisons was only 0.0564 ($I = 0.9451$). The degree of genic differentiation found among 47 populations of *Cerion* on Little Bahama Bank is well within the limits found among conspecific populations of comparable land snails. Greater interpopulation variation has been detected among the *Helix aspersa* inhabiting two adjacent city blocks in Bryan, Texas (Selander and Kaufman, 1975), among eight populations of *Theba pisana* in Israel (Nevo and Bar, 1976), and among ten populations of *Cepaea nemoralis* in North America (Brussard, 1975). As a generalization emerging from a rapidly increasing number of studies, comparison of local populations typically produces values of D in the range 0.001–0.01, while subspecific comparisons exhibit $D = 0.004$–0.351, and specific comparisons yield $D = 0.05$–2.73 (Nei, 1975). In the *willistoni* group of *Drosophila*, for example, average values of D are: 0.03 between geographic populations; 0.23 between subspecies and semispecies; and 0.66 between sibling species (Ayala, 1975). Clearly, on the basis of these generalizations, we should synonymize *C. bendalli* with *C. abacoense* and treat the Little Bahama Bank *Cerion* as a single variable species. We choose not to do this for several reasons.

First, variation in structural gene products tells us nothing, *per se*, about the development of reproductive isolation. Although a large number of allelic substitutions usually precede the completion of reproductive isolation (typically about 20 per 100 loci (Ayala, 1975)), there are many exceptions. Species pairs characterized by very low values of D include *Drosophila persimilis* and *D. pseudoobscura*, 0.05 (Prakash, 1969); *Thomomys bottae* and *T. umbrinus*, 0.009–0.054 (Patton et al., 1972; Patton, 1973); and the semispecies of *Drosophila paulistorum*, 0.025 (Richmond, 1972). At the other extreme, levels of genic divergence are similar between various sibling species of *Drosophila*, 0.67 (Ayala, 1975); humans and chimpanzees, 0.62 (King and Wilson, 1975); and local populations of a pocket gopher *Geomys bursarius*, (Rogers' $D = 0.65$–0.89) (Penney and Zimmerman, 1976). Values of D do not by themselves permit us to make unequivocal taxonomic decisions.

Secondly, the genic and morphometric surveys, taken together, both indicate that something notable is going on in the area of interaction between morphotypes. Although we find no increased variability in shell form, *Cerion* from this area are significantly more variable genically than samples collected elsewhere. They are polymorphic for alleles not found in either adjacent "parental" population (6-Pgdh-1^b and Est-2^b). A similar phenomenon was discovered in the hybrid zone between *Mus musculus musculus* and *M.m. domesticus* in Denmark (Hunt and Selander, 1973). Populations in this area also display higher levels of P and H, as well as increased intersample variation. This is particularly marked at The Crossing where between morphotype gene flow is presumably restricted by an intervening hill. Average values of D between samples on the east and west side of the hill are 0.0068 and 0.0003 respectively; D values between sam-

ples on either side of the hill average 0.0235. We tentatively interpret this situation as an interaction between two partially differentiated taxa possessing slightly different coadapted gene complexes.

Moreover, on New Providence Island, the same two morphotypes (under different names) interact to yield a "classic" hybrid zone, with unique phenotypes and greatly increased morphological variability in the intermediate samples. In fact, wherever the two morphotypes interact in the Bahamas (and they do on several islands), the hybrid zones are marked and narrow. We have never failed to find some evidence—either morphological (as on New Providence) or genetic (as on Abaco and in partly completed studies of several zones on Long Island)—of abrupt change, marked discontinuity, or greatly increased variability. The two morphotypes never blend evenly, and we take this as a sign that their mixtures involve two at least moderately discordant entities. We believe that this discordance deserves some taxonomic recognition above the subspecific level. The morphotypes are not mere geographic variants. (Simple geographic variants do abound as well; we designate as such the Pongo Carpet samples of *C. bendalli* because their morphological transitions to normal populations are smooth and because they share with adjacent samples of normal *C. bendalli* a genetic anomaly peculiar to their region—see Gould et al., 1974.) Structural gene products, in any case, do not control the alteration of developmental (allometric) rates that lie at the core of differences between morphotypes of *Cerion*. We shall have to learn how to study the genetics of eukaryotic regulation before the fundamental problems of *Cerion* are resolved.

Finally, we are now studying a series of hybrid zones involving *Cerion* of radically different morphology elsewhere in the Bahamas. Our preliminary electrophoretic surveys suggest that some of the most distinctive morphotypes (recognized as separate subgenera) of *Cerion* have differentiated to a lesser extent than semispecies in groups like *Drosophila willistoni*. Until we know more about genic variation in *Cerion* as a whole, we will treat the mottled and ribby morphotypes as semispecies. Until we know more about them and their interactions (repeated under the guise of many different species names throughout the Bahamas and Cuba), we will recognize *C. bendalli* and *C. abacoense* as taxonomic species. In doing so we heed Lewontin's (1974) closing dictum that "context and interaction are of the essence."

ACKNOWLEDGMENTS

We thank John Hevelin for spending so much time measuring all the snails so carefully; Margaret Wu, Janet Quensen, Dana Marek and, especially, Sarah Burgess for their excellent help in the electrophoresis laboratory; Tom and Amy Schoener and William Gillis for sharing their expertise in Bahamian natural history with us. This work was supported by N.S.F. Grant BMS-72-02213-A03. Publication was also partially supported by the Coles Fund.

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NOTE ADDED IN PROOF

Since the above study was completed, a quantitative system of identifying allozymes has been developed (Woodruff and Burgess, in preparation). In future papers, *Cerion* allozymes will be characterized by their mobilities (under specified conditions) relative to the mobility of analogous allozymes derived from *C. incanum*. *C. incanum* from the Florida Keys is an appropriate standard as it is genetically invariant throughout most of its range (Woodruff, D.S., 1978, Evolution and adaptive radiation of *Cerion*: a remarkably diverse group of West Indian land snails. Malacologia 17: 223–239). Allozymes described here as 6-Pgdh-1^b, Mdh-1^b, Mdh-2^b, Got-1^b, and Lap-1^a are identical in their mobility to those of *C. incanum* and henceforth will be designated with the superscript 1.00 rather than a letter. For example, 6-Pgdh-1^b will now be 6-Pgdh-$1^{1.00}$.

In the course of quantifying the relative mobility of various allozymes, an error was discovered in the scoring of the Est-2 system as reported above. While *C. abacoense* and *C. bendalli* share a common set of Est-2 alleles, the allozyme here reported as Est-2^f does not have the same mobility in its commonest form in each species. Est-2^f, the commonest allozyme of *C. abacoense* and the populations from the areas of interaction, is now correctly designated Est-$2^{1.00}$. Est-2^f of *C. ben-*

dalli, on the other hand, is now known to migrate a little further. (This common *C. bendalli* allele is also present, though rare, in *C. abacoense*. Thus it remains true that neither species has a unique allele.) Consequently, Table 13 and Fig. 14 are incorrect with respect to their allozyme frequencies and the calculated interspecific genetic distances are slight underestimates. This finding does not significantly change our overall conclusions. A corrected data set, together with three years' additional data from the zone of interaction, will be reported in Woodruff and Gould (in prep.).

APPENDIX: LIST OF LOCALITIES

Specimens described in this paper may be found in the Museum of Comparative Zoology, Harvard University. The authors' collection sites are described below. Grid references are to the Grand Bahama and Abaco (Bahamas 1: 25,000 series) map series prepared by the Directorate of Overseas Surveys. Localities are arranged geographically from west to east. More precise data are available from the authors.

Loc.	Grid Ref.	General Area
Grand Bahama—*C. bendalli*		
212	QV 7293 29382	near Freeport airport
211	QV 7324 29351	junction of E. Sunrise Hwy and Shearwater Dr., Lucaya.
208	QV 7435 29388	near Blair House on Barbary Beach rd.
204	QV 7423 29436	site in pine forest, Lucaya Estate.
207	QV 7589 29488	forest site, North Perimeter Parkway, 1.0 km N. of Queens Hwy.
209	QV 7454 28497	North Perimeter Parkway
205	QV 7532 29459	Queens Highway, 0.8 km E. of Grand Bahama Hwy junction.
202	QV 7703 29483	High Rock
199	QV 7834 29591	North Riding Point—site A.
200	QV 7831 29599	North Riding Point—site B.
201	QV 7871 29548	The Gap
Little Abaco—*C. bendalli*		
213	TE 2202 2980	north coast at Crown Haven.
214	TE 2286 29792	Wood Cay village
216	TE 2436 29779	Little Abaco end of causeway between Little Abaco and Great Abaco.
Great Abaco—*C. bendalli*		Great Abaco end of causeway between Little Abaco and Great Abaco.
217	TE 2437 29780	
218	TE 2497 29752	Great Abaco Highway, 0.3 km W. Cooperstown (Pongo Carpet site 9 in Gould et al. 1974).
224	TE 2502 29750	Cooperstown (Pongo Carpet site 7).
223	TE 2510 29741	4.85 km N. of Pongo Carpet (site 6)
222	TE 2511 29740	4.75 km N. of Pongo Carpet (site 5)
226	TE 2517 29733	3.8 km N. of Pongo Carpet (site 4)
220	TE 2528 29723	2.4 km N. of Pongo Carpet (site 3)
219	TE 2531 29721	2.1 km N. of Pongo Carpet (site 2)
316	TE 2543 29707	Pongo Carpet (site 1)
228	TE 2725 29524	Rock Bluff road, Treasure Cay.
229	TE 2716 29529	Beach Way, Treasure Cay.
230	TE 2704 29542	Treasure Cay rd., 1.8 km NW of Loc. 229.
231	TE 2694 29550	Junction Treasure Cay rd and Great Abaco Hwy.
233	TE 2707 29495	Great Abaco Hwy. 5.9 km S. of Loc. 231.
240	TE 2866 29404	Bustick Bight
241	TE 2872 29394	Great Abaco Hwy, 1.1 km SE. of Loc. 240.
247	TE 2970 29383	John Cash Point, Marsh Harbour.
246	TE 2927 29273	Fossil locality exposed in road cut.
243	TE 2945 29275	Snake Cay rd., W. of causeway to Tuggy Cay.
245	TE 2949 29275	Tuggy Cay
244	TE 2953 29274	Snake Cay

APPENDIX [continued]

Loc.	Grid Ref.	General Area
Great Abaco—area of interaction between *C. bendalli* and *C. abacoense*		
261	TE 2916 29105	Cherokee Sound jetty
260	TE 2909 29095	Casuarina Point road junction
501	TE 2907 29095	0.5 km N. of Rocky Point
308	TE 2904 29093	0.3 km N. of Rocky Point
307	TE 2902 29092	Rocky Point
306	TE 2900 29092	0.3 km S. of Rocky Point
310	TE 2893 29093	approx. 1.0 km W. of Rocky Point
309	TE 2888 29098	1.6 km W. of Rocky Point
305	TE 2893 29088	2.9 km N. of Loc. 259
304	TE 2882 29078	1.6 km N. of Loc. 259
311	TE 2874 29074	NW. corner of Bahama Palm Shores estates.
249	TE 2845 29059	Great Abaco Hwy., 8.5 km S. of Cherokee rd. junct.
253	TD 2812 28943	Chalk Sound jetty.
255	TD 2809 28931	Great Abaco Hwy., Crossing Rocks estate junct.
251	TD 2594 28783	Sandy Point.
Great Abaco—*C. abacoense*		
259	TE 2873 29066	Bahama Palm Shores estate gazebo.
520	TE 2856 29050	2.2 km S. of Loc. 259.
521	TE 2848 29046	3.0 km S. of Loc. 259.
254	TD 2818 28942	Crossing Rocks Bay track: east end.
257	TD 2816 28933	Crossing Rocks estate beach: north end.
252	TD 2815 28925	Crossing Rocks estate beach: south end.
250	TD 2813 28617	Hole-in-the-Wall lighthouse.

US ISSN 0027-4100

Bulletin OF THE
Museum of
Comparative
Zoology

The American Orb-weaver Genera *Colphepeira, Micrathena* and *Gasteracantha* North of Mexico (Araneae, Araneidae)

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VOLUME 146, NUMBER 9
8 SEPTEMBER 1978

THE AMERICAN ORB-WEAVER GENERA *COLPHEPEIRA*, *MICRATHENA* AND *GASTERACANTHA* NORTH OF MEXICO (ARANEAE, ARANEIDAE)

HERBERT W. LEVI[1]

ABSTRACT. *Colphepeira* has only one species from the southeastern United States. There are four species of *Micrathena* north of Mexico, three common ones in eastern North America from New England to the tropics, one uncommon from Arizona to Guatemala. All *Micrathena* known, perhaps 50 species, are tropical American, the three extending their range north belong each to a different species group. Even though tropical and widespread in the eastern states, *M. mitrata* and *M. gracilis* appear absent from southern Florida. All *Micrathena* species have only a sliver of the canoe-shaped tapetum left, the latter a characteristic of most of the superfamily Araneoidea. The cosmotropical genus *Gasteracantha* has only one or two species in the Americas, *G. cancriformis* in the warmer parts of North America.

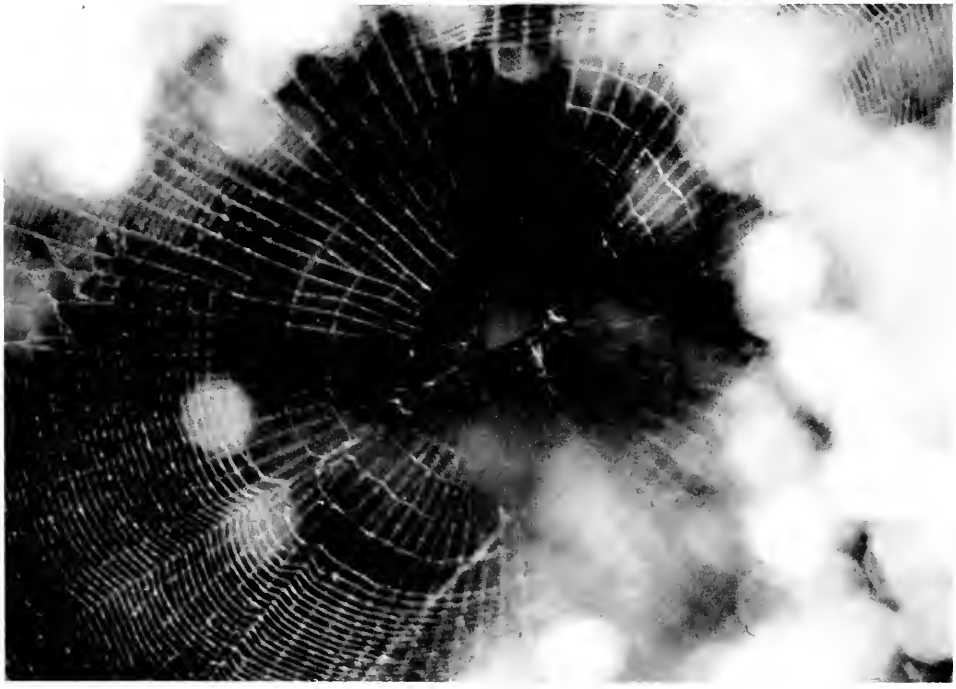
INTRODUCTION

Homann (1950, 1971) reported diversity in secondary eye structure within the spider family Araneidae. The tapetum of the secondary eyes is usually canoe-shaped: with a crease through the middle dividing the tapetum into two parts facing each other (Figs. 4, 5, 75, 76). This is characteristic for members of the superfamily Araneoidea and some related families including Agelenidae, Gnaphosidae, Clubionidae, and Amaurobiidae. *Meta* and *Zygiella* have a large canoe-shaped tapetum, like Theridiidae, however the tapetum appears reduced in *Araneus* (and also *Colphepeira*, Figs. 4, 5) with rows of rhabdomes arranged in loops toward the median side in the posterior median eyes. In some (*Pachygnatha*, and also *Linyphia*) only the lateral eyes have the canoe-shaped tapetum left. *Tetragnatha* have lost all tapetum. Some arachnologists consider the absence of epigynum in *Pachygnatha* and *Tetragnatha* a primitive feature and the two genera ancestral, related to the haplogyne spiders. Out-comparison (all relatives have a canoe-shaped tapetum, and an epigynum) would indicate that the loss of both structures may be secondary. To learn more about these relationships, the tapetum has to be examined (Figs. 4, 5, 19, 20, 75, 76).

Already Homann's eye studies indicated that *Colphepeira* belongs to the Araneinae, not close to *Meta* or *Theridiosoma* as previously thought. My study of *Colphepeira*'s genitalia confirms Homann's conclusions. A new observation, not previously reported, is that *Micrathena* species have only remnants of a tapetum in the posterior median eyes. Perhaps this is only an adaptation to *Micrathena*'s diurnal habits or perhaps it will be of use for figuring out phylogenies.

Also of interest are the relatively large accessory setae below the tarsal claws of *Micrathena*. *Micrathena* may be a good experimental animal for studying the handling of silk (a subject about which we know little), because its setae against which silk strands are held by the median claws are larger than those of other genera.

[1] Museum of Comparative Zoology.



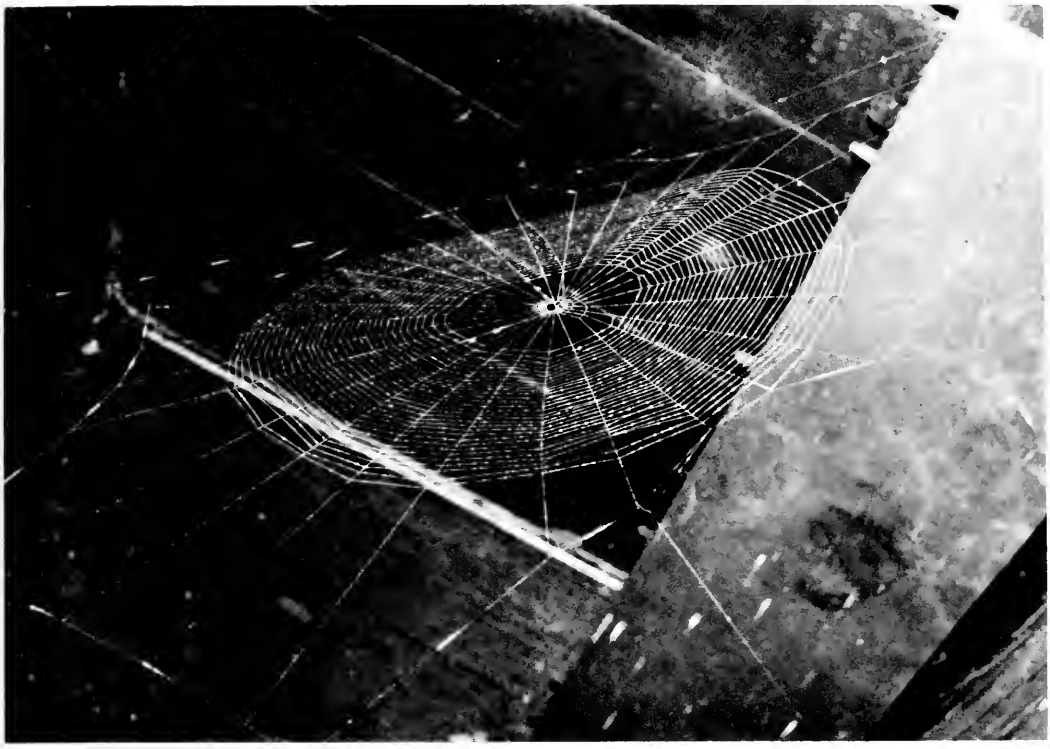


Plate 2. *Gasteracantha cancriformis* (Linnaeus) web, spider removed, dusted with cornstarch. Viscid area 17 cm in diameter. Web was built at 45° angle in porch corner of abandoned Florida house: lower left, floor; above and far right, walls. Notice tufts of silk on frame lines and on some radii.

Colphepeira contains only one small-sized species and is related to *Singa* and perhaps *Mangora*. *Micrathena* and *Gasteracantha* are tropical spiders; *Micrathena*, with more than 50 species, are all tropical American. Three of these have successfully extended their range from the tropics to temperate eastern North America (Map 2). Each of the three belongs to a different species group. I believe *Gasteracantha* and *Micrathena* to be specialized Araneidae which have lost some of their palpal sclerites secondarily, and *Micrathena* do not attack-wrap prey (Robinson, personal communication). The lack of attack-wrapping is probably not primitive but a secondary loss. *Micrathena* and *Gasteracantha* orb-webs have open hubs (Plates 1, 2). *Micrathena* rests in the center of the web in an unusual position (Plate 1) and controls web tension. Unlike other araneid genera *Micrathena* have strong fourth legs, used to hold its position in the web (Plate 1). Both *Micrathena* and *Gasteracantha* are diurnal spiders.

I would like to thank colleagues for

←

Plate 1. *Micrathena gracilis* (Walckenaer) in web, Virginia. The lower photograph is about life-size. Web dusted with cornstarch. Notice the unusual position of the spider in the open hub and the use of the fourth leg (in upper photograph).

making collections available. P. H. Arnaud and R. X. Schick of the California Academy of Sciences, D. Bixler, J. A. Beatty, J. Carico, R. Crabill of the National Museum of Natural History, C. Dondale of the Canadian National Collections, S. I. Frommer of the University of California Riverside collections, W. R. Icenogle, B. J. Kaston, H. Dybas and J. B. Kethley of the Field Museum of Natural History, T. Kronestedt of the Natural History Museum, Stockholm, R. E. Leech, G. Uetz and J. D. Unzicker of the Illinois Natural History Survey, S. C. Johnson, W. Peck of the Exline-Peck collection, N. Platnick of the American Museum of Natural History, W. T. Sedgwick, W. Shear, W. Staręga of the Polish Academy of Science, Warsaw, H. K. Wallace, H. V. Weems of the Florida State Collection of Arthropods, F. R. Wanless of the British Museum, Natural History. The mapping and typing were done by Susan Hunt. The research and its publication were made possible by National Science Foundation grants BMS 75-05719 and DEB 76-15568.

METHODS

The method of examination, study, and illustration are those of other studies in this series on North American orb-weavers. However in *Micrathena* and *Gasteracantha*, measurement of total length is the length in midline from the anterior margin of the carapace to between the posterior abdominal humps or spines.

The tapetum of the secondary eyes was examined by near-vertical illumination (with a fiber-light) on the eye. The spider is kept submerged in alcohol and positioned on washed sand, which permits odd positions and very minor changes in angles. (Because of reflections, sand is a poor background for most observations; the background should be black.) The magnification of the stereoscopic dissecting microscope is about 50 times for the larger species, 100 times for the smaller. If the eye lens has become opaque in preservation the spider can be cleared in clove oil for examination. The posterior dorsal eyes were illustrated with the left eye flat and the right at an angle, anterior is on top (Figs. 4, 19, 75). The left lateral eyes were illustrated diagrammatically, first the anterior (left) flat under the microscope, then the spider was shifted for the posterior eye (right) flat under the microscope. The illustrations produced are thus composites (Figs. 5, 20, 76). The rows of rhabdomes can be seen in microscope mounts of the eyes with a compound microscope.

Following American and British dictionary definitions but not arachnological vocabulary, spines are immovable, rigid, pointed humps or thorns, as found on the abdomen of *Micrathena* and *Gasteracantha*. The movable heavy setae covering the integument are called macrosetae.

Colphepeira Archer

Colphepeira Archer, 1941, Geol. Surv. Alabama, Mus. Paper, 18: 12. Type species *Epeira catawba* Banks by original designation. The name is feminine.

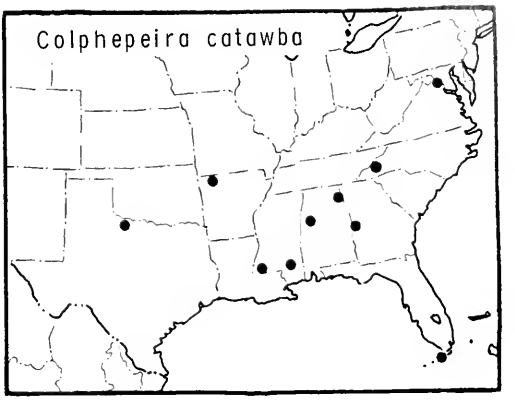
Diagnosis. Colphepeira differs from many other araneid genera by the closely spaced eyes (Figs. 1–3). Unlike *Mangora* and *Singa*, it has a hirsute carapace and abdomen with short setae on granules and the shape of the abdomen is higher than long with posterior dorsal tubercles (Figs. 1, 6, 7). It differs from *Mangora* by the lack of the characteristic long trichobothria on the third tibia.

Description. The carapace, abdomen, and legs are covered with scattered short setae. The setae are cylindrical, distally tapering to a blunt point, basally with a narrow neck and sitting in the center of a disc. The sides of the setae have some blunt teeth (Fig. 9). The eyes are subequal to each other in the female, and the anterior are larger in the male. The posterior eye row is recurved. The median eyes are slightly more than their diameter apart, and the anterior medians are less than two diameters from the laterals, the posterior medians 2.5 diameters from the laterals.

The thorax has a shallow depression in the female (Fig. 3) and a transverse, procurved mark in the male. The posterior part of the head is slightly swollen. The height of the clypeus is slightly more than the diameter of the anterior median eyes (Fig. 2). The sternum, like the carapace, is lightly sclerotized and slightly granulate. The chelicerae are weak, without a basal boss, and have two teeth on the anterior margin, two on the posterior and denticles and one tooth in between (Fig. 8). The chelicerae have a proximal anterior projection under the clypeus as in Theridiidae (Fig. 8). The proximal articles of the legs, especially the femora, are also slightly granulate. The first legs are longest, the fourth second in length, the third shortest. The metatarsus and tarsus together are shorter than the patella and tibia. The abdomen is higher than long with posterodorsal and posterior tubercles (Figs. 1, 6, 7). The lung covers are smooth and, like those of *Meta*, lack the transverse grooves found in species close to *Araneus*. The leaflets of the book-lung in a microscope mount appear to consist of series of parallel tracheae attached to each other side by side.

The males are like females, slightly smaller and have a more distinct, transverse, thoracic depression and a slightly higher clypeus, 1.5 diameters of the anterior median eyes. The endite has a tooth facing a tooth on the proximal end of the palpal femur. The distal margin of the first coxa has a hook that fits into a groove on the second femur. The legs are not modified except that the anterior tibia is slightly sinuous.

Genitalia. The soft epigynum is covered with setae (Fig. 9) and has a soft annulate scape (Figs. 9, 10). The openings appear on the posterior face (Figs. 10, 11). There are fertilization ducts. The male palpus has a soft conductor (C in Figs. 14, 15), bearing a basal tooth, a median apophysis (M), which has a hook, and a very large terminal apophysis (A) which covers conductor and embolus (E) distally. The terminal apophysis extends and covers most of the bulb laterally (Figs. 12–15).



Map 1. Distribution of *Colphepeira catawba* (Banks), north of Mexico.

Relationship. A similar large terminal apophysis (A in Fig. 15) is found in some species of *Singa* (Levi, 1972) and *Mangora* (Levi, 1975). The resemblance of the palpus (Fig. 14) to that of *Singa hamata* (Clerck) is striking in the shape of the small median apophysis (M), the soft conductor (C), and the large terminal apophysis (A). The embolus of *Colphepeira* is simpler, and *Colphepeira* lacks a subterminal apophysis. Other similarities to *Singa hamata* and *Mangora* are the lightly sclerotized epigynum, with a soft broadly attached scape and the closely spaced eyes. The genitalia also resemble those of *Cercidia* (except for *Cercidia*'s large median apophysis). All these related genera *Colphepeira*, *Singa*, *Mangora*, and *Cercidia* have the eyes relatively closely spaced, unlike those of the larger-sized *Araneus*, *Micrathena*, *Gasteracantha* and those of numerous other araneid genera. *Colphepeira*, unlike most araneid genera but like *Mangora*, does not have distinct contrasting ventral abdominal marks.

After he examined the tapetum of the secondary eyes (Figs. 4, 5) Homann (1950) first reported that *Colphepeira* is more

closely related to *Araneus* than to *Meta* or *Theridiosoma*.

Distribution. Only one species of *Colphepeira* is known, *C. catawba*, found in the southeastern United States (Map 1).

Colphepeira catawba (Banks)
Figures 1–15; Map 1

Epeira catawba Banks, 1911, Proc. Acad. Natur. Sci. Philadelphia, 63: 450, pl. 34, fig. 4, ♀. Female holotype from Ashville, Buncombe County, North Carolina in the Museum of Comparative Zoology, lost. There is no old E. B. Bryant catalog card in the file for this species as there is for other Banks types.

Aranea catawba:—Roewer, 1942, Katalog der Araneae, 1: 859.

Colphepeira catawba:—Archer, 1941, Geol. Surv. Alabama, Mus. Paper, 18: 13, pl. 1, figs. 3, 4, pl. 2, figs. 1–3. 1953 Amer. Mus. Novitates, no. 1622: 22, figs. 32–34.

Araneus catawba:—Bonnet, 1955, Bibliographia Araneorum, 2: 452.

Description. Female from Arkansas: carapace black with paired yellowish white patches lacking pigment. Sternum spotted black and yellow-white. Coxae yellow-white. Legs yellow-white with narrow black rings. Dorsum of abdomen with paired streaks (Figs. 1, 7). Venter with black and white spots and no distinct marks. The abdomen slightly higher than long, with four posterodorsal tubercles closely grouped on each side and a pair of tubercles on the posterior face (Fig. 7). Total length, 3.5 mm; carapace, 1.2 mm long; 1.0 mm wide. First femur, 1.2 mm; patella and tibia, 1.4 mm; metatarsus, 1.3 mm; tarsus, 0.5 mm. Second patella and tibia, 1.2 mm; third, 0.8 mm; fourth, 1.0 mm.

Male from Arkansas with color pattern less distinct than female. Abdomen shape like that of female. Total length, 1.6 mm; carapace, 0.9 mm long, 0.9 mm wide. First femur, 1.0 mm; patella and tibia, 1.2 mm; metatarsus, 0.6 mm; tarsus, 0.4 mm. Second patella and tibia, 1.1 mm; third, 0.6 mm; fourth, 0.7 mm.

Variation. Some specimens have little black pigment, others are almost completely black. Total length of females 2.2 to 3.8 mm; carapace 1.0 to 1.3 mm long, 0.9 to 1.1 mm wide. Total length of males, 1.6 to 2.2 mm; carapace 0.9 to 1.2 mm long, 0.9 mm to 1.0 mm wide.

Diagnosis. This species can only be confused with *Dolichognatha* species, which are of similar size and appearance. *Dolichognatha*, a relative of *Tetragnatha*, has four small tubercles on the abdomen, and *Colphepeira* has four tubercles posterodorsal on each side and in addition a pair posteriorly (Figs. 1, 6, 7). *Dolichognatha* species have their chelicerae elongate; *Colphepeira* do not (Fig. 2). The *Dolichognatha* epigynum has a depression with a dark spot on each side; *Colphepeira* has a fleshy scape (Figs. 9, 10). The *Dolichognatha* male palpus appears rather simple, *Tetragnatha*-like, but with a complicated paracymbium. That of *Colphepeira* has a terminal apophysis, median apophysis, and a simple paracymbium (Figs. 12–15).

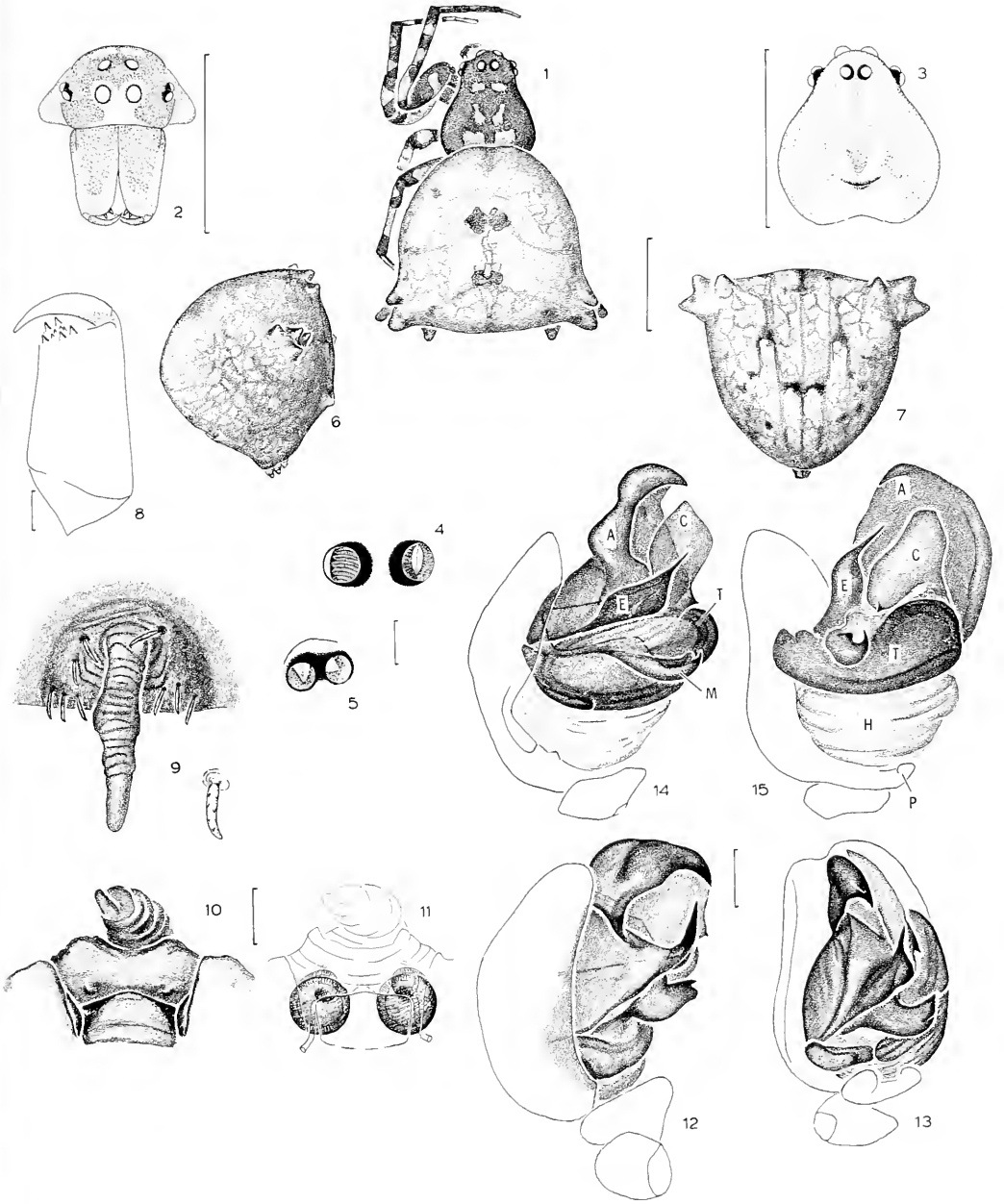
Natural History. According to Archer (1941) *Colphepeira catawba* makes its horizontal orb-web near the ground between tree roots in thin open second-growth woods with grassy undergrowth. The web is 7 to 9 cm diameter with about 60 spirals and a small, poorly defined hub. The egg-sac hangs with debris, suspended on a horizontal line just above the web. The spider has its retreat under loose bark and feeds on small ants.

Distribution. Southeastern United States, Virginia, southern Florida to Sonora (Map 1).

Records. Virginia. Fairfax Co.: Great Falls, ♀ (N. Banks). *Georgia.* Troup Co.: West Point, 7 Sept. 1949, ♀ (A. Archer). *Florida.* Monroe Co.: 2 mi SE of Mara-

→

Figures 1–15. *Colphepeira catawba* (Banks) 1–11. Female. 1. Dorsal view. 2. Eye region and chelicerae. 3. Carapace. 4. Posterior median eyes. 5. Left lateral eyes. 6. Abdomen from side. 7. Abdomen, posterior view. 8. Left chelicera from posterior. 9–11. Epigynum (with enlarged seta). 9. Ventral. 10. Pos-



terior. 11. Posterior view, cleared. 12–15. Male, left palpus. 12. Mesal. 13. Ventral. 14. Mesal, expanded. 15. Ventral, expanded.

Scale lines. 0.1 mm, except Figures 1–7, 1.0 mm.

Abbreviations. A. terminal apophysis; C, conductor; E, embolus; H, hematodocha; M, median apophysis; P, paracymbium; T, tegulum.

thon, 15 Dec. 1962, juv. (W. Ivie). *Alabama.* Cherokee Co.; May's Gulfe, 11 Aug. 1948, 13 Oct. 1949, ♀♀ (A. Archer). Tuscaloosa Co.: Tuscaloosa, 2 Oct. 1941, ♀ (A. Archer). *Mississippi.* Forrest Co.: Camp Shelby, 1945–1946, ♀, ♂ (A. Archer). Wilkinson Co.: Centreville, Jan.–July 1944, ♀ (A. Archer). *Arkansas.* Carroll Co.: Berryville, Aug. 1938, summer 1941, Sept. 1944. ♀, ♂ (C. Wilton). *Texas.* Wilbarger Co.: 4 mi NW of Elliott, 21 Oct. 1964, ♂ (K. W. Haller). *Sonora.* Guaymas, on beach, 13 Sept. 1966, ♀ (J., W. Ivie), not mapped, received after completion of paper.

Micrathena Sundevall

Micrathena Sundevall, 1833, Conspectus Arachnidum, London, p. 14. Type species *Epeira clypeata* Walckenaer, the only species listed in "section one" of the genus. The name is feminine. The synonymy problems of generic names are discussed by Bonnet, 1957 (Bibliographia Araneorum, 2: 2858).

Diagnosis. Micrathena females differ from those of other genera in having a smooth, shiny carapace with a light rim on each side (Figs. 18, 31, 45, 59) and in particular, from *Gasteracantha*, by having the carapace longer than wide in the female, at times with pairs of dimples (Fig. 31) or lateral spines (in tropical species) unlike that of any other genera. The female abdomen is usually longer than wide, trapezoidal, or square armed with spines, sclerites and a sclerotized ring around the spinnerets (Figs. 17, 30, 44, 58), while that of *Gasteracantha* is usually wider than long. Males lack the carapace rim and the abdominal spines and have a smooth, sclerotized abdomen with a ring around the spinnerets. The male abdomen is longer than wide, not like that of *Gasteracantha.* The median eyes are never projecting as are those of *Gasteracantha.* The posterior legs of both sexes, especially the femora, are longer than the anterior legs or subequal in length, unlike those of most other araneid genera. The posterior median eyes have the canoe-shaped tapetum reduced to a very narrow, lateral sliver. When viewed through the lens, it may be hidden by the curvature of the eyeball (Figs. 19, 32, 46, 60). The mesal side contains rhabdomes without tapetum, arranged in rows of a variable number of loops, few, perhaps 5 to 6 in number in *M. gracilis* (Fig. 60), about 8 to 9 loops in the other species (Figs. 19, 32, 46). The narrow lateral tapetum is unlike that of most species of Araneidae (Fig. 75). The lateral eyes may be separated from each other by as much as their diameter; the rhabdomes to the sides of the tapetum are not arranged in rows.

Description. The carapace is smooth and shiny in the female and has a unique light rim on each side (Figs. 18, 31, 45, 59). Posterior median eyes are 1.2 to 1.5 times the diameter of anterior medians, laterals subequal or slightly smaller than anterior medians. The median eyes are separated by their diameter to 1.5 diameters. The laterals are several diameters from medians, but may be up to slightly more than their diameter from each other (Fig. 47). The height of the clypeus is equal to or slightly more than the diameter of the anterior median eyes (Fig. 57). The chelicerae are slightly longer than wide, strong with three to four teeth on the anterior margin, three to four on the posterior. The legs are usually not banded. However, sometimes they are slightly lighter in color than the carapace and sometimes slightly granulated (especially the long femora) bearing very short setae. The abdomen is often brightly colored, always modified with spines, tubercles, or folds. The spinnerets are surrounded by a sclerotized ring.

The males are smaller than the females and have the abdomen lightly sclerotized. In the males, it is greater in length than in width, but lacks the spines and tubercles of the female. Thus it is quite difficult to associate with the females of the same species (Figs. 16, 28, 41, 55). The palpal femur lacks the proximal tooth, and there is no facing tooth on the endite. The first coxae sometimes have a hook, sometimes not; the hook is absent in the four species

north of Mexico. The distal articles of the legs may not be modified and only sometimes have macrosetae; in *M. funebris* the first femur has macrosetae on the distal end (Fig. 16).

Genitalia. The epigynum is usually a heavily sclerotized knob with openings at the base of the posterior face (Figs. 21–23, 34–36, 48–50, 62–64). There is no annulate scape. Together with the shape of the abdomen, the epigynum is a diagnostic feature but has been slighted by previous authors.

The palpal patella has one macroseta in *M. funebris*; in *M. gracilis* and *M. sagittata* the macroseta is present, but small. The paracymbium (P in Fig. 40) differs in different species (Figs. 25, 38, 52, 66), unlike other araneid genera but as in *Zygiella*. The bulb lacks a terminal apophysis but has a transparent flap which arises from the base of the embolus (E) and surrounds it. It may be homologous with the missing terminal apophysis (Figs. 27, 40, 54, 68). The embolus tip (E) rests in the conductor (C). The conductor is sometimes a complex sclerite and at its base another sclerite may appear, the paramedian apophysis (PM) (Figs. 40, 68). The median apophysis varies greatly in different species: a sclerotized, split hook in *M. funebris* (M in Fig. 27), the tip sclerotized in *M. mitrata* (Fig. 40), forked in *M. sagittata* (Fig. 54) and reduced in *M. gracilis* (Fig. 68). The sclerites of the palpus are only lightly sclerotized, unlike the sclerotized epigynum, carapace and spines.

Natural History. Micrathena species are diurnal and the spiders rest in the open hub of the orb-web (Plate 1). The spider hangs in a characteristic position, controlling the tension of the web while in the hub. The spinnerets are up, the dorsal surface of the abdomen parallel to the ground (Plate 1) and at an angle to the web plane. The orb has many radii and spirals. No doubt the long fourth legs are an adaptation to the unusual position in the web. Unlike most araneids, *Micrathena* species do not attack-wrap (M. Robinson, personal communication). There is no retreat. All species, north of Mexico, mature in fall in the northern part of their range. Little is known of egg-sacs and life histories.

Distribution. All species known are American. There may be as many as 50 or more tropical American species, with only four extending their range into the temperate area north of Mexico: three in the eastern United States, one in the Southwest (Map 2).

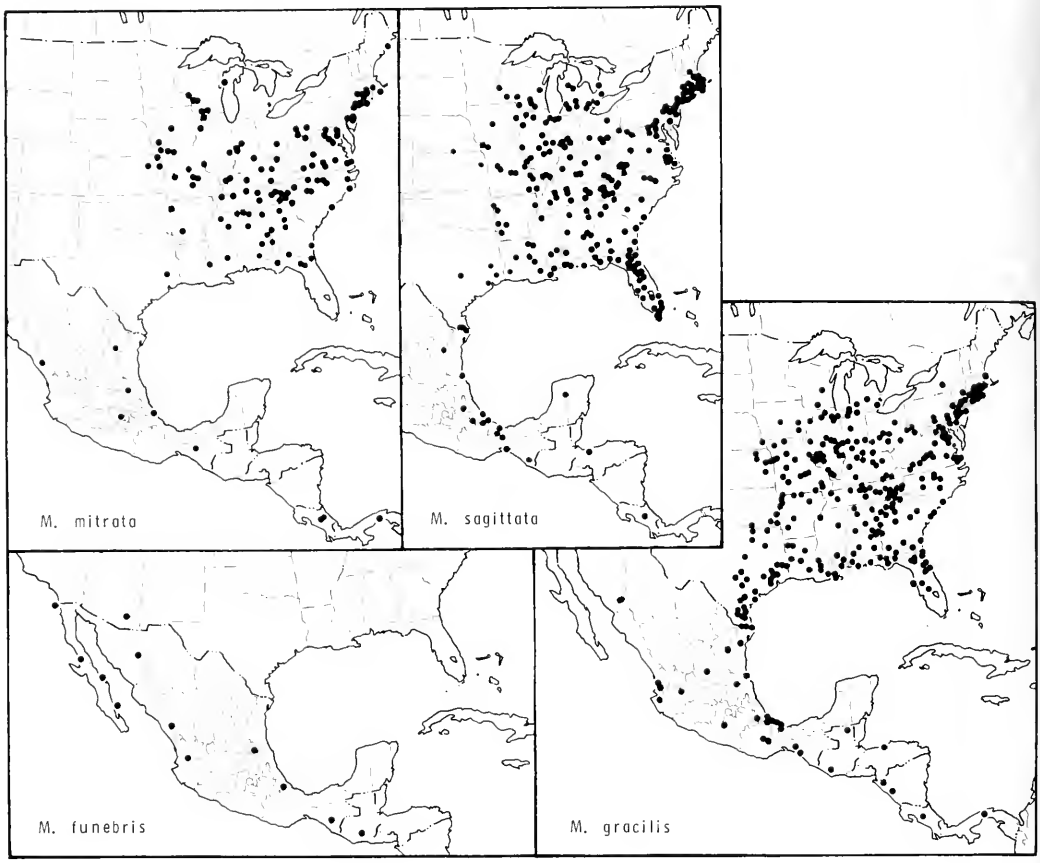
Note. In all species, the genitalia are quite variable, and thus the species are difficult to delineate. The four species north of Mexico, however, are not closely related to each other and are easily separated.

KEY TO FEMALE *MICRATHENA* NORTH OF MEXICO

1. Female abdomen with 5 pairs of conical tubercles (Figs. 58, 59); eastern United States to South America ..... *gracilis*
– Female abdomen with 3 or 2 pairs of spines or tubercles (Figs. 18, 31, 45) 2
2(1) Abdomen with only two pairs of posterior conical tubercles (Figs. 30, 31); carapace with 3 pairs of dimples (Fig. 31); eastern United States to South America (Map 2) ..... *mitrata*
– Abdomen with 3 pairs of tubercles or spines (Figs. 17, 44, 45) and carapace without paired dimples (Figs. 18, 45) 3
3(2) Abdomen much wider behind than anteriorly and with anterior, lateral and large posterior, dorsal spines (Figs. 44, 45); eastern United States to South America (Map 2) ..... *sagittata*
– Abdomen as wide behind as in front without anterior dorsal spines or tubercles, but with dorsolateral, posterior dorsal and posterior ventral tubercles (Figs. 17, 18); Arizona, Baja California to Central America (Map 2) ..... *funebris*

KEY TO MALE *MICRATHENA* NORTH OF MEXICO

1. Abdomen wider behind than in front (Fig. 41); median apophysis of palpus with two branches (Figs. 53, M in 54); paracymbium a recurved hook pointing dorsally (Fig. 52); eastern United States to South America (Map 2) ..... *sagittata*
– Abdomen as wide behind as in front (Figs. 16, 28, 55); median apophysis and paracymbium otherwise (Figs. 26, 39, 67) 2



Map 2. Distribution of *Micrathena* species north of Mexico.

2(1) Abdomen more than twice as long as carapace (Fig. 55); posterior end of abdomen longer on venter than dorsum (Fig. 56); eastern United States to South America (Map 2) ..... *gracilis*

– Abdomen less than 1.5 times as long as carapace, not longer on venter (Figs. 16, 28, 29) 3

3(2) First femur with distal macrosetae (Fig. 16); paracymbium with large granulate sculpturing (Fig. 25); median apophysis a semicircular hook on proximal end of bulb (Figs. 26, M in 27); Arizona, Baja California to Central America (Map 2) ..... *funebris*

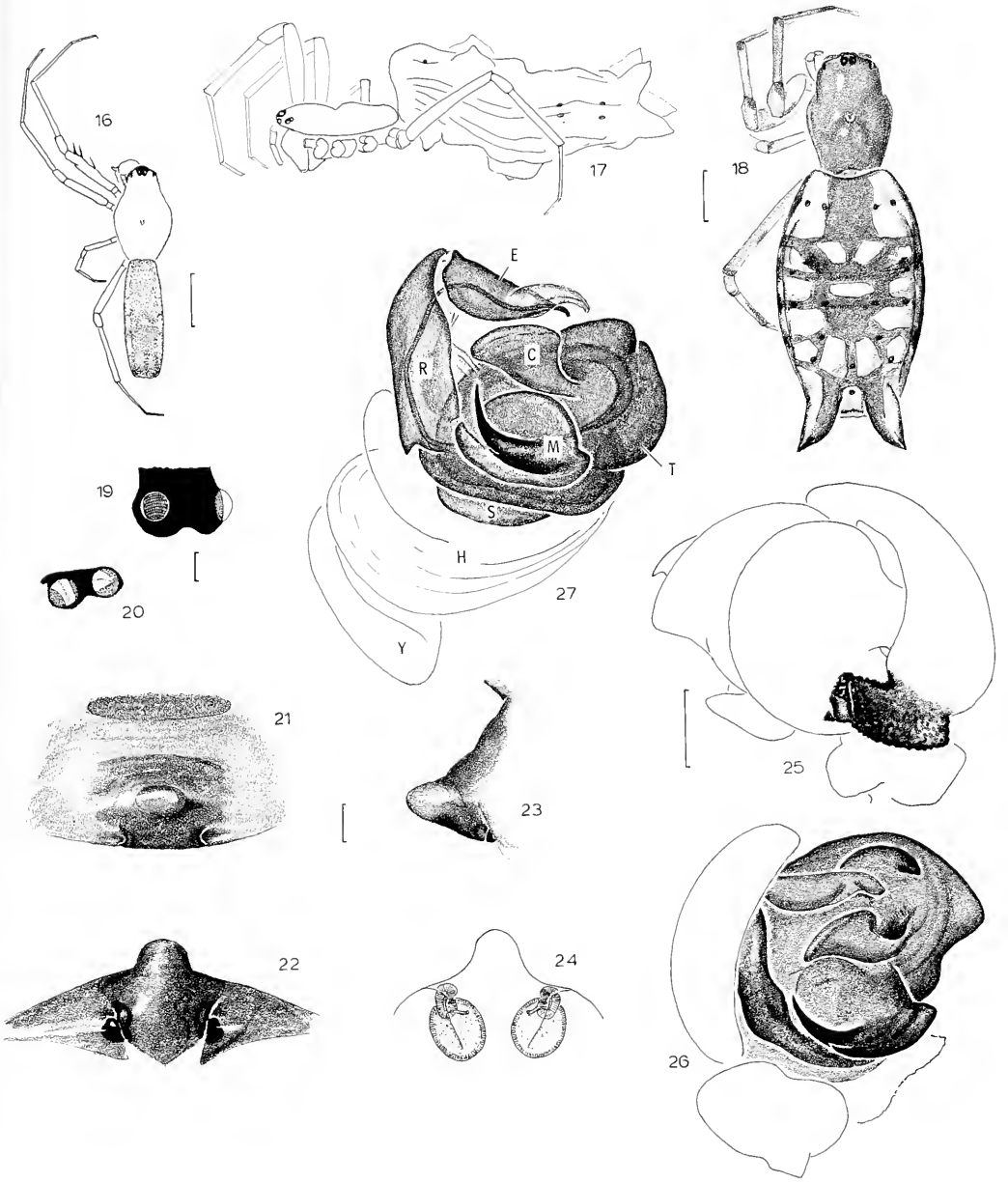
– First femur without distal macrosetae (Fig. 28); paracymbium smooth and small (Fig. 38); median apophysis with distal end pointed and bent back (Figs. 39, M in 40); eastern United States to South America (Map 2) ..... *mitrata*

Micrathena funebris (Marx in Banks) Figures 16–27, Map 2

Acrosoma funebre Marx in Banks, 1898, Proc. California Acad. Sci., 3rd ser., 1(7): 249. Female syntypes from Calmilla Mines and Sierra San Nicholas in the California Academy of Sciences, destroyed; and two syntypes from Mazatlan in the Museum of Comparative Zoology, examined.

Acrosoma maculata Banks, 1900, Canadian Entom., 32: 100. Female holotype from "Arizona" in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Micrathena granulata F.P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 532, pl. 50, fig. 12, ♂. Male holotype from Teapa, Mexico in the British Museum, Natural History, examined. Reimoser, 1917, Verh. Zool. Bot. Ges. Wien, 67: 117. Roewer, 1942, Katalog der Araneae, 1: 958. Bonnet, 1957, Bibliographia



Figures 16–27. *Micrathena funebris* (Marx in Banks). 16. Male. 17–24. Female. 17. Lateral. 18. Dorsal. 19. Posterior median eyes. 20. Left lateral eyes. 21–24. Epigynum. 21. Ventral. 22. Posterior. 23. Lateral. 24. Posterior, cleared. 25–27. Male left palpus. 25. Lateral. 26. Mesal. 27. Submesal, expanded.

Scale lines. 0.1 mm; except Figures 16–18, 1.0 mm.

Abbreviations. C, conductor; E, embolus; H, hematodocha; M, median apophysis; R, radix; S, subtegulum; T, tegulum; Y, cymbium.

Araneorum, 2: 2870. Chickering, 1961, Bull. Mus. Comp. Zool., 125(13): 423, figs. 78–82, ♂. NEW SYNONYMY.

Micrathena funebris:—Reimoser, 1917, Verh. Zool. Bot. Gesell. Wien, 67: 104. Roewer, 1942, Katalog der Araneae, 1: 958. Bonnet, 1957, Bibliographia Araneorum, 2: 2867. Chickering, 1961, Bull. Mus. Comp. Zool., 125(13): 414, figs. 55–59, ♀.

Micrathena maculata:—Reimoser, 1917, Verh. Zool. Bot. Gesell. Wien, 67: 10. Roewer, 1942, Katalog der Araneae, 1: 967. Bonnet, 1957, Bibliographia Araneorum, 2: 2871. NEW SYNONYMY.

Note. Chickering (1961) already suspected that the male named *M. granulata* belonged to the female *M. funebris*.

Description. Female holotype of *M. maculata*. Carapace brown, sternum black-brown. Legs much lighter, yellow-brown, indistinctly banded darker. Abdomen black with white patches (Fig. 18). The rim of the carapace is brown. Carapace with a circular depression in thorax (Fig. 18). Abdomen soft with four fleshy extensions posteriorly and an anterior pair of humps on each side (indistinct, if viewed from above, Figs. 17, 18). Total length 7.0 mm, carapace 2.3 mm long, 1.6 mm wide. First femur, 2.0 mm; patella and tibia, 2.2 mm; metatarsus, 1.5 mm; tarsus, 0.7 mm. Second patella and tibia, 1.9 mm; third, 0.9 mm. Fourth femur, 2.4 mm; patella and tibia, 2.2 mm; metatarsus, 1.6 mm; tarsus, 0.7 mm.

Male from Sonora: Carapace glossy brown; legs brown. Dorsum of abdomen gray with central white spots and a row of white spots along lateral margins (Fig. 16); sides gray; venter with a plate from pedicel and surrounding spinnerets lightly sclerotized and brownish black. First femur with strong macrosetae at distal end (Fig. 16). Sides of abdomen almost parallel (Fig. 16). Total length 4.1 mm, carapace 1.7 mm long, 1.1 mm wide. First femur, 1.6 mm; patella and tibia, 1.5 mm; metatarsus, 1.0 mm; tarsus, 0.5 mm. Second patella and tibia, 1.4 mm; third, 0.8 mm. Fourth femur, 1.6 mm; patella and tibia, 1.4 mm; metatarsus, 1.1 mm; tarsus, 0.5 mm.

Variation. The palpus of males from southern Mexico and Guatemala differs in having a shorter sclerotized portion of the median apophysis and a more sclerotized paramedian apophysis. Females vary in total length 5.8 to 7.2 mm, carapace 2.4 to 2.6 mm long, 1.5 to 1.7 mm wide. Males vary in total length 4.0 to 4.1 mm, carapace 1.7 to 2.0 mm long, 1.1 to 1.3 mm wide.

Diagnosis. This species is similar to *M. mitrata*. Females differ in their lack of the paired dimples on the carapace (Fig. 18), and the openings of the epigynum are not in a depression (Figs. 22, 24). There is a pair of tubercles anterodorsal on the abdomen (Fig. 17), lacking in *M. mitrata*. The male palpus differs from *M. mitrata* in having a large granulate paracymbium (Fig. 25) and a split sickle-shaped median apophysis on the proximal end of the palpal bulb (Figs. 26, M in 27).

Natural History. Specimens have been collected sweeping weeds at 975 m elevation in Sonora. The webs in Arizona were fairly abundant and were found one to two feet from the ground, attached to stems of Johnson grass (*Sorghum halepense*). They were found near water, at a 825 m elevation (J. Beatty, personal communication).

Distribution. From Baja California and Arizona to Guatemala (Map 2).

Records (north of Mexico). *Arizona.* Pima Co.: Sabino Pond, Santa Catalina Mts., 825 m el. 26 June, 1960, ♀♀; 10 July 1962, ♀♀ (J. Beatty).

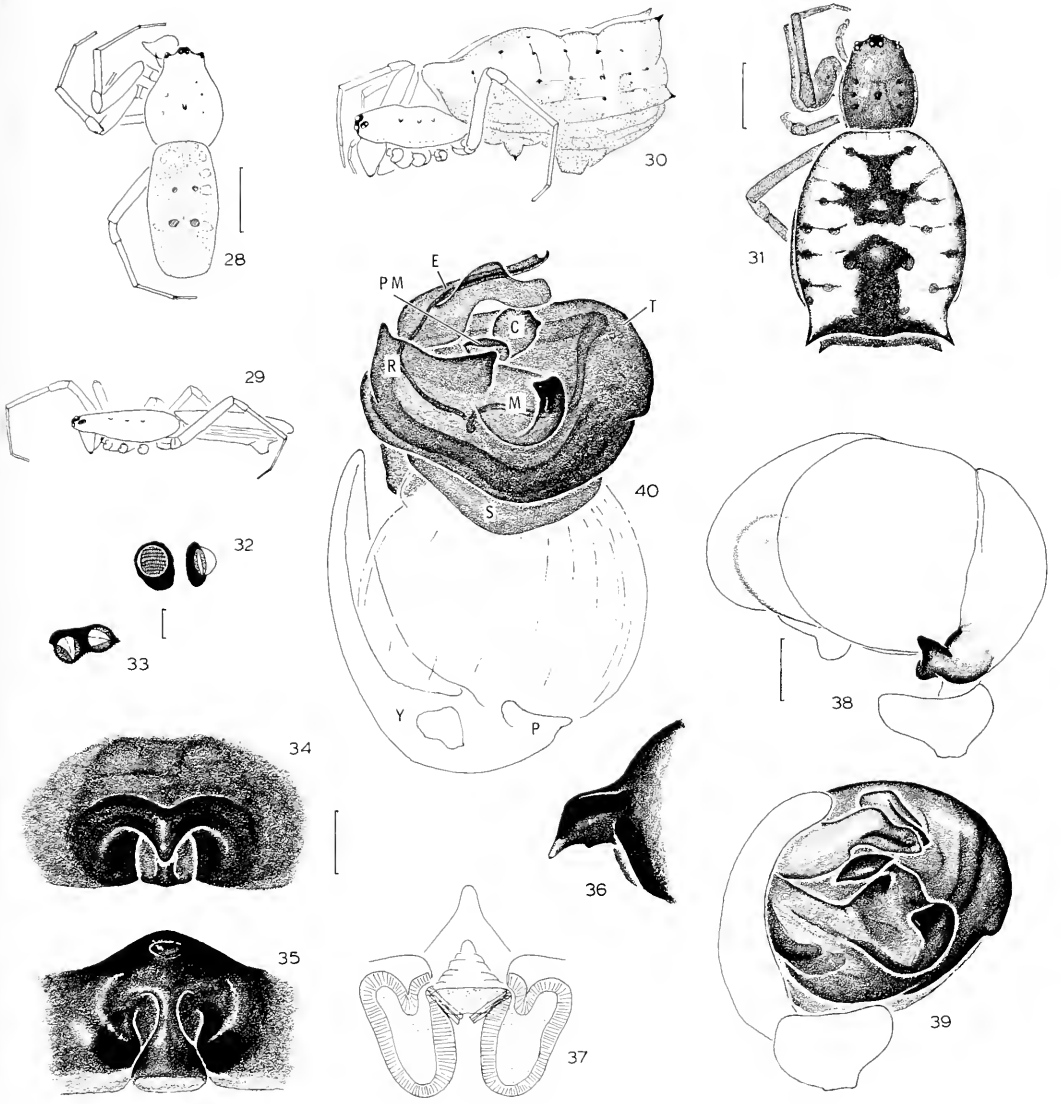
Micrathena mitrata (Hentz)
Figures 28–40, Map 2

Epeira mitrata Hentz, 1850, J. Boston Natur. Hist. Soc., 6: 22, pl. 3, fig. 11, ♀. Syntypes from North Carolina and Alabama in the Boston Society of Natural History, destroyed.

Acrosoma mitrata:—Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 327, pl. 38, fig. 9, ♀. Emerton, 1902, Common Spiders, p. 189, fig. 438. ♀.

Acrosoma reduvianum:—McCook, 1893, American Spiders, 3: 213, pl. 21, figs. 6, 7, ♀, ♂. Not *Plectana reduviana* Walckenaer, 1841 (= *M. gracilis*).

Micrathena mitrata:—F.P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 538.



Figures 28–40. *Micrathena mitrata* (Hentz). 28–29. Male. 28. Dorsal. 29. Lateral. 30–37. Female. 30. Lateral. 31. Dorsal. 32. Posterior median eyes. 33. Left lateral eyes. 34–37. Epigynum. 34. Ventral. 35. Posterior. 36. Lateral. 37. Posteriodorsal. 38–40. Male left palpus. 38. Lateral. 39. Mesal. 40. Submesal, expanded.

Scale lines. 0.1 mm; except Figures 28–31, 1.0 mm.

Abbreviations. C, conductor; E, embolus; M, median apophysis; P, paracymbium; PM, paramedian apophysis; R, radix; S, subtegulum; T, tegulum; Y, cymbium.

Reimoser, 1917. Verhandl. Zool. Bot. Ges. Wien, 67: 104. Roewer, 1942, Katalog der Araneae, 1: 966. Kaston, 1948, Connecticut State Geol. Natur. Hist. Surv., 70: 220, figs. 694–695, ♀, ♂. Bonnet, 1957, Bibliographia Araneorum, 2: 2872.

Micrathena reduviana:—Comstock, 1912, Spider Book, p. 517, fig. 563, ♀. Comstock, 1940, Spider Book, rev. ed., p. 530, fig. 563, ♀. Not *Plectana reduviana* Walckenaer, 1841 (= *M. gracilis*).

Description. Female from Virginia: Carapace brown with white thoracic rim. Sternum dark brown. Legs brown, slightly lighter than carapace. Dorsum of abdomen white with black marks (Fig. 31). Sides white with black marks (Fig. 30). Venter black. There is a thoracic depression and three pairs of dimples on each side of thorax (Fig. 31). Abdomen with four short posterior spines (Figs. 30, 31). Total length 5.0 mm, carapace 1.7 mm long, 1.4 mm wide. First femur, 1.7 mm; patella and tibia, 1.7 mm; metatarsus, 1.2 mm; tarsus, 0.5 mm. Second patella and tibia, 1.4 mm; third, 0.9 mm. Fourth femur, 1.7 mm; patella and tibia, 1.6 mm; third, 1.1 mm; fourth 0.4 mm.

Male: carapace brown, posterior median eyes on black spots. Sternum black. Legs brown. Dorsum black with paired white pigment spots. Venter black. Carapace with three pairs of dimples (Fig. 28). First coxa with a very small hook. Abdomen rectangular in dorsal outline (Fig. 28). Total length 3.5 mm, carapace 1.4 mm long, 1.2 mm wide. First femur, 1.3 mm; patella and tibia, 1.2 mm; metatarsus, 0.9 mm; tarsus, 0.5 mm. Second patella and tibia, 1.0 mm; third, 0.7 mm. Fourth femur, 1.4 mm; patella and tibia, 1.0 mm; metatarsus, 0.8 mm; tarsus, 0.5 mm.

Variation. The dorsal abdominal black marks are smaller in specimens from Guatemala and Panama. Females vary in total length from 4.7 to 6.0 mm long, carapace 1.7 to 2.2 mm long, 1.4 to 1.9 mm wide. Males vary in total length from 3.0 to 3.7 mm, carapace 1.5 to 1.8 mm long, 1.1 to 1.2 mm wide. The largest female came from Mexico.

Diagnosis. Unlike other species north of Mexico *M. mitrata* has three pairs of dimples on the carapace (Fig. 31). The female differs from *M. funebris* in the absence of the anterodorsal tubercle on the abdomen (Fig. 30) and the presence of openings of the epigynum in a depression (Figs. 34, 35). The male palpus has a smaller, differently shaped, smooth paracymbium (Fig. 38), and a median apophysis folded back on itself, its tip sclerotized (Figs. 39, M in 40).

Natural History. Micrathena mitrata is found in deciduous forest, woodland, under trees, sometimes in shrubs and usually in the shade.

Distribution. From Maine to Wisconsin and Kansas, south to Mexico and Panama, but absent from the Florida peninsula (Map 2).

Micrathena sagittata (Walckenaer)
Figures 41–54, Map 2

Plectana sagittata Walckenaer, 1841, Histoire Naturelle des Insectes, Aptères, 2: 174. The name was applied to Abbot illustration of Georgia Spiders, p. 8, fig. 50. Photocopy of the Abbot manuscript in the Museum of Comparative Zoology, examined.

Epeira spinea Hentz, 1850, J. Boston Soc. Natur. Hist., 6: 21, pl. 3, fig. 9, ♀. Syntypes from Atlantic states in the Boston Society of Natural History, destroyed.

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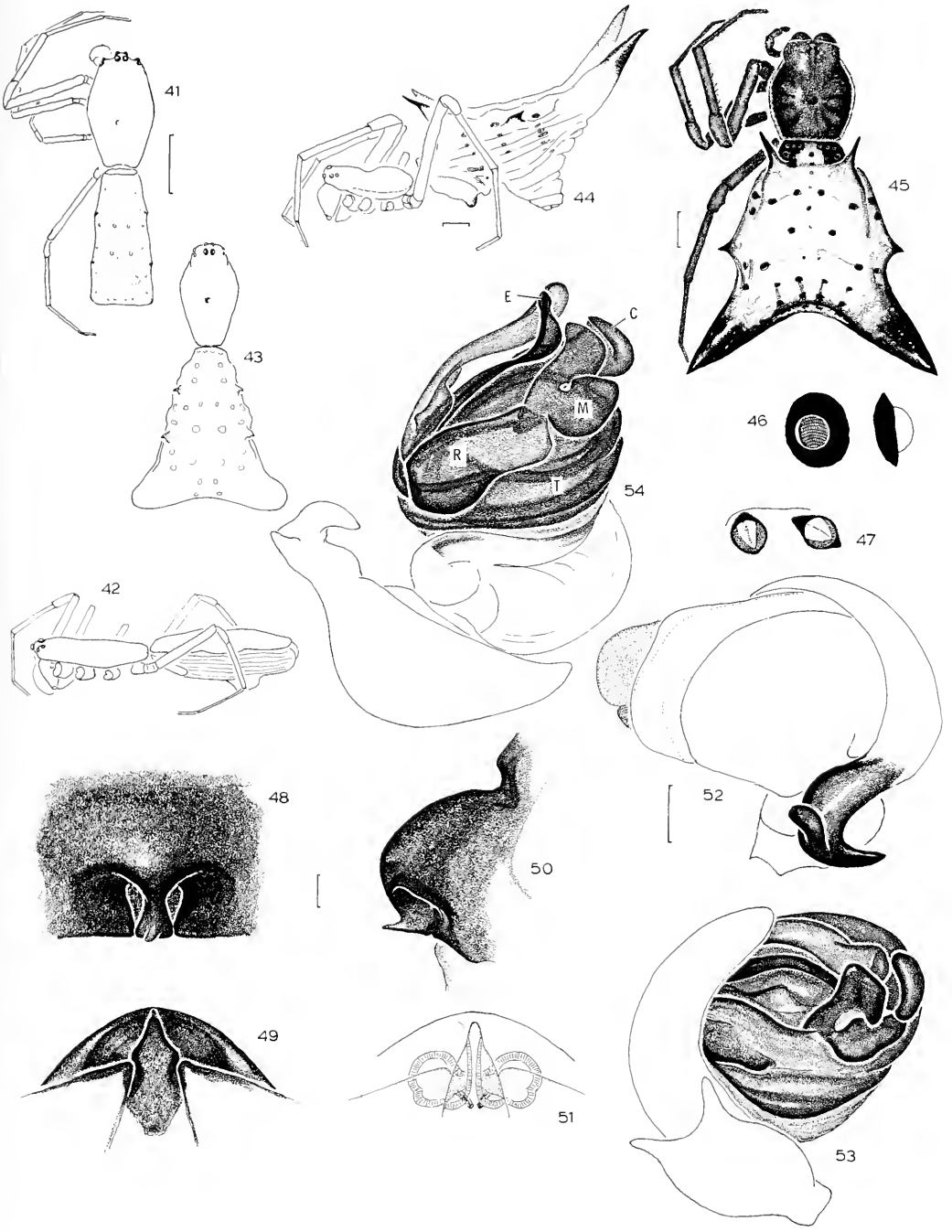
Figures 41–54. *Micrathena sagittata* (Walckenaer). 41–42, Male. 41. Dorsal. 42. Lateral. 43. Subadult male. 44–51. Female. 44. Lateral. 45. Dorsal. 46. Posterior median eyes. 47. Left lateral eyes. 48–51. Epigynum. 48. Ventral. 49. Posterior. 50. Lateral. 51. Posterior, cleared. 52–54. Male left palpus. 52. Lateral. 53. Mesal. 54. Mesal, expanded.

Scale lines. 0.1 mm; except Figures 41–45, 1.0 mm.

Abbreviations. C, conductor; E, embolus; M, median apophysis; R, radix; T, tegulum.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Acrosoma bovinum Thorell, 1859, Oefv. Svensk Vet. Ak. Forh., 16: 301, ♀. Female holotype from Alabama, lost (not in Natural History Museum, Stockholm).

Acrosoma spinea:—Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 326, pl. 38, figs. 5–8, ♀, ♂; 1902, Common Spiders, p. 190, figs. 437, 440–442, ♀, ♂, web.

Acrosoma sagittatum:—McCook, 1893, American Spiders, 3: 214, pl. 21, figs. 8, 9, ♀, ♂.

Micrathena sagittata:—F.P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 536, pl. 51, figs. 20, 21, ♀, ♂. Comstock, 1912, Spider Book, p. 514, figs. 189, 558–561, ♀, web. Reimoser, 1917, Verhandl. Zool. Bot. Gesell. Wien, 67: 140, pl. 9, fig. 29, ♀. Petrunkevitch, 1930, Trans. Connecticut Acad. Sci., 30: 259, figs. 111–114, ♀, ♂. Comstock, 1940, Spider Book, rev. ed., p. 527, figs. 189, 558–561, ♀, web. Roewer, 1942, Katalog der Araneae, 1: 967. Kaston, 1948, Connecticut Geol. Natur. Hist. Surv. 70: 219, figs. 690–693, 2028, ♀, ♂, web. Bonnet, 1957, Bibliographia Araneorum, 2: 2876.

Micrathena comstocki Archer, 1951, Amer. Mus. Novitates, no. 1487: 10, figs. 15–17, ♀. Female holotype from Royal Palm State Park [Royal Palm Area, Everglades National Park], Dade County, Florida in the American Museum of Natural History, examined. NEW SYNONYMY.

Micrathena sagittata emertoni Archer, 1951, Amer. Mus. Novitates, 1487: 10, figs. 18, 22, ♀. Female holotype from Norwell, Plymouth Co., Massachusetts, in the American Museum of Natural History. NEW SYNONYMY.

Description. Female from Virginia: carapace brown, darker on sides of thorax. Sternum, legs brown. Dorsum of abdomen white to yellow with black sclerotized disks; black anteriorly above carapace and posterior spines black (Fig. 45). Sides black with white patches. Venter black around spinnerets, with paired white patches. Abdomen with three pairs of spines, the posterior ones largest (Figs. 44, 45). Total length from between the posterior spines 8.0 mm, carapace 3.1 mm long, 2.5 mm wide. First femur, 3.3 mm; patella and tibia, 3.0 mm; metatarsus, 1.9 mm; tarsus, 0.9 mm. Second patella and tibia, 2.8 mm; third, 1.6 mm. Fourth femur, 3.7 mm; patella and tibia, 3.0 mm; metatarsus, 2.1 mm; tarsus, 0.9 mm.

Male from Virginia: carapace brown. Posterior median eyes on black spots. Sternum, legs brown. Dorsum of abdomen black, white on lateral margin and posterior white marks. Sides black, venter black and brown. Posterior median eyes 1.2 diameters of anterior medians. Laterals subequal to anterior median eyes. Abdomen trapezoidal, dorsoventrally flattened (Fig. 41). Total length 4.7 mm, carapace 1.9 mm long, 1.2 mm wide. First femur, 1.6 mm; patella and tibia, 1.5 mm; metatarsus, 1.0 mm; tarsus, 0.6 mm. Second patella and tibia, 1.2 mm; third, 0.8 mm. Fourth femur, 1.8 mm; patella and tibia, 1.4 mm; metatarsus, 1.0 mm; tarsus, 0.6 mm.

Variation. The abdomen of the female may be white to golden orange in color. The posterior abdominal spines of specimens from southern Florida are longer than those from more northern areas. Interestingly some Mexican specimens have minute posteroventral spines like related tropical species. Females vary in total length 5.4 to 8.6 mm, carapace 2.9 to 3.5 mm long, 2.2 to 2.7 mm wide. Males vary in total length 4.2 to 5.9 mm, carapace 2.0 to 2.5 mm long, 1.3 to 1.6 mm wide.

Diagnosis. Micrathena sagittata females are recognized by having three pairs of spines with the posterodorsals the largest (Figs. 44, 45), and there are no posteroventral spines in specimens north of Mexico as there are in some related tropical species. The openings of the epigynum are in depressions on the posterior face of a bulge (Figs. 48–51). The male, unlike other species of the area, has a trapezoidal abdomen, widest posteriorly (Fig. 41) and a distinct, biforked median apophysis (Figs. 53, M in 54). The paracymbium, unlike that of other North American species, is recurved, pointing back (Fig. 52) with a spur on its side. Juveniles also have a triangular abdomen (Fig. 43).

Natural History. This species is found on shrubs in deciduous forest and woods.

Distribution. From southern New Hampshire to Minnesota, Nebraska, south to Costa Rica.

Micrathena gracilis (Walckenaer)
Plate 1; Figures 55–68; Map 2

Epeira gracilis Walckenaer, 1805, Tableau des Araneides, p. 65. "An unpublished species from Carolina, communicated by M. Bosc."

Plectana gracilis Walckenaer, 1841, Histoire Naturelle des Insectes, Aptères, 2: 193. The name is applied to the Abbot illustration of the Spiders of Georgia nos. 47, 48. Photocopy of the Museum of Comparative Zoology, examined. I consider this the date of the name.

Plectana reduviana Walckenaer, 1841, Histoire Naturelle des Insectes, Aptères, 2: 201. Name for Abbot illustration Spiders of Georgia no. 49. Photocopy in Museum of Comparative Zoology, examined.

Acrosoma matronale C. L. Koch, 1845, Die Arachniden, 11: 68, fig. 887. Female from Mexico, lost (not in Berlin Museum).

Epeira rugosa Hentz, 1850, J. Boston Natur. Hist. Soc., 6: 21, pl. 3, fig. 10. Type from southern states in the Boston Natural History Society, destroyed.

Acrosoma rugosa:—Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 326, pl. 38, fig. 10, ♀; 1902, Common Spiders, p. 189, fig. 439, ♀.

Acrosoma gracile:—McCook, 1893, American Spiders, 3: 212, pl. 21, figs. 1–4, ♀, ♂.

Micrathena matronalis:—Simon, 1895, Histoire Naturelle des Araignées 1: 852, fig. 902, ♀.

Micrathena gracilis:—F.P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 528, pl. 50, fig. 3, pl. 51, fig. 16, ♀, ♂. Comstock, 1912, Spider Book, p. 516, fig. 562, ♀. Reimoser, 1917, Verhandl. Zool. Bot. Ges. Wien, 67: 87, pl. 1, fig. 1, ♀. Comstock, 1940, Spider Book, rev. ed., p. 529, fig. 562, ♀. Roewer, 1942, Katalog der Araneae, 1: 966. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 219, pl. 33, figs. 688, 689, ♀, ♂. Bonnet, 1957, Bibliographia Araneorum, 2: 2868. Chickering, 1961, Bull. Mus. Comp. Zool., 125: 421, figs. 72–77, ♀, ♂.

Micrathena nigrior Chamberlin and Ivie, 1936, Bull. Univ. Utah, biol. ser. 3(5): 58, figs. 134–135, ♀. Four female syntypes from Barro Colorado Island, Panama Canal Zone, in the American Museum of Natural History, examined.

Description. Female from Virginia: carapace brown, darker on sides and middle of thorax. Sternum maculated white and brown. Legs brown. Dorsum of abdomen whitish with dark spots and dark brown sclerotized spots and dark brown spines (Fig. 59). Sides brown with white spots and dark brown sclerotized spots. Thoracic depression small, round (Fig. 59). Dorsum of abdomen with three pairs of spines and two pairs of posteriorly directed spines (Figs. 58, 59). Total length 8.5 mm, carapace 3.0 mm long. 2.2 mm wide. First femur, 2.3 mm; patella and tibia, 2.2 mm; metatarsus, 1.4 mm; tarsus, 0.9 mm. Second patella and tibia, 2.0 mm; third, 1.4 mm. Fourth femur, 2.7 mm; patella and tibia, 2.2 mm; metatarsus, 1.5 mm; tarsus, 0.8 mm.

Male: carapace brown, thoracic region darker. Legs brown. Dorsum of abdomen whitish, venter blackish. There is a round, circular thoracic depression (Fig. 55). Total length 4.8 mm, carapace 1.4 mm long, 0.9 mm wide. First femur, 0.8 mm; patella and tibia, 0.9 mm; metatarsus, 0.6 mm; tarsus, 0.4 mm. Second patella and tibia, 0.9 mm; third, 0.6 mm. Fourth femur, 1.2 mm; patella and tibia, 0.8 mm; metatarsus, 0.5 mm; tarsus, 0.4 mm.

Variation. The species is quite variable in color. Females vary in total length 7.0 to 10.8 mm, carapace 2.6 to 3.7 mm long, 1.7 to 2.5 mm wide. Males vary in total length 4.2 to 5.1 mm, carapace 1.3 to 1.6 mm long, 0.9 to 1.0 mm wide.

Diagnosis. The female can readily be recognized by the often gray abdomen with ten spines (Figs. 58, 59) and by the laterally flattened tip of the cone of the epigynum (Figs. 62–65). The male as well as juvenile males have an elongate abdomen more than three times as long as wide (Figs. 55, 56), the palpus has a round hookshaped paracymbium (Fig. 66), a complex conductor (C) difficult to make out (the basal lobe is probably the paramedian apophysis) and a minute median apophysis with a filamentous attachment (Figs. 67, M in 68).

Natural History. Micrathena gracilis is found in dense woods, the web in shaded areas, often on bushes. A study of the web was published by B. E. Dugdale (1969); the orb observed had 44 radii and about as many spirals. The orb had a radius of 17 cm.

Distribution. The species is found from

eastern Massachusetts, Michigan, Wisconsin, Nebraska, Texas, Sonora, to Panama, absent from southern Florida (Map 2).

Gasteracantha Sundevall

Gasteracantha Sundevall, 1833, Conspectus Arachnidum, p. 14. *Gasteracantha cancriformis* is the type species since the only other species name originally included is *G. hexacantha*, a synonym of *G. cancriformis*. The name is feminine. Dahl, F. 1914, Mitt. Zool. Mus. Berlin, 7: 235–301. Benoit, 1962, Ann. Mus. Royal de l'Afrique Centrale, 8 ser., sci. zool., 112: 1–70. Emerit, 1974, Faune de Madagascar, 38: 1–216.

Vibradellus Chamberlin, 1925, Bull. Mus. Comp. Zool., 67: 214. Type species by original designation and monotypy *V. carolinus* Chamberlin (= *Gasteracantha cancriformis*).

Note. Sundevall cited Latreille, 1831 as author of the name *Gasteracantha*. However, *Gasteracanthe* Latreille (1831 Cours d'Entomologie, p. 530) is a *nomen nudum* since no species are included; it is thus an invalid name since it lacks an indication (ICZN, Art. 16, V). Bonnet (1957) also erroneously cites Latreille (1831) as author.

The list of synonymy of *Gasteracantha* is incomplete; a complete list is found in Emerit, 1974. There are two excellent revisions for the genus available, one of African species by Benoit and one of Madagascan species by Emerit. Both point out that *Gasteracantha* species are generally variable and difficult to separate. But this had been noted previously by Dahl (1914) in his world-wide study.

Diagnosis. The female carapace is almost square in outline (Figs. 71, 72) not longer than wide nor rebordered on the sides as that of *Micrathena*. It is high in front. Unlike related African genera, there is only one transverse row of black discs on the anterior of the abdomen dorsum; the abdomen has one or two pairs of spines laterally and one pair posteriorly (Figs. 71, 72). There is a sclerotized, central bulge on the venter of the abdomen of the female between genital groove and spinnerets, not present in *Micrathena* (Figs. 71, 73). Unlike *Micrathena*, *Gasteracantha* has a large canoe-shaped tapetum in the posterior median eyes (Fig. 75). Together with *Micrathena*, *Gasteracantha* differs from other genera in having the spinnerets on a cone or their base surrounded by a sclerotized annulus (Fig. 73).

Description. *Gasteracantha* species are brightly colored. The sclerotized, square carapace is high in the head region and has a deep thoracic groove (Figs. 71, 72). The eyes are subequal, small, the anterior median eyes their diameter apart, the posterior medians more than their diameter. All secondary eyes have a canoe-shaped tapetum (Figs. 75, 76). The laterals on each side are far from the medians (Fig. 74). The height of the clypeus equals the diameter of the anterior median eyes (Fig. 74). The heavy chelicerae of *G. cancriformis* have five teeth on the anterior margin, four on the posterior margin. The legs are short and thick, and the tarsi are very short. The female abdomen is a sclerotized shield with sclerotized lateral spines and dorsal sclerotized discs.

Males are minute (Figs. 69, 70, notice different scale) and less often collected. The median eye area is slightly projecting (Figs. 69, 70). The male lacks the tooth on the proximal end of the palpal femur and a tooth on the endite present in many Araneidae. None of the coxae and none of

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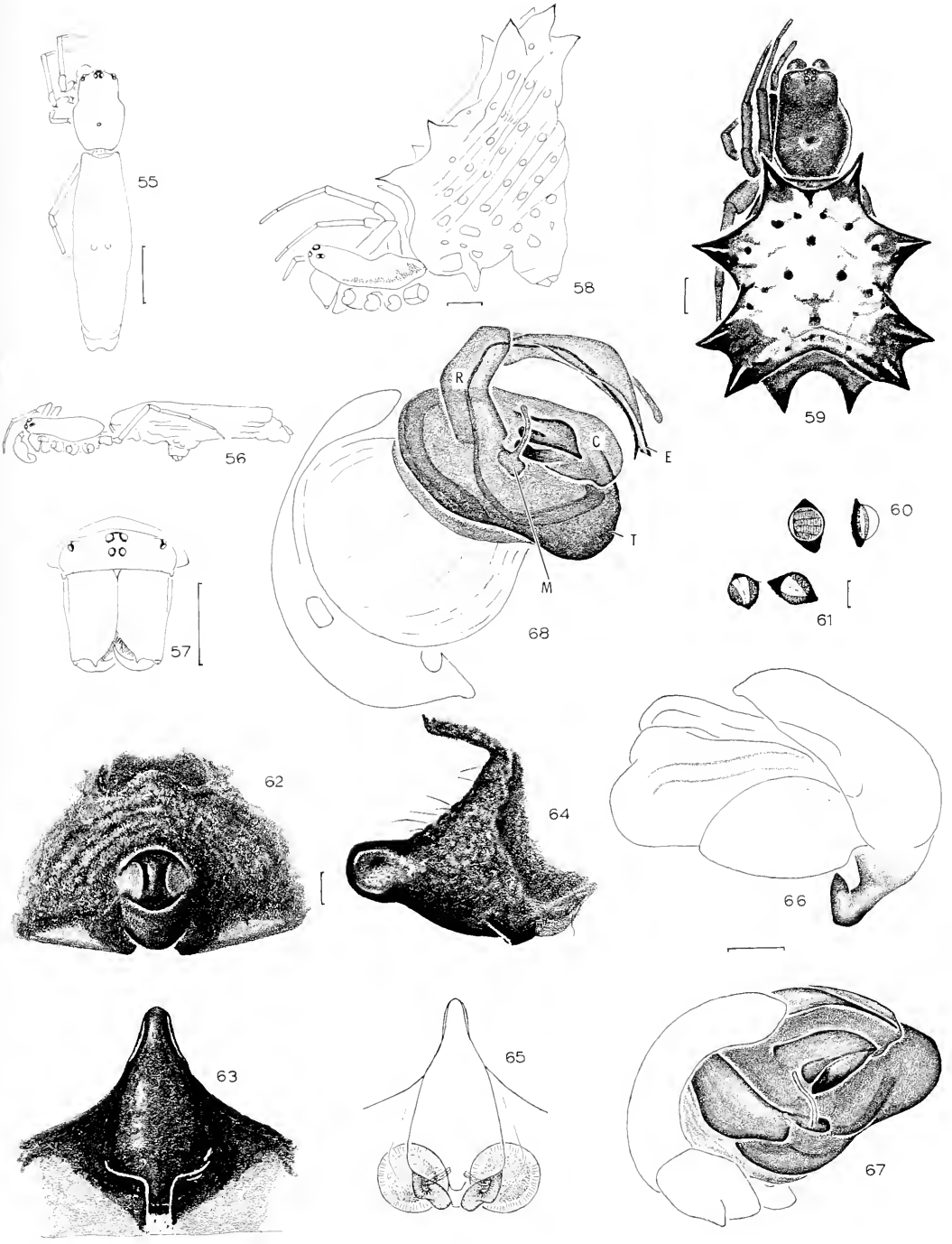
Figures 55–68. *Micrathena gracilis* (Walckenaer). 55–56. Male. 55. Dorsal. 56. Lateral. 57–65. Female. 57. Eye region and chelicerae. 58. Lateral. 59. Dorsal. 60. Posterior median eyes. 61. Left lateral eyes. 62–65. Epigynum. 62. Ventral. 63. Posterior. 64. Lateral. 65. Posterior, cleared. 66–68. Male left palpus. 66. Lateral. 67. Mesal. 68. Mesal, expanded.

Scale lines. 0.1 mm; except Figures 55–59, 1.0 mm.

Abbreviations. C, conductor; E, embolus; M, median apophysis; R, radix; T, tegulum.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the distal articles of the legs are modified. Since the abdomen lacks the prominent spines of the females and also the ventral protuberance, males are difficult to associate with matching females in other parts of the world where there are several species.

Genitalia. The epigynum is a heavily sclerotized projection with a median lobe (Figs. 77–80). The openings can be seen on each side of a septum on the posterior face (Fig. 79). The internal genitalia (Fig. 81) are difficult to make out because of heavy sclerotization.

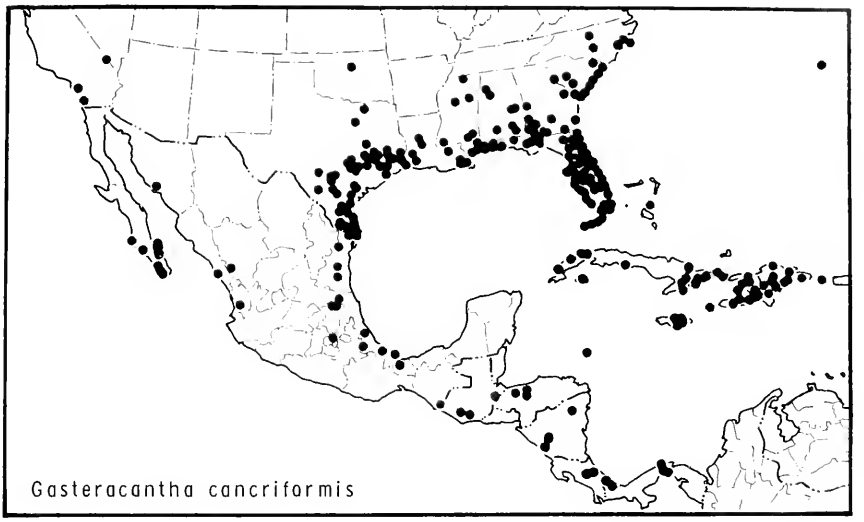
The palpus is relatively simple. In mesal view of the contracted palpus three sclerites are visible: distally the filiform embolus (Figs. 83, F in 84); in the center a round sclerite with its distal edge folded and sculptured, the paramedian apophysis (PM); and proximally the median apophysis (Figs. 83, M in 84). In the expanded palpus (Fig. 84) the radix (R) becomes completely free and transparent hematocha-like material, probably the conductor (C), appears behind the embolus (E). The embolus lacks the parallel lobe (perhaps the terminal apophysis) of *Micrathena.* In the expanded palpus, the paramedian apophysis (PM) slips down and behind the median apophysis (M) as result of pressure from the soft conductor (C) (Fig. 84). The *Mastophora* palpus is similar but lacks a paramedian apophysis (Levi, in press). The palpal patella lacks strong setae. The paramedian apophysis (PM) was called terminal apophysis by Emerit (1968a, 1974). This sclerite is in the same position and of similar appearance as the paramedian apophysis of *Acanthepeira* and other genera (Levi, 1976; in press). The *Acanthepeira* paramedian apophysis is doubtless the same structure as that of the complex palpus of *Eriophora* (Levi, 1970) which was studied by Comstock (1910). The origin of this structure may perhaps be seen in the *Verrucosa* palpus (Levi, 1976, figs. 8, 9) in which it appears to be the basal end of the conductor. It is also close to the conductor in *Wagneriana* and *Wixia* (Levi, 1976, figs. 69–71, 98). The hematodocha-like material (C) behind the embolus (E) is believed to be the conductor, because of similar structures in similar positions in *Acanthepeira*, *Wagneriana*, *Wixia*, and *Scoloderus*. Since *Gasteracantha* lacks a sclerotized conductor and also additional lobes on the embolus (including a terminal apophysis), I believe the palpus to be simplified secondarily.

Relationship. Gasteracantha is close to *Micrathena* and also to *Mastophora.* The structure of the palpus, particularly the lateral (rather than proximal) position of the tegulum (Figs. 83, 84), the mesal position of all sclerites, and the presence of the paramedian apophysis (PM) and conductor suggest close relationship with *Acanthepeira*, *Wagneriana*, *Wixia*, and *Scoloderus* (Levi, 1976). Further indication of a highly specialized araneid are the widely separate eyes, the square carapace (Figs. 71, 72, 74) and the modified structure of the abdomen.

Natural History. Gasteracantha biology is better known than that of many other araneids (*Araneus diadematus* excepted) thanks to the beautiful researches of M. Emerit. His many studies on Madagascan *Gasteracantha versicolor* are listed in Emerit (1974).

Species. Gasteracantha is a cosmotropical genus. As far as we know, there are only one or perhaps two species in America, both known to Linnaeus 200 years ago; *G. tetracantha* (Linnaeus) in the West Indies and *G. cancriformis* (Linnaeus) found from the southern United States to Argentina.

The literature indicates two species in the Americas, both originally described by Linnaeus from Jamaica: *Gasteracantha cancriformis* and *G. tetracantha.* According to the literature, *G. tetracantha* occurs from California and Arizona to the Greater Antilles. The California and Arizona records come from specimens of the George Marx collection, well-known for erroneous



Map 3. North American distribution of *Gasteracantha cancriformis* (Linnaeus).

records. None were found in recent collections and the species probably does not occur in the Southwest. (There is a specimen in the N. Banks collection from "Cal." which probably also originated with Marx.) Although large collections were available from Jamaica, only one species, *G. cancriformis*, is found and the Linnaeus record may also be a locality error. *Gasteracantha tetracantha* occurs in Puerto Rico, the Virgin Islands, and the Bahamas to the north, exactly those areas where *G. cancriformis* is absent. Many specimens appear to be intergrades having six spines and only a few have completely lost the anterior pair. The intergrades come from the north and the Bahamas, not from the west. I hope to obtain more specimens from the region to determine whether there are one or two species in the West Indies.

Numerous names have been given to populations of *G. cancriformis* but as far as I know there are never two different populations overlapping except perhaps in the West Indies. The niche of the numerous African *Gasteracantha* species seems occupied by species of *Micrathena* in the Americas.

Gasteracantha cancriformis (Linnaeus)
Plate 2; Figures 69–84; Map 3

Aranea cancriformis Linnaeus, 1767, Systema Naturae, 12 ed., p. 1037. Specimens described from Jamaica, probably lost.

A. hexacantha Fabricius, 1787, Mantissa Insectorum, 1: 344. Name given with one line of description, but no locality.

Gasteracantha velitaris C. L. Koch, 1838, Die Arachniden, 4: 33, pl. 269, ♀. Female from Brazil.

Plectana elipsoides Walckenaer, 1841, Histoire Naturelle des Insectes, Aptères, 2: 155. Name given to fig. 118, p. 13 of Abbot, Drawings of the Insects of Georgia in America, photocopy examined.

Plectana quinqueserrata Walckenaer. 1841, Histoire Naturelle des Insectes, Aptères, 2: 157. Female from Guyana in Walckenaer's collection, lost.

Plectana sexserrata Walckenaer, 1841, Histoire Naturelle des Insectes, Aptères, 2: 157. Female from Cayenne.

Plectana atlantica Walckenaer, 1841, Histoire Naturelle des Insectes, Aptères, 2: 167. Female from St. Domingo.

Gasteracantha rubiginosa C. L. Koch, 1845, Die Arachniden, 11: 55, pl. 878. Female from St. Domingo, West Indies.

Epeira cancer Hentz, 1850, J. Boston Natur. Hist. Soc., 6: 23, pl. 3, fig. 13, ♀. Females from South Carolina and southern Alabama in the Boston Natural History Society, destroyed.

Gasteracantha insulana Thorell, 1859, Oefv. Svensk

Vet. Akad. Förh., 16: 302. Female from Galapagos Islands in the Natural History Museum, Stockholm, examined.

Gasteracantha columbiae Giebel, 1863, Z. Gesammt. Naturw., 21: 312. A black individual from Colombia, lost (not in Halle (Saale) with the Giebel collection).

Gasteracantha kochii Butler, 1873, Trans. Entomol. Soc. London, p. 169. New name for *G. hexacantha*:—C. L. Koch, 1838, Arachniden, 4, pl. 117, fig. 268. Female from Pará [Belem, Brazil].

Gasteracantha oldendorffi Holmberg, 1876, An. Agric. Rep. Argentina, 4: 143. Female from Noter del Río Guayguiraro, [Entre Rios], Argentina, destroyed.

Gasteracantha callida O.P.-Cambridge, 1879, Proc. Zool. Soc. London, p. 284, pl. 26, fig. 7, ♀. Female holotype from Trinidad, West Indies, in the Hope Museum, Oxford University, Oxford, not examined.

Gasteracantha raimondii Taczanowski, 1879, Horae Soc. Entomol. Rossicae, 15: 106, pl. 1, figs. 25, 26, ♀. Five female syntypes from Lima, Chorillos and Montana de Nancha, Peru, in the Polish Academy of Sciences, examined.

Gasteracantha raimondii unicolor Taczanowski, 1879, Horae Soc. Entomol. Rossicae, 15: 107. Two females from Lima, Peru.

Gasteracantha proboscidea Taczanowski, 1879, Horae Soc. Entomol. Rossicae, 15: 108, pl. 1, fig. 27, ♂. Two male syntypes from Lima, Peru in the Polish Academy of Sciences, examined.

Gasteracantha rufospinosa Marx, 1883, Entomol. Amer., 2: 25, figs. a–f, ♀, ♂. Female and male from Crescent City, Florida, lost (not in National Museum of Natural History).

Gasteracantha maura McCook, 1893, American Spiders, 3: 210, pl. 13, fig. 12, ♀. Numerous syntypes, "young and old from California, particularly the southern part . . . and from the islands off the coast," lost (not in Academy of Natural Sciences, Philadelphia).

Gasteracantha cancriformis:—McCook, 1893, American Spiders, 3: 211, pl. 14, fig. 9, ♀. F.P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 525, pl. 51, fig. 14, ♀. Petrunkevitch 1930. Trans. Connecticut Acad. Sci., 30: 249, figs. 103, ♀, ♂. Comstock, 1940, Spider Book, rev. ed., p. 526, fig. 556, 557, ♀, web. Roewer, 1942, Katalog der Araneae, 1: 949. Bonnet, 1957, Bibliographia Araneorum, 2: 1945.

Gasteracantha elliptica Getaz, 1893, An. Inst. Fis.-geogr. nac. Costa Rica, 4: 105, ♀. Female specimens from around San José, Costa Rica, depository unknown.

Gasteracantha biolleyi Banks, 1905, Proc. Entomol. Soc. Washington, 7: 20, fig. 3, ♀. Female holotype from Cocos Island in the Museum of Comparative Zoology, examined.

Vibradellus carolinus Chamberlin, 1925, Bull. Mus. Comp. Zool., 67: 214, ♂. Male holotype from South Carolina in the Museum of Comparative Zoology, examined.

Description. Female from Florida: carapace, sternum, legs brownish black. Dorsum of abdomen whitish, spines orange-yellow, muscle scars black. Venter black with white spots; spines and ventral sclerotized projection, orange. Total length 7.2 mm, carapace 3.2 mm long, 3.0 mm wide. First femur, 2.5 mm; patella and tibia, 2.6 mm; metatarsus, 1.4 mm; tarsus, 0.8 mm. Second patella and tibia, 2.4 mm; third, 1.6 mm; fourth, 2.4 mm.

Male from Florida: carapace brownish black; sternum black. Legs light blackish brown. Dorsum of abdomen dark gray with white spots; venter black with ventral paired white spots. Total length 2.2 mm, carapace 1.1 mm long, 0.9 mm wide. First femur, 0.8 mm; patella and tibia, 0.8 mm; metatarsus, 0.5 mm; tarsus, 0.3 mm. Second patella and tibia, 0.7 mm; third, 0.4 mm; fourth, 0.7 mm.

Variation. There are vast differences in color and shape (Fig. 85). Hispaniola and Jamaican specimens may have an orange carapace and legs. Almost all Florida specimens have orange spines. While black specimens occur occasionally throughout the range, all specimens from Mona Island (west of Puerto Rico) were black with light dorsal patches. Texas specimens were bright yellow in color (washed out in alcohol). The narrowest bodies were found on Mona Island and Jamaica, the widest

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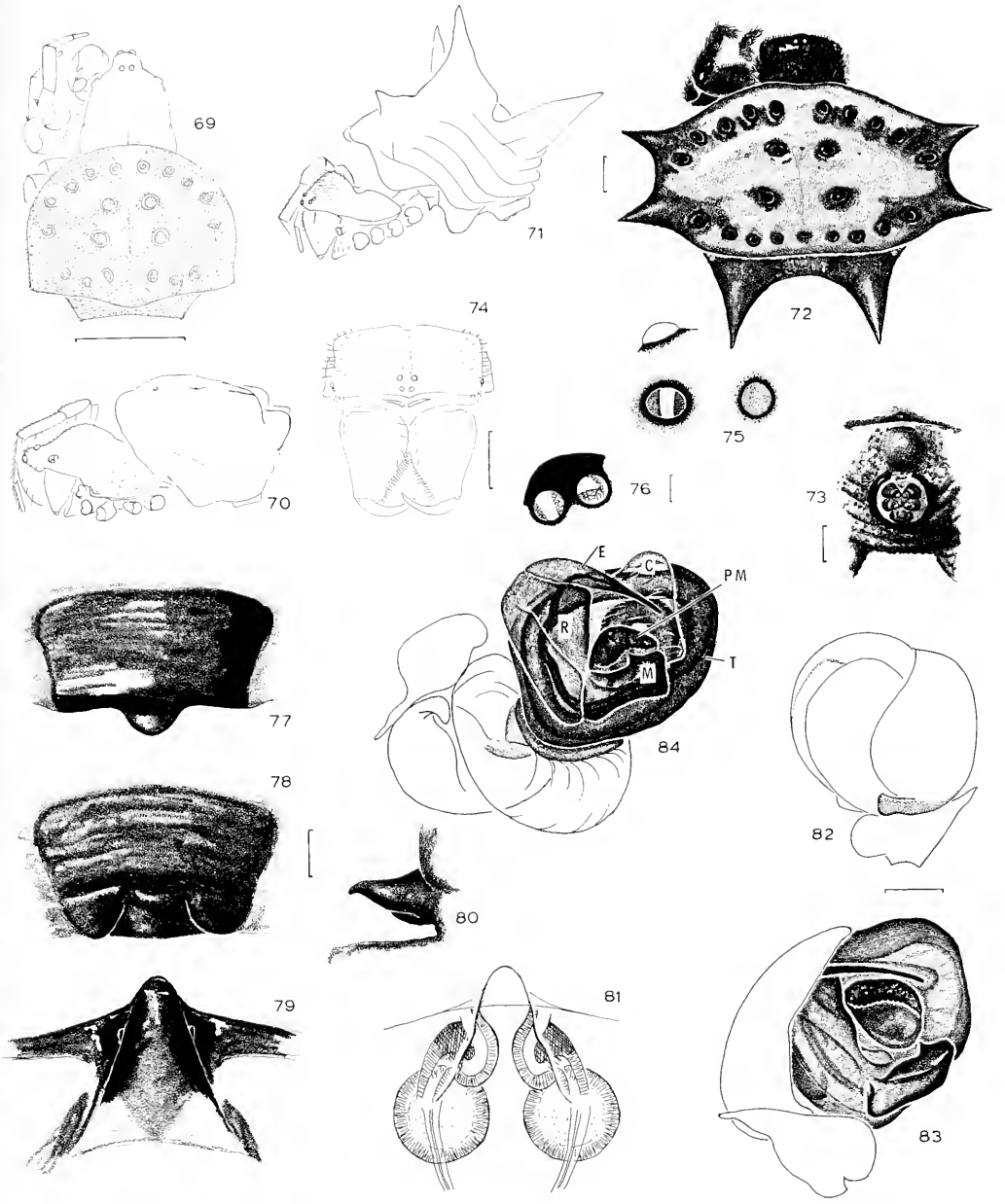
Figures 69–84. *Gasteracantha cancriformis* (Linnaeus). 69, 70. Male. 69. Dorsal. 70. Lateral. 71–81. Female. 71. Lateral. 72. Dorsal. 73. Abdomen, ventral. 74. Eye region and chelicerae. 77–81. Epigynum. 77. Anteroventral. 78. Ventral. 79. Posterior. 80. Lateral. 81. Posterior, cleared. 82–84. Male left palpus. 82. Lateral. 83. Mesal. 84. Mesal, expanded.



Scale lines. 0.1 mm; Figures 69–74, 1.0 mm.

Abbreviations. C, conductor; E, embolus; M, median apophysis; PM, paramedian apophysis; R, radix; T, tegulum.

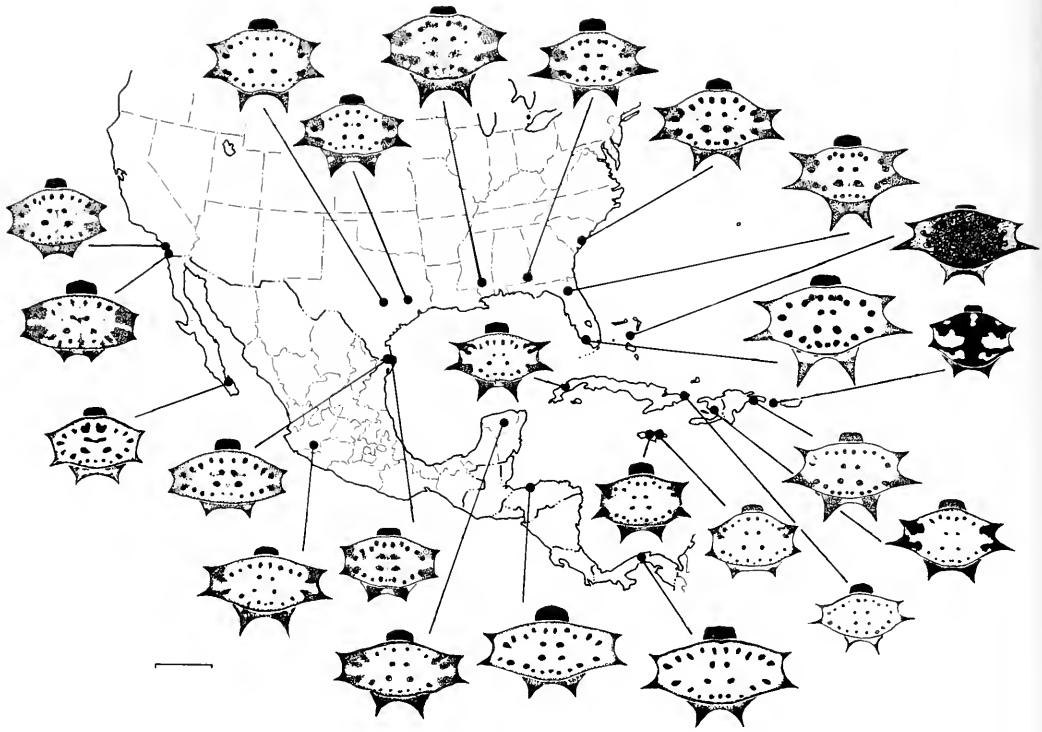


Figure 85. Geographic variation of *Gasteracantha*. Locality data clockwise: Torrey Pines State Park, San Diego Co., California; Laguna Beach, California; Austin, Texas; College Station, Texas; Hattiesburg, Mississippi; Houston Co., Alabama; Charleston, South Carolina; Gainesville, Florida; New Providence, Bahamas; Naples, Florida; Mona Island; La Romana, Dominican Republic; Momance, Haiti; Los Llanos, Cuba; Pinar del Río, Cuba; Port Antonio, Jamaica; Mandeville, Jamaica; Barro Colorado Island, Panama Canal Zone; Carmelina, Honduras; Chichen Itza, Yucatan; Atoyac, Jalisco; Most Southern Palm Grove, Cameron Co., Texas; Brownsville, Texas; La Paz, Baja California.

Scale line: 5.0 mm.

from Texas to Central America. The shortest stubbiest spines are found in Mona Island and California; the longest ones in Florida and the southeastern states. The most acute spines are found in Cuban specimens. A characteristic of Hispaniola and southern Florida specimens is that the second pair of spines is larger than the first pair. Since there are clines of these characters in various directions, it is not easy to segregate subspecies except for island populations.

Unusual variations are the additional round plates found at times on the dorsum of the abdomen. The specimen from Laguna Beach, California illustrated (Fig. 85) has an extra assymmetrical plate on the left anterior. Many specimens throughout the North American range have the median posterior plate split into two plates (Texas, South Carolina, and Dominican Republic, Fig. 85).

Total length of females is 5.8 to 8.6 mm, carapace 2.3 to 3.1 mm wide. Total length of males 1.9 to 2.7 mm, carapace 0.8 to 1.0 mm wide. Size variation is about the same throughout the southern states.

Species problems. Archer judging by museum labels, considered specimens from the western states to be *G. servillei* (Guérin)

and those from the eastern states to be *G. cancriformis*, with several subspecies. However collections from Austin, Texas had both specimens which Archer considered to belong to the western species and to the eastern species. Since there is no overlap of the two forms, but instead intermediates are found, I consider all to belong to one species. The eastern specimens were considered by Archer (unpublished) to belong to several different subspecies, but almost as many were labeled as intermediates (e.g. from northern Florida), as belonging to the subspecies.

Diagnosis. Females can be distinguished from West Indian *G. tetracantha* (Linnaeus) by the presence of six spines on the abdomen (Figs. 71, 72); *G. tetracantha* has only four. Males of *G. tetracantha* have the sclerites of the palpus, especially the paramedian apophysis, relatively smaller than those of *G. cancriformis* (Figs. 83, 84), although all parts are of the same shape.

Natural History. The striking appearance, conspicuous webs and diurnal habits make this one of the easily collected tropical spiders. The web is found between branches on shrubs and even on buildings (Plate 2). It is made in the morning and is usually inclined at an angle, sometimes near vertical (Plate 2). The outer threads are decorated with flocculent tufts of silk (Marples, 1969) and the spider rests in the open hub. Young Madagascan *Gasteracantha versicolor* may have a stabilimentum (Emerit, 1968b).

Adult males have been collected in Florida from November to February; in Alabama in August; in Texas in April, June, July, and October and in California during July. Adult females can be collected throughout the year in Florida and Texas.

Muma (1971) found *Gasteracantha cancriformis* webs in central Florida orchards in trees, between trees and also in mixed mesophytic woods at a height of less than 1 to more than 6 m. The female's web has 10 to 30 spiral lines, the viscid area spanning 30 to 60 cm diameter. The prey caught are flies, moths, and beetles. The spider completes the life cycle in a year. Females mature in late fall or early winter and are found from October to January. Adult males first appear in October and November when females are one-third to one-half adult size. Adult males hang from a single strand of silk adjacent to a female's web, one to three per web. The tiny males accomplish sperm induction just prior to courtship. Egg-sacs are flattened ovate masses of tangled white, yellow, and green silk, marked with a longitudinal stripe of dark green silk. They are found on the underside of leaves adjacent to the webs.

Distribution. Gasteracantha cancriformis is found from North Carolina to Southern California south to northern Argentina (Map 3). Specimens occasionally get transported; one female was found among fruit in Seattle.

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Bulletin of the Museum of Comparative Zoology

Revision of the Genera and Typical Species of the Family Ptychodontidae

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REVISION OF THE GENERA AND TROPICAL AMERICAN SPECIES OF THE SPIDER FAMILY ULOBORIDAE[1]

BRENT D. OPELL[2]

ABSTRACT. The cosmopolitan family Uloboridae contains 17 genera, four of which are newly described. Members of five genera construct orb-webs, members of three reduced webs derived from an orb, and members of the remaining genera webs of unknown form. Recognition of 14 synonyms and nine new species brings to 28 the number of known species in the nine uloborid genera found south of the United States (excluding members of the unrevised genus *Miagrammopes*). Scanning electron microscopy shows spiral capture thread to be joined to radii by fine cribellate fibrils and allows more precise identification of male palpal structure, facilitating cladistic analysis of intrafamilial relationship. This analysis shows the simplest of four tracheal patterns to be derived from more extensive patterns. Males of three genera have a newly discovered stridulatory apparatus, consisting of a file on the retrolateral endite surface and two or more picks on the cymbial tip. Uloborids are characterized by having broad, retrolateral patellar notches and a row of trichobothria on each femur. Presence of similar trichobothrial rows in several Araneidae genera indicates close relationship of the two families. Discovery of both haplogyne and entelegyne uloborids challenges the validity of classifying families solely by the degree of genitalic development.

INTRODUCTION

The spider family Uloboridae is represented throughout the world, but achieves its greatest diversity of species and genera in tropical and subtropical zones. Muma and Gertsch (1964) revised the North American members of this family and the present investigation began as a complementary study of the remaining American species and genera. However, it soon became apparent that a clear delineation of American genera required a reexamination of Lehtinen's (1967) comprehensive study of world uloborid genera. Results of this phase of study, while in essential agreement with most of Lehtinen's conclusions, both allowed and demanded a more critical look at uloborid intrafamilial phylogeny. *Miagrammopes* is the only Central or South American genus whose species are not included in this revision. Comprehensive treatment of this important and interesting genus will be presented in a future study.

Olivier described the first uloborid in 1789, placing it (*Zosis geniculatus*) into Linnaeus' genus *Aranea*. The genus *Uloborus* was erected by Latreille in 1806 for *U. walckenaerius* which, because of its orb-web, was allied with Araneidae. Walckenaer described the genus *Uptiotes* (*Hyptiotes*) in 1833 and four years later changed this genus name to *Mithras*, placing it in the family Mithras along with *Scytodes* and *Lycose*. When O. Pickard-Cambridge first described *Miagrammopes* in 1869 he suggested that it was related to *Mithras* and *Uloborus* and that these three genera had "strong affinity with the family Epeirides . . . [but] at present I do not feel sufficiently assured . . . to justify the establishment of a new family of Araneidea, while, at the same time, I confess myself quite unable to include them in any fam-

[1] This study was presented to the Department of Biology at Harvard University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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ily hitherto-characterized." During the same year Thorell recognized Uloborinae as a subfamily of Epeiroidae (Araneidae). In 1870, O. Pickard-Cambridge established the family Uloborides for the genera *Hyptiotes* and *Uloborus* and the family Miagrammopides for *Miagrammopes thwaitesii* and *M. ferdinandi.* Simon (1874) combined these two families to form Uloboridae and in 1892 extended this family to include the subfamilies Dinopinae (*Dinopis* and *Menneus*), Aebutininae (*Aebutina*), Uloborinae (*Uloborus* and *Sybota*), and Miagrammopinae (*Miagrammopes* and *Hyptiotes*). Pocock (1900) and Dahl (1904) removed the Dictynidae (Aebutininae) and Comstock (1913) the Dinopidae from the family Uloboridae. However, many workers (e.g., Gerhard and Kästner, 1937; Kaston, 1948; Bonnet, 1959) place these three families into the superfamily Dictynoidea. A historical review of higher-level spider classification is presented by Bristowe (1938), Bonnet (1959), and Lehtinen (1967) and need not be repeated here.

Most disagreement about placement of the Uloboridae centers around the cribellate-ecribellate controversy and a study of the family might be expected to deal at length with this problem i.e., can true spiders be divided into one monophyletic group whose members have a cribellum and another whose members lack this structure. However, I agree with Platnick's (1977) conclusion that the cribellum is a primitive character of all true spiders and that in some groups it has been lost or transformed to a colulus. For this reason attention is devoted to other characters which may prove more useful in studies of relationship.

ACKNOWLEDGMENTS

I wish to thank Herbert W. Levi for suggesting this study and for his encouragement and assistance throughout its duration. His excellent advice was always available but never imposed. Productivity of field studies in Panama and Colombia was significantly enhanced by the biological insights, knowledge, and hospitality of William Eberhard, Yael Lubin, and Mike Robinson. I hope the outcome of this investigation will facilitate their valuable studies of uloborid behavior. Fieldwork was financed by National Science Foundation Grant for Improving Doctoral Dissertation Research in the Field Sciences DEB 77-01571. The Smithsonian Tropical Research Institute's Barro Colorado Island and Cali, Colombia facilities were used during these field studies. Victor M. Patiño made it possible to conduct field studies at the Jardin Botánico near Mateguadua, Colombia and the Central Hydroeléctica Anchicayá (Valley de Cauca, Colombia) provided accommodations and access to grounds. In the early stages of this study I benefited from discussions with Raymond Forster and in the late stages Norman Platnick's comments proved extremely valuable. C. Bradford Calloway introduced me to techniques used in preparing specimens for the Scanning Electron Microscope. National Science Foundation Set-Up-Grant BMS-7412494 awarded to the Museum of Comparative Zoology purchases the SEM (operated by Edward Seling) used in this study. This publication is made possible by N.S.F. grant BMS 75-05719 awarded to Herbert W. Levi.

Specimens used during this research were made available by the following persons and institutions: Anna T. da Costa, Museu Nacional, Rio de Janeiro; Charles D. Dondale, Biosystematics Research Institute, Ottawa; William G. Eberhard; Raymond R. Forster, Otago Museum, Dunedin; Maria E. Galiano, Museo Argentina de Ciencias Naturales, Buenos Aires; M. Grasshoff, Senckenberg Museum, Frankfurt; Michel Hubert, Muséum National d'Histoire Naturelle, Paris; John A. Kochalka; Torbjörn Kronestedt, Naturhistoriska Riksmuseet, Stockholm; Herbert W. Levi, Museum of

Comparative Zoology, Harvard University; Yael Lubin; Norman I. Platnick, American Museum of Natural History; Gisela Rack, Zoologisches Institut und Zoologisches Museum, Universität Hamburg; David C. Rentz, California Academy of Sciences; W. Starega, Polska Akademia Nauk Instytut Zoologiezny, Warsaw; E. Taylor, Hope Department of Entomology, Oxford University; University of Vermont Collection; F. R. Wanless, British Museum (Natural History); Howard V. Weems, Jr.; Florida State Collection of Arthropods.

It is impossible to acknowledge the many individuals responsible for collecting the thousands of specimens which made this study possible, but their contributions are exemplified by those of Louis Peña of Santiago, Chile. His small collection presented to the Museum of Comparative Zoology contains one new species as well as males and females of two species each known previously from only a single specimen.

METHODS

Specimens from collections were prepared for study with the A.M.R. 1000 scanning electron microscope (SEM) by cleaning them in an ultrasonic cleaner or agitating them in ethanol, dehydrating them in ethanol, and critical-point-drying them in carbon dioxide. Prior to examination, specimens were mounted on double-sided Scotch tape affixed to a SEM stub and then sputter-coated, first with carbon and then with gold-palladium. Specially constructed SEM stubs, each consisting of a 4 mm high, 19 mm diameter, polished aluminum cylinder attached to a 20-mm diameter SEM stub by silver paint were used to collect web samples in the field. Double-sided Scotch tape on the cylinder's 2-mm-wide free rim served to anchor web samples and the 15-mm diameter cut-out tape circle placed on the cylinder's floor provided a nonconducting surface resulting in a black background when webs were studied with the SEM. Web samples were desiccated and sputter-coated (as described above) prior to examination. *Hyptiotes* male palpi were dissected before being critical-point-dried and *Miagrammopes* palpi after being critical-point-dried.

All female genitalia were examined with both a dissecting microscope and a differential interference contrast compound microscope. The female genital region of at least one specimen of each taxon was studied. Some genitalia were removed and optically cleared with and mounted in clove oil. In other cases nonsclerotized tissues were digested with hot 10% (weight/volume) potassium hydroxide and genitalia were then mounted (often *in situ*) in Hoyer's medium. The genital region of *Tangaroa* was studied both after being cleared in clove oil and as its nonsclerotized tissues were slowly eroded by 5% sodium hypochlorite. The latter method permitted study of exposed regions and the small gas bubbles generated by this process allowed examination of the passageway leading from the central spermatheca.

Specimens were prepared for tracheal studies by removing dorsal regions of the carapace and abdomen and digesting nonsclerotized tissues in hot 10% potassium hydroxide. Resulting preparations were first examined with a dissecting microscope in order to study abdominal patterns and then with an interference compound microscope in order to verify these observations and to study cephalothoracic tracheal patterns. In taxa represented by few specimens, tracheal patterns were determined by removing epigyna and carefully separating exposed muscles to determine the number and size of underlying tracheae entering the cephalothorax. Specimens with detached abdomens can be studied in a similar manner. In nearly all taxa tracheal patterns of both males and females were examined and were always found to be similar. Therefore, in the few genera

(*Purumitra*, *Orinomana*, and *Daramuliana*) where male tracheal patterns were not studied (because of lack of specimens), these patterns are most probably similar to those of females.

Webs to be photographed were first dusted with cornstarch (Eberhard, 1976b). Most web measurements were made from enlarged prints of such photographs taken at a carefully recorded distance.

NATURAL HISTORY

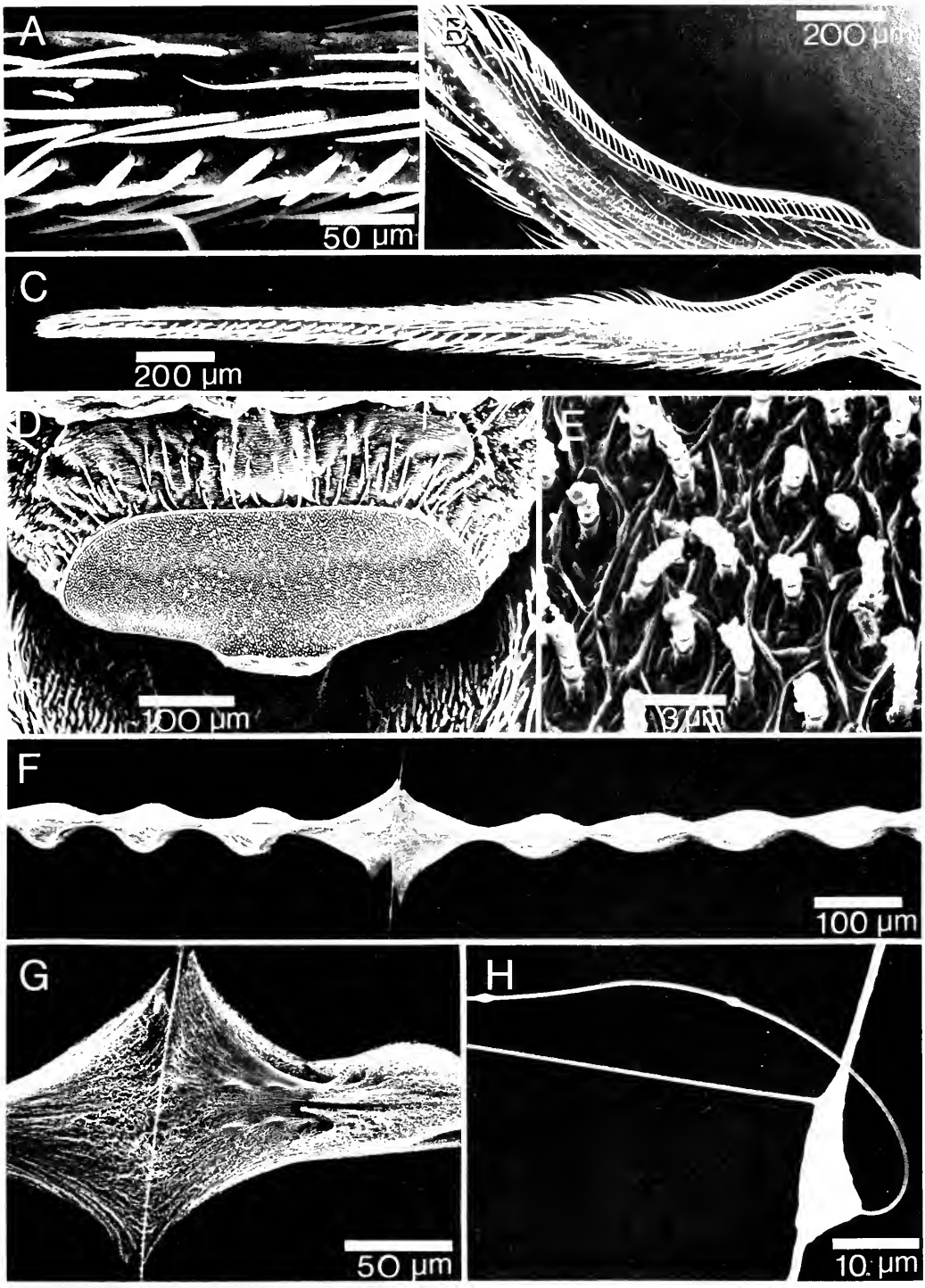
Uloborids are often referred to as "hackled-band-orb-weavers," although webs of only half of this family's 16 genera are known and members of only five of these genera (*Waitkera*, *Uloborus*, *Zosis*, *Octonoba*, and *Philoponella*) construct orb-webs. *Polenecia* females produce a vertical, slightly concave web and hang head down at the webs central attachment to a twin support (Wiehle, 1931). To construct this web the spider first lays down 25 to 32 radii, adds a single temporary spiral loop (which remains), and then deposits cribellar silk along the radii and framework threads. *Hyptiotes* also produces an apparently reduced vertical web which takes the form of an orb sector consisting of four radii across which cribellar capture "spirals" extend. *Hyptiotes* web construction and prey capture is discussed by several authors, including Comstock (1913), Gertsch (1949), and Nielsen (1932). Members of the genus *Miagrammopes* construct either a single horizontal capture thread with cribellar silk at its center or a horizontal resting line with one or several vertical or diagonal cribellar capture threads (Akerman, 1932; Lubin *et al.*, 1978).

Uloborid orb-webs are similar in construction to araneid webs. The former employ a cribellate capture spiral and are usually horizontal, whereas the latter have an adhesive capture spiral and are usually vertical. Eberhard (1969, 1971, 1972) discusses the building, structure, and ecology of the orb-web of *Uloborus diversus*. Uloborid cribellate silk consists of two axial (warp or supporting) strands onto which "puffs" of fine cribellate fibrils (Plate 1-F) are combed by the calamistrum (Plate 1-B, C) (Comstock, 1913; Friedrich and Langer, 1969). To accomplish this a spider places the tip of one fourth tarsus on the dorsal surface of the opposite fourth tarsus, bringing the calamistrum adjacent and parallel to the cribellum (Plate 2-A). Both legs are rapidly pumped up and down, combing out fine cribellar silk (with a diameter of about 30 nm and nodes about every 30 to 40 nm along its length, Plate 2-B) and placing it onto the axial threads. As Gerhard and Kästner (1937) and Gertsch (1949) note, this spinning behavior is similar to that of most cribellate spiders. Each pumping motion is presumably responsible for a single hackled-band "puff" as noted by Friedrich and Langer (1969) and Langer and Eberhard (1969). The spider uses the calamistrum of one leg to spin approximately half the cribellate strand spanning adjacent radii and then instantaneously switches to the other calamistrum with no noticeable interruption (Eberhard, 1972; personal observations).

The cribellate spiral threads extend directly across radii, forming a junction that corresponds to Jackson's (1971) "zero"

→

Plate 1. A. Ventral view of *Zosis geniculatus* female fourth tarsus showing erect macrosetae. B. Prolateral view of fourth metatarsus of *Zosis geniculatus* female showing one row of small setae and above it the large setae which form the calamistrum. C. Ventroprolateral view of *Zosis geniculatus* female fourth metatarsus and tarsus showing calamistrum and ventral row of erect macrosetae. D. Cribellum of *Zosis geniculatus* female. E. Spinning spigots of *Philoponella republicana* female cribellum. F. Cribellate silk and spiral-radius junction of *Uloborus penicillatus* female. G. Spiral-radius junction of *Uloborus penicillatus* female. H. Spiral-radius junction of *Mangaroa* sp. female. Horizontal strand is spiral.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F
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G
50 µm
H
10 µm

type (Plate 1-F, G). Eberhard (1976a) has shown that these junctions, in contrast to "nonzero" junctions of araneid orb-webs, do not allow the spiral to slip when it is stretched.

Scanning electron micrographs of *Uloborus penicillatus* (Plate 1-F, G) show the spiral flattened at its junction with the radius and the cribellate fibrils along this junction entangling the radius and responsible for attachment. This is in contrast with the spiral of *Mangaroa* (Plate 1-H) which is attached to the radius by adhesive. It appears that such adhesive junctions allow the spiral to slip through them whereas the entangled junctions of uloborids do not permit this to occur. Eberhard (1976a) has shown that the cribellate mat can pull free of its rigid axial threads, affording the uloborid spiral some elasticity when stressed. This movement may allow prey to come into contact with additional spiral strands. Perhaps the ability of a spiral to easily slide through its radius connections is more important in vertical webs where additional spiral strands wait below to intercept the sagging prey.

Stabilimenta are often added to the web after the capture spiral has been completed and take a variety of forms, none of which appear restricted to a single genus or species. The most common type of stabilimentum seems to be a linear silk band (occasionally two or more) of variable length which extends through the web's hub, usually with a central gap about as long as the spider's body. This type of stabilimentum is found in webs of *U. diversus* (Eberhard, 1969, 1973), *U. glomosus* (Emerton, 1902), *U. plumipes* (Wiehle, 1927), *Philoponella tingena*, and *P. republicana* (personal observations). Some *U. diversus* and *U. penicillatus* add a small spiral of dense silk to the hub of their webs (Eberhard, 1973; personal observation). *Zosis geniculatus* adds either a thin mat of silk to the hub of its web or several delicate, circular silk cogwheels around the perimeter of the hub's central mesh (Wiehle, 1927; personal observation). This species may also add a broad, linear stabilimentum to the web. As Eberhard (1973) points out, spiral and linear stabilimenta probably serve to conceal the spider from predators. However, the flimsy stabilimenta constructed by *Zosis geniculatus* seem ill suited for this purpose.

When the spider senses a prey in its orb-web it usually jerks the web several times forcefully (as noted by Marples, 1962) in a manner reminiscent of members of *Hyptiotes* (Comstock, 1913; Gertsch, 1949) and *Miagrammopes* (Lubin *et al.*, 1978). This behavior is sometimes repeated as the spider approaches its prey and may serve to further entangle the prey, evaluate its size, or assure that it is securely held by the web and will not attack the spider. As the spider nears the prey, one of its first legs often probes and lightly contacts the prey by swinging in a small circle similar to the exploratory movements that Eberhard (1972) describes during spiral construction. Maintaining its distance, the spider turns away from the prey, hangs from its first and second legs and uses its fourth legs to throw silk onto the prey. This silk often does not encircle the prey but soon entangles its thrashing appendages. After a short time the spider moves closer and begins a thorough wrapping of the prey which may take from about one minute for a small fruit fly to 20 minutes for an insect as large as the spider. This wrapping, conducted while prey is held and manipulated with the second and third pairs of legs, begins with the struggling prey still in the web's mesh and continues as the prey is partly or completely cut or torn from the web (larger prey are often left suspended by a thread at either end of the body and rotated on this axis during wrapping). The spread first legs support the spider and the fourth legs manipulate silk used for wrapping. The prey is then carried to the web's hub where additional layers of silk may be added before the

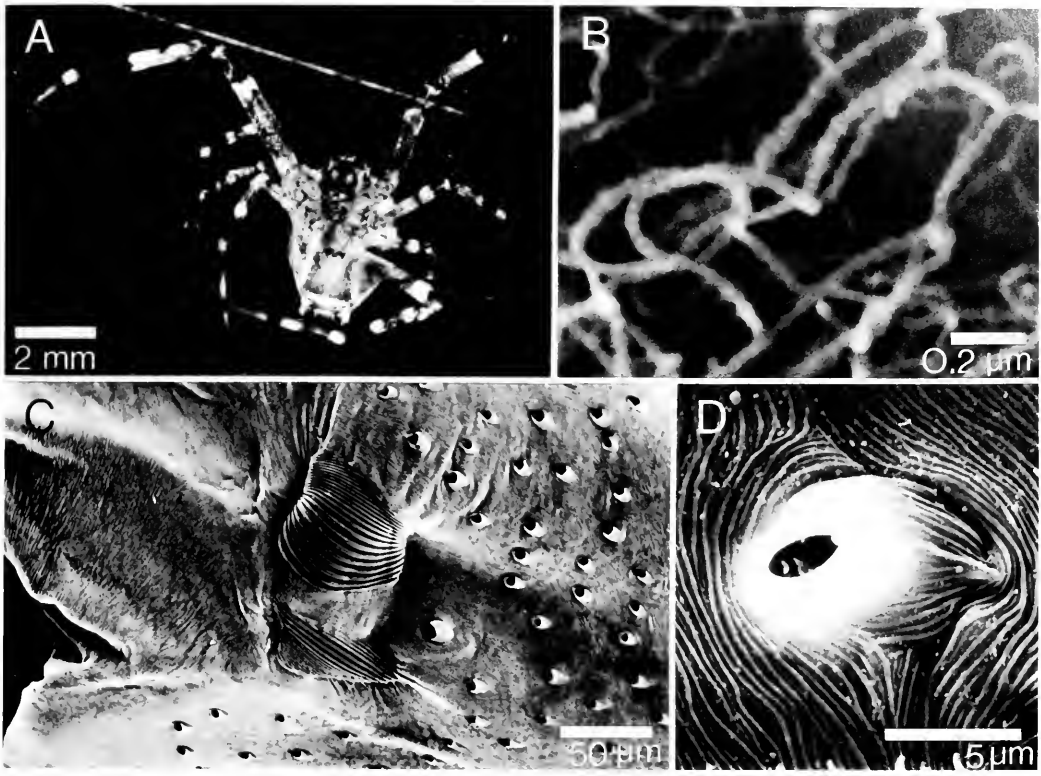


Plate 2. A. *Zosis geniculatus* female spinning cribellate silk. B. Cribellate silk strands of *Uloborus penicillatus* female. C. Retrolateral view of *Philoponella republicana* female first patella showing unsclerotized notch (left) bordering lyriform organs. D. First tarsal organ of *Zosis geniculatus* female.

spider grasps the prey with its palpal claws and begins to feed. Members of this family, lacking poison glands, both kill and digest prey by pouring digestive enzymes onto it. The prey's thick silk wrapping becomes transparent as it absorbs these enzymes and the extreme thickness of this covering may be useful for its absorptive properties rather than strictly for prey restraint. Uloborids do not use their chelicerae to pierce or knead prey and require as much as three hours to feed on a 5 to 6-mm-long beetle. Feeding, though slow, is thorough and when complete, only the prey's exoskeleton remains.

Convex eggsacs of *Polenecia* and *Hyptiotes* are form-fitted to and nearly indistinguishable from the surfaces of twigs on which they are constructed (Comstock, 1913; Scheffer, 1905; Wiehle, 1931). Members of the genera *Uloborus*, *Zosis*, *Philoponella*, and *Miagrammopes* construct suspended, stellate to cylindrical eggsacs. *Philoponella tingena* and *Zosis geniculatus* first construct a horizontal silk platform in their webs, deposit a cluster of 40 to 80 eggs under this platform, and then spin a form-fitting, convex covering around this egg mass, attaching its margins to those of the upper platform. Such eggsacs usually have five to eight marginal points which represent attachment sites of lines supporting the platform. These observations agree with those of *Uloborus diversus* made by Eberhard (1969). *Zosis geniculatus* leaves its thin-walled, pink to light purple egg-

sac in the orb's mesh where it is seemingly ignored. *Philoponella tingena* females, on the other hand, remove their thick-walled, dark gray eggsacs, resuspend them in a vertical orientation from the orb's perimeter or framework threads, and usually hang immediately above or beside them (Simon, 1891; pl. 4). It is not clear if *P. tingena* females remain with their eggsacs during the approximately twenty days required for spiderlings to emerge, but I observed several females with eggsacs daily for as long as eight days and each time the spider was hanging above her eggsac. *Uloborus diversus* females hang their eggsacs at the web's perimeter (Eberhard, 1969), but *U. glomosus* females arrange their eggsacs in the web's mesh (Emerton, 1883). Lubin *et al.* (1978) describe the structure and placement of *Miagrammopes* eggsacs.

Spiderlings molt once within the eggsac and emerge as second instars. Newly emerged *Philoponella tingena* spiderlings remained clustered near their eggsac about a day before ballooning away. These spiderlings and a few apparently third instar spiderlings constructed horizontal sheet webs similar to those described for *Uloborus diversis* (Eberhard, 1969), *U. walckenaerius* and *Zosis geniculatus* (Wiehle, 1927), *Philoponella vicina* (Peters, 1953), *U. plumipes* (Szlep, 1961), and *U. penicillatus* (personal observation). Initial stages in construction of these sheet webs are similar to early stages of orb-web construction seen in subsequent immature instars and mature females. However, second and a few third instar spiderlings lack a functioning cribellum and calamistrum and, unable to produce a usable capture spiral, begin laying down numerous fine secondary radii after the temporary spiral has been completed. Spiderlings attach these nonsticky radii only at the web's hub and perimeter. This allows these fine strands to be blown by air currents before they come in contact with and attach to primary radii, temporary spiral, and other secondary radii. This explains the sheet appearance of these essentially carefully constructed webs. Mature males of *Philoponella*, *Uloborus*, and *Zosis* also lack a cribellum and calamistrum and construct a sheet web similar to that made by second instar spiderlings.

Since Simon's (1891) description of *Philoponella republicana* colonies, little has been published on this interesting presocial behavior which is apparently common among members of the genus *Philoponella*. Gertsch (1949) briefly describes this phenomenon, Peters (1953) describes aggregations of *P. vicina*, and Struhsaker (1969) notes that *P. tingena* are found in colonies of various sizes and are sometimes associated with webs of *Nephila clavipes*. Observations on *P. tingena* show colonies of this species similar to those described by Simon.

Philoponella tingena colonies contain as many as 50 individuals of all ages and in larger colonies mature males and females are found in about equal numbers. A careful search yielded a few solitary individuals and numerous small colonies of two of three (usually immature) individuals. Colonies were commonly associated with the long, irregular threads of *Achaearanea* webs; however, I found several individuals and a few small colonies in irregular scytodid webs and the barrier strands of *Nephila clavipes* webs. *Achaearanea* webs, often constructed in the protective hollows of buttress tree roots, appear to provide a ready-made set of framework threads among which *P. tingena* can begin building their webs. By removing *Achaearanea* females to tree trunks lacking spider webs I was able to study colonization of their newly constructed webs. Not only did second instar *P. tingena* balloon to these webs and construct sheet webs, but larger juveniles as well as mature males and females arrived within six days. One colony of three males, two females, and two juveniles was established ten days after the *Achaearanea* female began constructing her web.

Sheet webs of second instar spider-

lings and orb-webs of immatures and mature females found with the colony's irregular framework threads are more or less horizontal. Mature males do not construct webs, but hang from framework threads, occasionally taking prey from the colony's sheet or orb-webs. Other than several apparently unsuccessful mating attempts, I observed no close interaction between individuals. Most juveniles and females hung from the hub of their respective webs and did not cluster in the center of the colony's framework threads as Gertsch describes. Females with eggsacs hung from framework threads, often those nearest the tree trunk.

INTRAFAMILIAL PHYLOGENY

Formulation of a clear hypothesis of uloborid intrafamilial relationship has been hindered by the: 1. traditional division of the family into subfamilies Uloborinae, Hyptiotinae, and Miagrammopinae and by emphasizing conspicuous carapace and web modifications of the latter two subfamilies while deemphasizing less striking, but potentially more significant forms of diversity within the Uloborinae, and 2. failure to carefully and fully study the family's diversity and employ a clearly defined method for translating this diversity into a phylogeny. This is not to say that uloborids have been neglected or that those studying them have been undiscerning. Rather, most studies treat the fauna of a limited geographical region and are concerned with the immediate task of describing and differentiating species.

By 1966 eight uloborid genera had been described, although, only five of these were widely recognized. In the first comprehensive treatment of the family since Simon (1892), Lehtinen (1967) described an additional eight genera and a new subfamily, Tangaroinae. Most of Lehtinen's genera are both valid and monophyletic, but his use of a chart for their description indicates only their distinctive features and subfamilial affiliation. Based on a study of web structure, Kaston (1964, 1966) suggests that uloborids evolved along two distinct and possibly polyphyletic lines: one leading via *Sybota* (nomenclatural changes make the cited genus *Polenecia*) to *Uloborus* and the other leading via *Hyptiotes* to *Miagrammopes*. However, the prevailing view of uloborids still seems best expressed by F. Pickard-Cambridge's 1902 statement that: "the spiders comprehended in this family probably have no near relations amongst existing forms; so that it is difficult to place them into any system of classification."

Whether one views this statement as a warning or a challenge depends largely on his evaluation and analysis of the family's diversity. Three such lines of diversity—male and female genitalia and the tracheal system—warrant separate consideration before being used as phylogenetic evidence.

Male Palpus. Despite extensive use of the uloborid male palpus to distinguish species, no attempt has been made to precisely define terms given to its various parts or to assure that these terms are used only for homologous structures. This problem seems to center around use of the term "conductor" for any sclerite serving to support and orient the embolus. By their comparison of the shape and size of the "conductors" of different genera and their failure to specify otherwise, Muma and Gertsch (1964), Lehtinen (1967), and others imply that these structures are homologous, when in fact, any one of five different sclerites may serve to support and orient the uloborid embolus. To avoid confusion, I will use the functional term *guide* for these five analogous structures and restrict the term *conductor* to its apparently original use for the specific uloborid sclerite defined below.

In selecting terms to describe the male palpus, I have retained and carefully defined terms historically associated with

TABLE 1. ABBREVIATIONS USED IN ILLUSTRATIONS.

MALE PALPUS:

STRIDULATORY FILE	SF
STRIDULATORY PICK	SP
CYMBIAL MACROSETAE	CM
FEMORAL TUBERCLE	FT
BASAL HEMATODOCHA	BH
SUBTEGULUM	ST
MIDDLE HEMATODOCHA	MH
TEGULUM	T
TEGULAR SPUR	TS
MEDIAN APOPHYSIS	MA
MEDIAN APOPHYSIS BULB	MAB
MEDIAN APOPHYSIS SPUR	MAS
EMBOLUS	E
SPERM RESERVOIR	RES
FUNDUS	F
CONDUCTOR	C
CONDUCTOR BASAL LOBE	CBL
CONDUCTOR SPIKE	CS
RADIX	R

FEMALE GENITALIA:

SPERMATHECA	S
FERTILIZATION DUCT	FD
ACCESSORY GLAND	AG
POSTERIOR PLATE	PP

FIGURE SCALE LINES:

a	0.1 mm
b	0.2 mm
c	0.5 mm
d	1.0 mm

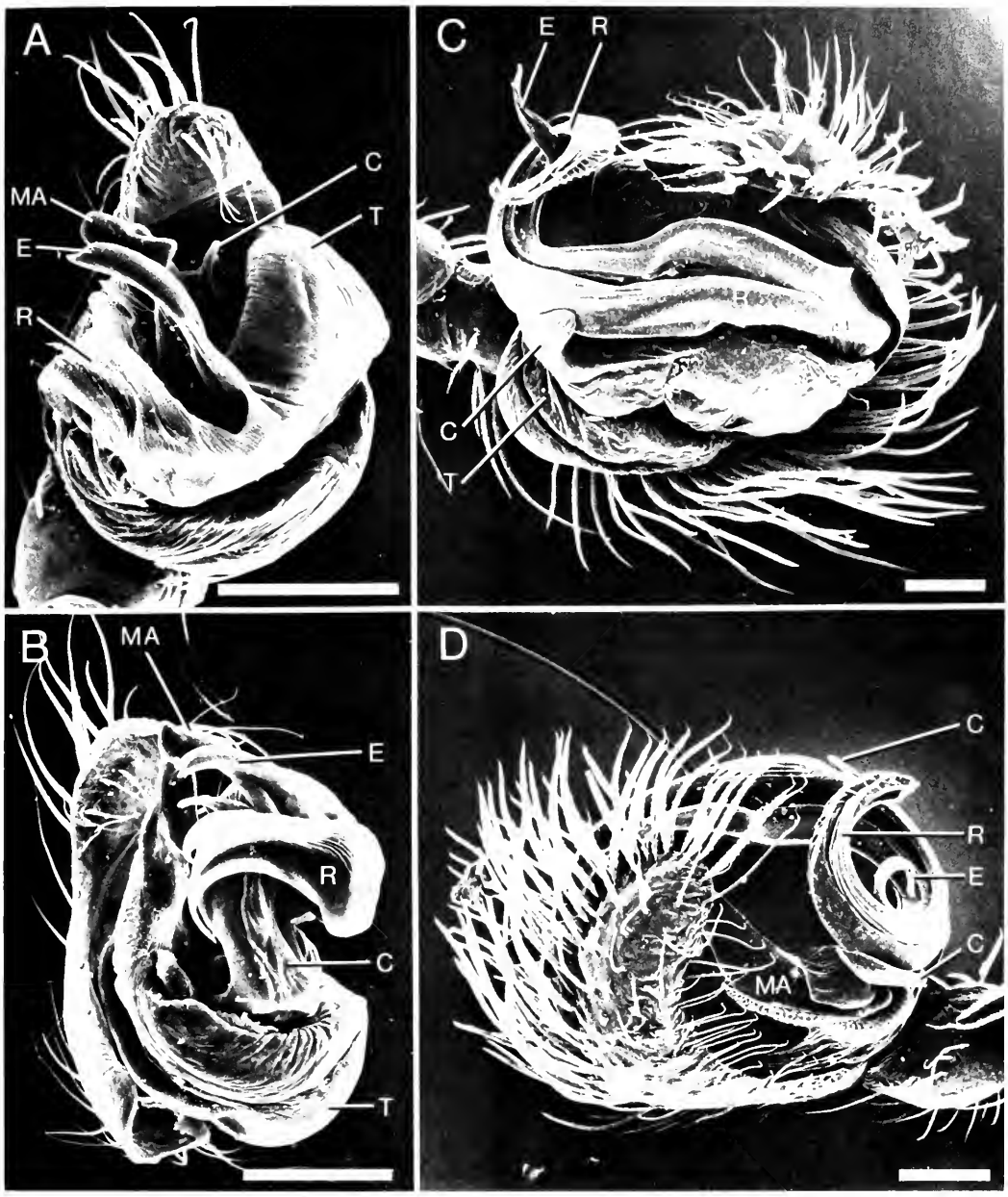


Plate 3. A. Retrolateral view of *Ariston mazolus* male left palpus. B. Prolateral view of *Ariston mazolus* male left palpus. C. Prolateral view of *Siratoba referena* male left palpus. D. Apical view of *Siratoba referena* male left palpus. All scale lines are 100 μm long.

the family and introduced additional terms only when it was necessary to distinguish previously unrecognized sclerites. Sclerites or projections arising from previously named structures are given names which reflect this attachment. Use of terminology common to other spider families does not imply that uloborid pal-

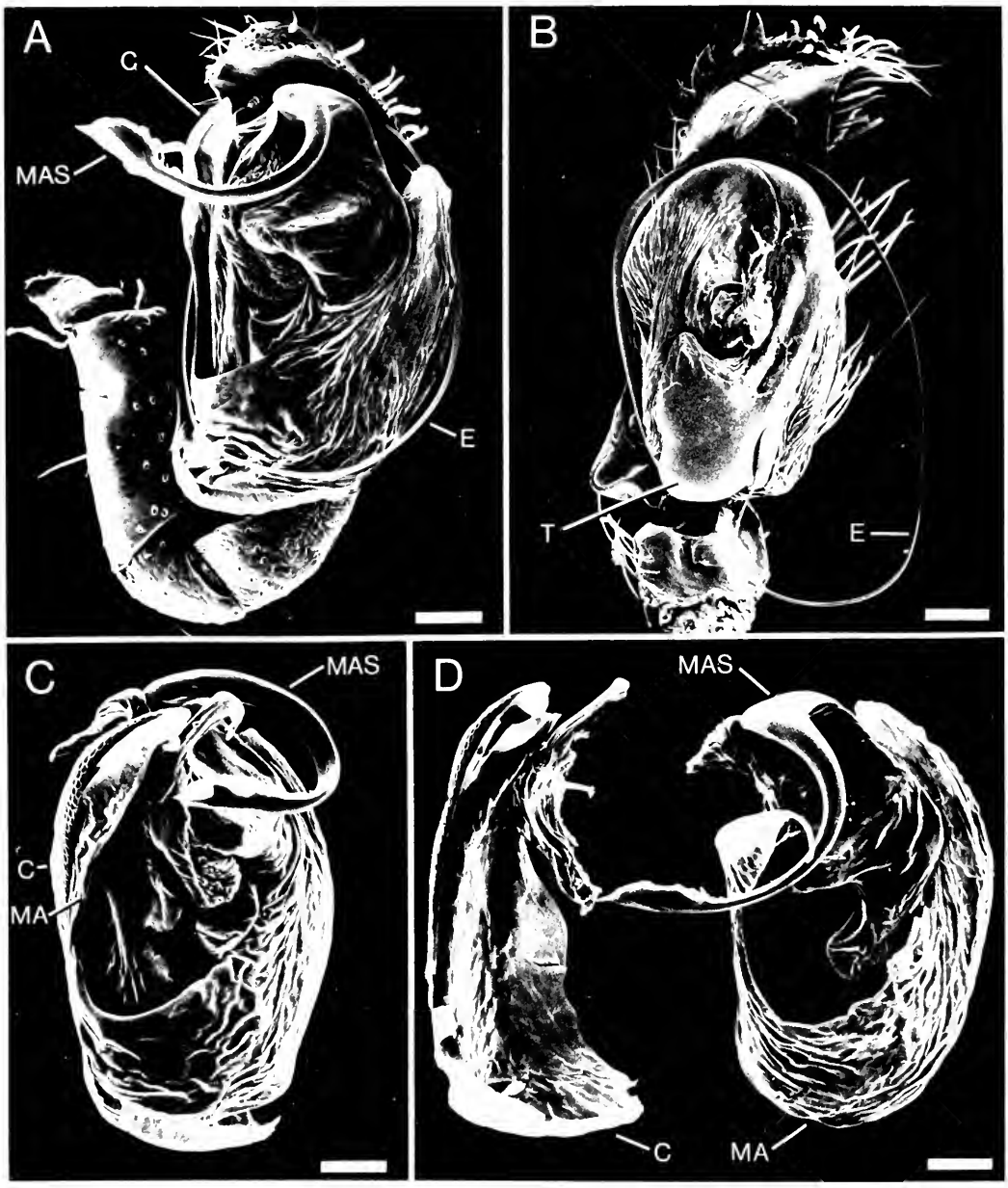


Plate 4. A. Retrolateral view of *Hyptiotes gertschi* male left palpus. B. Retrolateral view of *Hyptiotes gertschi* male left palpus with conductor and median apophysis removed. C. Retrolateral view of *Hyptiotes gertschi* male left palpus conductor and median apophysis removed from base of palpus. D. Conductor and median apophysis of *Hyptiotes gertschi* male left palpus removed and separated. All scale lines are 100 μm long.

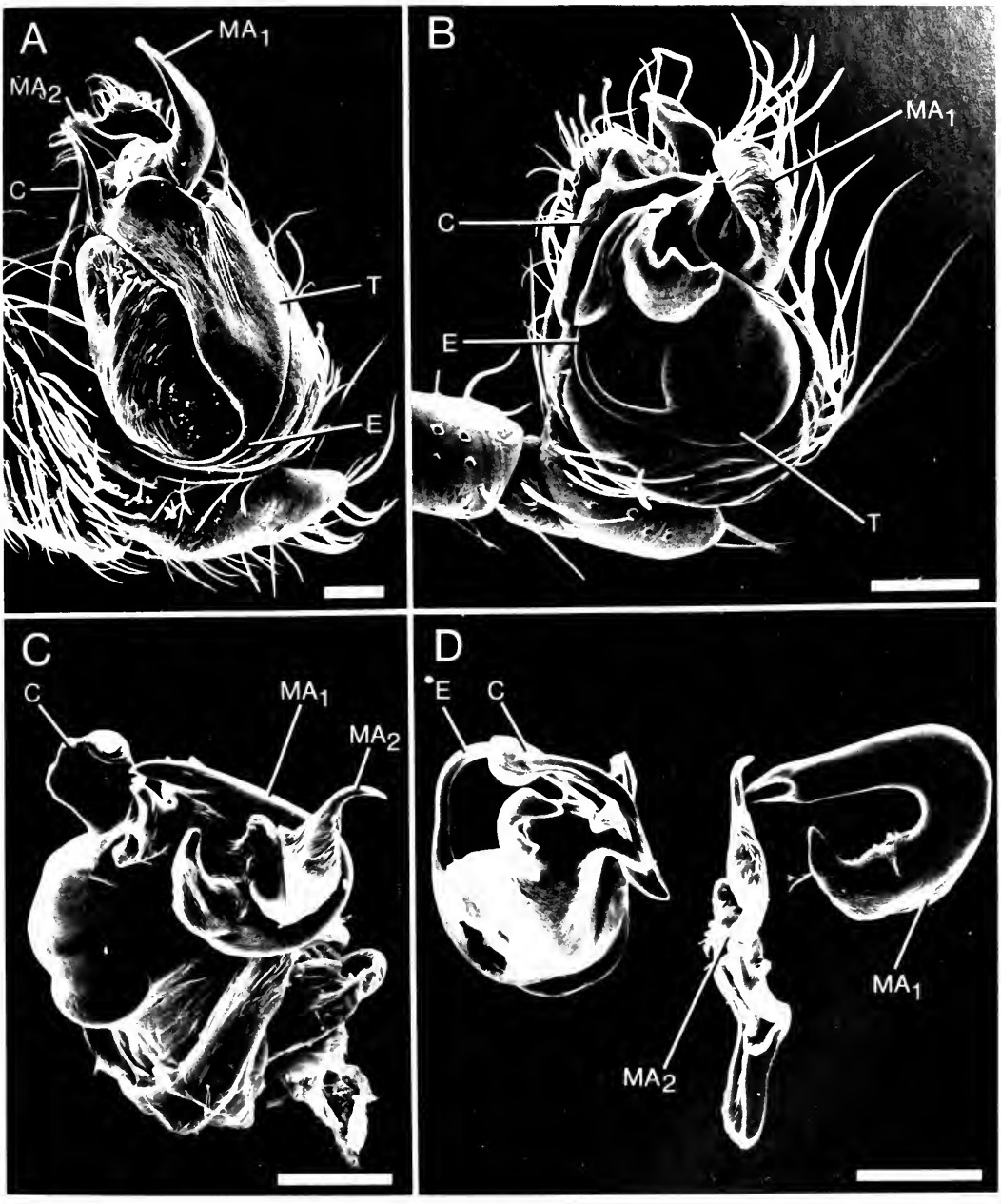


Plate 5. A. Retrolateral view of *Miagrammopes* sp. (from Tai Pin) male left palpus. B. Retrolateral view of *Miagrammopes simus* male left palpus. C. Apical view of *Miagrammopes simus* male left palpus with cymbium (attachment at lower right) removed. D. Apical region of *Miagrammopes simus* male left palpus separated to show components. All scale lines are 100 μm long.

pal structures are homologous to similarly named structures in these families. Rather, the primitive (simple) nature of the palpi of *Waitkera* indicates that most sclerites of uloborid palpi have evolved independently.

Endites of *Tangaroa*, *Waitkera*, and *Polenecia* have a small stridulatory file on their lateral surfaces (Figs. 19, 28, 46), described here for the first time. In *Tangaroa* two and in *Waitkera* three macrosetae, on the distal, ventral cymbial rim serve as picks (SP) (Figs. 19, 28). Two apparently homologous macrosetae (CM) (Plates 6-C, D; 7-C) found on the male palpi of most other uloborid genera serve no obvious function. The palpal femur of *Octonoba*, *Zosis*, *Philoponella*, and *Uloborus* has one or two proximal, ventral tubercles (FT) (Plate 7-A, C, D). The palpal patella and tibia of most genera each have a stout dorsal seta (Fig. 28). In *Sybota* and *Miagrammopes* a dorsal tibial extension protrudes over the tarsus (Plate 5-A, B; Fig. 90). The cymbium of *Tangaroa* folds over the distal part of the tarsus (Fig. 19), apparently serving as a guide for the embolus (E).

Hematodocha and Tegulum. The distal portion of the male palpus of all genera bears a basal hematodocha (BH) and subtegulum (ST) (Figs. 201, 215, 236). A middle hematodocha (MN) and tegulum (T) is present in *Octonoba*, *Purumitra*, *Zosis*, *Philoponella*, and *Uloborus* (Plate 7-A, D). In the remaining genera the region between the subtegulum and median apophysis (MA) is not pleated (Plates 3–6) and it is unclear whether this region represents a modified subtegulum, hematodocha, or tegulum. For this reason it is not named; although, its distal surface which gives rise to the median apophysis is termed the tegulum. In *Zosis*, *Octonoba*, and *Purumitra* a thin tegular spur (TS) arises from the lateral tegular surface and serves as an embolus guide (Plates 6-C; 7-C, D).

Embolus. In this study I recognize three divisions of the male sperm duct: 1. the free (projecting) embolus (E) containing an ejaculatory duct (ED), 2. a slender reservoir (RES), and 3. an enlarged fundus (F). Only in *Tangaroa* (Fig. 19) and possibly in *Siratoba* and *Ariston*, where the embolus is a flat sclerite, is it possible or necessary to distinguish this sclerite from the ejaculatory duct within. In the remaining genera the slender, sclerotized embolus closely conforms to the ejaculatory duct diameter. Examination of male palpi cleared in clove oil did not permit observation of taenidiae and, therefore, I define the reservoir and fundus by size and position rather than by wall structure as does Comstock (1910). The embolus arises from the dorsal or median tegular surface and, when the left tarsus is viewed apically, loops in a clockwise direction (Plates 3-D; 4-B; 5-A, B; 6-B–E, 7-C–D).

Radix. A radix (R) arises near the embolic base and appears to be a primitive feature of all uloborids except *Tangaroa*. In *Waitkera* the radix is a prominent scape (Figs. 28, 29) and in *Ariston* and *Siratoba* it functions as a guide (Plate 3, Figs. 68, 69). The radix of *Polenecia*, *Purumitra*, *Octonoba*, and Pacific *Philoponella* is a short flange and in the latter three genera is usually hidden by the median apophysis (Plate 6-D, E). Remaining genera lack a radix. Presence of the radix in some *Philoponella* and absence in others indicates that this sclerite's absence in this and all other genera but *Tangaroa* is the result of loss.

Median Apophysis. In all genera but *Tangaroa* a median apophysis arises from the tegulum's center and is usually partially or completely encircled by the embolus. The median apophysis of *Waitkera* consists of a small proximal lobe and a flat distal portion with a grooved ventral surface that forms a guide (Figs. 28, 29). In *Polenecia* (Figs. 46, 47) the median apophysis' distal portion is a flat plate and the proximal lobe is expanded, serving along with the conductor (C) as an embolus guide. Nearctic members of the

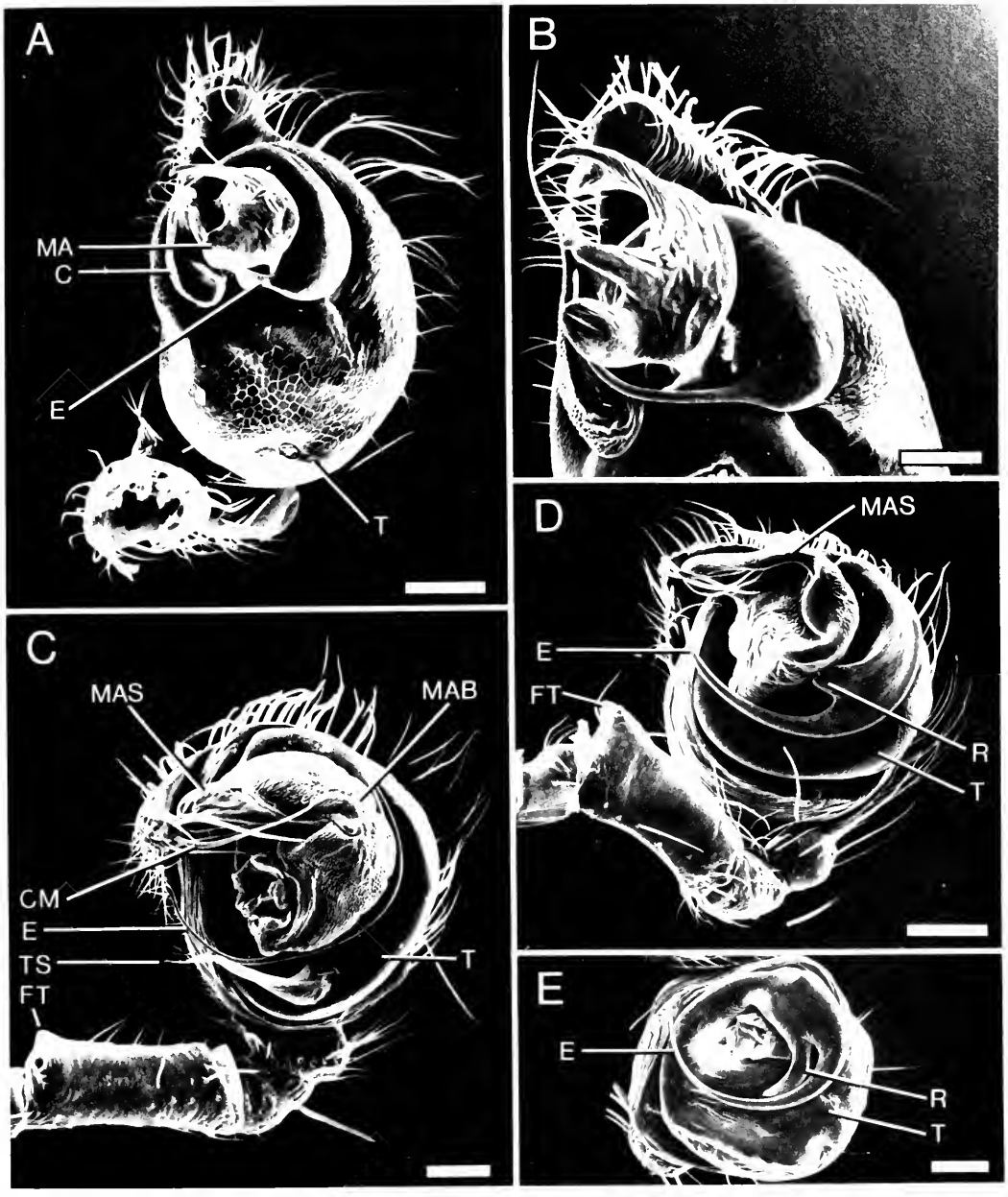


Plate 6. A. Retrolateral view of *Sybota abdominalis* male left palpus. B. Retrolateral view of apex of *Sybota osornis* male left palpus. C. Retrolateral view of *Octonoba* species 1 male left palpus. D. Retrolateral view of *Octonoba* species 2 male left palpus. E. Apical view of male left palpus of *Philoponella* sp. from Woodlark Island with bulb and conductor removed to expose embolus and radix. All scale lines are 100 μm long.

genus *Hyptiotes* have a long, curved, distally expanded median apophysis (Plate 4), whereas Palearctic and Oriental members have a short, flat median apophysis. In all members of this genus the proximal portion of the median apophysis is flat, curved, and tightly appressed to the grooved conductor to form a guide. This composite guide is termed the "conductor" by Muma and Gertsch (1964), Shear (1967), and Lehtinen (1967). Muma and Gertsch (1964) and Shear (1967) refer to the flattened tip of the proximal median apophysis lobe protruding from the conductor groove as the "radix." This term is unnecessary and inconsistent with the radix as defined above. Members of the genus *Siratoba* (Plate 3-C, D; Figs. 68, 69) have a proximal median apophysis lobe whose lateral surface forms a trough that accepts the conductor and radix-embolus unit. In this genus the distal lobe of the median apophysis is a flat sclerite with a concave terminus that appears to accept the tip of the proximal median apophysis lobe (Figs. 68, 69). The median apophysis of *Ariston* forms an elongate projection with an angular terminus (Plate 3-A, B). In *Sybota* the median apophysis is a broad sclerite with two or three distal projections (Plate 6-A, B). *Miagrammopes* is characterized by having an apical median apophysis with two lobes modified into projections of various shapes which are therefore difficult to designate as basal or apical. For this reason these lobes are designated MA_1 and MA_2 in Plate 5. Some members of the genus *Octonoba* have a concave median apophysis distal lobe which may serve as a guide (Plate 6-C, D). In other members the distal region of the median apophysis is rolled, forming a tube (Plate 7-D). Two regions can be distinguished in the median apophyses of members of the genera *Zosis*, *Ponella*, *Philoponella*, and *Uloborus*: a basal, hemispherical median apophysis bulb (MAB), probably homologous with the proximal median apophysis lobe described above, and a distal small, hooked median apophysis spur (MAS), probably homologous with the distal median apophysis lobe (Plate 7).

Conductor. The conductor (C) is a sclerite arising at the junction of the median apophysis and tegulum (Plates 3–7). In several genera the conductor's rugose surface aids in its identification (Plates 4-C, 6-B). No conductor is present in *Tangaroa*, *Purumitra*, *Octonoba*, or *Zosis*. However, in *Zosis*, *Purumitra* and *Octonoba* the small, unsclerotized lobe extending from the median apophysis bulb's center is probably homologous with the conductor (Plates 6-C; 7-C, D). The short, flat conductor of *Waitkera* (Figs. 28, 29) does not appear to function as an embolus guide. Conductors of *Polenecia*, *Hyptiotes*, *Siratoba* and possibly *Ariston* serve in conjunction with the median apophysis' basal lobe as a guide, while those of *Uloborus*, *Philoponella*, *Ponella*, *Miagrammopes*, and *Sybota* function independently as a guide. In many *Miagrammopes* the conductor, in addition to forming a trough in which the embolus lies, is also modified into a plate of various shapes (Plate 5-B–D). The conductor of *Polenecia* (Figs. 46, 47) consists of a broad basal plate with two distal projections, a small dorsal one and a longer, concave ventral one which, along with the basal portion of the median apophysis, serves as a guide. The same condition if found in *Hyptiotes* (Plate 4), but here the conductor is thinner and more extensive. In *Siratoba* (Plate 3-C, D; Figs. 68, 69) a Y-shaped conductor (C) lies proximal to the loop of the radix-embolus unit, apparently supporting it in its fork. The conductor of *Ariston* (Plate 3-A, B) extends distally under the radix and embolus, but its functional association with these sclerites is unclear. The conductor of *Miagrammopes*, *Sybota*, and *Uloborus* (Plates 5; 6-A, B; 7-A) is a trough-shaped basal lobe (CBL). In *Philoponella*, *Ponella*, and *Miagrammopes* a conductor spike (CS) is also present (Plates 5-A; 7-B).

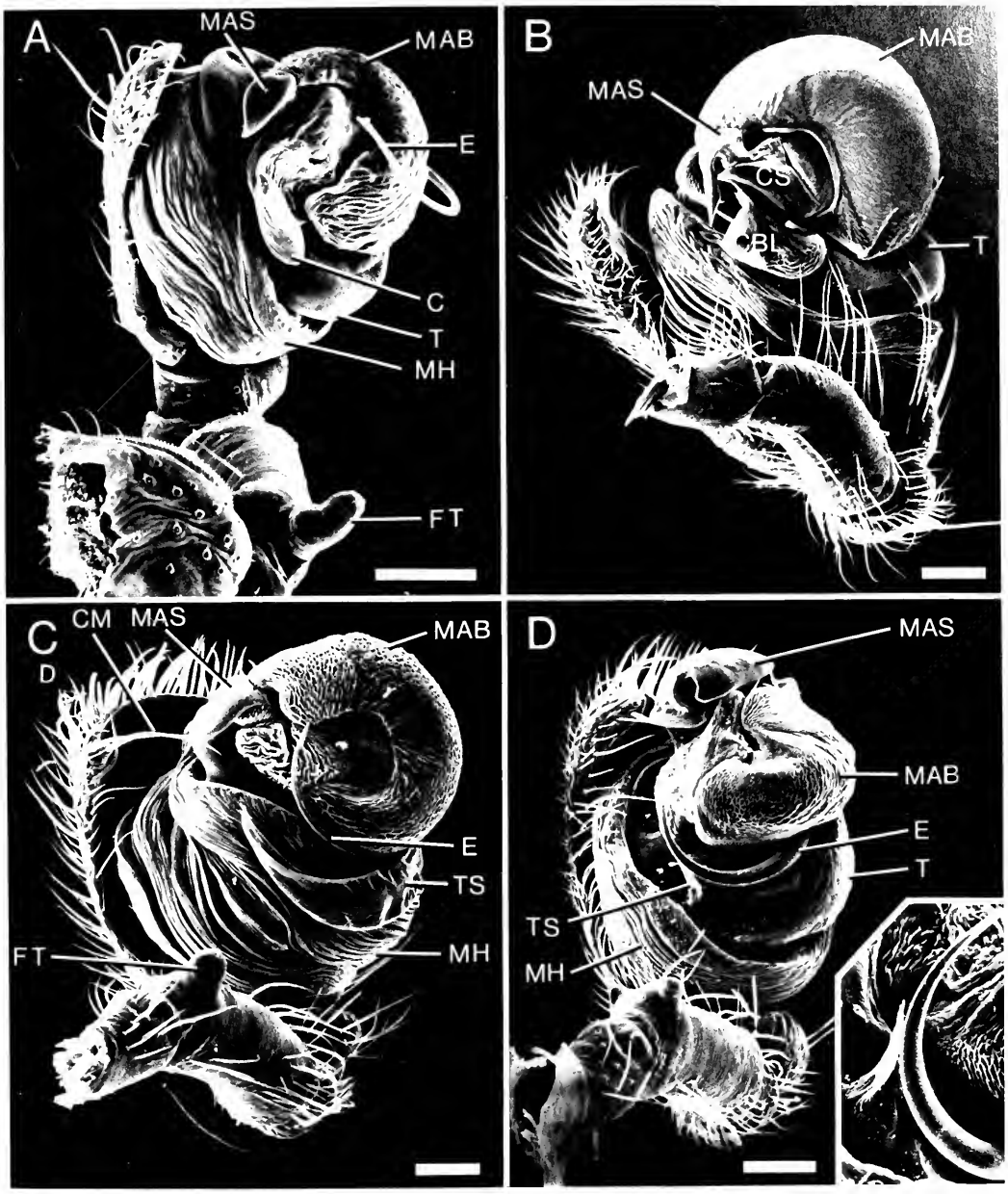


Plate 7. A. Retrolateral view of *Uloborus glomosus* male left palpus. B. Retrolateral view of *Philoponella republicana* male left palpus. C. Retrolateral view of *Zosis geniculatus* male left palpus. D. Retrolateral view of *Octonoba octonaria* left male palpus with insert showing tegular spur (small left projection) and embolus. All scale lines are 100 μm long.

Female Genitalia. The simplest female genitalia are found in *Tangaroa* and *Waitkera* where the epigastric furrow's anterior border is formed by a low, unsclerotized mound (Figs. 16, 30). In *Tangaroa* each of the two genital openings found on the epigastric furrow's anterior wall leads to a pair of blind spermathecae

(S) (Fig. 18). *Waitkera* females have a single median spermatheca which opens only into the vagina through a broad, hood-shaped dorsal passage (Fig. 31). Two small, blind, posterolateral accessory glands open at the posterior margin of the genital area. Chamberlain (1946) describes and illustrates an "epigynal" opening at each edge of the genital area's posteromedian indentation, apparently the openings of the glands described above.

Members of the genera *Polemecia*, *Ariston*, and *Hyptiotes* have a pair of blind accessory glands (AG) which appear to have an external opening distinct from the spermathecae and which may be either small (*A. albicans* and *A. mazolus*) (Figs. 34, 38) or large (*A. aristatus*, *Polenecia*, *Hyptiotes*) (Figs. 45, 54, 61, 62). In *Ariston* and *Polenecia* a pair of blind spermathecae arises from each genital opening (Figs. 34, 38, 45, 54). In *Hyptiotes* a long, coiled duct leads from each opening and may terminate in a fertilization duct (Figs. 61, 62). Muma and Gertsch (1964) misinterpret the accessory glands of *Hyptiotes* as spermathecae at the distal end of each long thin coiled duct. However, Wiehle (1927) correctly recognized the accessory glands and long sperm ducts as being unconnected. Females of *Ariston*, *Polenecia*, and *Siratoba* have a narrow to broad genital projection extending over a posteroventral concavity in which the openings are found (Figs. 32, 36, 43, 52, 65, 75). In *Hyptiotes* the genital area has a raised median ventral surface and a broad posterior plate whose narrow, median projection extends anteroventrally (Figs. 59, 60).

Members of the genera *Uloborus*, *Purumitra*, *Zosis*, *Octonoba*, *Daramuliana*, *Ponella*, and *Philoponella* have similar internal genitalia, characterized by a pair of external copulatory openings, each leading via a duct to a spherical spermatheca with a posterior fertilization duct (FD) (Figs. 139, 161, 180, 190, 200, 210). Epigyna of *Octonoba* and *Zosis* have two posterior lateral lobes whose posterodorsal margins form either a pair of atria (Figs. 184, 185) or a common atrium (Figs. 169, 171, 178, 179) in which copulatory openings are found. A sclerotized posterior plate (PP) lies dorsal to these atria (Figs. 171, 185). *Uloborus* has a similar epigynum, but lacks conspicuous atria, the epigynal copulatory openings being found at the posterior lobes' posterolateral margins (Figs. 138, 155). Epigynal openings of members of the genera *Daramuliana*, *Ponella*, and *Philoponella* lie anterior to the separated or medially united posterior lobes. In *Ponella* the posterior lobes are small mounds (Figs. 198, 199); whereas, in *Philoponella* and *Daramuliana* they appear to form the posterior rim of an oval or medially divided atrium, respectively, in which copulatory openings are found (Figs. 189, 208). Members of *Purumitra* have two pairs of sagittally divided median atria and two pairs of lateral atria (Fig. 160).

Female *Sybota*, *Siratoba*, *Orinomana*, and *Miagrammopes* have a duct (in *M. simus*, Fig. 96, a large bulb and a duct) leading from each epigynal opening to a large, blind spermatheca (Figs. 89, 94, 95, 96, 109, 119, 125, 128). At the base of each spermatheca (or of a thinner duct leading to it) arises either a fertilization duct or an expanded region giving rise to a fertilization duct. Members of *Sybota* are charaterized by having an epigynum with a prominent, well-sclerotized posterior plate, the tip of which is visible in ventral view as a median extension between lighter lateral areas at whose anterolateral margins the epigynal openings are situated (Figs. 105–108, 112, 113). The epigynum of *Orinomana* has a posterior indentation with openings situated at its lateral margins (Figs. 123, 124, 126, 127). *Siratoba* has a prominent epigynal hood which forms a posterior atrium housing openings at the ventrolateral margins of the posterior plate (Figs. 65, 66, 75, 76). Within the genus

Miagrammopes s.l. a variety of epigynal patterns is found, ranging from a simple posterior margin with lateral openings (Fig. 88) to a deeply notched posterior margin with posterolateral extensions, a posteromedian scape, and an anteromedian rim.

Discovery that members of the genus *Tangaroa*, *Waitkera*, *Polenecia*, *Ariston* and possibly *Siratoba* and *Hyptiotes* are haplogyne (*sensus* Wiehle, 1967; Cooke, 1969) shows Uloboridae to be an older lineage than previously thought. Members of *Tangaroa*, *Polenecia*, and *Ariston* lack fertilization ducts and have two pairs of spermathecae, each spermatheca connected by a duct to the genital opening on the epigastric furrow's anterior wall. Platnick and Gertsch (1976) and Platnick (1977) consider two pairs of spermathecae a primitive feature of spiders, but Platnick (1977) regards such structures in all non-hypochiloid araneomorphs as a modified single pair of spermathecae. Such modification no doubt explains the multiple spermathecae of many spiders. However, the striking similarity between female genitalia of *Hypochilis* (Gertsch, 1958; figs. 14, 16, 20, 21), *Hexathele* (Forster and Wilton, 1968; figs. 487–497, 510–514) and those of *Tangaroa*, *Polenecia* and *Ariston* (Figs. 18, 34, 38, 45, 54) suggests that genitalia of these three uloborid genera represent primitive haplogyne patterns and are not derived secondarily.

The single median spermatheca of *Waitkera* (Fig. 31) distinguishes it from other uloborids. However, the male palpal structure of *Waitkera* (Figs. 28, 29) suggests that this genus is allied with *Tangaroa* and *Polenecia* and the presence of a pair of small, presumptive lateral spermathecae indicates that a median pair of spermathecae may have fused to form the central spermatheca.

Female genitalia of *Orinomana*, *Sybota*, and most *Miagrammopes* are similar in having an anterior pair of blind spermathecae and a posterior pair of spermathecae (reduced in *Sybota abdominalis*) which give rise to fertilization ducts, making these genera entelegyne. I hypothesize that these spermathecae are homologous with those of *Tangaroa*, *Polenecia*, and *Ariston* and that, with the possible exceptions of *Hyptiotes* and *Siratoba*, fertilization ducts arose only once in entelegyne uloborids. Implicit in this hypothesis is homology between the posterior pair of *Orinomana*, *Sybota*, and *Miagrammopes* spermathecae and the single pair of spermathecae in the remaining entelegyne uloborids.

To my knowledge, no one has attempted to determine either histologically or developmentally whether fertilization ducts represent haplogyne ducts connecting the vagina and spermathecae or if they are newly evolved structures. The fertilization duct may have evolved in response to movement of the haplogyne genital openings from the deep recesses of the vagina to the posterior wall of the epigastric furrow and then to the ventral surface of the genital region. Only when these openings moved out of the epigastric furrow and were no longer able to supply sperm to eggs still within the protective recesses of the epigastric furrow, would there be selective pressure for evolution of a new set of tubes through which sperm could reach the eggs. This hypothesis considers female copulatory openings (into which the male inserts his embolus) of all spiders homologous and fertilization ducts apomorphic structures, derived one or several times.

If, on the other hand, one considers the fertilization ducts homologous with ducts connecting the spermathecae and vagina of haplogyne spiders, one is faced with the difficulty of explaining how male mating behavior and palpal structure responded to a sudden need to use a new and differently placed aperture for insemination. It is difficult to envision a spider so versatile or a population so diverse as to permit this. A similar problem arises if the fertilization duct is consid-

ered homologous with one of the paired lateral spermathecal ducts of haplogyne spiders and the other duct homologous with the bursa leading from an external opening. Only after the two spermathecae were connected by a newly evolved duct could the external opening be used by the male. This hypothesis is subject to the previous criticism and also questions what selective pressures could be called upon to explain evolution or movement of a nonfunctioning aperture.

These conclusions, if correct, support Shear's (1978) contention that "the haplogyne condition represents a grade and not a clade" by showing that the haplogyne-to-entelegyne transformation has occurred within a monophyletic lineage. Belief that Cribellata and Ecribellata represent separate and monophyletic lineages has been undermined by studies of Lehtinen (1967), Forster (1968), Baum (1972), and others and toppled by Platnick's (1977) analysis of this issue. This being the case, discovery of a single family with both haplogyne and entelegyne members supports Brignoli's (1975) conclusions by seriously challenging the validity of grouping either cribellate or ecribellate families solely on the degree of genitalic development.

Tracheal System. Bertkau (1878) reported and Lamy (1902) confirmed that *Uloborus walckenaerius* Latreille had a stout pair of tracheal trunks which extended from a common atrium into the cephalothorax where they divided into tracheoles which entered the legs. Lamy (1902) and Petrunkevitch (1933) found a similar pattern in *Miagrammopes*, but Petrunkevitch reported that in *Uloborus geniculatus* the two trunks split into tracheoles upon reaching the petiole. A study of the Uloboridae shows four basic tracheal patterns: 1. tracheoles restricted to abdomen (Fig. 1), 2. tracheoles extending into cephalothorax (Fig. 2), 3. four stout tracheal trunks extending into cephalothorax (Figs. 3, 5), and 4. two stout tracheal trunks extending into cephalothorax (Figs. 7, 9, 11). Within the cephalothorax only two patterns can be distinguished: one in which several small tracheoles serve each leg (Figs. 4, 6, 8, 10) and a second, found only in *Miagrammopes*, in which only one large trachea serves each leg (Fig. 12).

Tracheae always arise from a broad, common atrium near the cribellum. More extensive tracheal patterns are not associated with forward movement of the spiracle as in Hahniidae (Forster, 1970; Petrunkevitch, 1933), some Tetragnathidae (Levi, 1967), and Anyphaenidae (Platnick, 1974). From the atrium's lateral margin small tracheae, shown by Purcell (1909, 1910) to be homologous with book lungs, extend posteriorly, presumably to serve silkglands and spinnerets. From the atrium's anterior margin two stout median tracheal trunks extend into the abdomen (pattern 1) or the abdomen and cephalothorax (patterns 2–4). In the latter case each median trachea gives rise to a large lateral branch which divides into tracheoles that supply the abdomen. In pattern 3 these lateral branches arise just posterior to the median trunks' bifurcation.

The generally accepted view that in spiders an extensive tracheal system evolved primarily to reduce respiratory water loss is presented by Levi (1967) and is well documented for small spiders. Anderson (1970) accepts this explanation, but suggests and provides supporting evidence for the hypothesis that tracheal systems also evolved to supply increasing oxygen demands associated with increasing metabolic rates. Higher metabolic rates, he suggests, resulted when more reliable food supplies initiated more active forms of prey capture, increased fertility and more rapid development rates. Citing his findings and those of Davis and Edney (1952) and Dresco-Derouet (1960), who discovered that blockage of the tracheal spiracle caused no significant decrease in basal

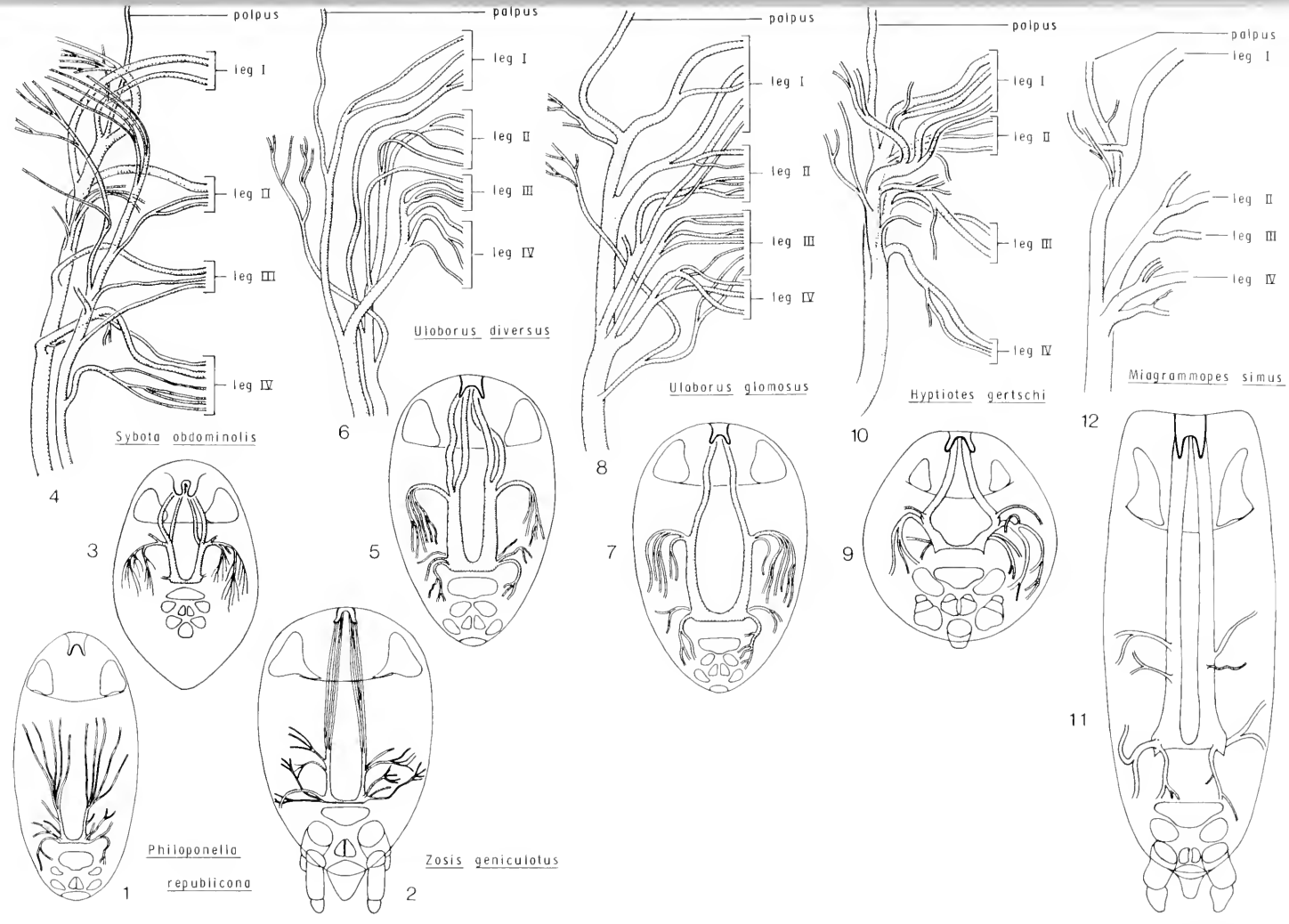


Figure 1. *Philoponella republicana* (Simon) abdominal tracheal pattern. Figure 2. *Zosis geniculatus* (Olivier) abdominal tracheal pattern. Figures 3–4. *Sybota abdominalis* (Nicolet). 3. Abdominal tracheal pattern. 4. Cephalothoracic tracheal pattern. Figures 5–6. *Uloborus diversus* Marx. 5. Abdominal tracheal pattern. 6. Cephalothoracic tracheal pattern. Figures 7–8. *Uloborus glomosus* (Walckenaer). 7. Abdominal tracheal pattern. 8. Cephalothoracic tracheal pattern. Figures 9–10. *Hyptiotes gertschi* Chamberlin and Ivie. 9. Abdominal tracheal pattern. 10. Cephalothoracic tracheal pattern. Figures 11–12. *Miagrammopes simus* Chamberlin and Ivie. 11. Abdominal tracheal pattern. 12. Cephalothoracic tracheal pattern.

(resting) metabolic rate, Anderson further hypothesized that it is largely during periods of activity that tracheae serve to prevent respiratory water loss and to provide large amounts of oxygen. Levi and Kirber (1976) cite studies supporting the hypothesis that tracheae are particularly important in supplying oxygen to the cephalothorax during periods of activity when, in order to generate hydrostatic pressure for leg extension, hemolymph circulation between cephalothorax and abdomen is thought to be stopped. A comprehensive reivew of studies relating to hydrostatic pressure and locomotion is presented by Anderson and Prestwich (1975) who also present evidence showing that during extreme activity retrograde flow and resulting accumulation of hemolymph in the abdomen is attenuated by: 1. closure of a valve between the heart and anterior aorta, 2. increased abdominal hemolymph pressure, 3. rigidity of the book lungs, and 4. large pressure drops as venous hemolymph passes through the book lungs. These findings indicate that circulation of oxygen-carrying hemolymph between abdomen and cephalothorax may not be completely blocked during activity or, if so, is stopped for only short intervals. Owing to proportional hemolymph distribution and maintained abdominal hemolymph pressure, flow is quickly restored when activity ceases. Anderson and Prestwich hypothesize that reliance on cephalothorax-generated fluid pressure for leg extension allowed more leg muscle mass to be devoted to flexion, thereby increasing strength for prey capture. Carrying this reasoning a step further, I suggest that some advanced tracheal systems may have evolved largely to supply the increased oxygen demands of these flexor muscles.

To summarize, an advanced tracheal system which extends into the cephalothorax may serve to: 1. reduce respiratory water loss, 2. increase total oxygen supply, 3. supplement or replace hemolymph-carried oxygen during periods of activity, and 4. supply oxygen specifically to leg flexor muscles. Although these four functions are not mutually exclusive, it is likely that tracheal patterns found in different families or even those found within a single family evolved under selective pressures favoring a certain function or set of functions.

Habitats, behavior and webs of many uloborid genera are unknown, but evidence suggests that tracheal patterns 3 and 4 of some genera serve largely to supply oxygen for extended or particularly strenuous leg flexure. Members of the genera *Polenecia*, *Hyptiotes*, *Miagrammopes*, construct reduced, highly specialized webs (see Natural History) and have tracheal pattern 4. *Hyptiotes* and *Miagrammopes* (perhaps *Polenecia* as well) support and flex the web while waiting for prey and vigorously jerk the web to ensure prey entrapment. Tracheal patterns of *Sybota* and *Orinomana*, shown by this study to be closely related to *Miagrammopes*, may facilitate similar specializations of web and behavior.

Among genera known to construct orb-webs (*Waitkera*, *Zosis*, *Octonoba*, *Philoponella*, and *Uloborus*) all four tracheal patterns are represented. Size ranges of these genera are similar with smaller species belonging to *Philoponella* (tracheal pattern 1). In Panama and Colombia I collected specimens of *Philoponella*, *Uloborus* (tracheal patterns 3 and 4), and, less often, *Miagrammopes*, in the same habitat. However, in captivity members of the latter genus appeared least resistant to desiccation and members of *Uloborus* less resistant than *Philoponella*. A large *Zosis geniculatus* (tracheal pattern 2) population discovered in Panama Canal Company warehouse B by Yael Lubin thrives in the apparent absence of free water.

Tracheal patterns are usually considered to evolve from simple to more extensive patterns. However, the following analysis of uloborid intrafamilial phylog-

eny indicates that the more extensive tracheal pattern 4 is either primitive in the family or has evolved independently at least five times. I favor the former explanation because of its greater parsimony. The literature, however, provides no insight into selective pressures responsible for reduction of the tracheal system and seems to dismiss this possibility.

Apparent desiccation resistance of *Philoponella* and *Zosis* indicates that tracheal patterns 1 and 2 are not detrimental in this regard. Web-hanging postures and relatively smaller femur diameters suggest that members of these genera expend less energy during web monitoring and prey entrapment and therefore may require less oxygen. In this case a well-developed tracheal system might prove disadvantageous because it would require an added initial investment of tissue and perhaps slightly raise basal metabolic rate and respiratory water loss.

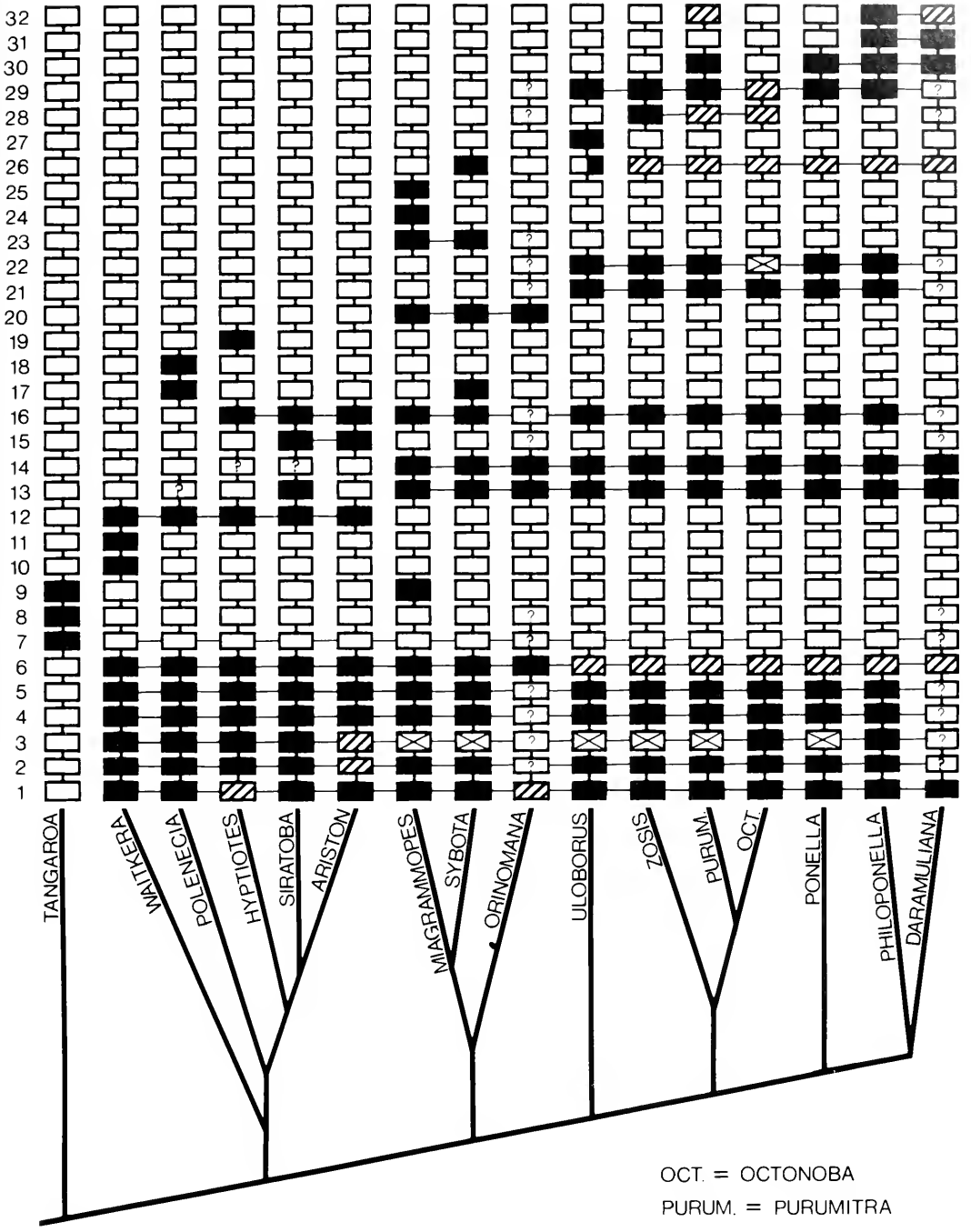
Discussion. Members of the family Uloboridae possess six potentially synapomorphic (shared, uniquely derived) characters: 1. loss of poison glands, 2. presence of a ventral row of macrosetae on the fourth metatarsae and tarsae (Plate 1-A, C), 3. two apical cymbial setae on the male palpus, 4. production of an orb-web or web derived from an orb, 5. presence of a row of trichobothria on the second through fourth femora, and 6. stout tracheal trunks which extend into the cephalothorax. Absence of a plesiomorphic character is generally not admissible as phylogenetic evidence. However, the fact that all uloborid genera are united by the five other characters listed above and are the only araneomorph spider genera to lack poison glands seems good reason to consider this loss a character uniting all uloborids. This character, however, offers little insight into interfamilial relationship. Ventral macrosetae occur on the metatarsi and tarsi of other spiders, but those of uloborids are larger, more perpendicular, and more precisely in register than those present in other spiders I have examined. These macrosetae appear to handle silk used to wrap prey (see Natural History) and, as uloborids rely heavily on this ability, the extreme development of this setal row may be considered a family character. The structure of these macrosetae distinguishes them from setae of the theridiid comb row, also situated on the fourth tarsus. Two prominent setae on the apex of the male's palpal tarsus (Plate 3-A, 6-C, D) appear homologous with and derived from stridulatory picks of *Tangaroa*, *Waitkera*, and *Polenecia* palpi (Figs. 19, 28, 46). Until similar stridulatory apparati or setae are discovered in other spider groups, these setae must be considered unique to the family Uloboridae.

I interpret behavior responsible for orb-web production as an apomorphic (primitive) character of the family Uloboridae and the behavior of *Polenecia*, *Hyptiotes*, and *Miagrammopes* as a modification of this behavior. Several ingenious schemes have been proposed to explain the monophyletic or (more often) polyphylyetic origin of the orb-web from various simple web types (e.g., Kaston, 1964, 1966; Kullmann, 1972), but these remain largely untested by morphological or behavioral evidence. This study is not intended to be a comprehensive treatment of interfamilial relationship, rather it attempts to present a clearly defined hypothesis of uloborid intrafamilial relationship which will facilitate these broader studies. Presence of femoral trichobothria on the legs of all uloborids (Fig. 206) as well as the legs of some araneids provides support for the relation of these groups and monophyletic evolution of the orb-web. Uloboridae have a single row of prolateral femoral trichobothria on the third and fourth legs and a single retrolateral row on the second legs. The first femur has either a single or double row of dorsal trichobothria. It is generally recognized that members of the genus *Leucauge* have two rows of

Table 2: Characters Used in Table 3

Character	Primitive State ☐	Derived State a ■ b ▨
1 Calamistrum length/metatarsus IV	Less than half	a. half b. more than half
2 Embolus in cross section	Flat	a. round b. crescent
3 Radix	Absent	a. present b. bifurcate
4 Length of male palpal femur	4 x diameter	3 x diameter
5 Conductor	Absent	Present
6 Female genital projection	Absent	a. median b. lateral
7 Median apophysis	Present	Absent
8 Male first femur	Straight	With distal crook
9 Anterior lateral eyes	Present	Absent
10 Median spermatheca	Absent	Present
11 Macrosetae on cymbial margin	Two	Three
12 Accessory glands	Absent	Present
13 Dorsal trichobothria on ♀ femur I	1 row	2 rows
14 Female genitalia	Haplogyne	Entelegyne
15 Embolus guide	Does not include radix	Includes radix
16 Stridulatory apparatus	Present	Absent
17 Posterior abdomenal extension	Absent	Present
18 Apical cymbial spine	Absent	Present
19 Anterior half of carapace	Rounded	Narrowed
20 Posterior lateral eye tubercules	Absent	Present
21 Large middle hematodocha	Absent	Present
22 Median apophysis	Does not form a bulb	Forms a large bulb
23 Male palpal tibia	Small	With extension
24 Anterior median eyes	Present	Absent
25 Endite length	One-and-one-third width	Twice width
26 Cephalothoracic tracheal trunks	Two	a. four b. absent
27 Setal tuft on female tibia I	Absent	Present
28 Tegular spur	Absent	a. large b. small
29 Median apophysis spur	Absent	a. claw-like b. concave
30 Female genital openings	Posterior	Ventral
31 Tracheoles	Pass into cephalothorax	Restricted to abdomen
32 Epigynal atrium	Absent	a. undivided b. divided

TABLE 3. CLADOGRAM OF ULOBORIDAE GENERA USING CHARACTERS DESCRIBED IN TABLE 2. BOXES MARKED WITH AN X REPRESENT A CHARACTER STATE REVERSAL.



prolateral trichobothria on the fourth femora. It this were the only araneid genus to have such trichobothria their presence might be explained by convergence. However, the tetragnathid genus *Agriognatha* has a single row of trichobothria on the dorsal surface of the first femur, the dorsoretrolateral surface of the second femur, and the prolateral surfaces of the third through fourth femora. The Metinae genus *Alcimosphenus* and *Leucauge argyra* (the latter previously placed in the Metinae genus *Plesiometa*) have dorsal trichobothria on the first femur and two rows of trichobothria on the dorsal surface of the second femur and the prolateral surfaces of the third through the fourth femurs.

Based on the synapomorphic characters of orb-web production and the presence of rows of femoral trichobothria, the family Araneidae appears to be the only family with which Uloboridae may be objectively allied. This hypothesis may be shown false by discovery that these trichobothrial rows are not homologous or that they are shared by members of other families.

The extensive tracheal pattern which I interpret as primitive within the Uloboridae is also found in members of other families and, for this reason, cannot at this time be regarded as a synapomorphic character of uloborids. However, this character does separate Uloboridae from Dinopidae which have a four-branched tracheal system restricted to the abdomen.

Most characters (Table 2) used in the cladistic analysis (Table 3) of generic relationship are discussed above and can also be found in genus descriptions. In the seven cases where two derived states are designated for a character each state is treated as an alternate possibility and designation of a state as "b" in Table 2 does not imply that it was derived from state "a." Ensuing analysis of this data can provide some directional evidence as in the case of Character 6 where "b" appears derived from "a" and Character 26 where "a" and "b" appear independently derived. The structure serving as an embolus guide in haplogyne spiders appears to be homologous with the median apophysis of *Waitkera* (Figs. 28, 29) and, for this reason, I consider presence of a median apophysis a primitive character of uloborids and its absence in *Tangaroa* a derived condition.

Tangaroa is distinguished by derived states of Characters 7, 8, and 9 and the remaining fifteen genera by derived states of Characters 1 through 6. *Waitkera* is the only genus with derived states of Characters 10 and 11 and is united with *Polenecia*, *Hyptiotes*, *Siratoba*, and *Ariston* by the derived state of Character 12. The remaining ten genera share derived states of Characters 13 and 14. *Miagrammopes*, *Sybota*, and *Orinomana* are united by the derived state of Character 20 and the remaining seven genera by derived states of Characters 6, 21, 22, and 29. *Uloborus* is characterized by the derived state of Character 27 and the remaining six genera by Character 26-b. *Zosis*, *Purumitra* and *Octonoba* share the derived state of Character 28 and the remaining three genera share the derived state of Character 30. Other shared, derived characters further define the cladogram presented in Table 3.

Conclusions on relationships of uloborid genera (Table 3) differ from traditional division of the family into three subfamilies and more precisely place the genera. I have chosen not to present a formal classification for the family Uloboridae at this time. I do so not out of disagreement with arguments favoring a well-defined and detailed classification, but out of the belief that this investigation will stimulate additional studies which will test and improve this hypothesis of intrafamilial relationship. Because a cladogram is translated directly into a cladistic classification, lack of a hierarchical scheme does not prevent a clear understanding of the underlying hypoth-

esis of relationship nor preclude its testing.

Uloboridae Thorell

Uloborinae Thorell, 1869, N. Act. Reg. Soc. Sci., Upsalaiensis, (3)7: 1–108 (In Epeiroidae). Type genus *Uloborus* Latreille, 1806.
Uloboridae:—O. Pickard-Cambridge, 1870, Zool. Rec., 7: 207–224.

Diagnosis. Members of the family Uloboridae are distinguished from all other spiders by the lack of poison glands. They are the only cribellate spiders which spin an orb-web, have a row of trichobothria on femora II through IV (Fig. 206), and have a prominent ventral row of macrosetae beginning on the distal half to third of metatarsus IV and extending nearly the full length of tarsus IV (Plate 1-A, C).

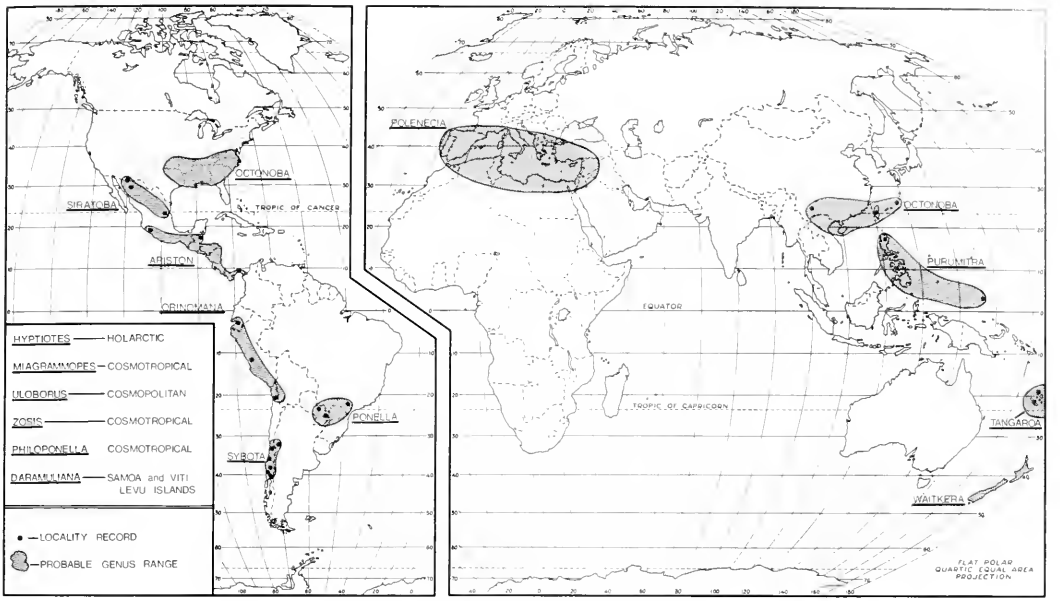
Description. The carapace of most uloborids is oval (Figs. 13, 23, 72) to pear-shaped (Figs. 40, 132, 162), but that of *Hyptiotes* is anteriorly constricted (Fig. 55) and that of *Miagrammopes* nearly rectangular (Figs. 78, 86). In males of some genera the anterior median eyes are situated on a small median mound (Figs. 14, 193). The thoracic groove of females and in many genera of males is a shallow pit (Figs. 13, 14, 40). Males of *Zosis*, *Ponella*, and *Philoponella* have a broad, transverse thoracic groove (Figs. 163, 193, 217). All eyes are nearly equal in size and lack a tapetum. In members of the genus *Tangaroa* anterior lateral eyes are reduced to small pigment spots (Figs. 13, 14) and in members of the genus *Miagrammopes* the anterior eyes are absent (Figs. 78, 80). The eight eyes of the remaining 14 genera are arranged in two rows. When viewed from above the anterior row is procurved in *Polenecia* (Fig. 50), straight in *Hyptiotes* (Fig. 55) and recurved in the remaining genera (Figs. 13, 23, 120). The posterior eye row is nearly straight in *Philoponella* (Figs. 204, 205) and in some *Miagrammopes* (Figs. 78, 80) and recurved in the remaining genera (Figs. 13, 23, 55). Posterior lateral eyes of *Hyptiotes*, *Sybota*, *Orinomana*, and *Miagrammopes* are on conspicuous lateral tubercles (Figs. 55, 78, 79, 100, 121). The sternum of most *Miagrammopes* species is divided (Figs. 81, 82, 92, 93) and in the remaining genera entire, being widest between the first and second coxae (Fig. 164). The labium is not rebordered and, although free from the sternum (Figs. 81, 82, 164), its separation from the latter is not easily discernible in most genera. Endites of *Miagrammopes* species are about twice as long as wide and in others about one-and-one-third times as long as wide. Endite serrulae of all genera are formed by a single row of closely spaced denticles (Plate 7-A). Chelicerae lack a prominent boss and their prolateral and retrolateral fang furrow margins each have a cluster of many small teeth and in some genera one or more larger teeth. Each fang's median surface has a row of small denticles which runs nearly its entire length. Its tip lacks a poison opening. Palpal tarsus of immatures and females each bears an apical serrate claw. The first leg tarsal organ of female representatives of all genera except *Tangaroa*, *Siratoba*, *Orinomana*, *Purumitra*, and *Daramuliana* was examined with the scanning electron microscope and found to be dome-shaped with a central pit (Plate 2-D). The first femur has dorsal trichobothria arranged in one or two rows (Table 3). The second femur has a single row of trichobothria which is proximally dorsal, becoming distally retrolateral (Fig. 206). The third and fourth each have a single row of trichobothria which is proximally dorsal and distally prolateral. Plumose setae are present on legs. Each leg has three tarsal claws, the dorsal two being serrate. Leg formula (longest to shortest): I, IV, II, III. Paired patellar lyriform organs (Plate 2-C) are retrolateral and situated at the proximal margin of a broad, open, weakly sclerotized notch (Figs. 58, 84, 166). In Plate 2-C this weakly sclerotized notch is recognized by the absence of setal sockets.

The fourth metatarsus is laterally compressed in the proximal region which bears the dorsal calamistrum (Plate 1-B, C). Although only one row of calamistral setae is well developed, a prolateral row of short setae (Plate 1-B) adjacent to the primary row betrays the double nature of the calamistrum. A row of stout, nearly perpendicular, ventral setae each with a spiraled shaft and small, hooked tip (Plate 1-A) extends from the center or distal third of the fourth metatarsus to the tip of tarsus IV. Presumably, these setae serve to handle silk during prey wrapping (see Natural History). The pedicel's lorum (Fig. 168) consists of a broad, anterior, shield-shaped plate, a smaller, posterior, H-shaped plate, and a pair of small lateral plates each bearing a lyriform organ (not shown). Abdomen shape is quite variable and ranges from oval (Figs. 24, 40, 42, 56) to peaked (Figs. 74, 122) to cylindrical (Figs. 78, 86). Abdomen of *Polenecia* and *Sybota* have a narrow posterior extension (Figs. 51, 114, 116). The four dorsal humps present in some genera (Figs. 56, 148, 149) appear to correspond to attachment points of the four pairs of dorsal-ventral abdominal muscles. In many genera only one pair of humps is visible (Figs. 120, 122, 132, 195, 260). The heart has three pairs of ostia which in light colored specimens can be seen through the integument (Figs. 40, 98, 133, 159, 195). The cribellum is undivided and bordered anteriorly by a weakly sclerotized region which bears fine setae (Plate 1-D). Cribellum and calamistrum are absent in second instar spiderlings when they emerge from the egg-sac as well as in mature males. In males the area previously occupied by the cribellum does not bear a colulus, but has a weakly sclerotized integument similar to that present anterior to a functioning cribellum. Just anterior to the cribellum is a single median spiracle whose broad, shallow atrium gives rise to a pair of lateral chambers, each giving rise to a stout anterior trunk and several smaller posterolateral tracheae (Figs. 1, 2, 3, 5, 7, 9, 11). A more extensive discussion of the tracheal system is found under Intrafamilial Phylogeny. Anterior spinnerets appear to have three segments: a large basal segment; a very short, ringlike middle segment; and a short, dome-shaped apical segment. Median spinnerets have a single segment and posterior spinnerets have two cylindrical segments, the proximal one being longer. The anal tubercle has two segments. A detailed discussion of male and female genitalia appears under Intrafamilial Phylogeny and Map 1 summarizes the distribution of the family's 16 known genera.

Note. Type specimens of *Uloborus minutus* Mello-Leitão and *U. tetramaculatus* Mello-Leitão were not examined during the course of this study. Types of *U. collinus* and *U. trillineatus* described by Keyserling should be housed in Polska Akademia Nauk Instytut Zoologiezny, Warsaw, Poland, but appear to have been lost. *Uloborus formosus* Marx (in Banks) was destroyed in the 1906 California earthquake. The type specimen of *U. niger* Mello-Leitão belongs to the family Dictynidae and the type specimen of *U. ater* Mello-Leitão is an immature male. *Uloborus sexmucronatus* Simon, the type and only known species of Lehtinen's genus *Astavakra* should be housed in the Muséum National d'Histoire Naturelle, Paris, but could not be located. Consequently, this is the only described genus of Uloboridae not treated in this study.

Generic Key for Uloborid Males
(Males of *Orinomana* are unknown)

1. Posterior lateral eyes (PLE) on prominent lateral tubercles (Figs. 55, 80, 103) 2
– PLE not on lateral tubercles 4
2(1). Anterior eyes absent (Figs. 80, 87); endites and labium at least twice as long as wide (Figs. 82, 92); Cosmotropical ..... *Miagrammopes*
– Anterior eyes present (Figs. 55, 103); endites and labium length equal to or less than 1.3 width 3
3(2). Anterior half of carapace conspicuously



Map 1. Distribution of uloborid genera.

narrowed (Fig. 55); in dorsal view anterior median eyes (AME) separated from anterior carapace edge by at least two eye diameters (Fig. 55); length of femur I equal to carapace length; median ocular quadrangle four times as wide posteriorly as anteriorly; Holarctic and Oriental (Map 1) ..... *Hyptiotes*

– Carapace oval (Fig. 103); in dorsal view AME at anterior edge of carapace (Fig. 103); length of first femur 1.5 to 1.7 times carapace length; median ocular quadrangle 1.5 to 2.0 times as wide posteriorly as anteriorly; western South America (Map 1) ..... *Sybota*

4(1). Anterior median eyes (AME) on a conspicuous anterior projection (Fig. 14); ALE absent, represented only by small, dark spots; first femur with a distal crook (Fig. 21); South Pacific islands (Map 1) ..... *Tangaroa*

– AME not on a conspicuous projection; ALE present; femur I without a distal crook 5

5(4). Palpus with a large, dome-shaped median apophysis bulb and a small, claw-shaped median apophysis spur (Plate 7-A–C) .. 6

– Palpus otherwise; median apophysis bulb flattened (Plates 6-C, D, 7-D; Figs. 28, 46, 47, 157), reduced (Plate 3-C, D; Figs. 68, 69), or median apophysis is a long projection (Plate 3-A, B) 9

6(5). Palpus without a conductor and with a broad, flat tegular spur serving as an embolus guide (Plate 7-C); first femur (Fig. 167) with one prolateral and three dorsal macrosetae; cosmotropical ..... *Zosis*

– Palpus with a conductor and without a tegular spur (Plate 7-A, B; Figs. 201, 218, 253, 270); first femur with two or three prolateral, one or two retrolateral, and two dorsal macrosetae (Fig. 202) 7

7(6). Palpus with a large conductor extending along the distal embolic surface and having a long, thin projection at its base (Fig. 201); first tibia with three prolateral, three retrolateral, and four dorsal macrosetae (Fig. 202); southeastern South America (Map 1) ..... *Ponella*

– Palpus either without a conductor along the distal embolic surface (Plate 7-A) or if conductor is longer it consists of a basal lobe and a long conductor spur (Plate 7-B); first tibia with at least four prolateral, four retrolateral, and six distal macrosetae 8

8(7). Carapace oval with a broad, transverse thoracic groove (Fig. 217); posterior eye row nearly straight; clypeus height in anterior view 0.7 to 1.5 AME diameter; conductor spur present (Plates 7-B; Figs. 218, 236); first femur without numerous trichobothria; cosmotropical ..... *Philoponella*

– Carapace pear-shaped with conspicuously narrowed cephalic region and a narrow thoracic depression (Figs. 133, 142); pos-

terior eye row recurved such that a line touching PMEs' posterior margins passes anterior to the PLEs by half a PLE diameter; clypeus height half an AME diameter; conductor spur absent (Plate 7-A; Figs. 135, 143); first femur with numerous trichobothria (Fig. 131); cosmopolitan ..... *Uloborus*

9(5). Median apophysis spur a broad, concave or enrolled sclerite (Plates 6-C, D; 7-D); tegular spur usually present (Plates 6-C, 7-D) 10

– Palpus otherwise 11

10(9). Male carapace length greater than 1.4 mm; length of first femur 1.5 to 1.7 that of carapace; median apophysis bulb reduced, median apophysis spur concave (Plates 6-C, D, 7-D); southeastern United States, China and adjacent Pacific islands (Map 1) ..... *Octonoba*

– Carapace length less than 0.9 mm; length of first femur twice that of carapace; median apophysis bulb large and laterally flattened; median apophysis spur broad with a central depression (Fig. 157); Pacific islands (Map 1) ..... *Purumitra*

11(9). Embolus short, pointed, and free from guide for most of its length (Figs. 28, 29, 46, 47); cymbium with two or three short, stout apical macrosetae; each endite's lateral surface with a lobe bearing stridulatory ridges (Figs. 28, 46, 47) 12

– Embolus either broad and flat (Plate 3-A B) or resting in a grooved radix (Plate 3-C, D; Figs. 68, 69); cymbium without such spines; endite lacks a lateral lobe and stridulatory file 13

12(11). Anterior eye row recurved (Fig. 23); first tibia with six prolateral, two retrolateral, six dorsal, and no ventral macrosetae (Fig. 27); cymbium with three stout distal marginal macrosetae (Fig. 28); palpus with a pointed, grooved median apophysis serving as an embolus guide and with a long thin radix (Figs. 28, 29); New Zealand (Map 1) ..... *Waitkera*

– Anterior eye row procurved (Fig. 50); first tibia with two prolateral, two retrolateral, one dorsal, and six ventral macrosetae (Fig. 49); cymbium with two stout distal, marginal macrosetae and a thin distal cymbial extension (Figs. 46, 47); palpus with a thin proximal median apophysis lobe and a broad flat conductor with a thin apical lobe together as a guide; radix not conspicuous (Fig. 46, 47); Mediterranean (Map 1) ..... *Polenecia*

13(11). Radix a thin, broad sclerite, bifurcate at its tip and not surrounding embolus (Plate 3-A, B); PME at least twice as far from one another as from PLE (Fig. 41); total length about 1.4 mm; southern Mexico through Central America (Map 1) ..... *Ariston*

– Radix a large, coiled sclerite whose grooved inner surface holds the embolus (Plate 3-C, D; Figs. 68, 69); PME 1.0 to 1.5 times as far from one another as from the PLE (Fig. 72); total length about 2.7 mm; southwestern United States and central Mexico (Map 1) ..... *Siratoba*

Generic Key for Uloborid Females

1. Abdomen with a prominent posterior projection extending beyond spinnerets (Figs. 51, 102, 116) 2

– Abdomen without such a posterior projection (Figs. 15, 24, 56, 74, 122, 197) 3

2(1). Posterior lateral eyes (PLE) near carapace border on prominent lateral tubercles (Figs. 100, 115); anterior eye row recurved when viewed dorsally; epigynum without a midventral posterior projection (Figs. 105, 112, 117); Chile (Map 1) ..... *Sybota*

– PLE not near carapace border and not on lateral tubercles (Fig. 50); anterior eye row procurved when viewed dorsally; epigynum with a midventral posterior projection (Figs. 52, 53); Mediterranean (Map 1) ..... *Polenecia*

3(1). Anterior eyes lacking (Fig. 78); endites and labium at least 1.5 times as long as wide (Figs. 81, 92); cosmotropical ..... *Miagrammopes*

– Anterior eyes present, although anterior lateral eyes (ALE) may be reduced; length of endites and labium 1.3 or less their width (Fig. 164) 4

4(3). ALE reduced, represented only by dark pigment spots (Fig. 13); genital area when viewed ventrally a low, weakly sclerotized mound (Fig. 16); South Pacific islands (Map 1) ..... *Tangaroa*

– ALE present; genital area either weakly sclerotized with a central peak and a posteromedian groove (Fig. 30) or distinctly modified and (usually) well sclerotized (Figs. 32, 59, 65, 169, 178, 198, 208, 236) 5

5(4). Posterior lateral eyes (PLE) on distinct lateral tubercles (Figs. 23, 55, 121) 6

– PLE not on distinct lateral tubercles (Figs. 72, 175, 186, 192) 8

6(5). Anterior half of carapace conspicuously narrower that posterior half (Fig. 55); anterior eye row straight; median ocular area's anterior border one-fourth the width of its posterior border; length of first femur less than that of carapace; Holarctic; Oriental (Map 1) ..... *Hyptiotes*

– Carapace oval or pear-shaped (Figs. 23, 121); anterior eye row recurved; median

ocular area's anterior border three-fifths to five-sixths as wide as its posterior border; length of first femur at least 1.4 that of carapace 7

7(6). Anterior eye row recurved such that a line across the anterior median eyes' (AMEs') posterior margins passes along the ALEs' anterior border (Fig. 23); in dorsal view the clypeus does not project anteriorly; abdomen rounded in lateral view (Fig. 24); genital area a weakly sclerotized mound with a central peak and a posteromedian notch (Fig. 30); New Zealand (Map 1) ..... *Waitkera*

– Anterior eye row recurved such that a line across the AMEs' posterior margins passes through the anterior third of ALE (Fig. 121); in dorsal view the clypeus extends anteriorly a distance equal to one AME diameter; abdomen peaked in lateral view (Fig. 122); epigynum well sclerotized, flattened, and with a posterior indentation (Figs. 123, 126); western South America (Map 1) ..... *Orinomana*

8(4). Epigynum with a pair of posterolateral lobes (Figs. 137, 154, 178, 184, 198) 9

– Epigynum with one or more ventral atria (Figs. 160, 189, 208, 239, 250) or with a posteriorly directed median projection (Figs. 32, 36, 43, 65, 75) 12

9(8). Posterior eye row recurved such that a line across the posterior median eyes' (PMEs') posterior margins passes along or anterior to the PLEs' anterior margins (Figs. 132, 175); posterior epigynal lobes slender and their bases contiguous (Figs. 137, 154, 178, 184) 10

– Posterior eye recurved so that such a line passes through the center of the PLEs (Figs. 162, 192); posterior epigynal lobes broad and their bases separated by a distance equal to the width of each (Figs. 169–171, 198, 199) 11

10(9). Posterior eye row recurved such that a line across the PMEs' posterior margins passes along the PLEs' anterior margins (Fig. 175); width of cephalic region at the ALEs two-thirds the maximum carapace width (Fig. 175); median ocular area's anterior width and length 0.7 its posterior width; epigynum's posterior surface with a conspicuous atrium or pair of lateral atria (Figs. 179, 185); United States and China and adjacent Pacific islands (Map 1) ..... *Octonoba*

– Posterior eye row recurved so that such a line passes anterior to the PLEs by a distance equal to at least one-fourth a PLE diameter (Figs. 132, 148); cephalic region at ALE half the carapace width; median ocular area square; epigynum's posterior surface without conspicuous atria (Figs. 138, 146); cosmopolitan ..... *Uloborus*

11(9). Epigynum with two low, rounded posterolateral mounds anterior to which the openings are found (Figs. 198, 199); total length less than 4 mm, southeastern South America (Map 1) ..... *Ponella*

– Epigynum with two flattened, ventrally or posteriorly directed lobes whose ventrolateral surfaces each bear a triangular sclerite and whose posterior surfaces form lateral atria in which openings are found (Figs. 169–171); total length greater than 6 mm; cosmotropical ..... *Zosis*

12(8). Epigynum with a single median, ventral atrium (Figs. 32, 36, 43, 65, 75, 208, 239, 250, 266, 275) 13

– Epigynum with two or more atrial divisions (Figs. 160, 189) 15

13(12). Epigynum with a ventral atrium (Figs. 208, 239, 250, 266, 275); total length 2.9 mm or greater; posterior eyes about equally spaced (Figs. 216, 260); cosmotropical ..... *Philoponella*

– Epigynum with a ventromedian projection extending over a posterior atrium (Figs. 32, 43, 65, 75) or if median projection is less distinct (Fig. 36) total length 2.5 mm or less and PME three times as far from one another as from PLE (Figs. 40, 41) 14

14(13). Carapace length and width equal (Fig. 41); PME 2.5 to 3.0 times further from one another than from PLE (Figs. 40, 41); clypeus height in anterior view half or less an AME diameter; total length less than 2.5 mm; epigynum without a distinct posterior plate (Figs. 33, 37, 44); southern Mexico through Central America (Map 1) ..... *Ariston*

– Carapace 0.8 times as wide as long (Fig. 72); posterior eyes about equally spaced (Figs. 71, 72); clypeus height 0.8 to 1.0 AME diameter, total length 3.0 mm or greater; epigynum with a distinct posterior plate (Figs. 66, 76); southwestern United States and central Mexico (Map 1) ..... *Siratoba*

15(12). Epigynum with two lateral atria (Fig. 189); median ocular area's anterior width half its posterior width (Fig. 186); carapace three-fourths as wide as long; total length 4.0 to 4.6 mm; Australia and Pacific islands (Map 1) ..... *Daramuliana*

– Epigynum with an anterior and posterior median atrium, each divided by a median septum, and a pair of anterior and posterior lateral atria (Fig. 160); median ocular area nearly square (Fig. 159); carapace width and length equal; total length about 3.0 mm; Pacific islands (Map 1) ..... *Purumitra*

Tangaroa Lehtinen
Figures 13–22, Map 1

Tangaroa Lehtinen, 1967, Ann. Zool. Fennici, 4: 199–468. Type species by original designation *Uloborus tahitiensis* Berland, 1934, Ann. Soc. ent. France, 103: 321–336. Male holotype and 3 female paratypes in Muséum National d'Histoire Naturelle, Paris, examined. The genus name is feminine.

Diagnosis. Males and females are distinguished from those of all other genera by lack of ALE (Figs. 13, 14). Males also differ from those of other genera by presence of: 1. AME on an anterior projection (Fig. 14), 2. a distal crook in femur I (Fig. 21), and 3. a palpus with a folded cymbial tip and only a flattened embolus (Fig. 19). Females are also differentiated by weakly sclerotized genitalia in the form of a low mound (Figs. 16, 17).

Description of Type Species. Total length of female 4.6 to 5.6 mm. Carapace 0.85 times as wide as long. In lateral view cephalic region rises slightly from shallow thoracic depression to PME. In females it then slopes downward and in males upward to AME. Thoracic region slopes gradually to the petiole. Male and female ALE absent, represented only by darkly pigmented areas (Figs. 13, 14). At AME carapace width 0.35 its maximum width. Male AME on conspicuous, anterodorsal projection (Fig. 14). Posterior eye row recurved such that line across posterior margins of PME passes anterior to PLE. Median ocular area in females nearly square (slightly wider than long) (Fig. 13) and in males trapezoidal, anterior edge slightly wider than posterior edge and length slightly less than posterior width (Fig. 14). In anterior view clypeus height of females equal to AME diameter and of males 2.0 to 2.5 times AME diameter. Female sternum two-thirds and male sternum four-fifths as wide as long. Female palpal femur laterally flattened and calamistrum one-third as long as metatarsus IV. Female first femur 2.1 times and male first femur 1.9 times carapace length. Male first femur bears four dorsal, four prolateral, and three retrolateral macrosetae. Tibia I bears seven dorsal, eight ventral, five prolateral, and five retrolateral macrosetae. Distal third of the male first tibia forms a crook whose concave ventral surface bears stout macrosetae at its posterior margin (Fig. 21). Abdomen width and height about half its length (Fig. 15). Two stout tracheal trunks extend into cephalothorax.

Male palpus. Endite with a small, lateral stridulatory file just dorsal to serrate edge (Fig. 19). Two macrosetae on distal, median surface of cymbium serve as picks. Femur lacks ventral tubercles. Cymbium large, its broad distal portion folded laterally, apparently serving as guide for embolus. Within this broad fold and near the embolus' base is a dark, oval region which close examination shows to be part of the heavily sclerotized sperm duct and not a median apophysis (Fig. 19, 20). No middle hematodocha is present. Unlike other uloborids, the embolus is flattened and is not closely associated with a guide.

Genital Region. In ventral view this region appears as a lightly sclerotized, convex shield (Fig. 16). In posterior view its central, unsclerotized region has two median openings (Fig. 17), each leading to a pair of lobed spermathecae (Fig. 18). No fertilization duct leads from either spermatheca.

Natural History and Distribution. In

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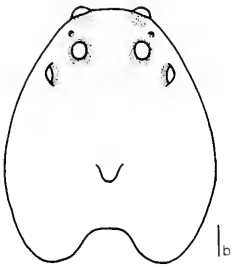
Figures 13–22. *Tangaroa tahitiensis* (Berland). 13. Dorsal view of female carapace. 14. Dorsal view of male carapace. 15. Lateral view of female abdomen. 16. Ventral view of female genitalia. 17. Posterior view of female genitalia. 18. Dorsal view of cleared female genitalia. 19. Retrolateral view of left male palpus. 20. Retrolateral view of embolus (black), sperm reservoir, and fundus. 21. Prolateral view of male left, first femur, patella, and tibia. 22. Dorsal view of female right first femur showing trichobothria. Figures 23–27. *Waitkera waitkerensis* (Chamberlain). 23. Dorsal view of female carapace. 24. Lateral view of female abdomen. 25. Lateral view of female carapace. 26. Dorsal view of female right first femur. 27. Prolateral view of male left first femur, patella, and tibia.



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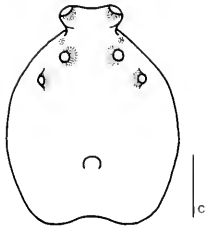

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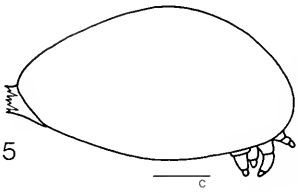

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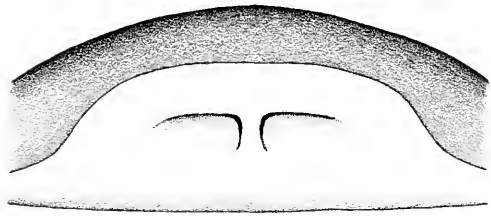

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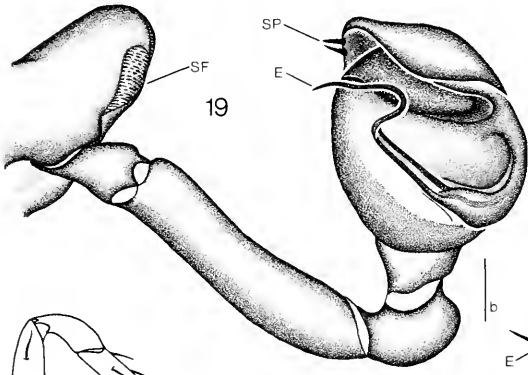

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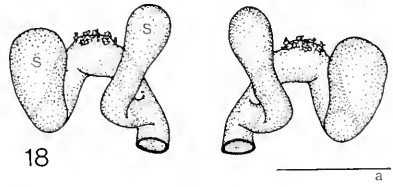

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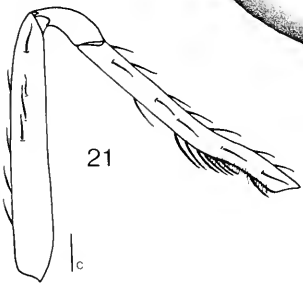

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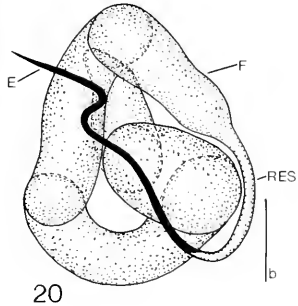

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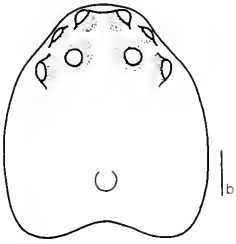

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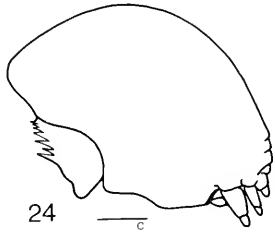

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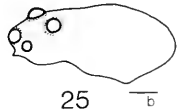

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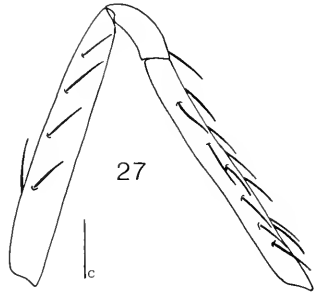

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addition to the type species found on Tahiti in the Society Islands and Rapa in the Tubuai Islands, this genus contains *Tangaroa* (*Uloborus*) *dissimila* (Berland, 1924), found on New Caledonia and the New Hebrides island of Epi (Map 1). Webs of neither species are known.

Waitkera new genus
Figures 23–31, Map 1

Tangaroa [part]:—Lehtinen, 1967, Ann. Zool. Fennici, 4: 199–468.

Type. Type species *Uloborus waitkerensis* Chamberlain, 1946, Rec. Auckland Inst. Mus., 3(2): 85–97. Female holotype and three paratypes from Watershed Reservoir, Waitker Hills, Auckland, New Zealand collected by G. Chamberlain. Holotype and one paratype in G. Chamberlain collection, two paratypes in Auckland Museum. The genus name is feminine and is derived from the locality of the type species.

Diagnosis. Like *Sybota* and *Orinomana*, *Waitkera* females have PLE on distinct lateral tubercles (Fig. 23). Unlike *Sybota* (Figs. 102, 114, 116) the abdomen of *Waitkera* (Fig. 24) does not have a prominent posterior extension and unlike *Orinomana* (Figs. 120, 122), it is not peaked. Posterior eye row of *Waitkera* males and females only slightly recurved such that a line across PMEs' posterior margins passes through PLEs' centers (Fig. 23). In *Sybota* (Figs. 100, 115) and *Orinomana* (Fig. 121) (males of the latter are unknown) such a line passes along PLEs' anterior borders or through anterior one-fourth of their diameters. First femur of *Waitkera* males and females twice as long as carapace, in *Sybota* and *Orinomana* 1.3 to 1.7 times carapace length. Genitalic region of *Waitkera* females (Fig. 30) a weakly sclerotized mound, that of *Sybota* (Figs. 105, 112, 117) and *Orinomana* (Figs. 123, 126) well sclerotized. Male palpus of *Waitkera* (Figs. 28, 29) has flattened, pointed median apophysis serving as embolus guide; prominent radix, and three short, stout marginal cymbial macrosetae. Palpus of *Sybota* (Plate 6-A, B) has well-developed conductor, two- or three-pronged median apophysis, and lacks radix.

Description. Male total length 2.9 mm, carapace length 1.1 mm, and sternum length 0.7 mm. Female total length 3.5 mm, carapace length 1.1 mm, and sternum length 0.7 mm. Carapace width equal to length. Cephalic region rises slightly from thoracic depression and thoracic region slopes gradually to petiole (Fig. 25). At ALE cephalic region three-fifths carapace width (Fig. 23). Both eye rows recurved, posterior such that a line across posterior margins of PME passes through center of PLE. Lateral eyes on slightly raised tubercles. Median ocular area five-sixths as wide anteriorly as posteriorly and as long as its anterior width. Clypeus height in anterior view equal to one AME diameter. Sternum 0.64 as wide as long in females and 0.71 in males. Female palpal femur not laterally compressed. Female first femur 1.9 times carapace length, male first femur 2.1 times carapace length. Female calamistrum half as long as metatarsus IV. Male first femur with two dorsal, four prolateral, and three retrolateral macrosetae (Fig. 27). First tibia with six dorsal, six prolateral, and two retrolateral macrosetae. Female abdomen two-thirds as wide and five-sixths as high as long (Fig. 24); maximum width and height attained half way along length. Male abdomen cylindrical, half as wide and high as long. Carapace gray with broad light lateral margins and narrow median stripe extending from thoracic pit through median ocular area. Endites, labium, and sternum gray,

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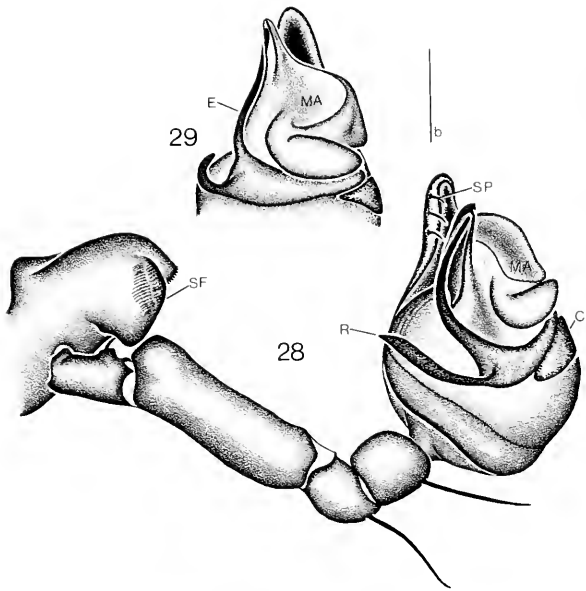
Figures 28–31. *Waitkera waitkerensis* (Chamberlain). 28. Retrolateral view of left male palpus. 29. Dorsolateral view of distal region of left male palpus. 30. Ventral view of female genitalia. 31. Dorsal view of cleared female genitalia. Figures 32–34. *Ariston albicans* (O. Pickard-Cambridge). 32. Ventral view of female genitalia. 33. Posterior view of female genitalia. 34. Dorsal view of cleared female genitalia. 35. Dorsal view of first female femur. Figures 36–38. *Ariston mazolus* n. sp. 36. Ventral view of female genitalia. 37. Posterior view of female genitalia. 38. Dorsal view of cleared female genitalia.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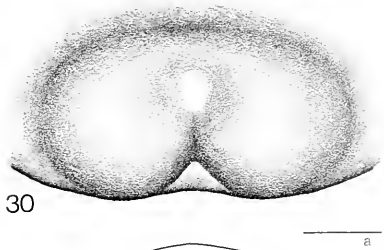
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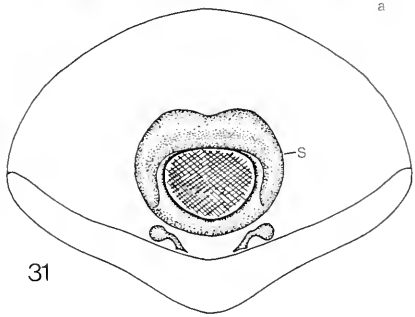
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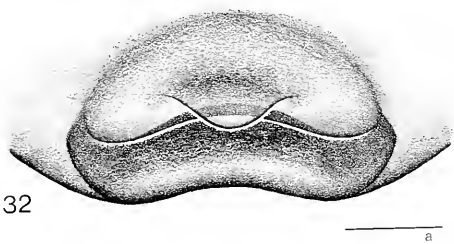
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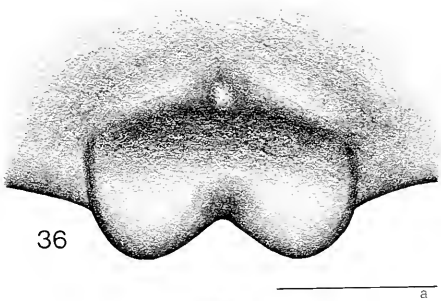
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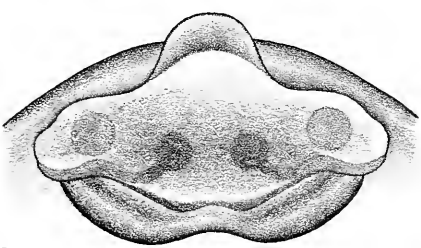
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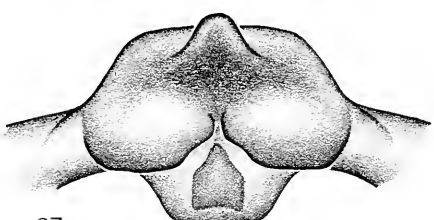
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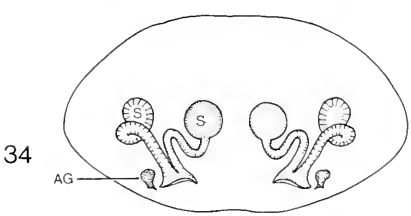
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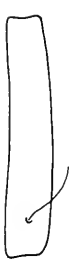
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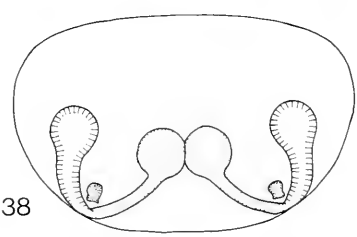
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the latter with narrow white median stripe. Tibiae gray with wide white proximal and median rings. Dorsum of abdomen white with five to six posteromedian gray chevrons. Sides with transverse, light gray stripes. Venter of abdomen gray with white book lung covers, white paraxial stripes just behind epigastric furrow, and three pairs of white spots just anterior to cribellum. Two stout tracheal trunks extend into cephalothorax.

Male Palpus. Lateral lobe on each endite bears stridulatory ridges (Fig. 28). Three stout macrosetae on posterodistal cymbial rim serve as picks. There are no ventral femoral tubercles or middle hematodocha. Short, curved embolus lies in trough on posterolateral face of flat, distal median apophysis lobe (Figs. 28, 29). Smaller, proximal median apophysis lobe lies between distal lobe and embolus base.

Female Genitalia. Genitalic area not heavily sclerotized (Fig. 30), consisting of ventral mound with central peak and posterior notch. Chamberlain (1946) describes an epigynal opening at each dorsal margin of this notch, but these appear to be openings of small, blind lateral bulbs (Fig. 31). Large, blind, spherical, median spermatheca opens only into the vagina through broad, hood-shaped opening. Implications of this haplogyne (*sensus* Wiehle, 1967) condition are discussed under phylogeny.

Natural History and Distribution. The single known species in this genus constructs small orb-webs among shrubs and grass (Forster, 1967) and is known only from New Zealand (Map 1).

Ariston O. Pickard-Cambridge
Figures 32–45, Plate 3-A, B; Map 1

Ariston O. Pickard-Cambridge, 1896, Bio. Cent.-Amer., Zool., Arachnida, 1: 161–224. Type species by monotype *Ariston albicans* O. Pickard-Cambridge, 1896, *ibid.* The generic name is masculine.

Note. The small, generalized uloborids which have been placed in *Ariston* appear to form two distinct genera, separated by differences in eye arrangement and features of male and female genitalia. In addition to *A. albicans* the now-restricted genus *Ariston* contains two new species, *A. aristus* and *A. mazolus*. *Ariston referens* and a new species have been placed into the new genus *Siratoba*.

Diagnosis. *Ariston* is the only known uloborid genus with mature females having a total length of less than 2.5 mm and, besides *Siratoba* (Figs. 65, 75), the only American genus whose members have a posterior epigynal hood (Figs. 32, 36, 43). In *Ariston* the posterior atrium formed by this hood lacks the prominent posterior plate found in members of *Siratoba* (Figs. 66, 76). *Ariston* is found from southern Mexico through Central America and *Siratoba* has been collected only from southwestern United States and central Mexico. In *Ariston* (as compared with *Siratoba*) females, PMEs separated by a distance at least two (Fig. 41) (in *Siratoba* no more than one-and-one-half, Fig. 72) times that separating AMEs, PME separation two-and-one-half to three (one-and-one-half in *Siratoba*) times that of the PME-PLE separation, PME and PLE mounds are confluent (in *Siratoba* separate) in anterior view, clypeus height equal to or less than half (in *Siratoba* four-fifths to one) AME diameter, carapace length and width about equal (in *Siratoba* carapace 0.80 as wide as long), first femur 1.8–2.0 (in *Siratoba* 1.5) times carapace length, and abdomen oval (Figs. 40, 42) (in *Siratoba* with middle peak, Figs. 71, 74), three-fourths (in *Siratoba* half) as wide and three-fourths as high as long. The only known males

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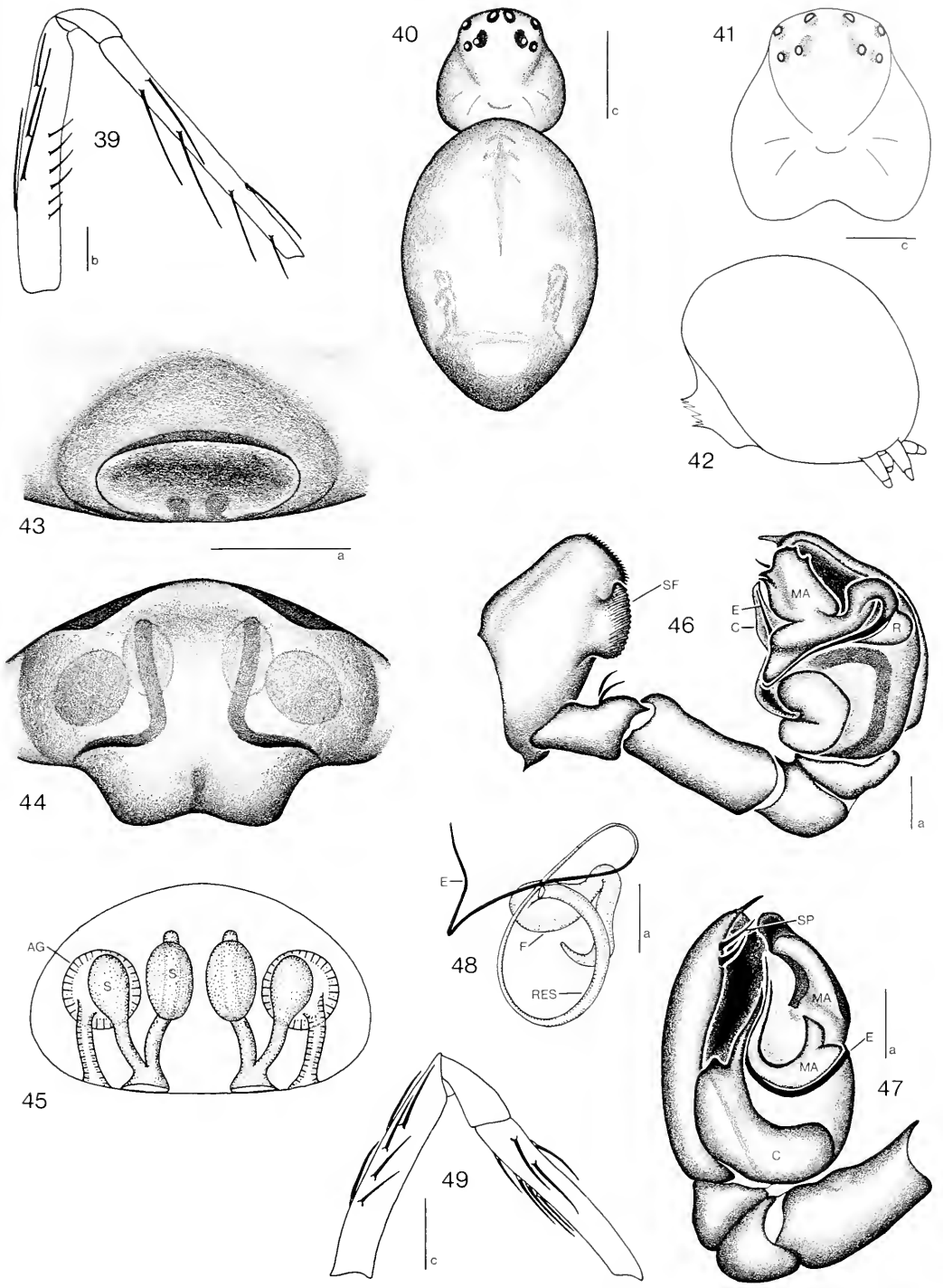
Figure 39. *Ariston mazolus* n. sp., prolateral view of male left first femur, patella, and tibia. Figures 40–45. *Ariston aristus* n. sp. 40. Dorsal view of female. 41. Female carapace. 42. Lateral view of female abdomen. 43. Ventral view of female genitalia. 44. Posterior view of female genitalia. 45. Dorsal view of cleared female genitalia. Figures 46–49.



Polenecia producta (Simon). 46. Retrolateral view of left male palpus. 47. Prolateral view of left male palpus. 48. Retrolateral view of embolus (black), sperm reservoir, and fundus. 49. Prolateral view of male, left, first femur, patella and tibia.

belong to *A. mazolus* and are distinguished as the smallest adult male uloborids known (total length less than 1.4 mm) and the only known uloborid males to have a series of six ventroprolateral macrosetae on femur I (Fig. 39), a bifurcate radix (Plate 3-A, B), and a short, flat embolus with a blunt tip.

Description. Carapace width and length equal. Cephalic region rises slightly from shallow thoracic depression, at level of ALE is about 0.6 carapace width. Both eye rows about equally recurved such that a line across posterior margin of median eyes passes along anterior margin of lateral eyes (Fig. 41). Median ocular area about as wide anteriorly as posteriorly and about four-fifths as long as its anterior width. In anterior view, clypeus height of females half or less AME diameter and in males one-and-one-half times AME diameter. Sternum width about 0.68 length. Female palpal femur laterally flattened. Female first femur about 1.8–2.0 times carapace length. Female calamistrum half the length of metatarsus IV. Male first femur with six ventroprolateral, three dorsoprolateral, one dorsoproximal, and three retrolateral macrosetae (Fig. 39). Male first tibia has one prolateral, three retrolateral, one or two dorsal, and four ventral macrosetae. Female abdomen oval, height and width three-fourths length (Figs. 40, 42). Male abdomen cylindrical with diameter half its length. A pair of stout tracheal trunks extends into cephalothorax.

Male Palpus. Palpal femur lacks ventral tubercles and tarsus has an apparently reduced middle hematodocha. Median apophysis a heavily sclerotized, elongate projection with foot-shaped terminus that appears to support the short, broad, blunt embolus (Plate 3-A, B). Flat, curved radix arises proximal to embolus and terminates in two pointed prongs. Conductor arises between bases of median apophysis and radix and extends between distal portions of these sclerites.

Female Genitalia. A posteroventral hood of various widths (Figs. 32, 36, 43) extends over dorsal atrium in which openings are found (Figs. 33, 37, 44). Each opening leads to a pair of apparently blind spermathecae, the lateral pair usually having thicker walls than the median pair (Figs. 34, 38, 45). Lateral to spermathecal ducts is a pair of small (*A. albicans* and *A. mazolus*, Figs. 34 and 38, respectively) or large (*A. aristus*, Fig. 45) accessory glands which appear to have separate openings and to be homologous with those of *Waitkera*, *Polenecia*, *Hyptiotes*, and *Siratoba*.

Natural History and Distribution. The three species in this genus are found from southern Mexico through Central America (Map 1). Nothing is known of their web structure.

KEY TO *ARISTON* FEMALES
(Males are known only for *A. mazolus*)

1. Genitalia with a thin, anterior, overhanging rim about three-fourths as wide as the raised genital area; in ventral view posterior genital margin rounded (Fig. 43); Panama ---------- *aristus*
– Genitalia with a prominent median projection about one-fourth to one-third its width and forming a hood; in ventral view posterior genital margin indented (Figs. 32, 36); southern Mexico to Honduras ---------- 2
2(1). Genital hood one-third the genital region's width; in ventral view this region's posterior margin has a slight median depression (Fig. 32) as does its dorsal margin when viewed posteriorly (Fig. 33); clypeus height one-fourth or less the AME diameter; southeastern Mexico and Honduras ------ *albicans*
– Genital hood one-fourth the genital region's width; in ventral view this region's posterior margin has two lateral lobes separated by a deep median depression (Fig. 36) and in posterior view these lobes are separated by a deep notch (Fig. 37); clypeus height half or less the AME diameter; southwestern Mexico ---------- *mazolus*

Ariston albicans O. Pickard-Cambridge
Figures 32–35

Ariston albicans O. Pickard-Cambridge, 1896, Bio. Cent.-Amer., Zool., Arachnida, 1: 161–224. Three female syntypes from Teapa in the Mexican state of Tabasco, collected by H. H. Smith, in the British Museum (Natural History), examined.

Diagnosis. *Ariston albicans* females are distinguished from those of *A. aristus* by having a genital hood which is one-third (Figs. 32, 33) rather than three-fourths (Figs. 43, 44) the genital area's width, by this hood forming a prominent posteroventral projection rather than a thin anterior margin of a broad atrium, and by having an indented rather than rounded posterior genital margin when viewed ventrally. Accessory glands are one-third (Fig. 34) rather than one-and-one-half (Fig. 45) a spermathecal diameter. *Ariston albicans* females differ from those of *A. mazolus* by having a genital hood which is one-third (Fig. 32) rather than one-fourth (Fig. 36) the genital area's width and by having shallow rather than deep posterior and dorsal epigynal indentations when viewed ventrally (Figs. 32, 36) and posteriorly (Figs. 33, 37) respectively. Spermathecal ducts are looped (Fig. 34) rather than straight (Figs. 38, 45).

Description. Only females are known. Total length 2.1 to 2.2 mm, carapace length 0.7 mm, sternum length 0.5 mm. Clypeus height one-tenth to one-fourth AME diameter. Coloration similar to that of *A. aristus* (Fig. 40). Carapace, sternum and legs light tan. Dorsum of abdomen white, with tan median cardiac region; broad, posterior tan paraxial stripes and a pair of tan spots just posterior to abdomen's center. From the center of the genitalia's ventral surface a narrow, flat, dorsally concave hood projects posteriorly (Fig. 32). In ventral view (Fig. 32) genital area's posterior edge slightly emarginate. In posterior view (Fig. 33) genitalia's broad, central region is concave and its dorsal edge bordered by a thin, heavily sclerotized, medially emarginate rim. A genital opening is found at each ventrolateral margin of this dorsal rim and leads to a short bursa from which a pair of looped ducts originates. Each duct connects to an apparently blind spermatheca, the lateral one having thicker walls than the median one (Fig. 34). Lateral to the bursae is a pair of small, blind accessory glands.

Distribution. Southeastern Mexico and Honduras.

Ariston mazolus n. sp.
Figures 36–39, Plate 3-A, B

Types. Female holotype and three male paratypes from Miramar, Manzanillo in the Mexican state of Colima, collected on 15 January 1943 by F. Bonet, in the American Museum of Natural History. The specific epithet is an arbitrary combination of letters.

Diagnosis. The only known males of *Ariston* belong to this species and are diagnosed in the generic treatment. Females are distinguished from those of *A. aristus* by having a median genital projection which is one-fourth (Fig. 36) rather than three-fourths (Fig. 43) the genital area's width and by having an indented rather than smooth posterior genital margin when viewed ventrally. Accessory glands one-third (Fig. 38) rather than one-and-one-half (Fig. 45) spermathecal diameter. *Ariston mazolus* females differ from those of *A. albicans* by having a genital hood one-fourth (Fig. 36) rather than one-third (Fig. 32) the genital area's width, by having deep rather than shallow posterior and dorsal genital indentations when viewed ventrally (Fig. 36) and posteriorly (Fig. 37) respectively. Spermathecal ducts straight (Fig. 38) rather than looped (Fig. 34).

Description. Male. Total length 1.4 mm, carapace length 0.6 to 0.7 mm, sternum length 0.4 mm. Carapace, sternum, and legs tan. Abdomen with white dorsum and gray venter. Other features of the male given in the genus description.

Female. Total length 2.0 mm, carapace length 0.6 mm, sternum length 0.4 mm. Clypeus height half AME diameter. Coloration similar to that of males. Genitalia's anteroventral region forms a rounded ridge with an abrupt narrow median projection whose posterior surface is concave (Fig. 37). In posterior view a pair of lateral lobes separated by a deep

median notch is found dorsal to this projection (Fig. 37). Dorsal to these lobes is a median lobe with a more heavily sclerotized central region. A genital opening located dorsolateral to each lateral lobe leads via two ducts to a thick-walled lateral and a thin-walled median spermatheca (Fig. 38). Near the bifurcation of these ducts a small accessory gland is found.

Distribution. Known only from the type locality in southwestern Mexico.

Ariston aristus n. sp.
Figures 40–45

Types. Female holotype and paratype from Barro Colorado Island, Panama Canal Zone. Holotype collected August 1939 by A. M. Chickering, paratype 20–24 June by N. Banks, both in the Museum of Comparative Zoology. The specific epithet is an arbitrary combination of letters.

Diagnosis. Females are distinguished by a broad, posteroventral genital atrium bordered anteriorly by a narrow rim three-fourths the genital area's width (Fig. 43). In ventral view (Fig. 44) genitalia's posterior edge gently rounded and not emarginate as in other two species. Accessory glands of *A. aristus* one-and-one-half the spermathecal diameter (Fig. 45) rather than one-third the diameter as in the other two species (Figs. 34, 38).

Description. Only females are known. Total length 2.3 to 2.5 mm, carapace length 0.7 to 0.8 mm, sternum length 0.5 mm. Clypeus height half AME diameter. Coloration (Fig. 40) similar to that of *A. albicans*. A thin, broad anterior rim on the genital area's ventral surface borders a broad, shallow atrium (Fig. 43). In posterior view (Fig. 44) genital area's ventral surface concave, its dorsal surface convex, and its median dorsal margin with two dorsal lobes separated by a shallow depression. An opening located lateral to the base of each lobe connects to a short bursa giving rise to two straight ducts, each leading to an apparently blind spermatheca (Fig. 45). A large accessory gland lies ventral to each lateral spermatheca and opens externally via a separate duct.

Distribution. Known only from the type locality in Panama.

Polenecia Lehtinen
Figures 46–54, Map 1

Sybota [part]:—Simon, 1892, Histoire Naturelle des Araignées, 1(1): 1–256. Paris.

Polenecia Lehtinen, 1967, Ann. Zool. Fennici, 4: 199–468. Type species by original designation and monotypy *Uloborus productus* Simon, 1873, Mém. Soc. roy. sci. Liège, 2(5): 1–174. Seven mature and one immature female syntypes (No. AR-150) from Corsica, in Muséum National d'Histoire Naturelle, Paris, examined. The genus name is feminine.

Diagnosis. *Polenecia* and *Sybota* females are the only uloborids to have an abdomen with a prominent posterior projection (Figs. 51, 102, 114, 116). *Polenecia* males and females lack PLE tubercles (Fig. 50) like those found in male and female *Sybota* (Figs. 100, 103, 115) and are distinguished by being the only uloborids to have a procurved anterior eye row (Fig. 50). Males are characterized by a palpus (Figs. 46, 47) with: 1. a thin cymbial projection and two short, marginal cymbial macrosetae, 2. a broad conductor with a long, thin medial projection which, along with a thin proximal median apophysis extension, serves as an embolus guide, and 3. a lateral endite lobe which bears stridulatory ridges. *Polenecia* females, unlike *Sybota* females, have a posteriorly directed, midventral genital extension (Fig. 52).

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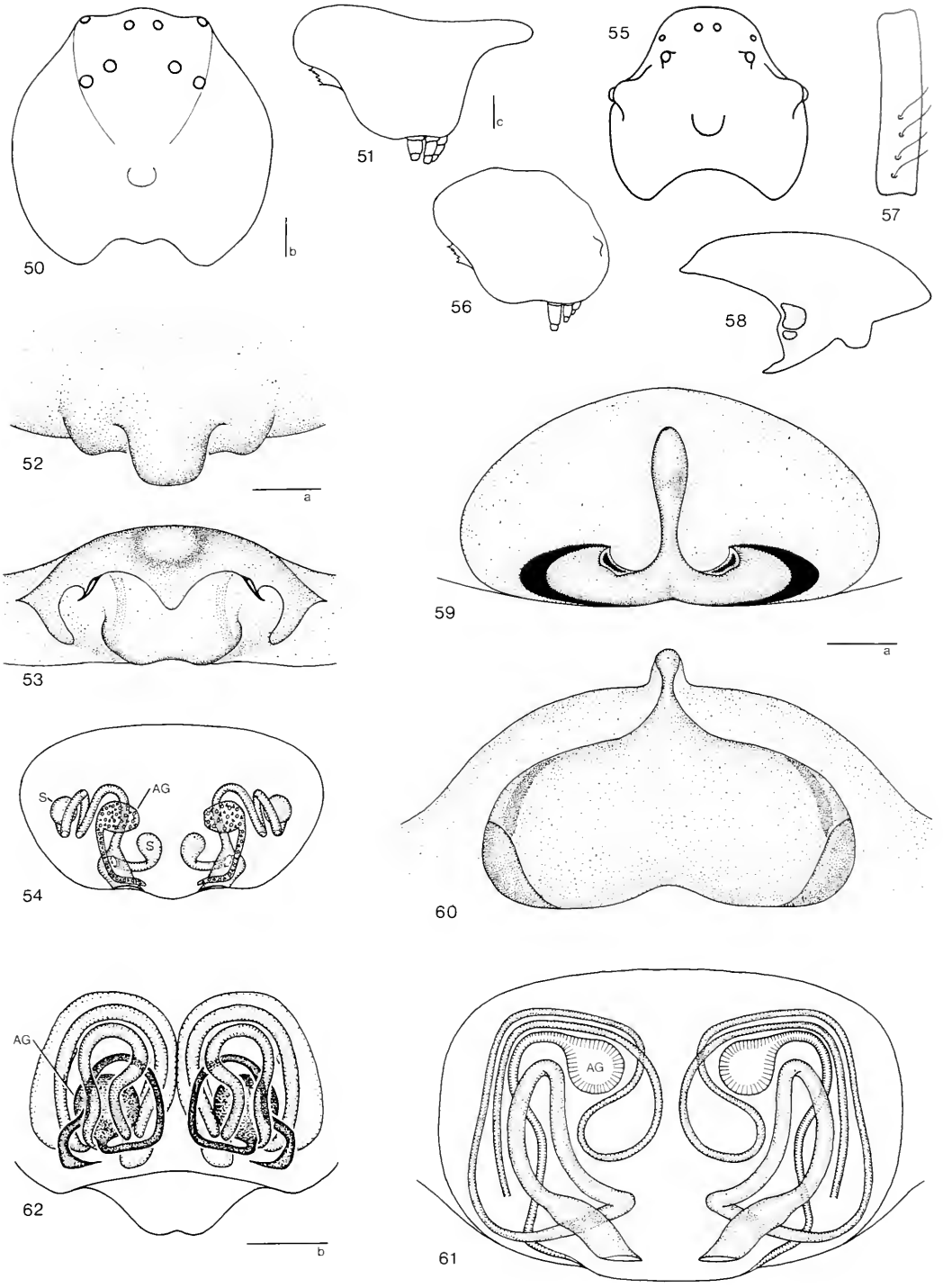
Figures 50–54. *Polenecia producta* (Simon). 50. Female carapace. 51. Lateral view of female abdomen. 52. Ventral view of female genitalia. 53. Posterior view of female genitalia. 54. Dorsal view of cleared female genitalia. Figures 55–61. *Hyptiotes cavatus* (Hentz). 55. Female carapace. 56. Lateral view of female abdomen. 57. Dorsal view of female, right, first femur. 58. Retrolateral view of female left first patella showing position of lyriform organs. 59. Ventral view of epigynum. 60. Posterior view of epigynum. 61. Dorsal view of cleared epigynum. Figure 62. *Hyptiotes paradoxus* C. Koch, dorsal view of cleared epigynum.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Description of Type Species. Female total length 3.8 mm, carapace length 1.2 mm, sternum length 0.9 mm. Male total length 2.6 mm, carapace length 1.0 mm, sternum length 0.8 mm. Carapace width and length equal. Cephalic region rises from shallow thoracic depression and at level of ALEs has a width half maximum carapace width. Although raised medially, cephalic region has no conspicuous eye tubercles (Fig. 50). Thoracic region slopes abruptly to petiole. Anterior eye row procurved. Posterior eye row recurved such that a line across posterior margins of PMEs passes along anterior margins of PLEs. In dorsal view anterior extension of the clypeus equal to one AME diameter and in anterior view height one to one-and-one-third AME diameter. Median ocular area's anterior width half and its length two-thirds its posterior length. Female sternum width half and male sternum width 0.6 its length. Prolateral surface of the female palpal femur concave. Female first femur 1.5 and male first femur 1.6 times carapace length. Female calamistrum 0.63 length of metatarsus IV. Male with weakly developed calamistrum two-thirds the length of metatarsus IV. First male femur with two dorsal, four prolateral, and three retrolateral macrosetae (Fig. 49). First male tibia with two separate and four clustered ventral, one dorsal, two prolateral, and two retrolateral macrosetae. Width and height of female abdomen two-thirds length. Prominent median tubercle arises from posterior third of female abdomen and extends posterodorsally for distance equal to one-fourth to one-third the abdomen's length (Fig. 51). Male abdomen cylindrical, compressed dorsoventrally and laterally constricted near center in a manner reminiscent of some casterine clubionids. A dorsomedian mound in the posterior third of male's abdomen bears a tuft of heavy setae. Male and female abdomen white with dense covering of light setae and darkly pigmented around base of spinnerets and booklung area. One male has a dark median, dorsal stripe. Male and female carapace tan with white guanine deposits near thoracic depression and lateral margins of thoracic region. Sternum has gray margins and brown central region. Legs without conspicuous markings. Two stout tracheal trunks extend inot cephalothorax.

Male Palpus. Femur without ventral tubercles and tarsus without middle hematodocha. Median apophysis' distal lobe a flat plate and its proximal lobe a long, flat spur which lies distal to the embolus and conforms to its curvature (Figs. 46, 47). Radix appears as a small lateral plate near embolus base. A broad, flat conductor located at the proximal, median surface of the tarsus has two lobes: a small lateral one and a long, thin, trough-shaped median lobe which, along with the median apophysis' proximal spur, serves as a guide for the embolus.

Female Genitalia. Genitalia a ventral mound with posteromedian lobe one-third the width of raised genital area (Fig. 52). In posterior view (Fig. 53) genital area's broad, weakly sclerotized dorsomedian region bordered ventrally and laterally by well sclerotized M-shaped edge of raised ventral region. An opening is found at each ventrolateral margin of weakly sclerotized median region and leads to a broad bursa giving rise to a small, blind median bulb and a long, coiled, anterior duct leading to a small, spherical, lateral spermatheca (Fig. 54). Fertilization ducts may lead from these anterolateral spermathecae, but none is visible. Dorsal to spermathecal ducts is a pair of large, apparently solid accessory glands whose ducts pass posteriorly, but do not connect with the bursae. These ducts probably have separate external openings as do those of *Waitkera waitkerensis.*

Natural History and Distribution. The only described species, *Polenecia producta,* constructs a circular or semicircular vertical web which lacks capture

spirals and has cribellate silk on the radii and framework threads (Wiehle, 1931). Eggsacs are attached to the twig which forms a central, vertical support for the web. This species is known from Corsica, Spain, Portugal, Algeria, Tunisia, and Syria (Map 1).

Hyptiotes Walckenaer
Figures 55–64, Plate 4-A–D; Map 1

Mithras [preoccupied] C. L. Koch, 1834, Arachniden. *in* Panzer, Faunae Insectorum Germaniae initia, 123: 9. Type species by monotypy *Mithras paradoxus* C. L. Koch, 1834, *ibid.*, disposition of types unknown. Preoccupied by *Mithras* Huebner, 1818, Verz. bekannt. Schmett., 5: 79—Lepidoptera.

Uptiotes Walckenaer, 1837, Histoire naturelle des Insectes, Aptères, 1: 277–279. Type species by monotypy *Uptiotes anceps* Walckenaer, 1837, *ibid.* [= *M. paradoxus* C. L. Koch]. Disposition of type specimens unknown.

Hyptiotes (emendation of *Uptiotes* Walckenaer, 1837, *op. cit.*): Erickson, 1845, Nomina systematica Generum Arachnidarum, p. 14. *in* Agassiz, 1846, Nomen. Zool. Index Univ. pp. 1–14.

Cyllopodia Hentz, 1847, Boston J. Nat. Hist., 5: 466. Type species by monotypy *Cyllopodia cavatus* Hentz, 1847. Female holotype from Alabama, collected in October by Hentz, specimen lost.

Note. The senior synonym *Uptiotes* has not been used in primary literature since 1845 and the emended name *Hyptiotes* has gained universal acceptance. Application is being made to The International Commission on Zoological Nomenclature for suppression of the name *Uptiotes* as an unused senior synonym provisions of amended Article 79 of the International Code of Zoological Nomenclature.

Diagnosis. *Hyptiotes* males and females are distinguished from those of all other genera by having: 1. anterior half of carapace abruptly narrowed to half the width of the posterior half (Fig. 55), 2. straight anterior eye row whose AMEs are three to four diameters from carapace's anterior rim, 3. median ocular area whose anterior width is one-fourth its posterior width, 4. carapace whose posterior half is flat or depressed and in lateral view slopes from petiole to PLEs, and 5. length of female first femur less than carapace length and male first femur equal to carapace length.

Description. Total length of females 2.3 to 5.0 mm, of males 2.0 to 3.0 mm. Carapace width equal to or slightly greater than length. Abdomen extends anteriorly over carapace, nearly reaching level of posterior eye row in many species. Posterior two-thirds of carapace flat or medially depressed and sloping upward from petiole to posterior eye row. The PLEs on conspicuous lateral tubercles and ALEs small and in some specimens difficult to see (Fig. 55). Anterior eye row straight and posterior eye row recurved such that a line along posterior margins of PMEs passes anterior to PLEs by a distance equal to three-fourths to one PLE diameter. Median ocular area's anterior width one-fourth and its length one-third its posterior width. In dorsal view clypeus extends anteriorly a distance equal to four to five AME diameters. Sternum width 0.5 to 0.6 its length. Female palpal femur flattened. Female first femur 0.7 to 0.9 carapace length. Male first femur 0.9 to 1.1 carapace length. Female calamistrum nine-tenths length of metatarsus IV. Males have a weak calamistrum four-fifths the length of metatarsus IV. Male first femur with two prolateral, three to seven retrolateral, and three to four dorsal macrosetae (Fig. 63). Male first tibia with eight to twelve prolateral, two to fifteen retrolateral, three to four dorsal, and zero to seven ventral macrosetae. Numerous stout setae are also present on tibia I of most males. Female abdomen two-thirds as wide and two-fifth to three-fourths as high as long (Fig. 56). Abdomen of many species with four pairs of small, lateral tubercles each bearing a tuft of flat setae. Male abdomen usually more slender and often lacking tubercles. Two stout tracheal trunks extend into cephalothorax.

Male Palpus. Femur lacks proximal, ventral tubercles and tarsus has no mid-

dle hematodocha. Median apophysis spur of American species forms a long, thin, curved extension with a broad, flattened tip (Plate 4-A–D). In Old World species median apophysis is a short, broad projection. Proximal portion of median apophysis flattened, expanded, and covering most of tarsus' proximal lateral surface. This flattened terminus lies in a groove of the large, flat conductor and with this sclerite serves as a guide for a long, thin embolus which makes one-and-one-half loops before terminating near median apophysis spur (Fig. 64). Between the grooved conductor terminus and median apophysis spur's base is a small, projecting sclerite that appears to be a conductor branch.

Epigynum. Epigynum's posterior face formed by a broad, sclerotized plate with a narrow ventromedian extension continuing onto the epigynum's ventral surface where it lies on a raised median ridge and terminates in a prominent tubercle (Figs. 59, 60). Epigynal openings lateral to this extension's base, each leading via a broad bursa to a long, coiled duct that presumably connects to the vagina (Figs. 61, 62). Among the coils of each duct is a thick-walled accessory gland (mistaken by Muma and Gertsch, 1964, for a spermatheca) whose long, thin duct appears to open at the epigynum's posterior margin independently of the epigynal openings. In Old World species (Fig. 62) the bursae are longer and the accessory glands larger and more posteriorly situated than in American species (Fig. 61).

Natural History and Distribution. Members of this genus construct a vertical, sectoral web consisting of four "radii," as discussed more fully under Natural History. This genus is represented in North America, Europe, Japan, and, according to Muma and Gertsch (1964), India and Ceylon (Map 1).

Siratoba new genus
Figures 65–77, Plate 3-C, D; Map 1

Type. The type species of *Siratoba* is *Ariston referens* Muma and Gertsch, 1964, Amer. Mus. Novitates, 2196: 17. The genus name is an arbitrary combination of letters and is feminine.

Diagnosis. *Siratoba* and *Ariston* are the only American genera whose female members have posterior genital hoods. Female *Siratoba* have a total length of 3.0 mm or more and have a prominent posterior plate in a genital atrium formed by the ventral hood (Figs. 66, 76); whereas, members of *Ariston* have a total length of less than 2.6 mm and lack such a plate (Figs. 33, 37, 44). *Siratoba* has been collected only from the southwestern United States and northern and central Mexico. *Ariston's* range extends from southern Mexico through Central America. *Siratoba* females are distinguished by having: 1. PMEs separated by a distance no more than one-and-one-half times that separating AMEs (Fig. 72), 2. PME separation one-and-one-half times that of the PME-PLE separation, 3. PME and PLE mounds separate in anterior view, and 4. abdomen with a middle peak (Figs. 71, 74). The only known males belong to *S. referena* and are distinguished by having a total length of about 2.7 mm and a conspicuous, coiled radix with a central groove in which the embolus lies (Figs. 68, 69; Plate 3-C, D).

Description. Carapace width 0.80 length. Cephalic region rises slightly from shallow thoracic depression and at level of ALE is about 0.70 carapace width. Both eye rows about equally recurved such that a line across posterior

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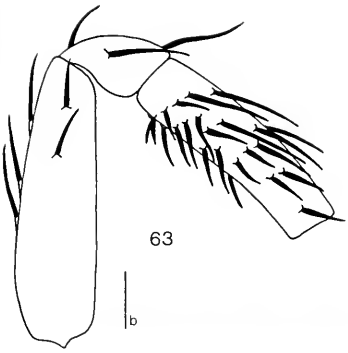
Figures 63–64. *Hyptiotes cavatus* (Hentz). 63. Prolateral view of male, left, first femur, patella, and tibia. 64. Retrolateral view of embolus (black), sperm reservoir, and fundus. Figures 65–74. *Siratoba referena* (Muma and Gertsch). 65. Ventral view of epigynum. 66. Posterior view of epigynum. 67. Dorsal view of cleared epigynum. 68. Apical view of left male palpus. 69. Retrolateral view of left male palpus. 70. Prolateral view of male, left, first femur, patella, and tibia. 71. Dorsal view of female. 72. Female carapace. 73. Dorsal view of female right first femur. 74. Lateral view of female abdomen.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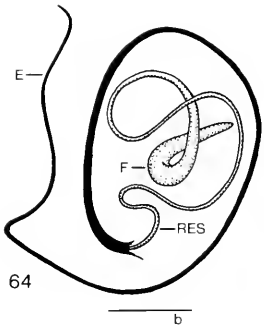
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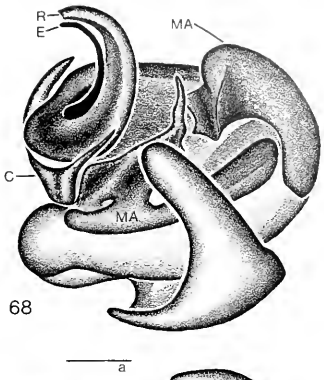
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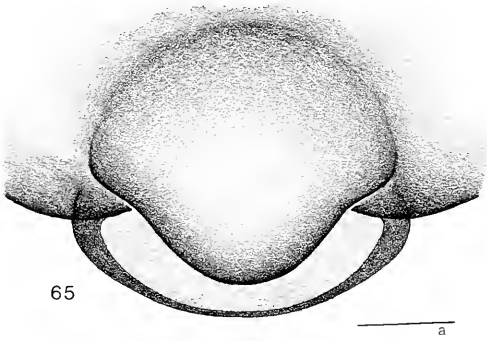
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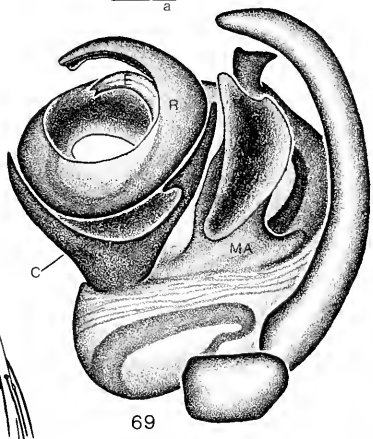
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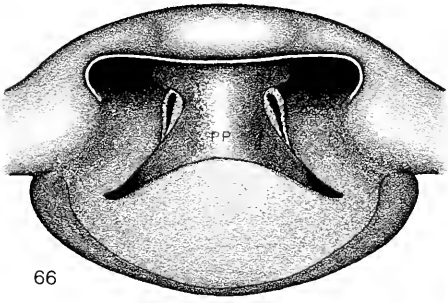
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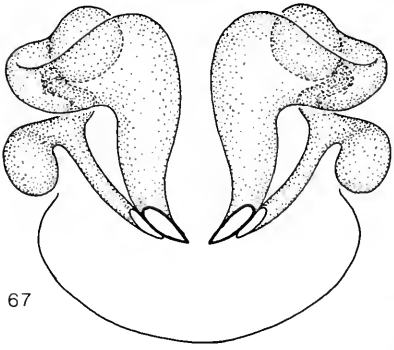
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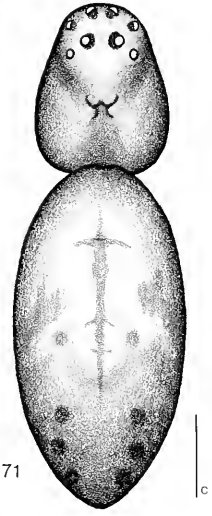
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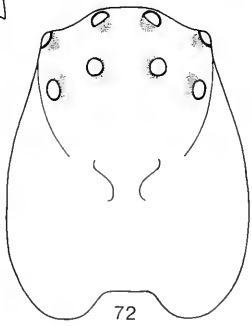
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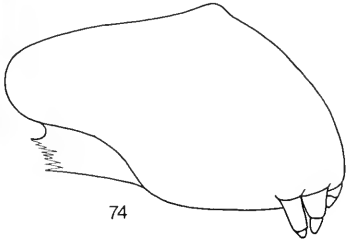
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margins of median eyes passes along anterior border of lateral eyes (Fig. 72). Median ocular area about four-fifths as wide anteriorly as posteriorly and its length equal to its anterior width. In anterior view clypeus height of females four-fifths to one AME diameter and in males one-and-one-half AME diameter. Sternum width 0.68 its length. Female palpal femur laterally flattened. Femur I about 1.5 times carapace length. Female calamistrum half the length of metatarsus IV. Femur I of males has six prolateral, three retrolateral, and one proximal dorsal macroseta (Fig. 70). Tibia I has three prolateral, retrolateral, dorsal and ventral macrosetae. Abdomen of male and female has a median central peak and its width and height are each half its length (Figs. 71, 74). Two stout tracheal trunks extend into cephalothorax.

Male Palpus. Palpal femur bears a proximal retrolateral lobe. Large, helical radix with concave inner surface forming a groove in which embolus lies (Figs. 68, 69; Plate 3-C, D). U-shaped conductor lies along the radix's proximal surface and its median lobe, along with part of the radix, appears to rest in the trough-shaped proximal median apophysis lobe. The proximal lobe terminus in turn appears to rest in the grooved tip of the flat distal median apophysis lobe.

Epigynum. A prominent, ventral hood (Figs. 65, 75) extends posteriorly over a dorsal atrium containing a median posterior plate (Figs. 66, 76). An epigynal opening is found at each ventrolateral corner of this plate (Figs. 66, 76). A large, thin-walled bursa leads from each opening and connects to an oval, anterior spermatheca (Figs. 67, 77). Posterolateral to the spermatheca is a smaller, spherical accessory gland which appears to connect both to the spermatheca's posterior surface and to the exterior near the epigynal opening. Connection between accessory glands and spermathecae is difficult to establish with certainty owing to the small size of specimens.

Distribution. This genus is represented only in the southwestern United States and northern and central Mexico (Map 1). Nothing is known of its natural history.

KEY TO *SIRATOBA* FEMALES
(Males of only *S. referena* are known)

1. Epigynal hood two-thirds as wide as the epigynum (Fig. 65); in ventral view the epigynum's posterior margin curved posteriorly, southwestern United States and northern Mexico ..... *referena*
- Epigynal hood one-third as wide as the epigynum (Fig. 75); in ventral view the epigynum's posterior margin curved anteriorly, central Mexico ..... *sira*

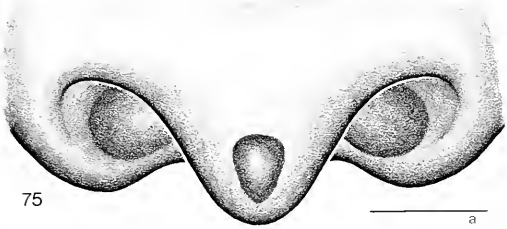
Siratoba referena (Muma and Gertsch) new combination
Figures 65–74, Plate 3-C, D

Ariston referens Muma and Gertsch, 1964, Amer. Mus. Novitates, 2196: 17. Male holotype from Cochise Stronghold, Dragoon Mountains, Arizona, collected 7 September 1950 by W. J. Gertsch, female allotype from Douglas, Arizona, collected 27 August 1939 by R. H. Crandell, both in the American Museum of Natural History, examined.

Diagnosis. The only known males of *Siratoba* belong to this species. Females are distinguished from those of *S. sira* by having an epigynal hood which is two-thirds (Fig. 65) rather than one-third (Fig. 75) the epigynal width and a posterior epigynal margin which, in ventral view, is curved posteriorly rather than anteriorly.

→

Figures 75–77. *Siratoba sira* n. sp. 75. Ventral view of epigynum. 76. Posterior view of epigynum. 77. Dorsal view of cleared epigynum. Figures 78–85. *Miagrammopes simus.* 78. Dorsal view of female. 79. Lateral view of female cephalothorax. 80. Dorsal view of male. 81. Female sternum, endites, and labium. 82. Male sternum, endites, and labium. 83. Ventral view of epigynum. 84. Retrolateral view of female first left patella. 85. Retrolateral view of embolus (black), sperm reservoir, and fundus. Figures 86–93. *Miagrammopes latens* Bryant. 86. Dorsal view of female. 87. Dorsal view of male. 88. Ventral view of epigynum. 89. Dorsal view of cleared epigynum. 90. Retrolateral view of left male palpus. 91. Prolateral view of left male palpus. 92. Female sternum, endites, and labium. 93. Male sternum, endites, and labium.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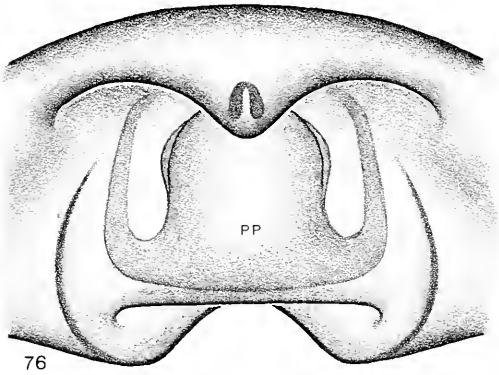
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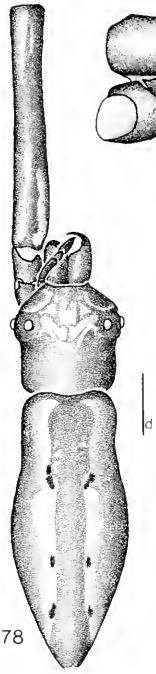
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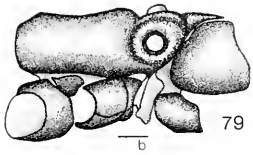
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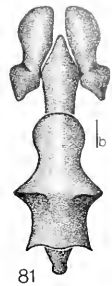
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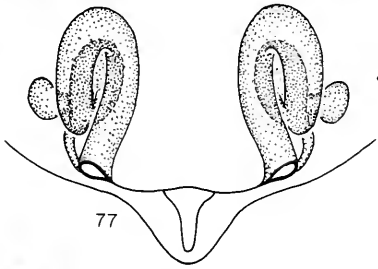
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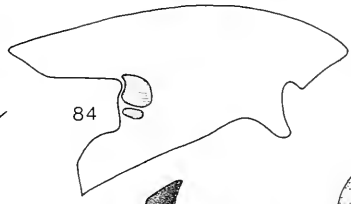
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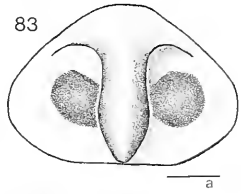
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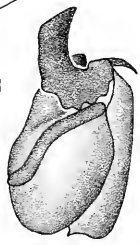
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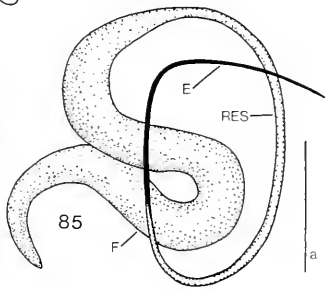
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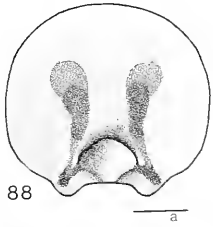
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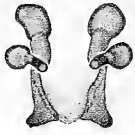
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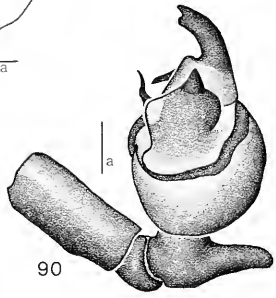
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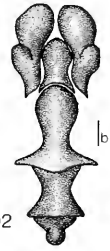
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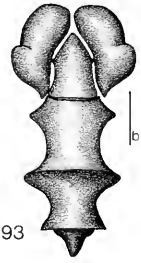
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Description. Male. Total length 2.7 mm, carapace length 0.9 mm, sternum length 0.7 mm. Carapace and legs tan, sternum gray. Dorsum of abdomen white, venter gray. Features of the male palpus are given in genus description.

Female. Total length 3.2 mm, carapace length 1.1 mm, sternum length 0.7 mm. Carapace and legs tan, sternum dark gray. Abdomen's dorsum white with three pairs of posterior and one pair of central gray spots (Fig. 71). Venter dark gray with narrow longitudinal stripe extending half the distance from epigastric furrow to cribellum. When viewed ventrally (Fig. 65), epigynum has a posteriorly directed hood two-thirds the epigynum's width and a posterior margin which curves posteriorly. In posterior view (Fig. 66) epigynum's dorsal surface convex and posterior plate dorsally concave, narrowing as it passes into hollow formed by hood. Epigynal openings at lateral margins of the posterior plate, each leading to a large, thin-walled, bulbous bursa which connects to a nearly spherical spermatheca. A lateral, spherical accessory bulb opens lateral to each epigynal opening and appears also to connect via a convoluted duct to the spermatheca (Fig. 67).

Distribution. Southwestern United States and northern Meixco.

Siratoba sira n. sp.
Figures 75–77

Types. Female holotype from entrance of cave at Taninul in the Mexican state of San Luis Potosí, collected 29 March 1940 by W. Bridges, in the American Museum of Natural History. The specific epithet is derived from the Greek term for cellar.

Diagnosis. Males of this species are unknown. Females are distinguished from those *S. referena* by having an epigynal hood which is one-third (Fig. 75) rather than two-thirds (Fig. 65) the epigynum's width and a posterior epigynal margin which, when viewed ventrally, is curved anteriorly rather than posteriorly.

Description. Female. Total length 2.9 mm, carapace length 0.9 mm, sternum length 0.6 mm. Carapace and legs light tan, sternum light gray with dark border. Dorsum of abdomen white, venter white with wide gray paraxial stripes. In ventral view (Fig. 75) epigynum's posteriorly directed hood one-third its width and epigynum's posterior margin curved anteriorly. Hood with dorsal pit near its tip (Figs. 75, 76). In posterior view (Fig. 76) epigynum's posterior margin concave and posterior plate's dorsal margin nearly straight. Sides of posterior plate nearly parallel and epigynal openings located along their borders. Each opening leads via a wide, thin-walled bursa to an oval spermatheca. A small accessory gland appears to connect to each spermatheca's lateral margin by a short duct and to open externally near the epigynal opening (Fig. 77).

Distribution. Central Mexico.

Miagrammopes O. Pickard-Cambridge
Figures 78–97, Plate 5; Map 1

Miagrammopes O. Pickard-Cambridge, 1869, J. Linn. Soc. London (Zool.), 10: 400. Type species by virtue of first listing in publication *M. thwaitesii* O. Pickard-Cambridge, 1869, *ibid.*

Note. Octavius Pickard-Cambridge (1870) established the family Miagrammopidae for the genus *Miagrammopes*, but Thorell (1873) considered Miagrammopinae as a uloborid subfamily. Lehtinen (1967) divides *Miagrammopes* (Miagrammopinae) into the following genera: 1. *Miagrammopes* O. Pickard-Cambridge, 1869, *op. cit.* Type species *M. thwaitesii* O. Pickard-Cambridge, 1869, *op. cit.* 2. *Ranguma* Lehtinen, 1967, Ann. Zool. Fennici, 4: 199–468. Type species by original designation *M. similis* Kulczynski, 1908, Ann. Mus. Nat. Hungary, 6: 484. 3. *Huanacauria* Lehtinen, 1967, *op. cit.* Type species by original designation *M. bambusicola* Simon, 1893, Ann. Soc. ent. France, 61: 421–462. 4. *Mumaia* Lehtinen, 1967, *op. cit.* Type

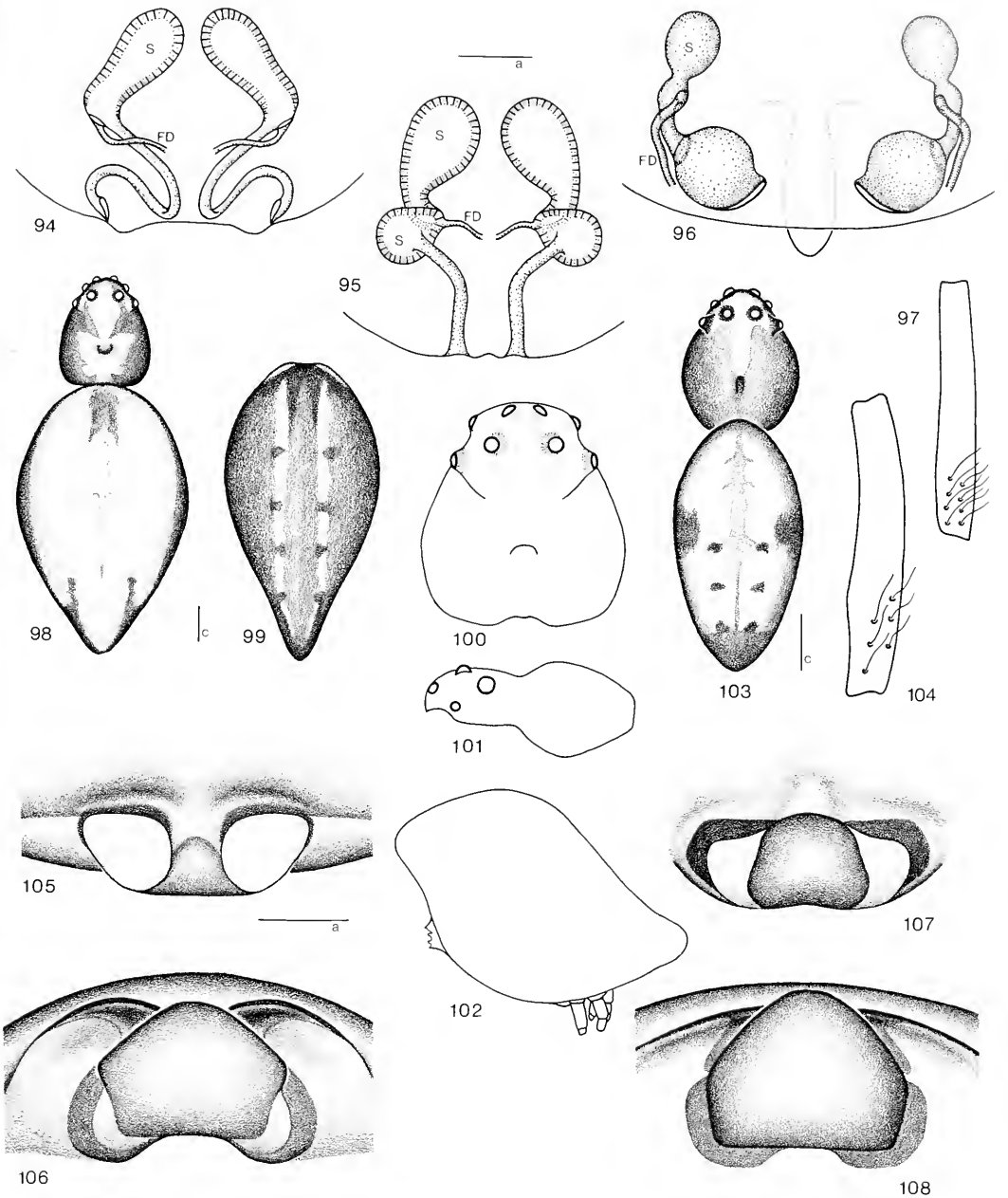


Figure 94. *Miagrammopes corticinus* Simon, dorsal view of cleared epigynum. Figure 95. *Miagrammopes bambusicola* Simon, dorsal view of cleared epigynum. Figures 96–97. *Miagrammopes simus*. 96. Dorsal view of cleared epigynum. 97. Dorsal view of female first right femur. Figures 98–108. *Sybota abdominalis* Nicolet. 98. Dorsal view of female. 99. Dorsal view of female abdomen. 100. Female carapace. 101. Lateral view of female carapace. 102. Lateral view of female abdomen. 103. Dorsal view of male. 104. Dorsal view of female first right femur. 105. Ventral view of epigynum. 106. Posterior view of epigynum. 107. Ventral view of epigynum. 108. Posterior view of epigynum.

species by original designation *Miagrammopes corticeus* Simon, 1892, *op. cit.*

I have examined type specimens of *Miagrammopes corticeus, M. similis,* and *M. bambusicola* as well as Neotropical, Australian and Oriental specimens of this group and believe it to represent a monophyletic assemblage. This is not to say that Lehtinen's division of this assemblage is unwarranted. I have not undertaken a comprehensive study of the miagrammopoid uloborids and for this reason will attempt neither to characterize nor synonymize Lehtinen's genera. Rather, I will deal with this assemblage as the traditional or broader genus *Miagrammopes sensu lato.* My phylogenetic conclusions, however, lead me to reject the subfamily ranking given to the group.

Diagnosis. Males and females of this genus are distinguished from all other uloborid genera by lacking anterior eyes (Figs. 78, 80, 86, 87), and by having a labium and endites which are two times as long as wide (Figs. 81, 82, 92, 93). The sternum of many species is very narrow and divided into two or three plates by flexible transverse areas (Figs. 81, 92, 93).

Description. Total length of males 2.8 to 3.5 mm, carapace length 1.0 to 1.2 mm, sternum length 0.5 to 0.6 mm. Total length of females 4.0 to 6.2 mm, carapace length 1.2 to 2.2 mm, sternum length 1.0 to 1.4 mm. Carapace width of both males and females three-fourths to slightly more than one times carapace length. In lateral view (Fig. 79) carapace nearly flat with first coxa extending from anterior surface. Anterior eyes absent. Posterior median eyes separated from carapace's anterior rim by a distance equal to 0.25 to 0.36 the carapace length (Figs. 78, 80). Posterior eye row either: 1. procurved such that a line across that anterior border of the median eyes passes through the lateral eyes or along their posterior margin, 2. straight, or 3. recurved such that a line across the median eyes' posterior margins passes anterior to the lateral eyes by as much as one PLE diameter. The PME and PLE nearly equal in size. The PLEs on distinct lateral tubercles. The PMEs may be from two to 20 times further from one another than from the PLEs (Figs. 78, 86). In addition to a shallow thoracic pit, a conspicuous depression is located medially or posteromedially to each PME. Sternum with conspicuous intercoxal projections and in many species divided by thin, flexible, transverse regions into 3 plates: one extending between the first two pairs of coxae, a second between the third coxae, and a third between the fourth coxae. Femur I 1.9 to 2.5 times as long as carapace in females and 1.5 to 1.7 times in males. Metatarsae I and IV laterally flattened and in females the latter has a row of stout spines extending along most of its ventral surface and a dorsal calamistrum which is 0.6 to 0.7 its length. Femur I of males lacks spines, but dorsal surface of tibia I has spines along its entire length. Abdomen of males and females cylindrical to spindle-shaped, width 0.25 to 0.40 length, usually attaining its maximum width and height near its center. Transverse, common spiracular groove noticeably forward of cribellum, situated one-eighth to one-sixth distance from cribellum to epigastric furrow. Two stout tracheal trunks extend into cephalothorax.

Male Palpus. Femur lacks ventral, lateral tubercles. Long, narrow lobe on patella's dorsal surface extends above the tarsal base (Plate 5-A, B; Fig. 90). Hematodocha absent. Median apophysis bulb and median apophysis spur modified in both shape and orientation (Plate 5). Conductor's proximal lobe serves as an embolus guide, but its distal spur may be simple (Plate 5-A) or modified (Plate 5-B–D).

Epigynum. Epigynum flat with openings at posterior. Each opening leads to a blind, anterolateral spermatheca whose posterior margin gives rise to either a fertilization duct (Fig. 94) or a lateral bulb from which a fertilization duct arises

(Figs. 89, 95). In *M. simus* (Fig. 96) each epigynal opening leads first to a large, oval bursa and then to a blind spermatheca.

Natural History and Distribution. Members of this genus are known to produce either a single horizontal capture thread with cribellar silk along its center or a horizontal resting thread to which one or several vertical or diagonal cribellar capture threads are attached (Akerman, 1932; Lubin *et al.*, 1978). The genus has a cosmotropical distribution.

Sybota Simon
Figures 98–119, Plate 6-A, B; Map 1

Sylvia [preoccupied] Nicolet, 1849, Aráchnidos. *in* Gay, Historia física y política de Chile. Zoologia 3: 465. Type species *Sylvia abdominalis* Nicolet, subsequent designation by Simon, 1892, Histoire Naturelle des Araignées, 1(1): 216, Paris. Preoccupied by *Sylvia* Scopoli 1769, Annus I: 154.—Aves.

Sybota Simon, 1892, *op. cit.* New name (Feminine) for homonym.

Diagnosis. *Sybota* and *Polenecia* females are the only uloborids to have a posterior abdominal projection extending beyond the spinnerets (Figs. 102, 110, 116). *Sybota* females and males have prominent PLE tubercles (Figs. 100, 103, 115); whereas those of *Polenecia* do not (Fig. 50). The anterior eye row of *Sybota* males and females is recurved rather than procurved as in *Polenecia*. *Sybota* males are characterized by having: 1. no hematodocha (Plate 6-A, B), 2. a well-developed conductor, and 3. a two- or three-pronged median apophysis. The posterior plate of *Sybota* females has a ventrally directed median extension on either side of which is a weakly sclerotized area (Figs. 105–108).

Description. Carapace width 0.7 to 1.0 its length. Female cephalic and thoracic regions each rise slightly from a shallow thoracic depression and attain about equal height (Fig. 101). Thoracic region slopes steeply to petiole. Male carapace nearly flat, rising slightly in ocular area and sloping gradually from thoracic pit to petiole. At ALEs cephalic region of males and females is half as wide as carapace (Figs. 101, 103). Ocular area raised and conspicuously set off from remainder of carapace (Figs. 100, 115). The PLEs on broad, prominent, laterally directed tubercles. In *S. mendoza* AMEs on an anterior tubercle (Fig. 115). Both anterior and posterior eye rows are recurved, posterior row such that a line across the posterior margins of PMEs passes along the anterior margins of PLEs (Figs. 100, 115). In anterior view female clypeus equal in height to AME diameter and male clypeus 1.4 times AME diameter. Male ALEs smaller than AMEs. Median ocular area one-and-one-half to two times as wide posteriorly as anteriorly and about two-thirds as long as its maximum width. Sternum width 0.6 to 0.7 its length. Female femur I 1.3 to 1.5 times as long as carapace; male femur I 1.5 to 1.7 times as long. Calamistrum half the length of metatarsus IV. Female palpal femur laterally compressed. Femur I of males with three or four dorsal, five or six prolateral, and three retrolateral spines. Tibia I with four or five ventral, two or three dorsal, seven proximal, and two retrolateral spines. Female abdomen half to three-fifths as wide and high as long and posteriorly narrowed into a conical projection which extends beyond spinnerets for a distance equal to one-fifth to one-third the abdomen's length (Figs. 98, 102, 110, 114, 116). Male's abdomen oval, about half as wide as long, dorsally flattened, and extended about one-sixth its length beyond spinnerets (Fig. 103). Four stout tracheal trunks extend into the cephalothorax.

Male Palpus. Femur without ventral tubercles and tibia with a distal lobe which extends beyond tarsal base. Long dorsal spine present on patella and tibia. Cymbium with two long spines on its distal median edge. Middle hematodocha absent and palpal sclerites situated quite distally (Plate 6-A, B). Median apophysis

terminal, flattened, and with three distally directed processes. Embolus curved around median apophysis' base, coming to lie in the groove of conductor's basal lobe.

Epigynum. Epigynum's posteromedian margin formed by posterior plate (Figs. 106, 113, 118) and, depending on the shape of this plate, either rounded (Fig. 112) or indented (Fig. 117) in ventral view. Lateral to this plate on epigynum's ventral surface is a pair of level or raised lighter areas, each with a low ridge at its anterior border (Figs. 105, 106). An epigynal opening is situated at each ventrolateral border of the posterior plate and leads via a short duct to an anterior bifurcation which connects with a blind spermatheca and a posterior bifurcation which gives rise to a fertilization duct (Figs. 109, 119).

Natural History and Distribution. The three known species in this genus appear restricted to central and southern Chile and the adjacent regions of Argentina (Map 1).

KEY TO *SYBOTA*

(Males of *Sybota mendozae* are not known.)

1. Males 4
– Females 2
2(1). Carapace width equal to length; AMEs not on conspicuous tubercle (Figs. 98, 100); posterior epigynal margin rounded slightly (Figs. 105, 112); posterior plate pentagonal or oval (Figs. 106, 113) 3
– Carapace width two-thirds length; AMEs on prominent anterior tubercle (Figs. 114, 115); posterior epigynal margin indented (Fig. 117); posterior plate diamond-shaped (Fig. 118) ..... *mendozae*
3(2). Posterior plate of epigynum pentagonal, 1.5 times as broad as high and without a ventromedian depression (Figs. 105–108); carapace with white median line in cephalic region and red pigment just anterior to thoracic depression (Fig. 98) ..... *abdominalis*
– Posterior plate oval, twice as broad as high and with a slight ventromedian depression (Figs. 112, 113); carapace dark gray with no white or red markings ..... *osornis*
4(1). Median apophysis of palpus with two prominent projections and a small central spur at the base of its broad lateral lobe (Plate 6-A); dorsum of abdomen predominantly white ..... *abdominalis*
– Median apophysis with three conspicuous distal projections, the middle one clearly set off (Plate 6-B); dorsum of abdomen dark gray ..... *osornis*

Sybota abdominalis (Nicolet)
Figures 98–109; Plate 6-A

Sylvia abdominalis Nicolet, 1849, Aráchnidos. *in* Gay, Historia física y política de Chile. Zoologia 3: 465–468. Female neotype from Pucatrihue in the Chilean province of Osonoro, collected 12 April 1968 by L. Peña, in the Museum of Comparative Zoology.

Uloborus abdominalis:—Simon, 1887, Ann. Soc. ent. France, 7(6): 195.

Sybota abdominalis:—Simon, 1892, Histoire Naturelle des Araignées, 1(1): 1–256, Paris. New generic name for preoccupied *Sylvia*.

Note. Nicolet (1849) described five species (*Sylvia abdominalis*, *S. similis*, *S. ater*, *S. rubiginosa*, and *S. vittata*) as belonging to his new genus *Sylvia* [preoccupied]. After examining Nicolet's specimens, Simon (1892) concluded that they were varieties of the same species and selected *S. abdominalis* as the type species for the replacement genus name *Sybota*. As Lehtinen (1967) noted, the Nicolet types no longer exist or, if they do, cannot be located in the Muséum National d'Histoire Naturelle in Paris. It is probably for this reason that all authors prior to Lehtinen accepted Simon's inclusion of *S. abdominalis* and *S. (Uloborus) productus* (Simon) in *Sybota*. When Lehtinen created the genus *Polenecia* with *P. productus* as its type species, he necessarily changed the meaning of several studies dealing with uloborid webs, e.g., Kaston (1964 and 1966) and Wiehle (1931). Because these two genera play an important role in studies of uloborid phylogeny and evolution of web forms, it seems appropriate to designate a neotype for *S. abdominalis*. Additionally, description of two new *Sybota* species supports the need to clearly associate this species name with a type specimen. In the absence of a clear definition of *S. abdominalis* I have as-

sociated this name with the Chilean species which appears more commonly in collections, shows the more extensive altitudinal and geographical distribution, and has the greater color variation.

Diagnosis. Females of this species are distinguished from those of *S. mendozae* by having a carapace width equal to (Fig. 100) rather than two-thirds the carapace length (Fig. 115), by having only a slightly recurved anterior eye row, and by having an epigynum whose posterior margin is rounded (Figs. 105, 107) rather than indented (Fig. 117), whose posterior plate is pentagonal (Figs. 106, 108) rather than diamond-shaped (Fig. 118), and whose spermathecae are large and elongate (Fig. 109). *Sybota abdominalis* females differ from those of *S. osornis* by having a pentagonal posterior plate (Figs. 106, 108) without a conspicuous ventromedian depression and by having a carapace with a median white line (Fig. 98) and a red pigment spot just anterior to the thoracic depression.

Males of *S. abdominalis* differ from those of *S. osornis* by having a palpal median apophysis with two (Plate 6-A) rather than three (Plate 6-B) conspicuous distal projections and by having white rather (Fig. 103) than a dark gray abdominal dorsum.

Description. Males. Total length 3.6 to 4.0 mm, carapace length 1.3 to 1.4 mm, sternum length 0.8 to 0.9 mm. Carapace (Fig. 103) dark gray with tan lateral margins and a median white stripe extending from thoracic depression to ocular region where it expands. Sternum gray with a central tan area. Abdomen (Fig. 103) white with a dark gray posterior tip, three pairs of dorsal gray spots, and lateral transverse gray stripes. Median apophysis of palpus with a long, thin projection and a short, broad lobe with a small spur on its mesal base (Plate 6-A).

Females. Total length 5.1 to 5.9 mm, carapace length 1.4 to 1.6 mm, sternum length 0.9 to 1.1 mm. Carapace (Fig. 98) gray with a median white area extending to ocular region. This white area is expanded in the thoracic region of lighter specimens and largely restricted to the cephalic region of darker specimens. Red pigment spot just anterior to thoracic depression. Abdominal coloration variable, ranging from completely white to a gray venter and white dorsum (Fig. 98), with or without a median dorsal gray stripe; to a white venter and gray dorsum with dorsal paraxial white stripes (Fig. 99). It is tempting to place specimens with the latter coloration into a separate species, but little other evidence supports this. Legs lack conspicuous markings and vary in color from tan to gray. In ventral view (Figs. 105, 107) the epigynum's posterior margin is rounded and lateral to the posterior plate's convex ventral tip are two lightly sclerotized areas, bordered laterally by dark, subsurface ducts. In posterior view (Figs. 106, 108) the posterior plate is pentagonal and no more than 1.5 times as broad as high. Ducts are short and looped, leading to large, elongate spermathecae (Fig. 109).

Distribution. Collected from the Chilean provinces of *Osorno*: Puyehue—500 m, Pucatrihue—200 m; *Cautin*: N.E. Villarrica—300 to 600 m; *Llanquihue*: Chamiza—0 to 100 m; *Santiago*: El "Golf"; *Concepcion*: Bosque Ramuntcho—0 to 100 m.

Sybota osornis n. sp.
Figures 110–113; Plate 6-B

Types. Female holotype and two male paratypes from Purranque in the Chilean province of Osorno, collected January–March 1955 by E. Reed, in the American Museum of Natural History. The specific epithet is a third declension noun in the genitive case, derived from the province of the type locality.

Diagnosis. Females of this species are distinguished from those of *S. mendozae* by having a carapace width equal to rather than two-thirds the carapace length, by having only a slightly recurved anterior eye row, and by having an epigynum whose posterior margin is rounded

(Fig. 112) rather than indented (Fig. 117), whose posterior plate is oval (Fig. 113) rather than diamond-shaped (Fig. 118), and whose spermathecae are large and elongate (Fig. 109). *Sybota osornis* females differ from those of *S. abdominalis* by having a broad oval posterior plate with a conspicuous ventromedian depression (Figs. 112, 113) and by having a dark gray carapace with no color markings.

Males of *S. osornis* differ from those of *S. abdominalis* by having a palpal median apophysis with three (Plate 6-B) rather than two (Plate 6-A) conspicuous distal projections and by having a dark gray rather than a white abdominal dorsum.

Description. Male. Total length 3.8 to 4.1 mm, carapace length 1.5 to 1.6 mm, sternum length 1.0 mm. Carapace darkly mottled with gray except for light areas near the thoracic depression, in the ocular area, and at the carapace margins dorsal to coxae III and IV. Sternum dark gray with a narrow median light stripe. Legs dark brown to gray, with no conspicuous markings. Abdomen gray with small dorsal white spots and paraxial ventral stripes. Palpal median apophysis with three distinct distal projections (Plate 6-B).

Females. Total length 6.4 mm, carapace length 1.8 mm, sternum length 1.1 mm. Carapace and sternum dark gray, sternum with a small tan center region. Dorsum of abdomen dark gray with white anterior tip and two small, widely separated white spots in the anterior half. Venter with a median gray stripe and two paraxial light stripes. A lateral white stripe extends along each side of the abdomen. Legs dark with no conspicuous markings. In ventral view (Fig. 112) the epigynum's posterior margin rounded. Lateral to the posterior plate's concave ventral tip are two lightly sclerotized areas, bordered laterally by dark, subsurface ducts. In posterior view (Fig. 113) posterior plate oval and at least twice as broad as high. Ducts short and looped, leading to large, elongate spermathecae.

Distribution. Known only from the type locality.

Sybota mendozae n. sp.
Figures 114–119

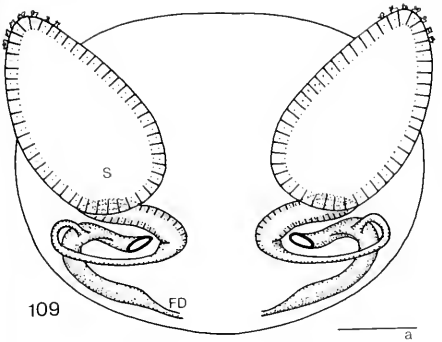
Types. Female holotype and three female paratypes from 7 km W of Mendoza, Argentina, collected in "chaparral" at an altitude of 1200 m, March–April 1958 by B. Patterson. Holotype and two paratypes in the Museum of Comparative Zoology, one paratype in the American Museum of Natural History. The specific epithet is a first declension noun in the genitive case, derived from the type locality.

Diagnosis. Males are not known. Females are distinguished from those of *S. abdominalis* and *S. osornis* by having a carapace whose width is two-thirds its length (Figs. 114, 115), by having AMEs on a prominent tubercle, by having the anterior eye row more strongly recurved than the posterior, and by having an epigynum whose posterior margin is indented rather than rounded (Fig. 117), whose posterior plate is diamond-shaped (Fig. 118) rather than pentagonal or oval, and whose spermathecae are small and spherical rather than large and elongate (Fig. 119).

Description. Female. Total length 5.6 to 6.8 mm, carapace length 1.7 to 1.9 mm, sternum length 1.0 to 1.3 mm. Carapace brown to light gray, lighter along anterior midline and darker in ocular region (Fig. 114). Sternum dark gray with brown anterior median stripe. Dorsum of abdomen

→

Figure 109. *Sybota abdominalis* Nicolet, dorsal view of cleared epigynum. Figures 110–113. *Sybota osornis* n. sp. 110. Lateral view of female abdomen. 111. Retrolateral view of male left embolus (black), sperm reservoir, and fundus. 112. Ventral view of epigynum. 113. Posterior view of epigynum. Figures 114–119. *Sybota mendozae* n. sp. 114. Dorsal view of female. 115. Female carapace. 116. Lateral view of female abdomen. 117. Ventral view of epigynum. 118. Posterior view of epigynum. 119. Dorsal view of cleared epigynum.



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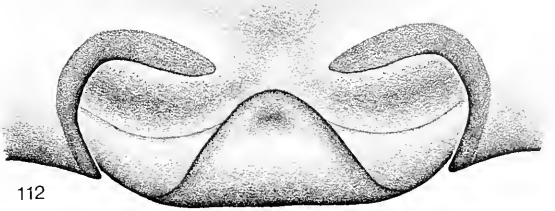

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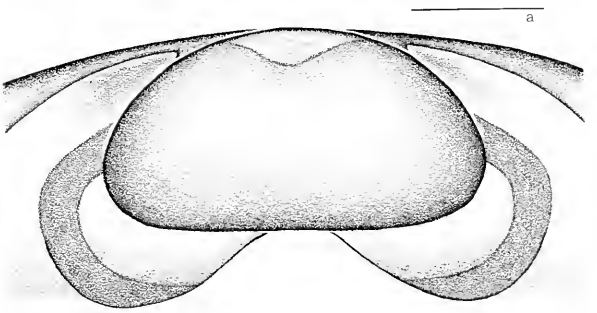

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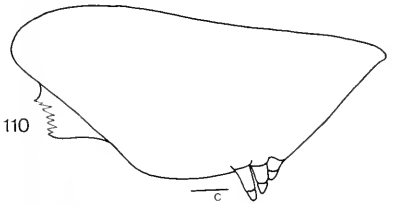

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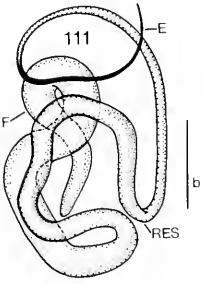

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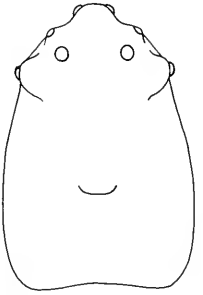

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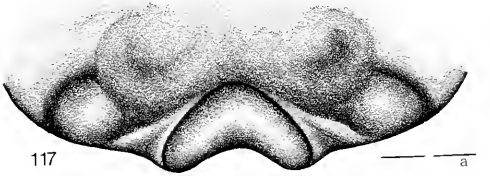

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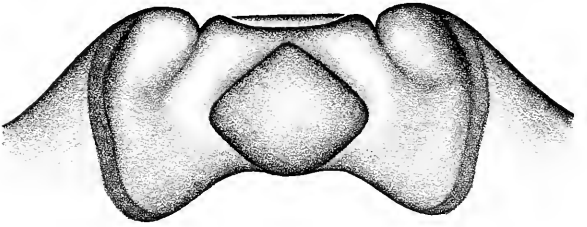

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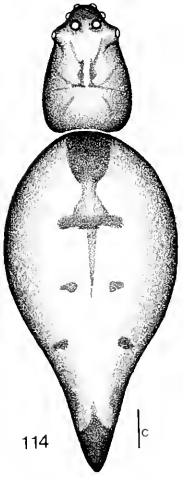

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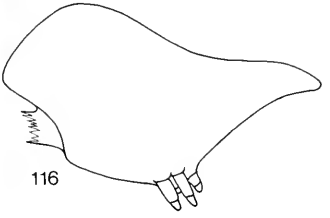

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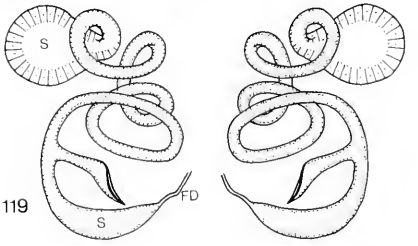

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all dark gray with slightly lighter paraxial areas or white with dark gray anterior median patch, gray transverse line in the anterior third of its length, three pairs of gray spots in the posterior half, and gray posterior tip (Fig. 114). Venter of abdomen with a median gray longitudinal stripe bordered by white patches or, in dark specimens, all gray. Abdomen's lateral surfaces all gray or white, mottled with dark gray spots. Legs brown with a dark gray longitudinal stripe on the dorsal surface of femur, patella, and tibia of leg I. Femora, tibiae, and metatarsi of legs II–IV each have a gray distal band. In ventral view (Fig. 117) epigynum's posterior margin indented with a pair of slightly raised lateral lobes lateral to the posterior plate's ventral tip. In posterior view (Fig. 118) posterior plate is pentagonal. Ducts are long and highly convoluted, leading to small, spherical spermathecae (Fig. 119).

Natural History and Distribution. This species is known only from the type locality in extreme western central Argentina. Darwin (1876) reported finding several webs which "consisted of a wedge-shaped segment" near Mendoza, the type locality of this species. Morphological modifications characteristic of this genus and species make its members likely candidates for the production of such apparently secondarily reduced webs.

Orinomana Strand
Figures 120–128; Map 1

Orinomus [preoccupied] Chamberlin, 1916, Bull. Mus. Comp. Zool., 60(6): 206. Type species by original designation and monotypy *O. lamprus* Chamberlin, 1916, *ibid.* Preoccupied by *Orinomus* Attems 1895, S.B. Akad. Wiss. Wien, Math.-naturw. Cl., 104(1): 166.—Myriapoda.

Orinomana Strand, 1934, Folia zool. hydrobiol., 6(2): 273. New name for *Orinomus* Chamberlin, 1916, preoccupied. The genus name is feminine.

Note. Mello-Leitão established the genus *Petrunkevitchia* for *P. venusta* Mello-Leitão, 1915, *op. cit.* To this genus was added *P. pusilla* Mello-Leitão, 1917, Arch. Esc. super. agric. medic. vet., 1(1): 3–19. Each species was described from a single male specimen which apparently no longer exists. Despite this, Lehtinen (1967) treats this genus as a senior synonym of *Orinomana* Strand, 1934 (*nom. nov.* for the preoccupied *Orinomus* Chamberlin, 1916, *op. cit.*, containing only the type species *O. lamprus* Chamberlin). However he considers *P. pusilla* not to be congeneric with *P. venusta*, but fails to assign it to another genus. On the following page (258) Lehtinen places *O. lampra* in the genus *Philoponella*. Owing to this confusion and inability to resolve the problem due to lack of specimens of *P. venusta* and *P. pusilla*, I have chosen to treat these two species and, therefore, the genus *Petrunkevitchia* as *nomina dubia*. The 1964 International Code of Zoological Nomenclature defines a *nomen dubium* as: "A name not certainly applicable to any known taxon." Mayr (1969) adds: ". . . owing to shortcomings in the original diagnosis or the type material."

Diagnosis. *Orinomana* females, along with those of *Waitkera* and *Sybota*, have prominent PLE tubercles (Fig. 121). *Orinomana* is distinguished from these genera by having: 1. a peaked (Fig. 122) rather than an oval (Fig. 24) or projecting (Fig. 102) abdomen, and 2. AMEs which are not on a slight, median mound and which are one diameter removed from the anterior carapace margin (Figs. 120, 121).

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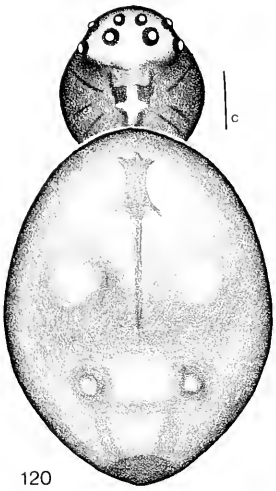
Figures 120–125. *Orinomana bituberculata* (Keyserling). 120. Dorsal view of female. 121. Female carapace. 122. Lateral view of female abdomen. 123. Ventral view of epigynum. 124. Posterior view of epigynum. 125. Dorsal view of cleared epigynum. Figures 126–128. *Orinomana mana* n. sp. 126. Ventral view of epigynum. 127. Posterior view of epigynum. 128. Dorsal view of cleared epigynum. Figures 129–130. *Uloborus glomosus* (Walckenaer). 129. Apical view of left male palpus. 130. Dorsal view of cleared epigynum. Figure 131. *Uloborus penicillatus* Simon, dorsal view of male left first femur.



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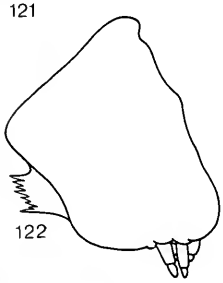

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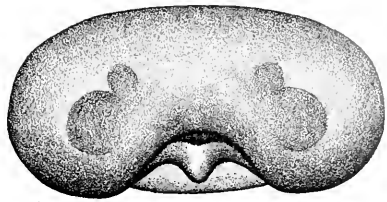

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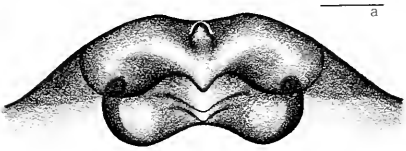

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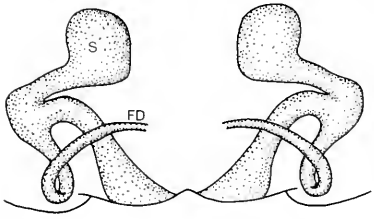

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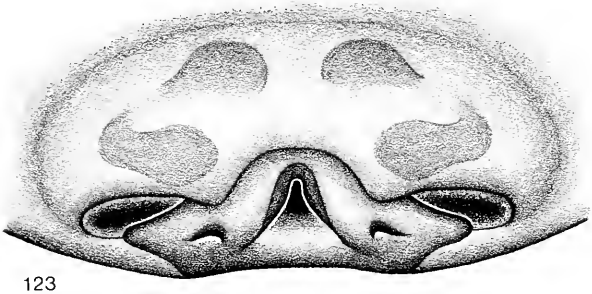

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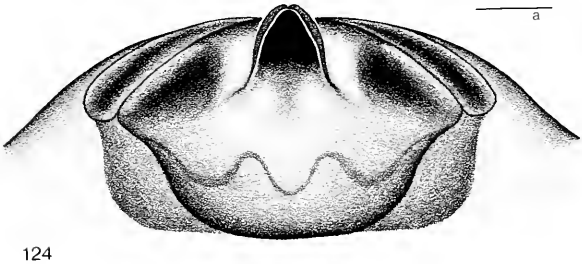

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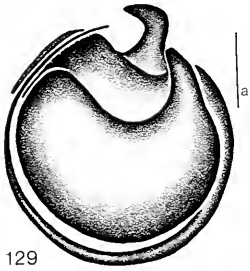

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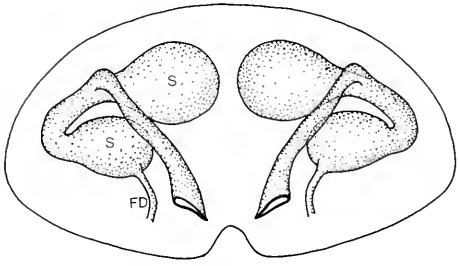

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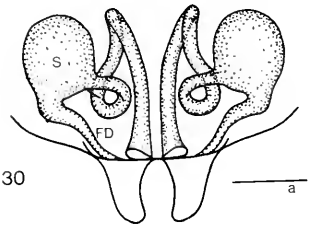

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Description. Carapace width and length equal. Cephalic region rises sharply from shallow thoracic depression and thoracic region slopes abruptly to petiole. The PLEs are on conspicuous lateral tubercles and the entire ocular area is on a distinct mound (Fig. 121). At ALEs cephalic region 0.6 carapace width. Both eye rows recurved so that a line across the median eyes' posterior margin passes through the anterior one-fourth of the lateral eyes' diameter. Median ocular area's anterior width three-fifths and its length three-sevenths its posterior width. In dorsal view clypeus extends forward of AMEs by a distance equal to one AME diameter. In anterior view clypeus height four-fifths an AME diameter. Sternum 0.6 as wide as long. Female palpal femur flattened. First femur 1.4 times as long as carapace. Calamistrum 0.7 times as long as metatarsus IV. Abdomen height and length nearly equal, width two-thirds to three-fourths length (Figs. 120, 122). Dorsum with a pair of large anterior tubercles and two pairs of small, paramedial tubercles posterior to these. Two stout tracheal trunks extend into cephalothorax.

Epigynum. Epigynum with a posteromedian notch or indentation and a pair of posterolateral depressions (Figs. 123, 124, 126, 127). An opening is found in each depression and the straight duct leading from it divides to connect to blind anterolateral spermatheca and either a long fertilization duct or a posterior spermatheca with a posteromedian fetilization duct (Figs. 125, 128).

Natural History and Distribution. Nothing is known of the natural history of this genus. Its members are found in the high Andes (3000 to 4000 m) from southern Ecuador to northern Chile.

KEY TO FEMALES OF *ORINOMANA*
(No males of this genus are known)

1. Sternum uniform brown; posterior epigynal margin with a sharp, V-shaped median notch (Fig. 123); abdomen white (Fig. 120) ..... *bituberculata*

– Sternum brown with a light median stripe; posterior epigynal margin with a rounded median indentation (Fig. 126); abdomen darkly colored ..... *mana*

Orinomana bituberculata (Keyserling), new combination
Figures 120–125

Uloborus bituberculatus Keyserling, 1882, Verh. zool.-bot. Ges. Wien, 31: 282. Two identified females from Peru in a vial labeled "type" in British Museum (Natural History), examined. Two identified females in vial labeled "Lima, Peru, leg. K. Yebki? Y. Sublemaa? detm. E. Keyserling, 177," in Polska Akademia Nauk Instytut Zoologiczny, Warsaw where Keyserling (1882 *op. cit.*) noted specimens to be, examined.

Orinomus lamprus Chamberlin, 1916, Bull. Mus. Comp. Zool., 60(6): 207. Female holotype from Urubamba (3160 m), Peru, collected 1919, in the Museum of Comparative Zoology, examined, NEW SYNONYMY.

Orinomana lampra:—Strand, 1934, Folia zool. hydrobiol., 6(2): 273.

Diagnosis. Orinomana bituberculata females are distinguished from those of *O. mana* by having a brown, unmarked sternum, a white abdomen (Fig. 120), a sharply notched posterior epigynal margin (Fig. 123), and two pairs of oval spermathecae (Fig. 125).

Description. Only females are known. Total length 4.8 mm, carapace length 1.2 mm, sternum length 0.8 mm. Carapace mottled brown with thin, light median stripe, a light ocular area with black encircled eyes, and a thin, light lateral margin (Fig. 120). Leg I tan mottled with gray; femur and tibia with faint proximal and median light rings; proximal two-thirds of metatarsus nearly white. Abdomen white with faint gray patches lateral to each dorsal tubercle (Fig. 120).

Epigynum. In ventral view (Fig. 123) posterior epigynal margin with a deep median notch and two broad, lateral depressions. Posterior epigynal surface (Fig. 124) nearly flat except for ventromedian notch. Two pairs of nearly equal-sized oval spermathecae (Fig. 125).

Distribution. This species is known only from the type locality in central Peru and from a female collected at Cerro Ti-

najillas (3100 m) in the southern Ecuadoran province of Azuay on 18 to 21 March 1965 by L. Peña.

Orinomana mana n. sp.
Figures 126–128

Type. Female holotype from Quismaa (ca. 4000 m) in the Chilean province of Tarapace, collected 5 June 1968 by L. Peña, in the Museum of Comparative Zoology. The specific name is an arbitrary combination of letters.

Diagnosis. *Orinomana mana* females are distinguished from those of *O. bituberculata* by having a light median sternal stripe, a darkly marked abdomen, a rounded posteromedian epigynal indentation (Fig. 126), and a single pair of spermathecae (Fig. 128).

Description. Only females are known. Total length 3.8 mm, carapace length 1.1 mm, sternum length 0.8 mm. Carapace coloration similar to *O. bituberculata* but the median stripe is broader and the lateral ocular area is brown not white. Carapace gray with a light median stripe. Leg I light brown with a light median femoral and a proximal tibial ring and a brown metatarsus. Dorsum of abdomen white overlain by dense black mottling to form a dark, median stripe and a dark chevron between each pair of light, dorsal tubercles. Venter of abdomen black with a thin median and a wide paraxial light stripe.

Epigynum. In ventral view (Fig. 126) posterior epigynal margin with a rounded median indentation containing two small central projections. In posterior view (Fig. 127) these projections appear dorsally directed. A single pair of spermathecae is present (Fig. 128).

Distribution. Known only from the type locality in northern Chile.

Uloborus Latreille
Figures 129–156, Plate 7-A; Map 2

Uloborus Latreille, 1806, Genera Crustaceorum et Insectorum, Aranéides, 1: 109, Paris. Type species by monotypy *U. walckenaerius* Latreille, 1806, *ibid.* Type specimens no longer exist.

Phillyra Hentz, 1850, Boston J. Natur. Hist. Soc., 6: 24. Type species by virtue of first listing in publication *P. mammeata* Hentz, 1850, *ibid.* The holotype of *P. mammeata* does not exist, but this species has long been recognized as a synonym of *Uloborus glomosus* (Walckenaer).

Veleda Blackwall, 1859, Ann. Mag. Natur. Hist., ser. 3, 3: 95. Type species by monotypy *V. lineata* Blackwall, 1859, *ibid.* The type species is a synonym of *U. walckenaerius.*

Philoponus Thorell, 1887, Ann. Mus. Civ. stor. nat. Genova, ser. 2, 5: 127. Type species by monotypy *Philoponus pteropus* Thorell, 1887, *ibid.*

Diagnosis. *Uloborus* males are distinguished by having: 1. a pear-shaped carapace with conspicuously narrowed cephalic region which is two-fifths the maximum carapace width (Figs. 133, 141, 150), 2. a posterior eye row recurved such that a line across posterior margin of PMEs passes anterior to the PLEs by half a PLE diameter, 3. clypeus height equal to half an AME diameter, 4. a conductor with only a proximal lobe (Plate 7-A, Fig. 129) and 5. numerous trichobothria on the first pairs of legs (Fig. 131). Females are similar to those of *Octonarius*, having slender posterolateral epigynal lobes whose bases are contiguous (Figs. 137, 145). Unlike *Octonarius*, they: 1. lack conspicuous posterodorsal atria (Figs. 138, 146), 2. have a cephalic region which at the ALEs is only half as wide as the carapace (Fig. 132), 3. have more conspicuously recurved eye rows, and 4. have a tuft of setae on distal region of the first tibia (Figs. 136, 153).

Description. Carapace width equal to 0.85 length. Cephalic and thoracic regions of females level, thoracic depression a shallow pit. Cephalic region of males curved slightly downward from thoracic depression. Both eye rows recurved. A line across AMEs' posterior margins passes anterior to the ALEs by a distance equal to one-fourth an ALE diameter in females and one ALE diameter in males. A line across PME's posterior margins passes anterior to the PLEs by a distance equal to one-fourth a PLE diameter in females and half a PLE diameter in males. Median ocular

area is square. In anterior view clypeus height equal to two-fifths to half an AME diameter. Sternum width 0.72 its length. Female palpal femur laterally compressed. Length of first femur 1.4 to 1.5 that of carapace. Female calamistrum half as long as metatarsus IV. Female first tibia with a distal tuft of setae forming a conspicuous brush. Male first femur with two prolateral, two retrolateral, and two dorsal spines. Male first tibia with ten prolateral, six retrolateral, and 12 dorsal spines. Female abdomen three-fourths as high and half as wide as long, usually with one pair of dorsal tubercles in the anterior third of its length. Male's abdomen half as wide and high as long and without tubercles. Tracheal system with either two or four stout tracheal trunks extending into cephalothorax.

Male Palpus. Femur with a pair of proximal, ventral tubercles and tarsus with a prominent middle hematodocha (Plate 7-A). Median apophysis bulb well developed and bears a terminal median apophysis spur. Conductor arises from median apophysis bulb's base and lacks the distal spur present in *Philoponella* males. In *U. segregatus* and *U. campestratus* the conductor is as long as broad (Figs. 143, 151); whereas, in *U. penicillatus* it is much longer than broad (Fig. 135).

Epigynum. Two weakly sclerotized posterolateral lobes extend from epigynum's posterior margin (Figs. 137, 154). A small sclerite is usually found at the tip of each lobe and a copulatory opening is found dorsal or dorsolateral to the base of each lobe. Each opening leads via a duct to an oval spermatheca from whose posterior margin a fertilization duct leads (Figs. 130, 139, 147, 156).

Natural History and Distribution. As far as is known, all members of this cosmopolitan genus spin horizontal orb-webs.

Note. Uloborus festivus Mello-Leitão female holotype is an immature specimen, *U. orsinus* Mello-Leitão female holotype has no abdomen, and *U. peruvanus* Keyserling female holotype has been dried and its genitalia cannot be studied. These three species must be treated as *nomina dubia.*

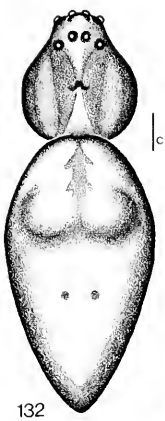
Confusion over the large number of *Uloborus* species names in the literature (most appearing only in original species descriptions and many belonging to what are now recognized as other genera) seems to have prevented many arachnologists from ascribing any name at all to members of this genus. Although the three *Uloborus* species redescribed in this study are clearly distinct from one another, each includes considerable color variability and may actually represent several sibling species which I am unable to distinguish at this time. This seems most likely in *U. aegrotus* and least likely in *U. cinereus.* With synonyms accounted for and the following three species delineated, names can be consistently ascribed to specimens and, as more information becomes available, the validity of the species described here more rigorously tested.

Key to *Uloborus* Males

1. Conductor lobe at least four times as long as wide (Fig. 135); carapace usually with three light stripes (Fig. 133) ---- *penicillatus*

→

Figures 132–139. *Uloborus penicillatus* Simon. 132. Dorsal view of female. 133. Dorsal view of male. 134. Ventral view of male left palpal femur. 135. Apical view of male left palpus. 136. Retrolateral view of female left first leg. 137. Ventral view of epigynum. 138. Posterior view of epigynum. 139. Dorsal view of cleared epigynum. Figures 140–147. *Uloborus segregatus* Gertsch. 140. Dorsal view of female. 141. Dorsal view of male. 142. Dorsal view of male. 143. Apical view of male left palpus. 144. Ventral view of male left palpal femur. 145. Ventral view of epigynum. 146. Posterior view of epigynum. 147. Dorsal view of cleared epigynum. Figures 148–156. *Uloborus campestratus* Simon. 148. Dorsal view of female. 149. Dorsal view of female abdomen. 150. Dorsal view of male. 151. Apical view of male palpus. 152. Ventral view of male left palpal femur. 153. Retrolateral view of male left first leg. 154. Ventral view of epigynum. 155. Posterior view of epigynum. 156. Dorsal view of cleared epigynum.



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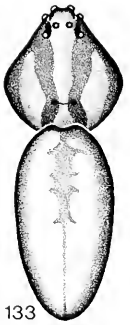
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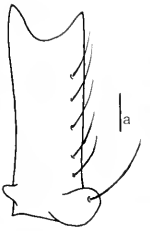

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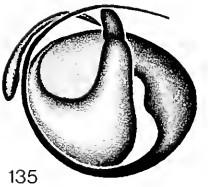
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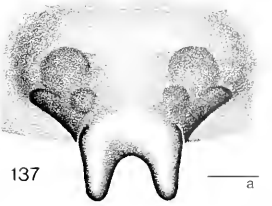

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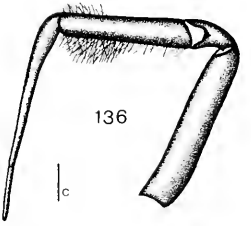

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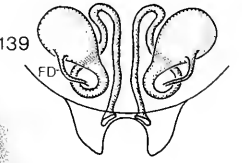

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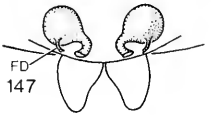

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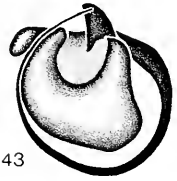

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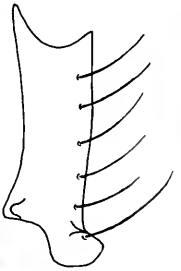
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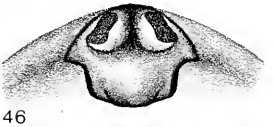
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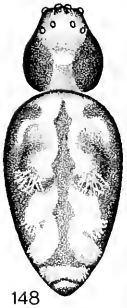
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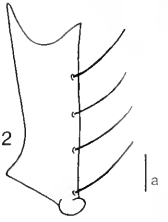

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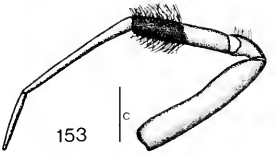

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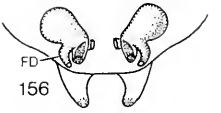

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– Conductor lobe as long as wide (Figs. 143, 151); carapace with a single median stripe (Fig. 141) or, if with three stripes a central guanine spot is present (Fig. 150) 2

2(1). Carapace with a central guanine spot (Fig. 150); median stripe broad; median apophysis bulb crescent-shaped, its prolateral notch twice as broad as deep (Fig. 151) ..... *campestratus*

– Carapace without a central white spot (Fig. 141, 142); median stripe narrow; median apophysis bulb semicircular, its prolateral notch as broad as deep (Fig. 143) ..... *segregatus*

KEY TO *ULOBORUS* FEMALES

1. Epigynal lobes separately connected to epigynal mound with their bases contiguous, forming a deep median "V" (Fig. 145); each lobe usually has a large, heavily sclerotized cap ..... *segregatus*

– Epigynal lobes have a common connection to epigynal mound with their bases forming a shallow median "U" (Fig. 137) or their bases separated from one another (Fig. 154); lobes with common base lack a large distal cap 2

2(1). Carapace with a large, central guanine spot and often with a broad, central light median stripe (Fig. 148); abdomen usually with four pairs of dorsal humps, each hump beset with a tuft of thick white setae (Figs. 148, 149); first tibia with a dark, distal band which in a few lighter specimens is very faint (Fig. 153) ..... *campestratus*

– Carapace without a white spot, lighter specimens have a narrow median white stripe and two paraxial white stripes (Fig. 132), darker specimens have only a central white stripe or a white posteromedian wedge; abdomen with only a single pair of anterior humps (Fig. 132); tibia 1 unmarked (Fig. 136) or, in dark specimens with a very narrow proximal band ..... *penicillatus*

Uloborus penicillatus Simon, new combination
Figures 131–139; Map 2

Uloborus penicillatus Simon, 1891, Proc. Zool. Soc. London, 1891: 554. Three female, one male, and immature syntypes (in three vials) from the British West Indies island of St. Vincent, collected by H. H. Smith, in the British Museum (Natural History), examined.

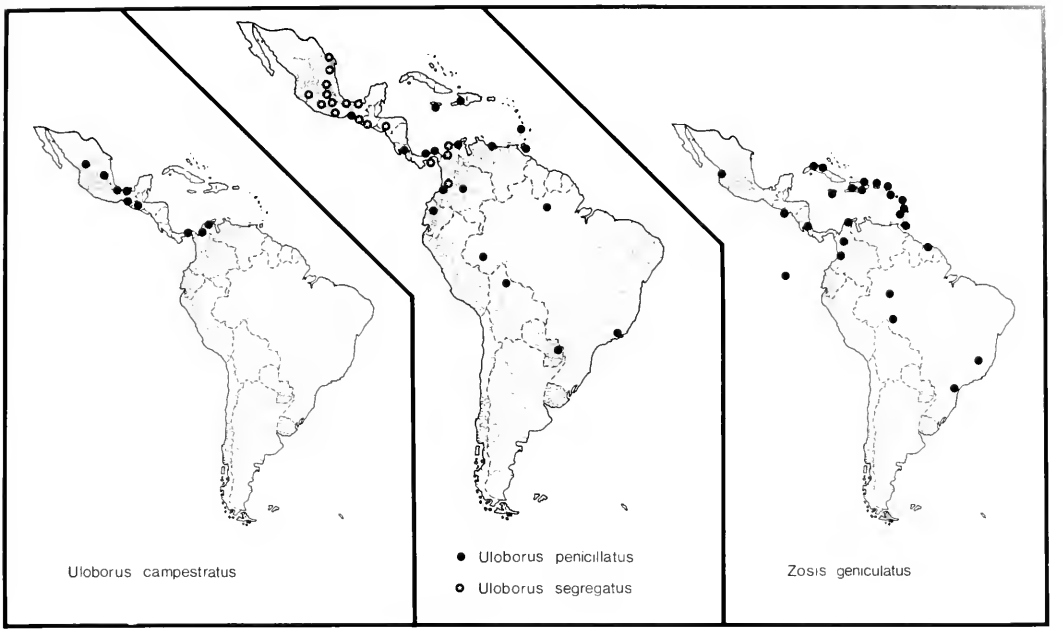
Uloborus aegrotus Simon, 1893, Ann. Soc. ent. France, 61: 424. Three female and three immature syntypes from Caracas and San Esteban, Venezuela, collected 27 December 1887 to 20 January 1888 and 29 February to 27 March 1888, respectively by E. Simon, in Muséum National d'Histoire Naturelle, Paris, examined. NEW SYNONYMY.

Uloborus maniculatus Simon, 1893, Ann. Soc. ent. France, 62: 299. Two female and one immature syntypes from San Paulo de Olivenca (de Mathan) in the Brazilian state of Amazonas, AR 45, in the Muséum National d'Histoire Naturelle, Paris, examined, NEW SYNONYMY.

Uloborus bucki Mello-Leitão, 1943, Arquivos do Museu Nacional, Rio de Janeiro, 37: 157. Female holotype from Porto Algere, Rio Grande do Sul, Brazil, collected by P. Buck, in Museu Nacional, Rio de Janeiro (No. 41. 720), examined, NEW SYNONYMY.

Uloborus plumipedatus Roewer, 1951, Abh. Nat. Ver. Bremen, 32(2): 154. New name for *U. plumipes* Mello-Leitão, 1947, Boletin Museu Nacional, Rio de Janeiro, 80: 6. Preoccupied by *U. plumipes* Lucas, 1846, Explor. Sci. Algérie, Zool. 1. Aranéides, p. 252. Two female, one immature, and two male syntypes from Garmo do Rio Claro in the Brazilian state of Minas Gerais, collected by J. C. Carvalho, in the Museu Nacional, Rio de Janeiro, examined, NEW SYNONYMY.

Diagnosis. In many respects this species is similar to *U. glomosus* from North America (Muma and Gertsch, 1964). Males are distinguished by having a conductor which is about five times as long as wide (Fig. 135) rather than three times as long as wide (Fig. 129) and by having a small median apophysis bulb with a deep prolateral notch (Fig. 135) rather than a large median apophysis bulb with a shallow notch (Fig. 129). Males are more easily distinguished from those of *U. segregatus* and *U. campestratus* by their long conductor (Fig. 135) and by the presence of small, less erect setae on the shaft of the palpal femur (Fig. 134). *Uloborus penicillatus* females are more difficult to distinguish from those of *U. glomosus*. The former usually lacks a proximal light tibial ring in all but dark specimens; whereas, most specimens of the latter have a conspicuous, though narrow, proximal light tibial ring. Epigynal lobes of *U. penicillatus* unite medially before joining the epigynal (Fig. 137) mound while those of most *U. glomosus* unite at the epigynal mound. *Uloborus penicillatus* females also differ from those of *U. segregatus* and *U. campestratus*, whose epigynal lobes unite at the epigynal mound (Fig. 145) or are separate at their attachment with the epigynal



Map 2. Distribution of *Uloborus campestratus*, *U. penicillatus*, *U. segregatus*, and *Zosis geniculatus*.

mound (Fig. 154). *Uloborus penicillatus* females lack the carapace guanine spot (Fig. 148), dark, distal tibial ring (Fig. 153), and four pairs of abdominal tubercles (Figs. 148, 149) found in *U. campestratus*. Epigynal lobes of *U. penicillatus* (Fig. 137) lack well sclerotized tips present in most *U. segregatus* specimens (Fig. 145).

Description. Female total length 4.4 to 7.2 mm, carapace length 1.4 to 1.7 mm, sternum length 0.8 to 1.2 mm. Male total length 3.0 to 4.2 mm, carapace length 1.1 to 1.3 mm, sternum length 0.6 to 0.9 mm. Female carapace tan to dark gray, lighter specimens with a light narrow median stripe and two light paraxial stripes (Fig. 132), darker specimens with only a median stripe. Male carapace tan with light median and paraxial stripes (Fig. 133). Female abdomen tan (Fig. 132) to dark gray. Male abdomen usually tan (Fig. 133), in a few specimens dusty gray. Two stout tracheal trunks extend into cephalothorax.

Male Palpus. Palpal femur's large retrolateral tubercle (Fig. 134) directed more perpendicular to femur's axis than in *U. segregatus* or *U. campestratus* (Figs. 144, 152). All setae but the one arising from the tubercle's tip smaller and less erect than in the other two species. Median apophysis bulb small with a deep prolateral notch (Fig. 135). Conductor at least five times as long as broad.

Epigynum. Epigynal lobes slender uniting at their bases to form a "U" which is often lighter than the remainder of the epigynum to which the lobes' common base attaches (Figs. 137, 138). Spermathecae oval, ducts long and convoluted (Fig. 139).

Natural History and Distribution. As far as is known members of this species construct tubular eggsacs with lengths at least ten times their diameters. This species is known from southern Mexico through Central America to Ecuador, Paraguay, and southeastern Brazil (Map 2).

Uloborus segregatus Gertsch
Figures 140–147; Map 2

Uloborus segregatus Gertsch, 1936, Amer. Mus.

Novitates, 852: 4. Male holotype and two male paratypes from Edinburg, Texas, collected 16 September 1935 by S. Mulaik. Two female paratypes from five miles SE of Welasco, Texas, collected 21 July 1935 by S. Mulaik. In the American Museum of Natural History, examined. Muma and Gertsch, 1964, Amer. Mus. Novitates, 2196: 26.

Diagnosis. As Muma and Gertsch (1964) note, males of this species are distinguished from those of *U. diversus* by having a palpal femur which is 2.5 rather than 4.5 times as long as broad. Females lack a dark, distal tibial ring present in *U. diversus*. *Uloborus segregatus* males differ from those of *U. penicillatus* by having a short conductor (Fig. 143), erect setae on the palpal femoral shaft (Fig. 144), and a single longitudinal stripe on the carapace (Figs. 141, 142). They differ from *U. campestratus* males by lacking a central white spot on the carapace's center and by having a larger retrolateral palpal femoral tubercle. *Uloborus segregatus* females are distinguished from those of *U. penicillatus* by having epigynal lobes which unite to form a "V" rather than a "U," and have sclerotized tips (Figs. 145, 146) and from those of *U. campestratus* by lacking a central guanine spot at the carapace's center and a dark, distal ring on the first tibia.

Description. Female total length 2.8 to 4.2 mm, carapace length 0.8 to 1.4 mm, sternum length 0.6 to 0.9 mm. Male total length 2.4 to 3.0 mm, carapace length 0.8 to 1.0 mm, sternum length 0.5 to 0.6 mm. Female and male carapace gray with a light median stripe. Abdomen of most females and darker males light dorsally and gray laterally with a complete or broken median gray stripe (Figs. 140, 141). Lighter males with a tan abdomen. Four stout tracheal trunks extend into the cephalothorax.

Male Palpus. Femoral shaft with six large, erect setae (Fig. 144). Median apophysis with a deep prolateral notch (Fig. 143). Conductor length and width equal.

Epigynum. Epigynal lobes unite separately to epigynal mound with their bases contiguous (Figs. 145, 146). Each lobe usually has a conspicuous sclerotized cap. Spermathecae round, ducts short (Fig. 147).

Natural History and Distribution. Vials of several specimens contained stellate eggcases similar to that shown in Fig. 233. This species is found from southeastern Texas through Colombia (Map 2).

Uloborus campestratus Simon, new combination
Figures 148–156; Map 2

Uloborus campestratus Simon, 1893, Ann. Soc. ent. France, 61: 424. Nine female and three male (see Note) syntypes from La Guiara, Caracas, and San Esteban, Venezuela collected by E. Simon from 27 December 1887 to 27 March 1888 in Muséum National d'Histoire Naturelle, Paris, examined.

Uloborus cinereus O. Pickard-Cambridge, 1898, Biol. Cent.-Amer., Zool., Arachnida. Araneida, 1: 265. Two female syntypes from Teapa in the Mexican state of Tabasco, collected by H. H. Smith, in British Museum (Natural History), examined, NEW SYNONYMY. Muma and Gertsch, 1964, Amer. Mus. Novitates, 2196: 28.

Uloborus spernax O. Pickard-Cambridge, 1898, *op. cit.* Female holotype from Teapa in the Mexican state of Tabasco, collected by H. H. Smith, in the British Museum (Natural History), examined, NEW SYNONYMY.

Note. Type material of *U. campestratus* contained nine females conspecific with *U. cinereus* and *U. spernax* plus three males conspecific with *Philoponella fasciata*. Simon describes females before males, and for this reason, I assert my authority as first revisor in establishing the synonymy listed above.

Diagnosis. Males and females are distinguished from those of other species by the presence of a large, white guanine spot at the carapace's center (Figs. 148, 150). *Uloborus campestratus* females are the only members of this genus to have four pairs of dorsal abdominal tubercles (Figs. 148, 149) and a dark ring on the distal half of the first tibia (Fig. 153).

Description. Female total length 2.4

to 4.0 mm, carapace length 0.8 to 1.3 mm, sternum length 0.5 to 0.8 mm. Male total length 2.0 to 2.4 mm, carapace length 0.9 mm, sternum 0.4 mm. Female carapace light tan to gray (Fig. 148), darker specimens with a broad, median light stripe. Male carapace of darker specimens with a broad median and two posterior paraxial stripes (Fig. 150). Female abdomen light tan (Fig. 149) to light gray, darker specimens with a median gray stripe and a pair of lobed, paraxial white stripes extending laterally to abdominal tubercles (Fig. 148). Male abdomen tan, without dorsal humps. Four stout tracheal trunks extend into cephalothorax.

Male Palpus. Palpal femur's retrolateral tubercle (Fig. 152) smaller than that of *U. penicillatus* and *U. segregatus* (Figs. 134, 144). Median apophysis bulb small, with a broad, shallow prolateral notch (Fig. 151). Conductor length and width equal.

Epigynum. Epigynal lobes broad and medially, widely separated at bases (Figs. 154, 155). Spermathecae oval with short ducts (Fig. 156).

Distribution. Florida and Gulf Coast states through Central America to Venezuela (Map 2).

Purumitra Lehtinen
Figures 157–161; Map 1

Purumitra Lehtinen, 1967, Ann. Zool. Fennici, 4: 261. Type species by original designation and monotypy *Uloborus grammicus* Simon, 1893, Ann. Soc. ent. France, 62: 68. Male holotype from Manila, Philippine Islands, in Muséum National d'Histoire Naturelle, examined. The genus name is feminine.

Note. Three female and two male specimens of *P. grammicus*, collected from epiphytes in the rainforest near Kolonia, on the Micronesian island of Ponape by M. Sabath on 27 January 1970 (in the Museum of Comparative Zoology); allow females of this genus to be described for the first time.

Diagnosis. Females are distinguished from those of other uloborid genera by having an epigynum with eight ventral atria (Fig. 160). The palp of *Purumitra* males (Fig. 157), like those of *Zosis* (Plate 7-C) and *Octonoba* (Plate 6-C) has a tegular spur, but unlike *Zosis* they have a broad, concave median apophysis spur and a small, narrow tegular spur. Their anterior eye row is strongly recurved such that a line across the AMEs' posterior margins passes half an ALE diameter anterior to the ALEs rather than along the ALEs' anterior border as in *Octonoba*. Unlike the males of either genus, their large median apophysis bulb is flattened and its lateral surface has a sclerotized ridge running between two depressions. *Purumitra* males are smaller than those of *Zosis* and *Octonoba*, having a carapace length of less than 0.9 mm.

Description of Type Species. Female total length 3.0 mm, carapace length 0.8 mm, sternum length 0.6 mm. Male carapace length 0.8 mm, sternum length 0.4 mm. Length and width of female carapace equal, male carapace 0.84 as wide as long. In lateral view cephalic region of female carapace level and straight thoracic region slopes to petiole. In males carapace highest just anterior to thoracic depression, its cephalic region sloping downward to ocular area and its rounded thoracic region sloping to petiole. Both eye rows of females and posterior eye row of males recurved such that a line across median eyes' posterior margins passes through anterior quarter of posterior eyes' diameter (Fig. 159). Anterior eye row of males more strongly recurved so that such a line passes half an ALE diameter anterior to ALE anterior margin. Median ocular area nearly square, its length and anterior width four-fifths its posterior width. Clypeus in anterior view three-fifths AME diameter. Sternum of female 0.69 and of male 0.78 as wide as long. Female palpal femur not flattened. Female calamistrum half as long as metatarsus IV. Femur I of females 2.0 and of

males 1.9 times carapace length. Abdomen teardrop-shaped (Fig. 159) without tubercles, its maximum width and height half its length and attained midway along its length. Coloration of males and females similar. Carapace very light tan with broad, brown paraxial stripes extending its full length (Fig. 159). Thoracic region with thin gray marginal stripes. Sternum tan with thin gray margins. Dorsum of abdomen white with a gray posterior tip, venter gray with a thin median longitudinal white stripe, and lateral abdominal surfaces white with a wide dorsal gray longitudinal stripe and a broken ventral gray longitudinal stripe. Numerous fine tracheoles extend into cephalothorax.

Male Palpus. No ventral femoral tubercles are visible. Broad cymbium with two apical macrosetae (Fig. 157). Small proximal portion of the tarsus includes a middle hematodocha and gives rise to a large, somewhat flattened median apophysis. Retrolateral face of median apophysis bulb with a heavily sclerotized, curved central ridge between two depressions (Fig. 157). Short, broad median apophysis spur with concave retrolateral depression. Embolus of intermediate length, supported along its proximal surface by a small tegular spur.

Epigynum. The heavily sclerotized ventral epigynal surface has a small anteromedian and a larger posteromedian atrium, each divided laterally by a thin median septum (Fig. 160). Also present are a pair of large, oval, anterolateral atria and a pair of smaller, triangular, posterolateral atria. An opening is located at each dorsolateral margin of the posterior median atria and leads via a very short duct to an oval spermatheca from whose posterior surface a fertilization duct arises (Fig. 161).

Natural History and Distribution. Nothing is known of this genus' natural history. Its only known species is found on central Pacific Islands of the Philippine and Caroline groups.

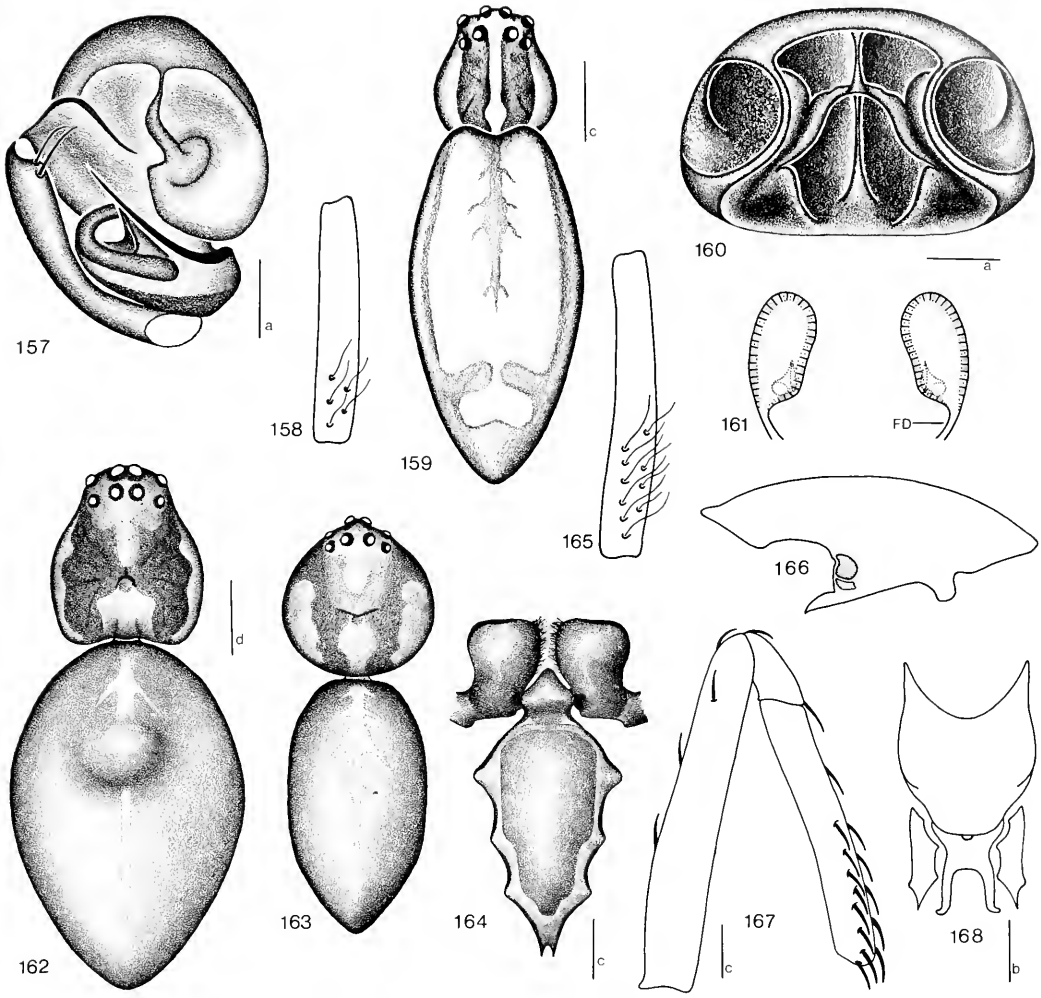
Zosis Walckenaer
Figures 2, 162–174, Plate 7-C; Map 2

Zosis Walckenaer, 1837, Histoire naturelle des Insectes, Aptères, Atlas: 12, pl. 20. Type species by monotypy *Zosis caraibe*. The genus name is masculine.

Orithyia Blackwall, 1858, Ann. Mag. Nat. Hist., 2(3): 331. Type species by original designation *Orithyia williamsii* Blackwall, 1858, *ibid.*

Diagnosis. *Zosis* males (Fig. 173, Plate 7-C) are distinguished by a large tubercle on the proximal, ventral surface of the palpal femur; a broad, flat tegular spur; a dome-shaped median apophysis bulb, and a clawlike median apophysis spur. Females are distinguished by broad, flattened epigynal lobes (Figs. 169, 170) which are medially separated, have posterolateral, triangular sclerites; and form a pair of posterior atria (Fig. 171) in which openings are found. Carapace (Figs. 162, 163) and leg (Fig. 174) color patterns are useful in distinguishing members of this genus.

Description. Female carapace width 0.8 carapace length, male carapace width 0.9 length. Female cephalic region rises only slightly from shallow thoracic depression, thoracic region flat. Conspicuous thoracic groove of males transverse and top of carapace flat, sloping anteriorly with ocular region lower than thoracic region. Female cephalic region at ALE half and male cephalic region 0.4 carapace width (Figs. 162, 163). Female clypeus height in anterior view half and male clypeus height one AME diameter. Anterior and posterior eye rows recurved, posterior such that a line across posterior margins of PME passes through anterior half of PLE diameter. Male AMEs on a mound and anterior eye row more strongly recurved than posterior (Fig. 163). In females the two rows about equally recurved (Fig. 162). Median ocular area nearly square. Sternum width 0.63 times length (Fig. 164). Prolateral surface of female palpal femur slightly flattened. Female first femur 1.8 times and male first femur 1.5 times as long as carapace. Fe-



Figures 157–161. *Purumitra grammica* (Simon). 157. Prolateral view of male palpus. 158. Dorsal view of female right first femur. 159. Dorsal view of female. 160. Ventral view of epigynum. 161. Dorsal view of cleared epigynum. Figures 162–168. *Zosis geniculatus* (Olivier). 162. Dorsal view of female. 163. Dorsal view of male. 164. Female sternum, endites, and labium. 165. Dorsal view of female right first femur. 166. Retrolateral view of female left first patella showing lyriform organs. 167. Prolateral view of male left first femur, patella, and tibia. 168. Dorsal view of female lorum.

male calamistrum half length of metatarsus IV. Male first femur with one distal prolateral and three dorsal macrosetae (Fig. 167). Tibia I with eight distal prolateral, seven retrolateral, and nine dorsal macrosetae. Width and height of female abdomen three-fifths its length, usually with a single, median tubercle in anterior third of its dorsum (Fig. 162). Male abdomen oval without tubercles, its height and width half its length (Fig. 163). Coloration of members of this genus is distinctive and given in detail under the species description. Tracheal system characterized by small tracheoles extending to cephalothorax (Fig. 2).

Male Palpus. Proximal ventral surface of femur with one small median and one large lateral tubercle (Plate 7-C). Two long setae project from the cym-

bium's tip. Middle hematodocha large and its dome-shaped median apophysis bulb bears a hooked median apophysis spur (Fig. 173, Plate 7-C). A broad, flat tegular spur serves as a guide for the embolus, running along its proximal surface and nearly meeting the median apophysis. The small, flat, unsclerotized lobe arising from the median apophysis bulb's center may be homologous with the well-formed conductors of *Philoponella*, *Ponella*, *Miagrammopes*, and *Uloborus*.

Epigynum. In ventral view two flattened, weakly sclerotized posterior lobes extend either posteriorly (Fig. 169) or ventrally (Fig. 170). Posterolateral or ventrolateral margins of the widely separated posterior lobes each have a triangular sclerite (Fig. 169). Posterior surface of each lobe forms an atrium at whose median margin an epigynal opening is located (Fig. 171). Dorsally, the two crypts merge and are bordered by the straight, ventral posterior plate border. In posterior view this plate is twice as wide as high. Duct leading from each epigynal opening loops twice before entering a spherical spermatheca from whose posterior surface a fertilization duct arises (Fig. 172).

Note. The cosmotropical species *Zosis geniculatus* is the only member of this genus I recognize for the New World. The smaller *Uloborus costalimae* Mello-Leitão, 1917 female which has a total length of 4.0 mm, a carapace length of 1.2 mm, and a median hump on the abdomen's dorsum may represent a second American species. However, the female holotype (and only specimen discovered in this study), collected from the Brazilian state of Alagoas by Costa Lima and housed in the Museu Nacional of Rio de Janeiro, Brazil, has been dried and is not in good enough condition to allow a useful redescription of this species.

Natural History and Distribution. This species appears to have good powers of dispersal, to be commonly associated with man-made structures, and to be quite resistant to desiccation. The latter two factors suggest that it may have been introduced into many areas through commerce. In the New World this cosmotropical species of orb-weavers is found from the Gulf Coast states of the United States through Central America and the West Indies, and into the northern two-thirds of South America.

Zosis geniculatus (Olivier)
Figures 2, 162–174, Plate 7-C; Map 2

Aranea geniculata Olivier, 1789, Araignée, Aranea. *in* Encycl. méth., Hist. nat., Inst. Paris, 4: 214.

Zosis caraibe Walckenaer, 1837, Histoire naturelle des Insectes, Aptères, Atlas: 12, pl. 20. Female holotype lost.

Uloborus zosis Walckenaer, 1841, Histoire naturelle des Insectes, Aptères, 2: 231.

Uloborus latreillei Thorell, 1858, Öfvers. Kongl. Vet. Akad. Förh., 15: 196.

Orithyia williamsii Blackwall, 1858, Ann. Mag. Nat. Hist., 2(3): 331. One male, one female, and one immature syntypes from Amboina Island, Amboina (Moluccas) Islands, bottle 161, tube 2, University Museum, Hope Department of Entomology, Oxford University, examined.

Uloborus domesticus Doleschall, 1859, Act. Soc. sci. Ind.-Neerl., 5: 46. Not with other Doleschall types in Rijksmuseum van Natuurlijke Historie, Leiden, Holland; presumed lost.

Uloborus williamsii:—O. Pickard-Cambridge, 1871, Proc. Zool. Soc. London, 1871: 617.

Uloborus geniculatus:—Thorell, 1890, Ann. Mus. civ. stor. nat. Genova, 10(2): 291. Bonnet, 1957, Bibliographia Araneorum, 2: 4762. Muma and Gertsch, 1964, Amer. Mus. Novitates, 2196: 37.

Zosis geniculatus:—Lehtinen, 1967, Ann. Zool. Fennici, 4: 277.

Description. Male total length 4.0 to 6.3 mm ($\bar{X}$ = 4.96, SD = 0.77, N in all cases = 13). Carapace length 1.6 to 2.5

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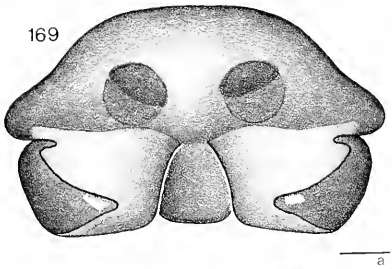
Figures 169–174. *Zosis geniculatus* (Olivier). 169, 170. Ventral view of epigynum. 171. Posterior view of epigynum. 172. Dorsal view of cleared epigynum. 173. Retrolateral view of male palpus. 174. Dorsal view of female left first femur, patella, and tibia. Figures 175–180. *Octonoba* species 3. 175. Female carapace. 176. Male carapace. 177. Retrolateral view of apical region of male left palpus. 178. Ventral view of epigynum. 179. Posterior view of epigynum. 180. Dorsal view of cleared epigynum.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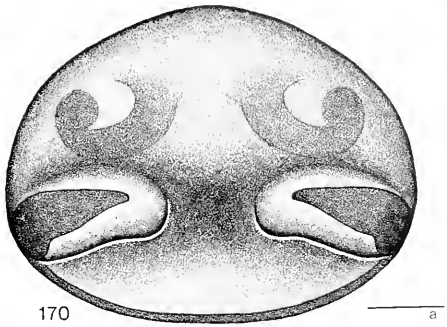
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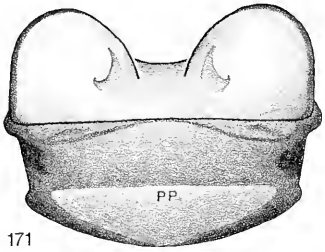
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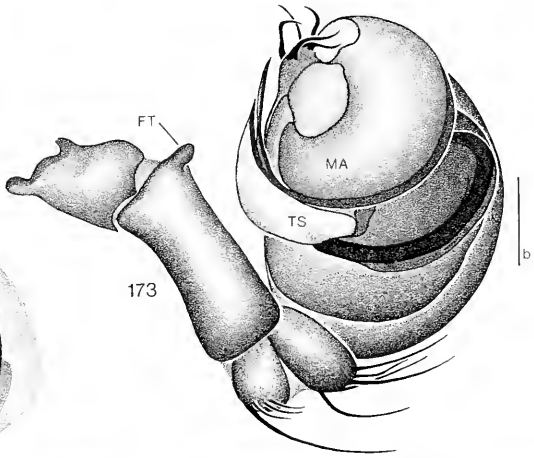
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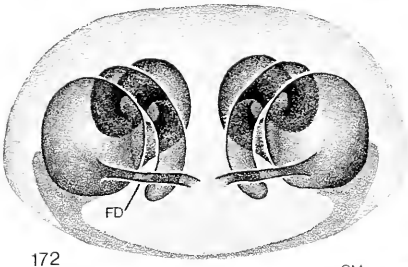
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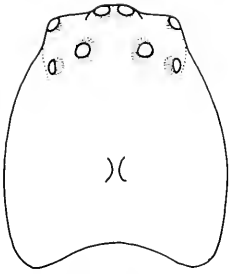
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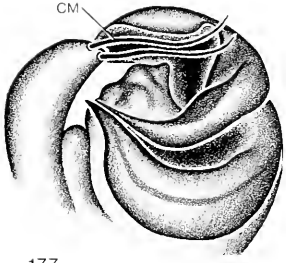
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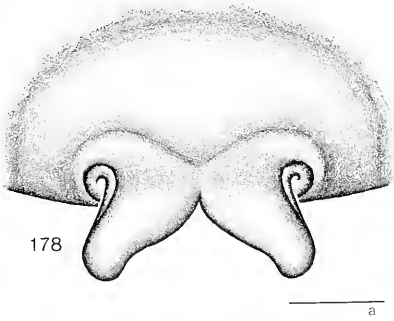
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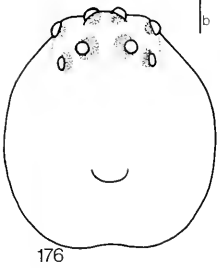
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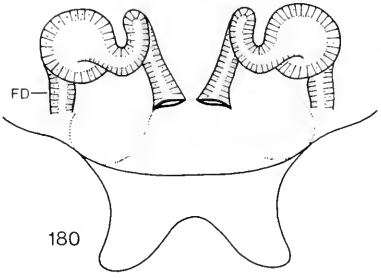
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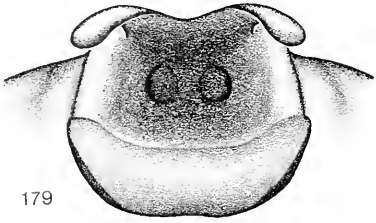
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mm ($\bar{X}$ = 2.03, SD = 0.23), sternum length 1.0 to 1.5 mm ($\bar{X}$ = 1.20, SD = 0.15). Female total length 6.3 to 8.4 mm ($\bar{X}$ = 7.21, SD = 0.47), carapace length 2.0 to 2.6 mm ($\bar{X}$ = 2.35, SD = 0.17), sternum length 1.2 to 1.8 mm ($\bar{X}$ = 1.52, SD = 0.15, N in all cases = 15). Coloration of males and females similar (Figs. 162), 163). Carapace gray to reddish brown with light lateral margins, cephalic region, and posterior median region. Sternum tan, often slightly darker in center than at margins (Fig. 164). Coloration of all legs similar to first leg (Fig. 174) except for four to six dark spots on proximal region of femur which are found only on legs I and II. Matatarsi and tarsi brown with no conspicuous bands. Abdomen usually white without conspicuous markings.

Octonoba new genus
Figures 175–185, Plates 6-C, D, 7-D; Map 1

Type. The type species of this genus is *Uloborus octonarius* Muma, 1945, Proc. Biol. Soc. Washington, 58: 91. Male holotype and female paratype from College Park, Maryland, collected 7 July 1943 by W. F. Jeffers and M. H. Muma, in the American Musum of Natural History, examined. The genus name is an arbitrary combination of letters and is feminine.

Note. Examined material contained four distinct *Octonoba* species, of which I am able to identify only *O. octonaria.* Consideration of the remaining three Oriental species is necessary for an understanding of the genus. Designation of these as species 1–3 is done for clarity and is not an attempt to name any of these species. To do so without careful examination of the types of all Oriental species likely to belong to this genus would be unwise. Lehtinen (1967) synonymizes *U. octonarius* and *U. sinensis* Simon, 1880 from China, placing the newly combined species into the genus *Zosis.* To this genus he also adds *U. varians* Bösenberg and Strand, 1906 from China and Japan (which he synonymizes with *U. defectus* Bösenberg and Strand and *U. dubius* Bösenberg and Strand, 1906), *U. sybotides* Bösenberg and Strand, 1906 from Japan, *Argyrodes yesoensis* Saito, 1934 from Japan. Lehtinen also places *U. mundior* Chamberlin and Ivie, 1936; *U. costalima* Mello-Leitão, 1917; and *U. ursinus* Mello-Leitão, 1917 into the genus *Zosis.* Lehtinen indicates he did not examine type specimens of *U. octonarius* and I cannot accept his synonymy of *U. octonarius* and *U. sinensis.* Type specimens of *Uloborus ursinus* and *U. costalimae* were damaged (the former's abdomen lost and the latter dried) and cannot be treated with certainty. *Uloborus mundior* is a synonym of *Philoponella republicana.* I agree with Lehtinen that *U. octonarius* is more closely related to *Zosis* than to any other genus (except possibly *Purumitra*) and that it bears a striking resemblance to several Oriental species. However, I believe that these species are more related to one another than any one is to *Zosis geniculatus* and for this reason propose *Octonoba* as a new genus.

Diagnosis. *Octonoba* males are distinguished from those of all other uloborids except *Purumitra* by having both an enlarged, concave median apophysis and a conspicuous hematodocha (Plates 6-C, D; 7-D). *Octonoba* males are distinguished from those of *Purumitra* by having: 1. a carapace length greater than 1.4

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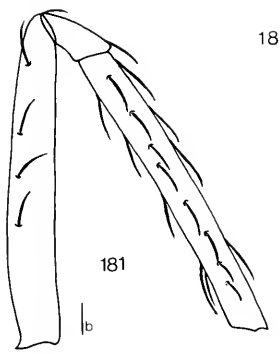
Figures 181–182. *Octonoba* species 3. 181. Retrolateral view of male left first femur, patella, and tibia. 182. Dorsal view of female right first femur. Figures 183–185. *Octonoba* species 1. 183. Prolateral view of male left first femur, patella, and tibia. 184. Ventral view of epigynum. 185. Posterior view of epigynum. Figures 186–191. *Daramuliana gibbosa* (L. Koch). 186. Female carapace. 187. Lateral view of female carapace. 188. Lateral view of female abdomen. 189. Ventral view of epigynum. 190. Dorsal view of cleared epigynum. 191. Dorsal view of female right femur. Figures 192–197. *Ponella lactescena* (Mello-Leitão). 192. Female carapace. 193. Male carapace. 194. Lateral view of female carapace. 195. Dorsal view of female. 196. Dorsal view of female right first femur. 197. Lateral view of female abdomen.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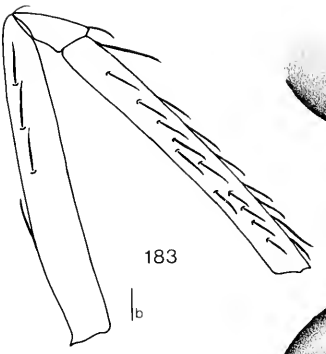
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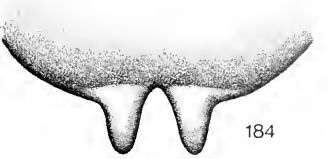
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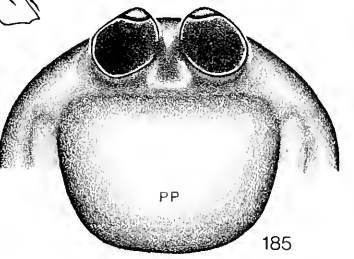
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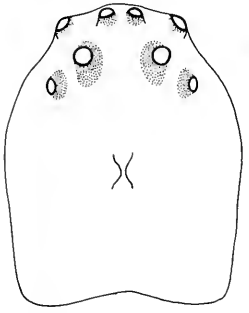
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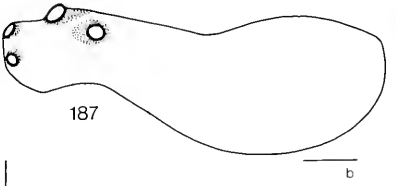
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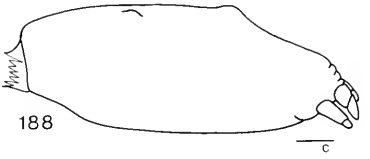
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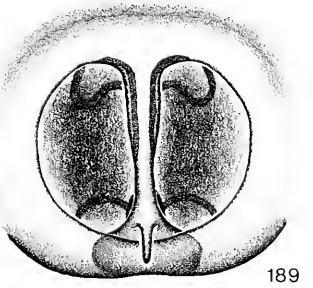
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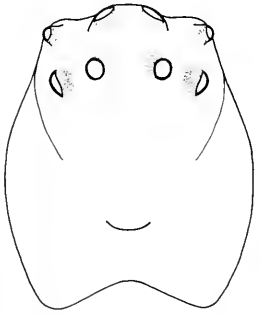
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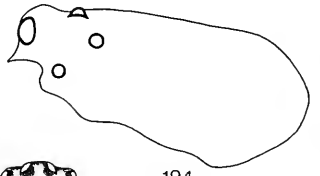
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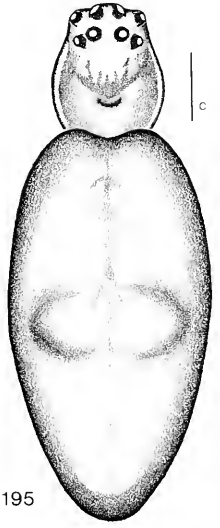
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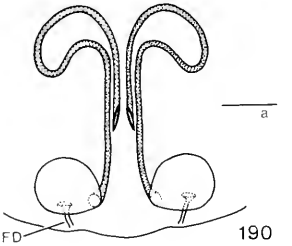
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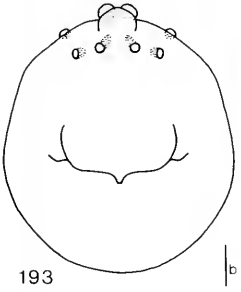
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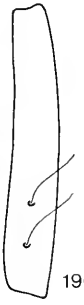
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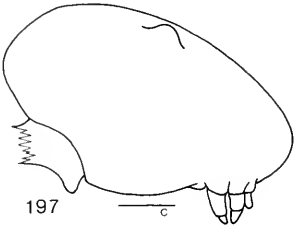
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mm rather than 0.9 mm or less, 2. first femur no greater than 1.7 (rather than twice) the carapace length, and 3. by having a more reduced median apophysis bulb. *Octonoba* and *Uloborus* females have slender, posterolateral epigynal lobes which are contiguous at their bases (Figs. 137, 145, 178, 184). The posterior eye row of *Octonoba* (Figs. 175, 176) recurved such that a line across the PMEs' posterior margins passes along the PLEs' anterior margins; whereas in *Uloborus* it passes at least one quarter PLE diameter anterior to the PLE (Figs. 132, 133). In *Octonoba* females the median ocular area's anterior width is 0.7 its posterior width; whereas the median ocular area of *Uloborus* is square. *Octonoba* females have a conspicuous atrium (Fig. 179) or pair of atria on the epigynum's posterodorsal surface (Fig. 185) which is absent in *Uloborus* (Figs. 138, 146).

Description. Female total length 4.2 to 5.2 mm, carapace length 1.5 to 1.6 mm, sternum length 0.9 to 1.0 mm. Male total length 4.0 to 4.8 mm, carapace length 1.4 to 1.8 mm, sternum length 0.8 to 1.0. Carapace width 0.85 to 0.88 its length. Cephalic and thoracic regions flat in lateral view, PMEs at the same height as shallow thoracic pit. At ALEs the cephalic regions' width two-thirds maximum carapace width in females and half in males (Figs. 175, 176). Both eye rows recurved such that a line across median eyes' posterior margins passes along anterior margin of lateral eyes (Figs. 175, 176). Median ocular area's anterior width and length 0.7 its posterior width. In anterior view clypeus height of males three-fifths an AME diameter and of females five-sixths an AME diameter. Sternum width 0.65 to 0.72 its length. First femur 1.50 to 1.65 times carapace length. Female palpal femur not flattened and calamistrum half as long as metatarsus IV. Male first femur with three to four prolateral, one to three retrolateral, and one dorsal macroseta (Figs. 181, 183). First tibia with 11 to 16 prolateral, three to four retrolateral, five to eight dorsal, and zero to five ventral macrosetae. Height and width of female abdomen 0.6 its length, with four pairs of small paramedian tubercles. Male abdomen half as wide and two-fifths to three-fifths as high as long. Carapace brown with a thin median light stripe and a pair of light, marginal, longitudinal stripes. Numerous fine tracheoles extend into cephalothorax.

Male Palpus. Femur with two nearly equal-sized proximal tubercles on a ventral mound (Plate 6-A, D). Two stout terminal spines extend from cymbium's tip. Middle hematodocha large and tegulum of two species a spur along embolus' proximal surface (Fig. 177, Plate 6-C). In *O. octonaria* (Plate 7-D) tegular spur small, apparently providing little support for embolus, but in species 1 where it is long and grooved (Plate 6-C), tegular spur probably affords some embolic support. In *O. octonaria* and species 1 median apophysis bulb is a small, convex, semicircular sclerite whose spur is enlarged and has a proximal surface that is either concave (species 1) (Plate 6-C) or rolled inward at the edges to form a tube (*O. octonaria*, Plate 7-D). A small irregular, unsclerotized lobe arising from the median apophysis bulb's center (Plate 7-D) may be homologous with the conductor of *Philoponella*, *Ponella*, *Miagrammopes*, and *Uloborus*. Reduction in size of the median apophysis bulb and tegular spur appears associated with enlargement of the median apophysis spur. This is seen when species 1 (Plate 6-C) and species 3 (Fig. 177), *O. octonaria* (Plate 7-D) and species 2 (Plate 6-D) are compared. In species 2 (Plate 6-D) where the median apophysis spur forms a U-shaped trough, the tegular spur is lost, and the median apophysis bulb reduced to a small, flat plate. The embolus of *O. octonaria* and species 1 is long and thin. That of species 2 (Plate 6-D) has a broad base and short central radix.

Epigynum. The epigynum consists of either: 1. a ventral mound with two pos-

terolateral lobes, each with a dorsal, circular atrium at its base (Figs. 184, 185), or 2. a ventral mound with two posterior lateral lobes extending over a common posterior atrium (Figs. 178, 179). The latter condition is similar to that of *Zosis geniculatus* (Figs. 169–171) and it is interesting to note that the male tegular spurs of both species are broad and long. The convex posterior plate is one-fourth to three-fourths as high as broad (Figs. 179, 185). A duct leads from each atrium or from each lateral margin of the common atrium to a spherical spermatheca from whose posterior surface a fertilization duct arises (Fig. 180).

Natural History and Distribution. Octonoba octonaria spins an approximately horizontal orb-web similar to many other uloborids (Eberhard, in preparation). This species is known only from the United States where its range extends from Maryland through Alabama, north-central Texas, and eastern Kansas. Species 1 comes from Kunming in the southwestern Chinese province of Yunnan, species 2 from Okinawa, and species 3 from Taiwan.

Daramuliana Lehtinen
Figures 186–191; Map 1

Daramuliana Lehtinen, 1967, Ann. Zool. Fennici, 4: 227. Type species by original designation *Uloborus gibbosus* L. Koch, 1871, Arachn. Austral., 1: 1, 228. Female holotype from Upolus, Samoa, in Zoologisches Museum, Hamburg, examined. The generic name is feminine.

Diagnosis. Daramuliana females are characterized by having: 1. a medially divided, circular, ventral epigynal atrium (Fig. 189), 2. a carapace whose width is 0.75 its length (Fig. 186), and an abdomen which is 0.38 as wide as long and has a median, dorsal tubercle in the posterior 0.57 of its length (Fig. 188).

Description of Type Species. Female. Total length 4.0 to 4.6 mm, carapace length 1.3 to 1.5 mm, and sternum length 0.8 to 0.9 mm. Carapace width three-fourths carapace length. Cephalic and thoracic regions each slope upward from a shallow thoracic depression (Figs. 186, 187). At ALEs cephalic area half as wide as carapace. Both eye rows recurved, the anterior such that a line across AMEs' posterior margin passes through anterior quarter of ALEs' diameter and posterior such that a line across PLEs' posterior margin passes two-thirds a PLE diameter anterior to PLEs' anterior margin (Fig. 186). Median ocular area's anterior width half and its length two-thirds its posterior width. Clypeus height in anterior view two-fifths AME diameter. Sternum width 0.42 length. Female palpal femur slightly flattened. First femur twice as long as carapace. Calamistrum half as long as metatarsus IV. Abdomen width and height 0.38 length, median tubercle in posterior 0.57 of the its length (Fig. 188). Fine tracheoles arising from two stout tracheal trunks appear restricted to the abdomen.

Epigynum. On the epigynum's ventral surface is a medially divided circular atrium (Fig. 189). An epigynal opening is found at the posteromedian margin of each atrial half, near the base of a small scape on the median septum's posterior margin. From each opening a long, thin duct extends anteriorly and then loops posteriorly to connect to a spherical spermatheca from whose posterior margin a ferlization duct arises (Fig. 190).

Natural History and Distribution. Nothing is known of the natural history of the members of this genus. Its two recognized species (Lehtinen, 1967) have been collected on Australia, Samoa, and on Viti Levu in the Fiji Islands.

Ponella new genus
Figures 192–202; Map 1

Type. Type species *Uloborus lactescens* Mello-Leitão, 1947, Boletim do Museu Nacional (N.S.), Rio de Janeiro, Zoologia, No. 80: 4. The genus name is an arbitrary combination of letters and is feminine.

Diagnosis. Members of this genus have a total length of less than 3.0 mm. *Ponella* (Fig. 193), *Zosis* (Fig. 163), and

Philoponella (Figs. 205, 217) males have an oval carapace with a wide, transverse thoracic groove and AMEs on a small mound. *Ponella* males are distinguished by having a long, narrow conductor which lies along the embolus' distal surface, lacks a basal lobe, and has a slender, distal branch (Fig. 201). First tibia of males (Fig. 202) has three prolateral, three retrolateral, and four dorsal macrosetae—fewer than either *Zosis* or *Philoponella*. *Ponella* females are distinguished by having a pair of low, widely separated, ventral epigynal mounds anterior to which a pair of openings is found (Figs. 198, 199).

Description. Carapace about 0.9 times as wide as long. Male thoracic groove deep and transverse and carapace dorsally flat (Fig. 193), slanting forward so that cephalic region is much lower than thoracic region. Transverse female thoracic groove narrow but conspicuous (Figs. 192, 195), cephalic and thoracic regions about equal in height (Fig. 194). At level of ALEs female cephalic region 0.70 times and male cephalic region 0.60 times carapace width. Male AMEs on a small, prominent, anteriorly directed mound (Fig. 193), but in females this mound is not distinct (Fig. 192). Both eye rows recurved, the posterior only slightly so such that a line across posterior margins of PMEs passes through center of PLEs. Such a line across AMEs' posterior margins passes across anterior margins of ALEs of females and in males 1 to 1.5 ALE diameters anterior to ALEs. In anterior view female clypeus height half an AME diameter and in males two AME diameters. Median ocular area of females square and of males slightly longer than wide. Sternum width 0.67 its length. First femur 1.1 times as long as carapace in females and in males equal to carapace length. Female calamistrum half as long as metatarsus IV. Male first femur with one dorsal, two distal prolateral, and two distal retrolateral macrosetae. Female abdomen half as wide and two-thirds as high as long, with two dorsal humps at or slightly anterior to its center (Figs. 195, 197). Male abdomen oval without humps, its width and height two-thirds its length. Fine tracheoles extend into the cephalothorax.

Male Palpus. Femur with two proximal, ventral processes; a large lateral one and a smaller median one. No conspicuous macrosetae visible on distal cymbial rim. Middle hematodocha well developed giving rise to a median apophysis consisting of a flat bulb with a large lateral hooked spur (Fig. 201). Conductor with a short cylindrical proximal lobe and a long, thin distal branch about five times as long as wide and with proximal surface trough-shaped to receive the embolus.

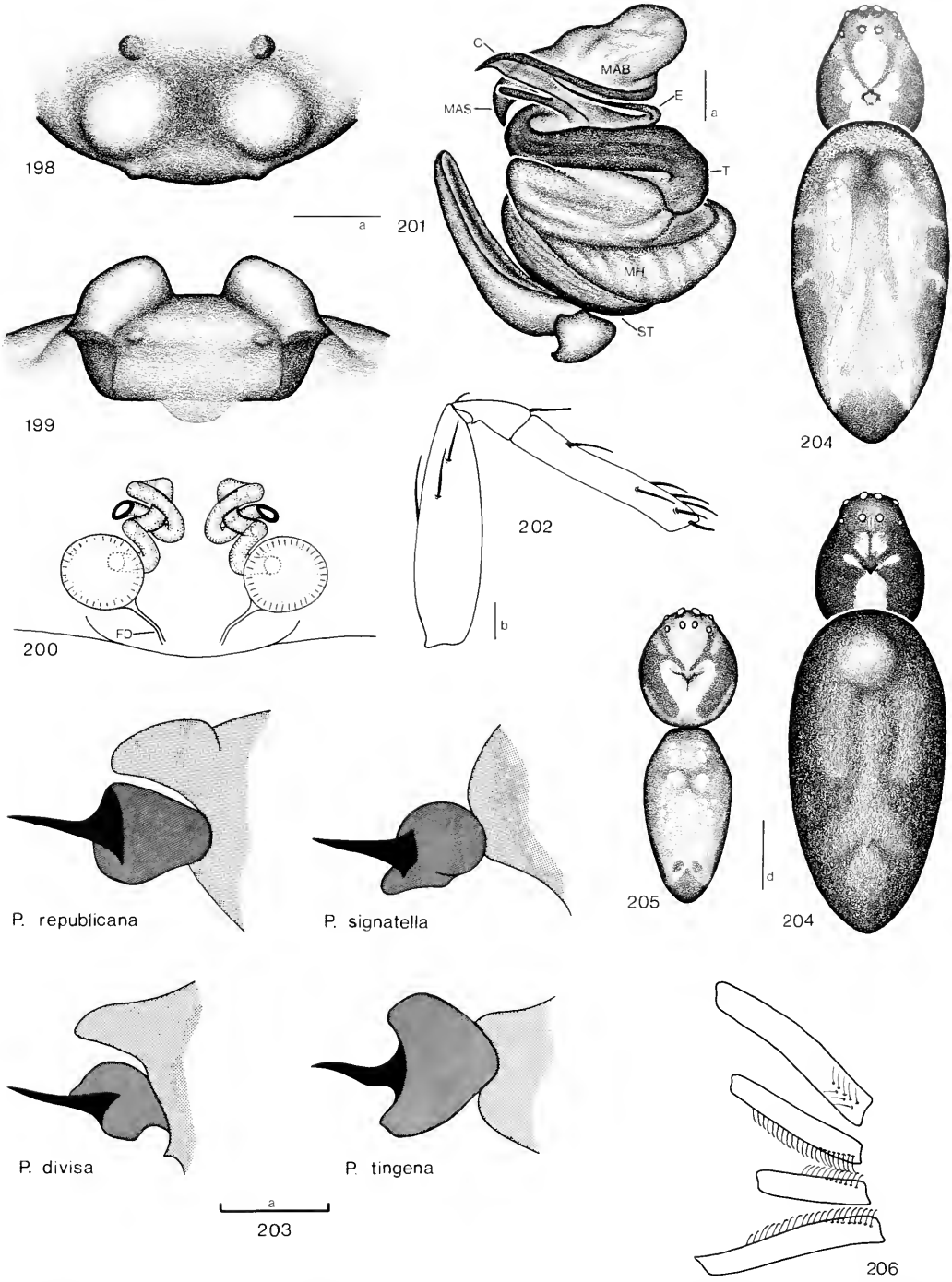
Epigynum. In ventral view (Fig. 198) two light, slightly raised posterior lobes appear near epigynum's posterior edge. Anterior to these is a pair of small, inconspicuous openings. In posterior view (Fig. 199) a posterior plate extends between the lobes and bears a pair of small midlateral bumps. From each opening a duct makes four loops before connecting with a large, thick-walled spermatheca from whose posterior margin a fertilization duct arises (Fig. 200).

Natural History and Distribution. The one described species of this genus has been collected from Paraguay and southern Brazil. One female was collected with a chain of three flat, stellate eggsacs, each about 4.0 × 2.8 mm.

Ponella lactescena (Mello-Leitão), new combination
Figures 192–202; Map 1

Uloborus lactescens Mello-Leitão, 1947, Boletim do Museu Nacional (N.S.), Rio de Janeiro, Zoologia, No. 80: 4. Immature female and one mature male syntypes from Carmo do Rio Claro in the Brazilian state of Minas Gerais, collected by J. C. M. Carvalho, in the Museu Nacional of Rio de Janeiro, Brazil, examined.

Description. Male. Total length 2.8 mm, carapace length 1.3 mm, sternum length 0.7 mm. Fourth coxae separated by a distance equal to the width of each. Carapace tan with no conspicuous color



Figures 198–202. *Ponella lactescena* (Mello-Leitão). 198. Ventral view of epigynum. 199. Posterior view of epigynum. 200. Dorsal view of cleared epigynum. 201. Retrolateral view of male left palpus. 202. Prolateral view of male left first femur, patella, and tibia. Figure 203. Apical views of left median apophysis spurs of *Philoponella republicana* species group. Figures 204–206. *Philoponella republicana* (Simon). 204. Dorsal view of female. 205. Dorsal view of male. 206. Dorsal view of female left femora, showing position of trichobothrial rows.

markings. Sternum tan with light gray anterior margin and center. Dorsum of abdomen light with flecks of white and with light gray posterior tip. Venter with gray patch between booklung covers and a broad, light gray median area. Legs tan.

Female. Total length 3.0 to 3.5 mm, carapace length 0.9 to 1.1 mm, sternum length 0.7 mm. Carapace light gray with narrow white border, lighter ocular region, and darker patch at posterior cephalic region (Fig. 195). Eyes encircled by dark gray rings. Sternum dark gray. Dorsum of abdomen light with no markings except gray posterior tip in some specimens. Venter dark gray with two think widely spaced white paraxial stripes running its entire length. Legs with no conspicuous color markings.

Distribution. Eastern Paraguay and southern Brazil.

Philoponella Mell-Leitão
Figures 1, 203–288, Plates 6-E, 7-B; Maps 3–5

Philoponella Mello-Leitão, 1917, Arch. Esc. Sup. Agr. Med. Veter., 1(1): 8. Type species by original designation and monotypy *Uloborus republicanus* Simon, 1891, Ann. Soc. ent. France, 60: 8. The genus name is feminine.

Note. Until Lehtinen, 1967, Ann. Zool. Fennici, 4: 258, resurrected this genus, the name *Philoponella* was not recognized by anyone other than its author. However, its first formal synonymy with *Uloborus* was by Roewer, 1954, Katalog der Araneae, 2(b): 1344. This genus corresponds with the *Uloborus republicanus* species group Muma and Gertsch, 1964, Amer. Mus. Novitates, 2196: 29. In addition to the type species, *U. republicanus*, this species group contained *U. variegatus*, *U. oweni*, *U. arizonicus*, and "a series of similar species from the Americas."

Diagnosis. *Philoponella* males are distinguished by having: 1. an oval carapace with a broad, transverse thoracic groove (Figs. 205, 217), 2. a nearly straight posterior eye row with about equally spaced eyes, 3. a clypeus height 0.6 to 1.5 an AME diameter, 4. a well-developed conductor spur (Plate 7-B), and 5. a first tarsus with four to five prolateral, four to five retrolateral, and six to eight dorsal macrosetae. Females are characterized by having: 1. a nearly straight posterior eye row with about equally spaced eyes (Figs. 204, 216), and 2. a ventral epigynal atrium whose posterior margin is formed by two lateral lobes (Figs. 208, 239, 250, 287).

Description. Carapace width 0.9 to 1.0 mm long. At ALEs cephalic region of females gradually narrowed to about half maximum carapace width; that of all males except those of *P. tingena* less conspicuously narrowed, making their carapace oval (Figs. 205, 217). Cephalic region rises slightly from a narrow transverse or semicircular thoracic groove to the ocular area. The AMEs on a low anteriorly directed mound, more prominent in males than in females. Eyes in two recurved rows, posterior row only slightly curved so that a line across PMEs' posterior margins passes through or posterior to the PLEs' centers (Fig. 204). Median ocular area is either square or 0.8 as wide anteriorly as posteriorly. The AME-ALE separation two to three times AME separation and PME-PLE separation 0.6 to 1.0 times PME separation. Clypeus height in anterior view 0.7 to 1.5 times an AME diameter. Sternum width 0.67 length. Endites 1.3 and labium 1.1 times

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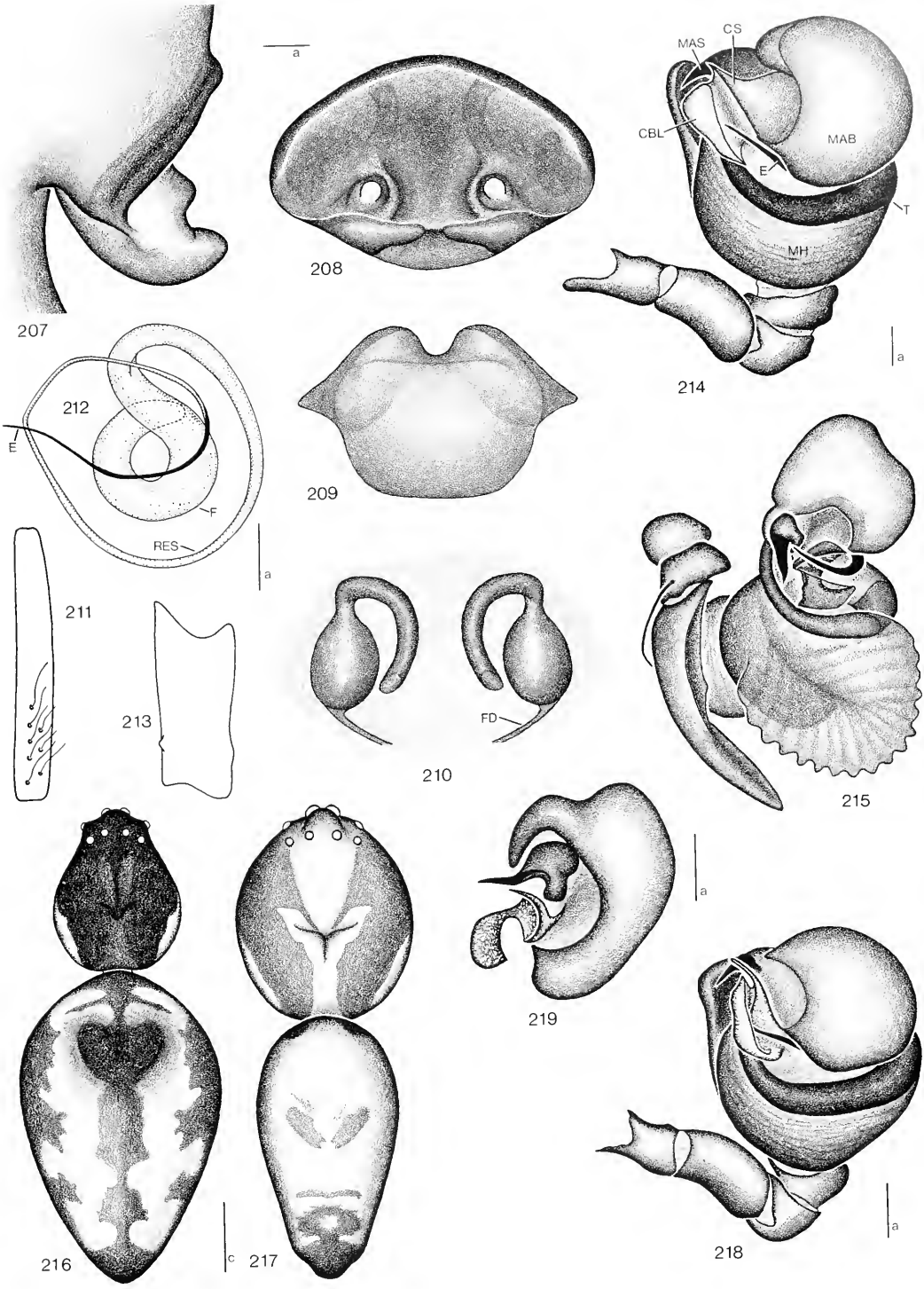
Figures 207–215. *Philoponella republicana* (Simon). 207. Lateral view of epigynum. 208. Ventral view of epigynum. 209. Posterior view of epigynum. 210. Dorsal view of cleared epigynum. 211. Dorsal view of female first femur. 212. Retrolateral view of left embolus (black), sperm reservoir, and fundus. 213. Ventral view of male, left palpal femur. 214. Retrolateral view of male left palpus. 215. Retrolateral view of expanded male left palpus. Figures 216–219. *Philoponella divisa* n. sp. 216. Dorsal view of female. 217. Dorsal view of male. 218. Retrolateral view of male left palpus. 219. Apical view of male left palpus.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as long as wide. Female palpal femur not flattened, calamistrum half as long as fourth metatarsus. Male first femur with three prolateral, one or two retrolateral, and one or two dorsal macrosetae. Male first tibia with four or five prolateral, four or five retrolateral, and six or eight dorsal macrosetae. Abdomen width and height one-third to one-half its length. In females it attains its maximum width about midway along its length and in males in the anterior third of its length. Abdomen height usually attained at or slightly anterior to widest area. Fine tracheoles which arise from two stout tracheal trunks are restricted to the abdomen (Fig. 1).

Male Palpus. Femur's ventral surface with one or two small, proximal tubercles (Figs. 213, 269). Tarsus with two long, apical cymbial setae and a large middle hematodocha (Plate 7-B). A grooved conductor blade arises near the proximal, ventral border of the median apophysis bulb and continues as a narrow, heavily sclerotized conductor spike into the proximity of the median apophysis spur. Proximal conductor lobe may be nearly square, weakly sclerotized, and often difficult to see as in the *republicana* group (Figs. 214, 215; Plate 7-B) or it may be longer than broad, heavily sclerotized, and conspicuous as in the *vittata* (Fig. 270) and *semiplumosa* (Fig. 253) groups.

Epigynum. Females are characterized by a well sclerotized epigynum with a large, deep, central atrium (Figs. 208, 239, 250, 287) bordered by precipitous anterior (except in *P. vittata*, Fig. 266) and posterior rims. Posterior rim bears an epigynal opening at each anterior lateral margin and may be continuous (Figs. 250, 275, 287) or comprised of two distinct lobes joined medially (Figs. 208, 239). Openings may be at the atrium's center (Fig. 250) or in the atrium's posterior half (Figs. 208, 230, 266) and are separated by a distance of half (Fig. 208) to 0.8 (Fig. 250) the epigynum's width. Anterior and posterior rims may be contiguous (Figs. 250, 259, 275) or separated laterally by wide troughs (Figs. 208, 221, 239). Epigynal ducts make one or two loose 180° loops (Figs. 223, 268) or spiral tightly around themselves (Figs. 252, 277) before connecting to a pair of spermathecae from whose posterior margins fertilization ducts lead. The *republicana* species group appears more primitive than the *semiplumosa* group. In *semiplumosa* females there is more extensive coiling and spiraling of ducts (Fig. 252), more complete median fusion and anterolateral displacement of epigynal openings and closure of lateral epigynal troughs. Members of the *fasciata* species group have coiled epigynal ducts (Fig. 277) and closed epigynal troughs (Figs. 275, 287) indicating they are intermediate between the two other species groups.

Natural History and Distribution. Members of many species in this genus are found in colonies consisting of numerous orb-webs built in a common, irregular framework. Some webs are associated with those of spiders belonging to other families (see family Natural History section). In the New World, members of this genus are found from the extreme southern central United States southward as well as in the West Indies (Maps 3–5). The genus is also represented in Oriental and Australian regions.

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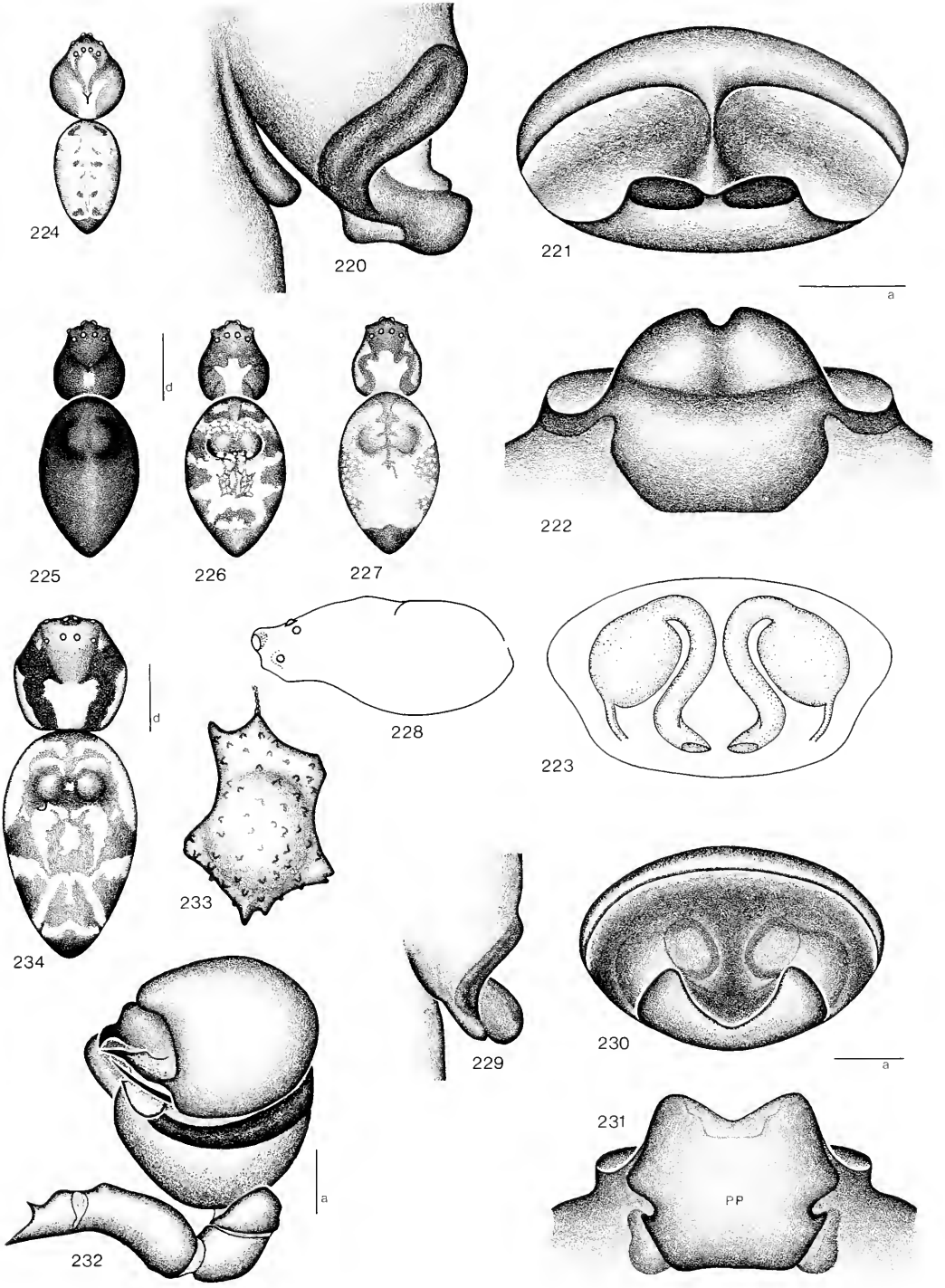
Figures 220–223. *Philoponella divisa* n. sp. 220. Lateral view of epigynum. 221. Ventral view of epigynum. 222. Posterior view of epigynum. 223. Dorsal view of cleared epigynum. Figures 224–232. *Philoponella tingena* (Chamberlin and Ivie). 224. Dorsal view of male. 225–227. Dorsal view of female. 228. Lateral view of female carapace. 229. Lateral view of epigynum. 230. Ventral view of epigynum. 231. Posterior view of epigynum. 232. Retrolateral view of left male palpus. 233. Eggsac. Figure 234. *Philoponella signatella* (Roewer), dorsal view of female.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KEY TO *PHILOPONELLA* FEMALES

1. Clypeus height 0.5 to 0.7 AME diameter; anterior rim of epigynal atrium broad, rounded, and not precipitous (Fig. 266); epigynal openings in posterior sixth of atrium; South America (Map 5) ---- *vittata*

– Clypeus height equal to AME diameter; anterior rim of atrium precipitous and usually narrow (Figs. 208, 239, 250, 275); epigynal openings in anterior half (Figs. 242, 250, 287) to posterior third (Figs. 208, 239) of atrium or, if more posterior, posterior rim projects conspicuously ventrally and has a length equal to that of the anterior rim (Figs. 284, 286) ---------- 2

2(1). Epigynal openings separated by half or less the atrium's width (Figs. 208, 230, 242); precipitous anterior and posterior rims separated by conspicuous lateral or posterolateral troughs (Figs. 208, 221, 239); posterior rim of epigynum 0.4 to 0.6 the epigynum's width and composed of two lateral lobes separated by a median depression or notch (Figs. 209, 222, 231, 240); (*republicana* species group)-------- 3

– Epigynal openings separated by at least three-fourths atrial width (Figs. 250, 259, 275, 287), or if less, posterior epigynal plate as high as wide (Figs. 284, 286); anterior and posterior rims not separated by wide, lateral troughs (Figs. 250, 259, 275); posterior rim at least three-fourths as wide as epigynal atrium and without a deep median indentation or notch (Figs. 250, 251, 275, 276, 287, 288) ------ 7

3(2). Epigynal atrium with a thin, median, longitudinal septum (Fig. 221); posterior margin with a shallow notch separating lobes (Fig. 222); epigynum's posterior face with a middle ridge (Figs. 220, 222); abdominal dorsum with two broad, light paraxial stripes (Fig. 216); Colombia ---- ---------- *divisa*

– Epigynal atrium without a septum (Figs. 208, 239); posterior margin with a deep notch (Figs. 209, 240) or a broad depression separating lobes (Fig. 231); epigynum's posterior face without a ventral rim (Figs. 207, 209, 229, 231, 238, 240); abdominal coloration otherwise (Figs. 204, 226, 234) ---------- 4

4(3). Epigynal atrium shallow with broad, laterally directed troughs (Figs. 208, 242); anterior rim and posterior lobes separated by a distance equal to half the atrial width (Figs. 208, 242); epigynal openings visible in ventral view (Fig. 208, 242) -- 5

– Epigynal atrium deep with posteriorly-directed troughs (Figs. 230, 239); anterior rim and posterior lobes separated by a distance equal to 0.30 the atrial width (Figs. 230, 239); epigynal openings located at the anterior margins of the posterior lobes and hidden in ventral view (Figs. 230, 239) ---------- 6

5(4). Epigynal openings on raised mounds in posterior third of atrium (Figs. 207, 208); total body length more than 5.4 mm; sternum usually dark gray and more than 1.1 mm long; abdominal dorsum with two pairs of light, lateral, longitudinal, diverging white stripes (Fig. 204); Panama and South America (Map 3) -- *republicana*

– Epigynal openings in depressions at atrium's center (Fig. 242); total body length less than 4.2 mm; sternum tan with gray posterolateral margins and less than 0.8 mm long; abdominal dorsum with a broad, light median stripe (Fig. 241); southern Mexico---------- *vicina*

6(4). Posterior epigynal lobes widely separated by a shallow depression (Fig. 231); anterior epigynal rim one-fifth as long as atrium (Fig. 230); total body length less than 4.0 mm; sternum less than 0.8 mm long; Costa Rica, Panama, and Colombia (Map 3). ---------- *tingena*

– Posterior epigynal lobes closely spaced and separated by a deep notch (Fig. 240); anterior epigynal rim half to a third the atrial length (Fig. 239); total body length more than 4.0 mm; sternum length more than 0.9 mm; Honduras through eastern Mexico (Map 3)---------- *signatella*

7(2). Epigynal atrium slightly longer than wide (Fig. 287); epigynal openings in anterior half of atrium (Fig. 287); posterior face of epigynum with two lateral grooves (Fig. 288); northeastern Colombia -- *bella*

– Epigynal atrium about twice as wide as long (Figs. 250, 259, 275, 284); epigynal openings at center of atrium (Figs. 250, 275) or in posterior half (Figs. 259, 284); posterior face of epigynum without lateral grooves (Figs. 251, 262, 276, 286) 8

8(7). Posterior face of epigynum as high as broad (Fig. 286); epigynal openings in the posterior quarter of atrium (Fig. 284); venter of abdomen usually with a dark W mark on a light field (Fig. 282); Paraguay ---------- *para*

– Posterior face of epigynum about twice as wide as high; epigynal openings at or slightly behind the atrium's center; venter of abdomen gray with light paraxial stripes---------- 9

9(8). Anterior atrial rim continues to the epigynum's posterior margin and encloses the broad, dorsally sloping lateral regions of the posterior rim (Fig. 275); large, longitudinal epigynal openings separated by a distance equal to 0.6 the atrial width; Paraguay and southeastern Brazil (Map 5) ---------- *fasciata*

– Anterior and posterior atrial rims end abruptly upon meeting at or slightly posterior to the atrium's center (Figs. 250, 257, 259); small, transverse epigynal openings are separated by a distance equal to 0.8 the atrial width; southwestern United States through Central America and the West Indies (Map 4); (*semiplumosa* species group) 10

10(9). Abdominal venter gray with two narrow, paraxial white stripes (Fig. 249) setose field anterior to cribellum smaller than cribellum; lengths of anterior and posterior epigynal rims equal (Fig. 250); ducts of most specimens do not show through atrial integument; total length less than 4.5 mm, sternum length less than 1.0 mm, southeastern Texas through Central America and the West Indies (Map 4) ..... *semiplumosa*

– Abdominal venter with two broad white stripes (Fig. 256); setose field equal to or larger than cribellum; anterior epigynal rim one quarter the length of the posterior rim (Figs. 257, 259); ducts of most specimens visible through atrial integument; total length greater than 4.6 mm, sternum length more than 1.0 mm 11

11(10). Epigynal atrium less than 0.5 mm wide and 0.4 as long as wide (Fig. 257); epigynum in posterior view without ventrolateral gray lines; most specimens darkly colored (Fig. 255); carapace less than 2.0 mm long; sternum less than 1.4 mm long; southwestern United States and northern Mexico (Map 4) ..... *oweni*

– Epigynal atrium more than 0.6 mm wide and 0.6 as long as wide (Fig. 259); posterior face of epigynum with dark lines (Fig. 262); most specimens with no dark color markings (Fig. 260); carapace more than 2.3 mm long, sternum more than 1.5 mm long; Arizona (Map 4) ..... *arizonica*

KEY TO *PHILOPONELLA* MALES

(Males of *P. vicina* and *P. bella* are unknown.)

1. Carapace high and cylindrical (Figs. 278, 279), transverse thoracic groove deep (Fig. 278), clypeus height twice AME diameter; palpal femur with a retrolateral tubercle whose length is three times its basal width (Fig. 281); median apophysis very small and flat (Fig. 208); Paraguay and southern Brazil (Map 5) ..... *fasciata*

– Carapace low with rounded margins; thoracic groove usually not deep (Figs. 205, 217); clypeus height equal to AME diameter; palpal femur's retrolateral tubercle, if present with a length equal to or less than its basal width (Fig. 269); median apophysis bulb not so reduced (Figs. 214, 235, 253, 270) 2

2(1). Conductor's proximal lobe at least three times as long as broad and easily seen although thin (Figs. 253, 270), at least 1.5 times as long as either the conductor spike or median apophysis spur's apical projection; median apophysis spur's apical (darkest) projection more robust, its length equal to or less than twice its basal width (Fig. 245); median apophysis spur's basal region surrounded by bulb along half of its perimeter (Fig. 245) 3

– Conductor's proximal lobe small, square, and usually difficult to see (Figs. 214, 215, 218, 232, 236), no longer than the conductor spike or median apophysis spur's apical projection (or conductor lobe short and with a long, thin, apical projection running parallel to the conductor spur, Fig. 283); median apophysis spur's apical (darkest) projection long and slender, about three times as long as its basal width (Figs. 203, 272); median apophysis spur's basal region surrounded by bulb along one quarter or less of its perimeter (Figs. 203, 272) 6

3(2). Conductor lobe large (Fig. 270); median apophysis bulb dome-shaped (Figs. 270, 271); dorsum of abdomen with three light chevrons (Fig. 265), venter with a light chevron midway between spinnerets and epigastric furrow; South America (Map 5) ..... *vittata*

– Conductor lobe small (Fig. 253); bulb flattened (Fig. 253); abdomen not so marked (Figs. 248, 258, 261); southwestern United States through Central America and West Indies 4

4(3). First tibia with eight or fewer dorsal macrosetae; carapace less than 1.4 mm long, sternum less than 0.8 mm long; southeastern Texas through Central America and West Indies (Map 4) ..... *semiplumosa*

– First tibia with nine to 12 dorsal macrosetae; carapace more than 1.6 mm long, sternum more than 0.9 mm long; southwestern United States and northwestern Mexico 5

5(4). Sternum dark; usually nine or ten dorsal spines on first tibia; carapace less than 1.8 mm long, sternum less than 1.1 mm long; palpal median apophysis bulb less than 0.6 mm wide; median apophysis spur's apical (darkest) projection 1.5 times as long as its basal width (Fig. 245); Map 4 ..... *oweni*

– Sternum light; usually 12 dorsal spines on first tibia; carapace more than 2.0 mm long, sternum more than 1.1 mm long; palpal median apophysis bulb more than 0.6 mm wide; median apophysis spur's

apical (darkest) projection two times as long as its basal width (Fig. 245); Map 4 ..... *arizonica*

6(2). Conductor lobe with a long, slender apical projection which extends parallel to and is about as long as the conductor spike (Fig. 283); median apophysis bulb with a small, apical lobe (Fig. 283); median apophysis spur's basal region with a long distal lobe (Fig. 272); first tibia with four dorsal macrosetae; Paraguay ..... *para*

– Conductor lobe square, without an apical projection (Plate 7-B; Figs. 214, 215, 218); median apophysis bulb without an apical lobe (Figs. 214, 218, 232, 235); spur's basal region without such a lobe (Fig. 203); first tibia with six to eight dorsal macrosetae (*republicana* species group, in part) 7

7(6). In apical view median apophysis bulb with a lobe which extends along the median surface of the median apophysis spur's basal region (Fig. 203); sternum usually dark gray 8

– Median apophysis bulb without such a lobe (Fig. 203); sternum tan to reddish brown with gray posterolateral margins 9

8(7). Total length more than 3.6 mm, sternum length more than 0.9 mm; median apophysis bulb diameter 0.4 mm; Panama and South America (Map 3) ..... *republicana*

– Total length less than 3.4 mm, sternum length less than 0.9 mm; median apophysis bulb diameter 0.3 mm; Colombia (Map 3) ..... *divisa*

9(7). Carapace more than 1.2 mm long, sternum more than 0.7 mm long; median apophysis bulb rounded-rectangular (Fig. 235), diameter 0.4 to 0.5 mm; carapace light tan with two anteriorly diverging longitudinal gray stripes (Fig. 237); eastern Mexico through Honduras (Map 3) ..... *signatella*

– Carapace less than 1.2 mm long, sternum less than 0.7 mm long; median apophysis bulb semicircular (Fig. 232), diameter 0.2 to 0.3 mm; carapace gray with either no color markings or with a wide median light longitudinal stripe (Fig. 224); Costa Rica through Colombia (Map 3) ..... *tingena*

The *Philoponella republicana* Species Group

This group contains *P. republicana*, *P. divisa*, *P. tingena*, *P. signatella*, and *P. vicina*. It does not correspond to the *Uloborus republicana* species group of Muma and Gertsch (1964) which is a synonym of the genus *Philoponella*.

Description. Clypeus height of males and females equal to AME diameter. Epigynal openings in posterior third (Fig. 230) to half (Fig. 208) of epigynal atrium and seaparated by a distance equal to half the atrium's width. Anterior and posterior atrial rims widely separated, forming broad lateral or posterolateral troughs (Figs. 208, 221, 239). Anterior rims precipitous and posterior rim composed of two lateral lobes separated by a depression or notch (Figs. 208, 209, 239, 240). Each female connecting duct makes a single loop before connecting with a spermatheca (Fig. 210). In *P. vicina* each duct connects to a small bulb which, in turn, connects with a spermatheca (Fig. 244). Conductor blade of male palpus short and square, about as high as long (Plate 7-B; Figs. 215, 218). Conductor spike shorter than slender median apophysis spur's apical projection (Figs. 232, 235, 236). Prolateral palpal femoral tubercle slightly larger than retrolateral tubercle and with a length slightly less than its basal width (Fig. 213).

Philoponella republicana (Simon), new combination

Plate 7-B; Table 4; Figures 1, 203–215; Map 3

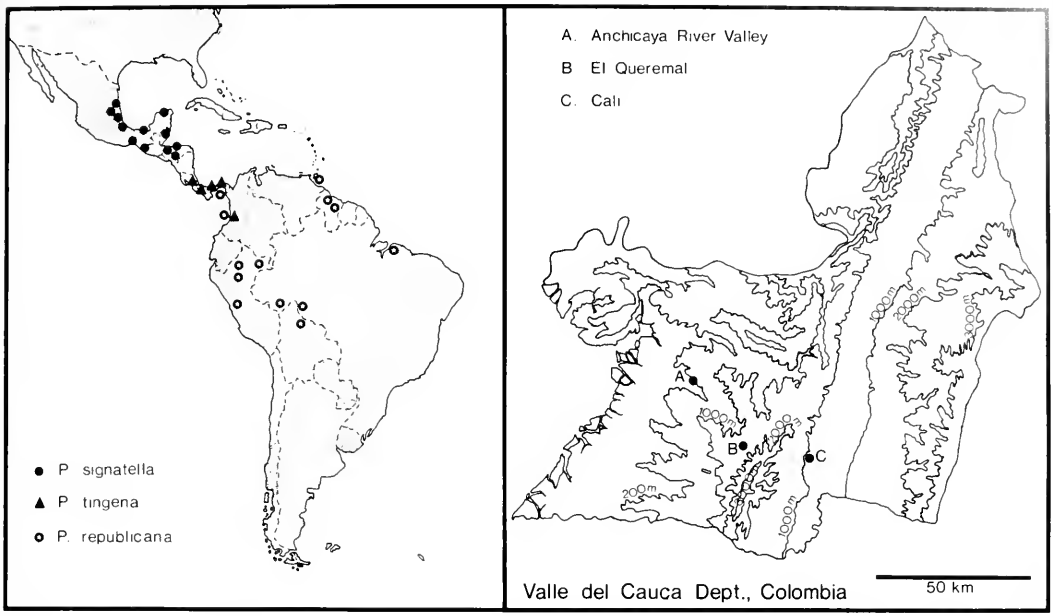
Uloborus republicanus Simon, 1891, Ann. Soc. ent. France, 60: 8. Five male and 56 female syntypes from the forests of San Esteban (6 km S of Puerto Cabello), Venezuela, collected by E. Simon on 29 February to 27 March 1888, in Muséum National d'Histoire Naturelle, Paris, examined. Bonnet, 1957, Bibliographia Araneorum, 2: 4768.

Uloborus cuminamensis Mello-Leitão, 1930, Sep. Arch. Mus. Nac., Rio de Janeiro, 32: 61. Female holotype (No. 1216) from Cuminá [Cuminapanema] River in the Brazilian state of Pará, in Museu Nacional, Rio de Janeiro, Brazil, examined, NEW SYNONYMY.

Uloborus mundior Chamberlin and Ivie, 1936, Bull. Univ. Utah, 27(5): 11. Female holotype, three male and ten female paratypes from Barro Colorado Island, Panama, collected by A. M. Chickering in 1928, in the American Museum of Natural History, examined, NEW SYNONYMY.

Zosis mundior:—Lehtinen, 1967, Ann. Zool. Fennici, 4: 277.

Note. Included with *U. republicanus*



Map 3. Distribution of *Philoponella signatella*, *P. tingena*, and *P. republicana* (left) and Colombian *P. tingena* (right).

syntypes were four male and two female *Philoponella servula* (=*P. vittata*). Simon clearly separated these two species in 1892 [1893]. As he collected both species at San Esteban during the same time period it is likely that these *P. servula* represent specimens he overlooked when sorting his collection. A female *Leucauge* and male *Nephila* were also included with the syntypes.

Diagnosis. *Philoponella republicana* females are distinguished by having a long, shallow, undivided epigynal atrium whose openings are situated on raised mounds and easily visible in ventral view (Fig. 208). Posterior lobes are low and wider than long (Figs. 208, 209). Females have a characteristic abdominal color pattern featuring two pairs of diverging white stripes (Fig. 204). Males are distinguished from all others of this species group but *P. divisa* by the presence of a median apophysis lobe which, in apical view, extends along the median surface of the median apophysis spur's basal region (Fig. 203). *Philoponella republicana* is larger than *P. divisa*, having a total length of more than 3.6 mm and a sternum length of more than 0.9 mm.

Description. Female. Total length 5.5 to 7.6 mm ($\bar{X}$ = 6.35, SD = 0.47, N = 40), carapace length 1.7 to 2.3 mm ($\bar{X}$ = 1.96, SD = 0.12), sternum length 1.1 to 1.4 mm ($\bar{X}$ = 1.26, SD = 0.08). Abdomen half as wide as long with a single broad, raised area in anterior fourth (Fig. 204). Dark forms with only faint light carapace and abdominal markings (Fig. 204). Lighter forms with light, trilobed carapace marking whose central lobe extends to front of carapace. Sternum black. Dorsum of abdomen with two or three recurved, nearly paraxial white chevrons; tip dark gray. Venter of abdomen with dark gray median area. Legs reddish brown or light gray with central light ring on femora and tibiae. Epigynal atrium open laterally, about half as long as wide (Fig. 208). Each opening on a raised area and easily visible in ventral view (Figs. 207, 209). Anterior epigynal rim about one-tenth as long as atrium. Ducts at their closest point separated by two diameters (Fig. 210).

Male. Total length 3.6 to 4.6 mm ($\bar{X}$ = 4.10, SD = 0.18, N = 40), carapace length 1.6 to 1.9 mm ($\bar{X}$ = 1.72, SD = 0.08), sternum length 0.9 to 1.1 mm ($\bar{X}$ = 0.98, SD = 0.04). Carapace light reddish brown dusted with gray (Fig. 205). Median light area in the shape of a posteriorly directed arrowhead extending full length of carapace. Sternum dark gray. Dorsum of abdomen tan, white pigment spots forming three fairly distinct chevrons, tip dark gray (Fig. 205). Venter of abdomen with median dark gray area about half as wide as abdomen. Legs light reddish brown. The palpal median apophysis bulb has a width of about 0.4 mm ($\bar{X}$ = 0.38, SD = 0.02, N = 40) and is crescent to semicircular shaped (Figs. 214, 215).

Natural History and Distribution. Found in Panama and South America (Map 3). The presocial nature of this species has been known since Simon's (1891) description and illustration of *P. republicana* from Venezuela (see family Natural History).

Philoponella divisa n. sp.
Plate 8-A–C; Table 5; Figures 216–223; Map 3

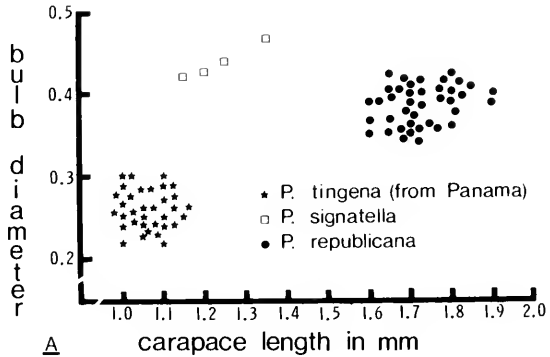
Types. Female holotype, one male and two female paratypes in the Museum of Comparative Zoology, one male and one female paratype in the American Museum of Natural History. All specimens from the Anchicayá River Valley near the Central de Anchicayá Limitada, Planta Hidraulica in the Colombian department of Valle del Cauca, collected 7 to 9 August by B. Opell. The specific epithet refers to the lateral division of the epigynal atrium.

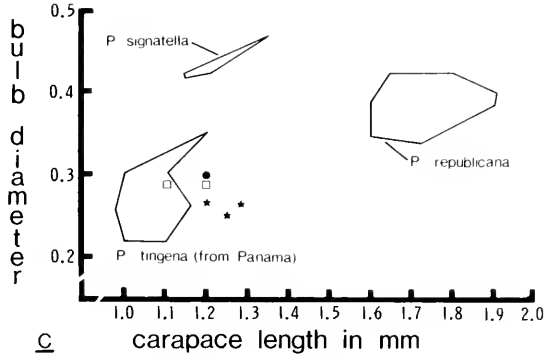
Diagnosis. Females are distinguished by their divided epigynal atrium (Fig. 221) and dorsal abdominal coloration (Fig. 216). Males are distinguished from all others of this species group but *P. republicana* by the presence of a large median apophysis lobe which, in apical view, extends along the median surface of the median apophysis spur's basal region (Fig. 203). *Philoponella divisa* males are smaller than those of *P. republicana*, having a total length of 3.4 mm or less and a sternum length of 0.9 mm or less.

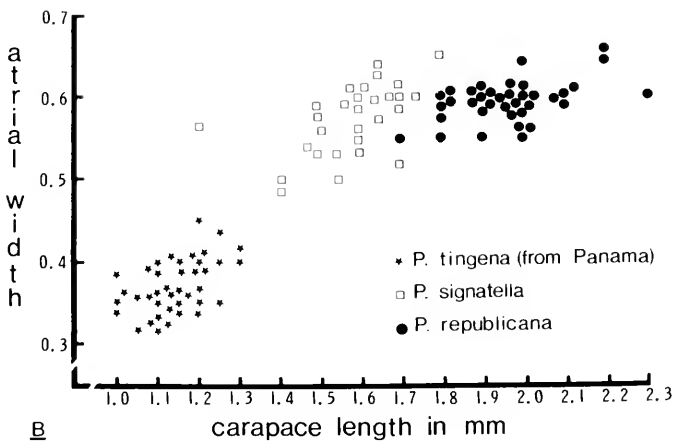
Description. Female. Total length 3.0 to 3.6 mm ($\bar{X}$ = 3.35, SD = 0.23, N = 9), carapace length 1.0 to 1.1 mm ($\bar{X}$ = 1.04, SD = 0.04), sternum length 0.7 to 0.8 mm ($\bar{X}$ = 0.72, SD = 0.04). Abdomen width and height about 0.6 its length with two dorsal humps in the anterior third of its length. Most specimens have a dark gray carapace with light posterolateral margins and a few have a light posteromedian longitudinal stripe (Fig. 216). Sternum dark gray to black. Abdomen dark gray to black with a pair of broad, light paraxial stripes on dorsum (Fig. 216) and venter. First femur dark gray with a narrow white ring in distal half of its length. Second through fourth femora gray with a white ring in proximal third and distal two-thirds of its length. Patellae dark gray. Tibiae gray with proximal and central white rings. Metatarsi and tarsi gray with narrow proximal white rings. In ventral view epigynal crypt about 0.2 as long as wide, divided by a thin median septum, and with low, closely spaced posteromedian lobes (Figs. 221). In posterior view raised posterior epigynal face with two lateral posterior lobes separated by a shallow notch (Fig. 222). A simple straight duct leads from each inconspicuous posteromedian epigynal opening to a spherical spermatheca (Fig. 223).

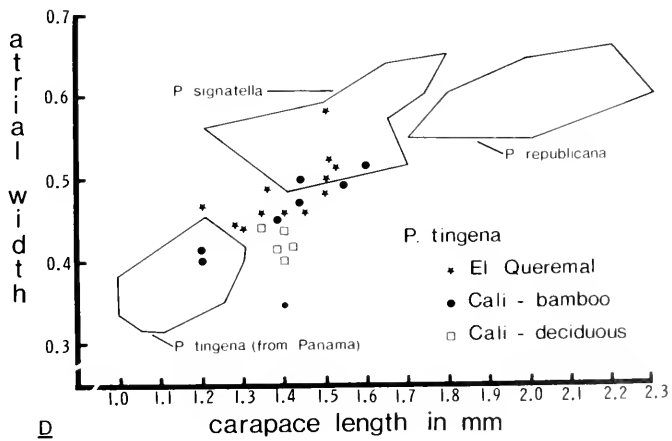
Male. Total length 2.6 to 3.4 mm ($\bar{X}$ = 3.02, SD = 0.22, N = 8), carapace length 1.3 to 1.4 mm ($\bar{X}$ = 1.38, SD = 0.35), sternum length 0.7 to 0.8 mm ($\bar{X}$ = 0.78, SD = 0.04). Carapace gray with a light median stripe and light posterolateral margins (Fig. 217). Abdomen tan with one or two mid dorsal paraxial spots and a gray posterior tip (Fig. 217). Legs white to tan, markings when present, of low contrast. First and second femora light gray with a narrow white ring in distal half of its length. Second through third femora tan. First, third, and fourth patellae tan, second patella light gray. First, second and fourth tibiae light gray with a narrow, central, white ring. Third tibia tan with

TABLE 4. ANALYSIS OF THE SPECIES IN THE *PHILOPONELLA REPUBLICANA* SPECIES GROUP: A. COMPARISON OF MALES. B. COMPARISON OF FEMALES, C. EVALUATION OF *P. TINGENA* MALES FROM THREE COLOMBIAN POPULATIONS (SEE D FOR KEY TO SYMBOLS), D. EVALUATION OF *P. TINGENA* FEMALES FROM THREE COLOMBIAN POPULATIONS.









a distal gray band. Metatarsi and tarsi tan. Median apophysis bulb semicircular (Fig. 218), length and width about 0.3 mm ($\bar{X}$ = 0.29 mm, SD = 0.01, N = 8).

Natural History and Distribution. Known only from the type locality in Colombia (Map 3). Specimens were collected from vegetation and rocks of roadside banks where their webs were always found adjacent to and connected with diplurid funnel webs. Several *P. divisa* webs were usually found together, but colonies did not exceed four individuals. Webs of immatures and mature females were diagonal to vertical (Plate 8-A–C; Table 5) and featured a signal line running from the hub to a peripheral support. The spider hung from this line near the support and moved to the hub only when prey vibrations were detected. As with other *Philoponella* species, males were observed hanging from framework threads of female and immature orb-webs.

Philoponella tingena (Chamberlin and Ivie), new combination

Plate 8-E–F; Tables 4, 5; Figures 224–232; Map 3

Uloborus tingens Chamberlin and Ivie, 1936, Bull. Univ. Utah, 27(5): 10. Female holotype and six female paratypes from Barro Colorado Island, Panama, Canal Zone, collected by A. M. Chickering in 1928, in the American Museum of Natural History, examined.

Diagnosis. Philoponella tingena and *P. signatella* are similar. Females of the former have a broad, shallow depression separating posterior epigynal lobes (Figs. 230, 231); whereas the latter has a deep notch separating lobes (Figs. 239, 240). *Philoponella tingena* males are smaller than *P. signatella* males, having a carapace length of less than 1.2 mm and a sternum length of 0.6 mm. Other features distinguishing these two species are found in *P. signatella* diagnosis.

Description. Female. Total length 2.8 to 4.0 mm ($\bar{X}$ = 3.45, SD = 0.30, N = 40), carapace length 1.0 to 1.3 mm ($\bar{X}$ = 1.14, SD = 0.08), sternum length 0.6 to 0.8 mm ($\bar{X}$ = 0.74, SD = 0.06). Abdomen two-thirds as wide as long with two distinct tubercles in anterior third. Some specimens entirely black with light gray rings in center of femora and tibiae of legs. Lighter species have a dark gray carapace with a wide, median, posterior, trilobed white area extending forward 0.6 the carapace length (Figs. 226, 227). The three lobes are of nearly equal length. Sternum light reddish brown with gray posterior lateral margins. Abdominal dorsum with three white chevrons or with closely spaced white pigment spots (Fig. 226, 227). Posterior tip gray. Abdominal venter with median light gray area. Legs tan or with color markings as in darker specimens. Epigynal atrium bordered posteriorly by two lobes which are widely separated by a shallow depression (Figs. 230, 231). Atrium open posterolaterally. Distance from posterior lobes to the anterior rim one-third epigynum's width and five times length of anterior rim. In ventral view epigynal openings usually hidden (Fig. 230), but sometimes visible just anterior and medial to posterior lobes. At their closest point ducts are separated by a distance of one diameter.

Male. Total length 2.2 to 2.8 mm ($\bar{X}$ = 2.50, SD = 0.13, N = 40), carapace length 1.0 to 1.2 mm ($\bar{X}$ = 1.06, SD = 0.05), sternum length 0.6 mm ($\bar{X}$ = 0.60, SD = 0.02). Carapace light tan often with light gray sides (Fig. 224). Sternum light tan. Dorsum of abdomen light tan with gray posterior tip and a few scattered white pigment spots (Fig. 224). Venter light tan or with a very faint gray median area. Legs light tan with a distal gray ring around tibiae and metatarsi of some or all legs. Semicircular median apophysis palpal bulb with an average diameter of 0.2 to 0.3 mm ($\bar{X}$ = 0.26, SD = 0.02, N = 40) (Fig. 232).

Species Variability. In Panama and Colombia *P. tingena* is sympatric with *P. republicana* (Map 3). In the Colombian

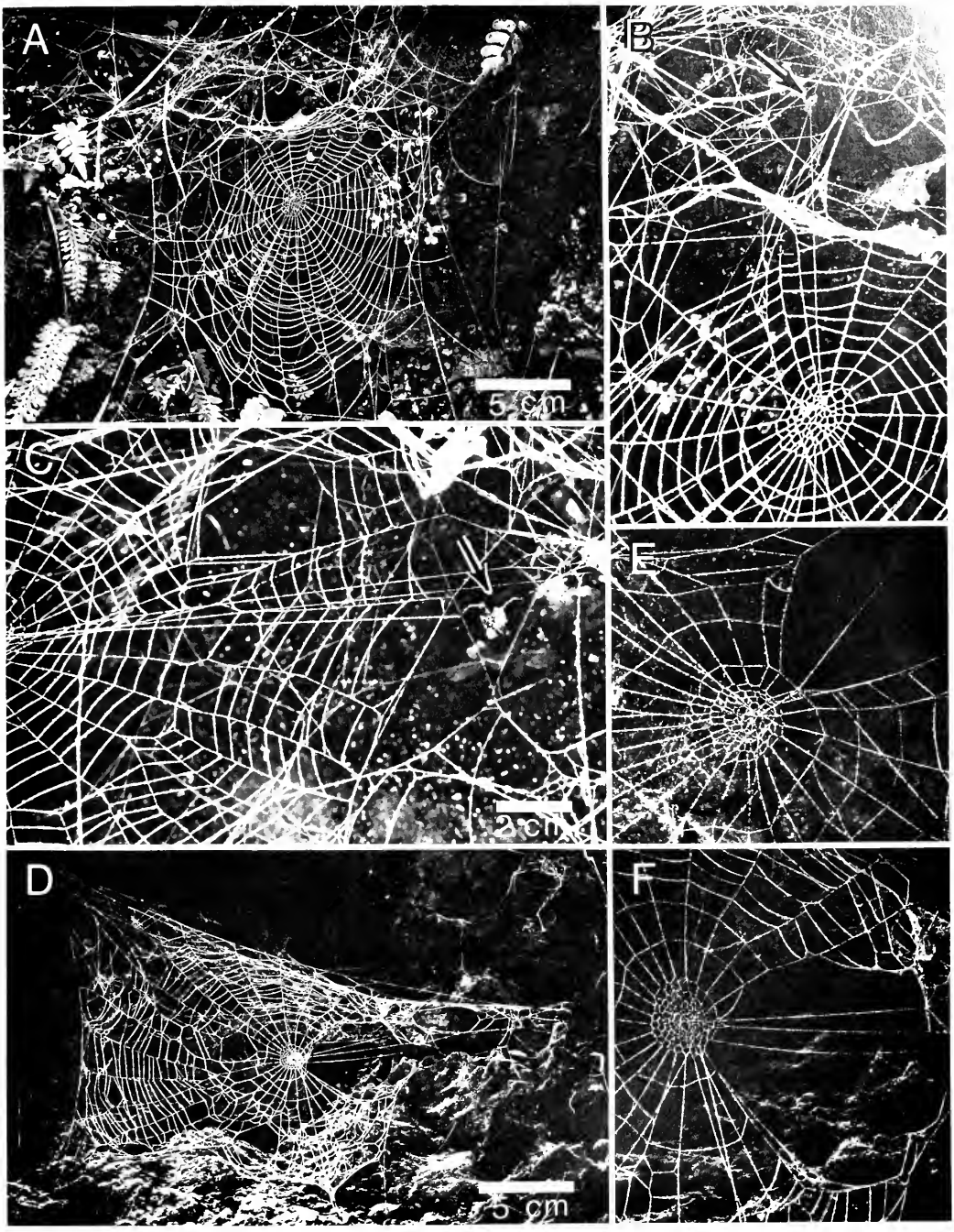


Plate 8. A. Web of *Philoponella divisa* female holotype. B. *Philoponella divisa* female holotype (arrow) hanging from a signal line at the orb's perimeter. C. *Philoponella divisa* female (arrow) feeding while hanging from a signal line at the orb's perimeter. D. Web of *Philoponella tingena* from El Queremal, Colombia (Map 3) with three signal lines extending through a vacant web sector (F). E. *Philoponella tingena* web from El Queremal, Colombia (Map 3) with a single signal line. F. Close-up of triple signal lines of web shown in D.

department of Valle del Cauca three local populations of *Philoponella* having individuals morphologically indistinct from, but larger than Panamanian *P. tingena* were studied: one from the faces of large boulders and roadside banks at El Queremal (1600 m), one from a bamboo forest south of Cali (1000 m), and one from a lowland deciduous forest near Cali (1000 m). The latter was found in colonies among buttress tree roots and its individuals produced a nearly horizontal, complete orb-web and rested at the web's hub while waiting for prey. Individuals of the former two populations were less often gregarious and the few colonies observed were small. Members of these two populations constructed diagonal or vertical webs with a vacant sector through which one to three signal lines ran (Plate 8-D–F) and rested at the attachment of the signal line(s) to a peripheral support. An insufficient web sample was obtained to permit detailed analysis of the deciduous forest population, but the webs of bamboo forest (*P. tingena* Cb) and El Queremal (*P. tingena* B) populations do not significantly differ (Table 5). Specimens from the bamboo forest are light tan to white in color with very few dark markings; whereas, those from the other two populations are predominantly dark gray to black. Additionally, the average egg diameter (for each species ten eggs from each of three eggsacs were measured, SD for each species = 0.02 mm) for Panamanian *P. tingena* was 0.53 mm and for the El Queremal populations 0.70 mm. Although this evidence suggests that two or perhaps all of these populations may be sibling species of *P. tingena*, additional study is required before this can be determined. Previous evidence can be challenged by arguments that: 1. color differences between populations are no greater than those found within some *Philoponella* species, 2. careful study of intraspecific web variability is needed to show that web structure is not influenced by environmental and predatory pressures, 3. size differences do not clearly separated the populations from one another (Table 4-C, D) and the trend for Colombian specimens to be larger than Panamanian specimens may represent clinal variation, altitudinal influence, or character displacement, and 4. data have been obtained from only restricted localities.

Distribution. Costa Rica, Panama, and Colombia (Map 3).

Philoponella signatella (Roewer), new combination

Table 4; Figures 234–240; Map 3

Uloborus signatus O. Pickard-Cambridge, 1898, Biol. Cent.-Amer., Arachnida-Araneida, 1: 264. One male and one female syntype from Teapa in the Mexican state of Tabasco, collected by H. H. Smith, in the British Museum (Natural History), examined.

Uloborus signatellus Roewer, 1951, Abh. Naturw. Ver. Bremen, 32(2): 1344. New name for *Uloborus signatus* O. Pickard-Cambridge, 1898, *op. cit.*, preoccupied by *Uloborus signatus* O. Pickard-Cambridge, 1876, Proc. Zool. Soc. Lond., 1876: 579 [=*U. plumipes* Lucas, 1846].

Diagnosis. Along with *P. tingena*, *P. signatella* females are characterized by having a deep, undivided atrium with posteriorly directed troughs, posterior lobes which are as high as wide, an atrium eight times wider than long, and openings not visible in ventral view (Figs. 230, 231, 239, 240). *Philoponella signatella* has closely spaced posterior lobes separated by a deep notch (Figs. 239, 240) rather than widely spaced lobes separated by a shallow depression as in *P. tingena* (Figs. 230, 231). Females of *P. signatella* are larger than those of *P. tingena*, having a total length greater than 4.0 mm and a sternum longer than 0.9 mm (Table 4). Anterior epigynal rim about half as long as the epigynal atrium in *P. signatella* (Fig. 239), a fifth as long in *P. tingena* (Fig. 230). Males of *P. signatella* and *P. tingena* are distinguished from others of their species group by the median apophysis bulb's lack of a prominent lobe which, when viewed apically,

TABLE 5. WEB CHARACTERS OF *PHILOPONELLA DIVISA* FROM THE ANCHICAYÁ VALLEY OF COLOMBIA (MAP 3), *P. TINGENA*-B FROM EL QUEREMAL, COLOMBIA (MAP 3), *P. TINGENA*-CB FROM A BAMBOO PATCH NEAR CALI, COLOMBIA (MAP 3), AND *P. REPUBLICANA* FROM THE ANGHICAYÁ VALLEY OF COLOMBIA (MAP 3).

		No. RADII	No. SPIRALS		DIAMETER FREE ZONE		DIAMETER CENTER MESH		AVERAGE SPIRAL SPACING			FRAMEWORK	
			MAX.	MIN.	MAX.	MIN.	MAX.	MIN.	UP	DOWN	SIDE	WIDTH	LENGTH
P. divisa					(mm)	(mm)	(mm)	(mm)	(mm)	(mm)	(mm)	(cm)	(cm)
1 singal line	RANGE	19-31	12-33	7-16	26-48	23-48	10-18	7-15	2.3-3.7	2.9-3.8	2.3-3.7	9-22	10-20
no vacant sector	MEAN	22.4	18.6	10.2	34.6	29.6	13.8	11.1	3.1	3.3	3.2	14.5	14.2
N=13	S.D.	3.0	6.1	2.7	6.9	7.0	2.3	2.0	0.5	0.3	0.4	3.2	3.2
P. tingena – B													
1-3 signal lines	RANGE	20-24	15-27	7-12	46-96	41-74	15-24	13-18	4.1-5.6	5.5-8.8	5.1-8.3	15-34	24-45
vacant sector	MEAN	22.3	19.7	9.5	65.4	55.6	18.9	15.0	4.9	7.2	6.6	21.8	34.9
N=6	S.D.	1.4	4.5	2.2	18.7	13.4	3.2	2.2	1.1	1.2	1.5	7.1	9.8
P. tingena – Cb													
1-2 signal lines	RANGE	19-22	20-29	8-10	48-77	39-60	15-24	12-18	3.5-6.8	4.0-4.8	3.5-5.0	11-16	18-21
vacant sector	MEAN	20.5	23.8	9.0	59.9	49.7	18.1	14.8	4.5	4.3	4.1	13.9	19.8
N=4	S.D.	1.3	4.1	0.8	12.5	8.4	4.0	2.5	1.6	0.4	0.7	1.9	1.7
P. republicana - A													
1 signal line no vacant sector		28	26	15	50.4	44.5	21.2	19.7	2.9	4.0	4.3	18.2	22.1

extends along the median surface of the spur's basal region (Fig. 203). *Philoponella signatella* males are larger than those of *P. tingena*, having a carapace length of 1.2 mm or more and a sternum length of 0.7 mm or more. The median apophysis bulb of *P. signatella* is large and somewhat rectangular (Fig. 235); whereas, that of *P. tingena* is smaller and semicircular (Fig. 232).

Description. Female. Total length 4.0 to 6.7 mm ($\bar{X}$ = 5.08, SD = 0.69, N = 29), carapace length 1.2 to 1.8 mm ($\bar{X}$ = 1.59, SD = 0.12), sternum length 0.9 to 1.2 mm ($\bar{X}$ = 1.07, SD = 0.07). Abdomen about twice as long as wide with two low adjacent tubercles in anterior third of dorsum (Fig. 234). Color similar to *U. tingens*, but in dark forms median light area of carapace about half as long as carapace. In light forms this white area extends anteriorly three-quarters the carapace length and the median lobe is twice as long as lateral lobes. Dorsal abdominal pattern as shown in Fig. 234. Epigynal crypt opens posteriorly and has two closely spaced posterior lobes separated by a deep depression (Fig. 239). Atrium's length about one-fifth the epigynum's width and two times the width of the anterior rim. In ventral view epigynal openings obscured by posterior lobes (Fig. 239).

Male. Total length 2.8 to 3.6 mm ($\bar{X}$ = 2.30, SD = 0.33, N = 4), carapace length 1.2 to 1.4 mm ($\bar{X}$ = 1.24, SD = 0.09), sternum length 0.7 to 0.8 mm ($\bar{X}$ = 0.75, SD = 0.04). Carapace light tan with wide, diverging lateral gray lines (Figs. 237). Sternum light tan with gray posterolateral margins. Abdomen's dorsum with nu-

merous white spots and gray posterior tip. Venter with faint gray median area bordered by a few white spots. Legs tan or with faint gray distal rings on tibiae and metatarsi. Median apophysis bulb of the palpus has an average diameter of 0.4 to 0.5 mm ($\bar{X}$ = 0.43, SD = 0.03, N = 4) and is rounded to rectangular in shape (Fig. 235).

Distribution. Honduras through eastern Mexico (Map 3).

Philoponella vicina (O. Pickard-Cambridge), new combination
Figures 241–244

Uloborus vicinus O. Pickard-Cambridge, 1898, Biol. Cent.-Amer., Arachnida-Araneidea, I, 266. Female holotype from Teapa in the Mexican state of Tabasco, collected by H. H. Smith, in the British Museum (Natural History), examined.

Note. This species is known only from the female syntype, upon which the following description is based.

Diagnosis. Females of *P. vicina* can be distinguished from those of *P. tingena* and *P. signatella* by having posterior epigynal lobes which are wider than long, by having laterally rather than posteriorly directed epigynal troughs, by having openings visible in ventral view, and by having an epigynal atrium which is two-thirds rather than one-third the length of the epigynum (Figs. 242, 243). *Philoponella vicina* is distinguished from *P. republicana* by having the epigynal openings in depressions at the center of the epigynum rather than on raised areas in the posterior third, by having an anterior rim one-eighth rather than one-sixteenth the length of the epigynum, by having a total body length less than 4.2 mm, and by having a tan rather than black sternum which is less than 0.8 mm long.

Description. Female. Total length 4.2 mm, carapace length 1.2 mm, sternum length 0.8 mm. Abdomen slightly more than half as wide as long with two small, but distinct humps in anterior quarter (Fig. 241). Carapace dark gray with a wide median light area extending anteriorly almost to the posterior eye row. Sternum tan with gray posterior lateral margins. Dorsum of abdomen with broad, light median area broken only by a gray patch between the humps and a smaller gray patch midway along the abdomen's length (Fig. 241). Sides of abdomen light gray, posterior tip dark gray. Venter of abdomen with a light gray median area. First femur with a distal light ring, second through fourth femora and all tibiae with proximal and median light rings. Metatarsi with a distal gray ring. Epigynal crypt opens laterally and is half as long as wide. Each opening is in a long depression at the anterolateral border of a wide posterior lobe (Fig. 242, 243). Anterior rim about one-fifth the atrium's length. Ducts separated by five of their diameters, each leading first to a bulb with a diameter half that of the spermatheca and then looping before connecting to a spherical spermatheca (Fig. 244).

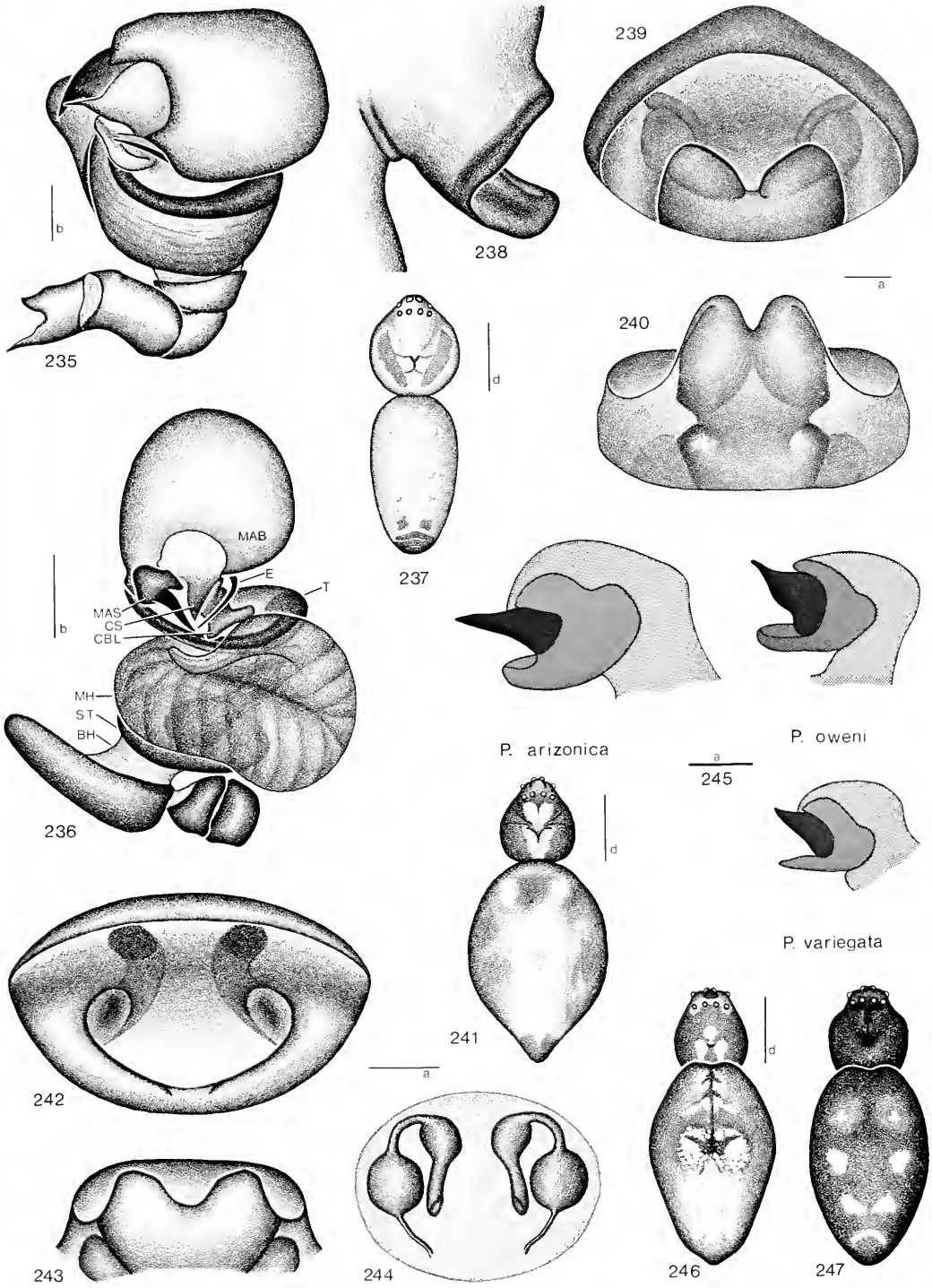
Distribution. Southern Mexico.

The *Philoponella semiplumosa* Species Group

Philoponella semiplumosa, *P. oweni*, *P. arizonica*, and *P. vittata* belong to this species group. Clypeus height of females equal to AME diameter. Clypeus height of males 1.5 to two AME diameters. Epigynal openings near the center of the atrium and separated by a distance equal to at least 0.8 the atrium's width (Figs.

→

Figures 235–240. *Philoponella signatella* (Roewer). 235. Retrolateral view of male left palpus. 236. Retrolateral view of expanded male left palpus. 237. Dorsal view of male. 238. Lateral view of epigynum. 239. Ventral view of epigynum. 240. Posterior view of epigynum. Figures 241–244. *Philoponella vicina* (O. Pickard-Cambridge). 241. Dorsal view of female. 242. Ventral view of epigynum. 243. Posterior view of epigynum. 244. Dorsal view of cleared epigynum. Figure 245. Apical views of left median apophysis spurs of male palpi of the *Philoponella semiplumosa* species group. Figures 246–247. *Philoponella semiplumosa* (Simon) dorsal views of females.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P. arizonica
P. oweni
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P. variegata
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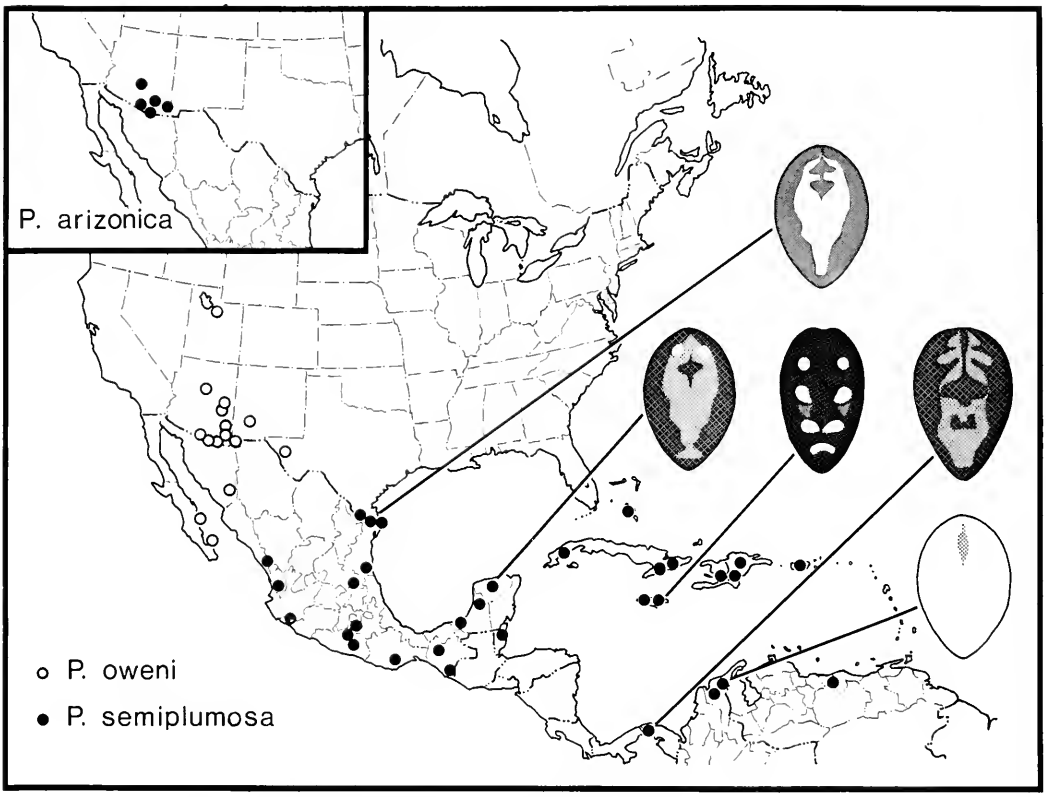


Map 4. Distribution of *Philoponella arizonica*, *P. oweni*, and *P. semiplumosa*.

250, 259, 266). Anterior and posterior atrial rims contiguous and lateral troughs absent. Anterior rim narrow and precipitous and posterior rim continuous without clearly defined lateral lobes (Figs. 251, 262, 267). Except in *P. vittata* (Fig. 268), each duct spirals tightly around itself before connecting with a spherical spermatheca (Fig. 252). Male palpus' conductor blade elongate and nearly three times as long as wide (Figs. 253, 270). Conductor spike longer than the broad median apophysis spur's apical region (Figs. 253, 270). Median apophysis bulb encompasses the median apophysis spur's basal region along 0.7 of its perimeter (Fig. 245). Retrolateral palpal femoral tubercle longer than prolateral tubercle and its length about equal to its basal width (Fig. 269).

Philoponella semiplumosa (Simon), new combination

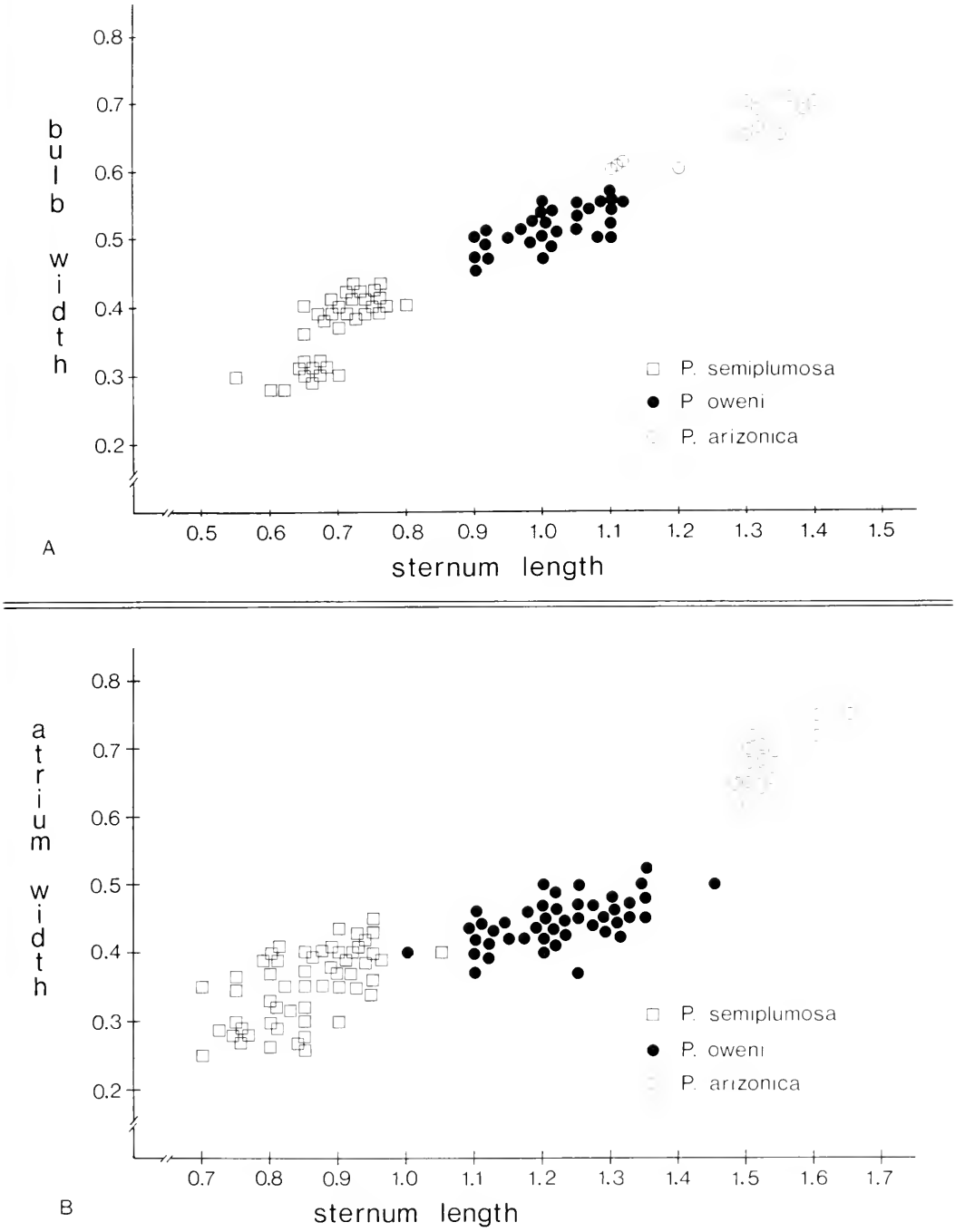
Table 6; Figures 245–254; Map 4

Uloborus semiplumosus Simon, 1893, Ann. Soc. ent. Fr., 61: 424. Three females from Caracas and San Esteban, Venezuela collected 27 December 1887 to 20 January 1888 and 29 February to 27 March 1888, respectively by E. Simon, in Muséum National d'Histoire Naturelle, Paris, examined.

Uloborus variegatus O. Pickard-Cambridge, 1898, Biol. Cent.-Amer., Arachnida-Araneidea, I: 266. Four female and four immature syntypes from Omilteme(i) in the Mexican state of Guerrero, collected by H. H. Smith, in the British Museum (Natural History), examined, NEW SYNONYMY.

Uloborus abstrusus Gertsch and Davis, 1942, Amer. Mus. Novitates, 1158: 18. Male holotype and female allotype from Xilitla in the Mexican state of San Luis Potosí, collected 22 December 1939, female and four immature paratypes from the same

TABLE 6. ANALYSIS OF SPECIES IN THE *PHILOPONELLA SEMIPLUMOSA* SPECIES GROUP.



locality, collected 2 December 1939 by A. M. and L. J. Davis, in the American Museum of Natural History, examined, NEW SYNONYMY.

Diagnosis. Females are similar to those of *P. oweni* and *P. arizonica*, but smaller, having a total length of less than 4.6 mm, a carapace length of less than 1.5 mm, and a sternum length of less than 1.0 mm. In females of *P. semiplumosa* the anterior epigynal rim about as long as the posterior rim (Fig. 250), rather than one-fourth as long (Figs. 257, 259). Internal epigynal ducts usually do not show through the atrium's integument as they do in the other two species. Venter of female's abdomen with narrow (Fig. 249) rather than wide (Fig. 256) paraxial white stripes setting off a median longitudinal gray stripe. Males are similar to those of *P. oweni* and *P. arizonica* but are smaller, having a carapace length of less than 1.4 mm, a sternum length of less than 0.8 mm, and a bulb width of less than 0.4 mm.

Description. Female. Total length 3.6 to 4.6 mm ($\bar{X}$ = 3.94, SD = 0.25, N = 37), carapace length 1.1 to 1.5 mm ($\bar{X}$ = 1.25, SD = 0.11), sternum length 0.7 to 1.0 mm ($\bar{X}$ = 0.85, SD = 0.07). Carapace dark gray with light, trilobed white patch in posterior half or black without light markings (Figs. 246–247). Sternum gray to black. Abdomen with prominent dorsal humps in anterior third. Dorsum light gray with white median area and dark gray sides (Fig. 246) to black with a posterior white chevron and three pairs of white spots (Fig. 247). Venter of abdomen gray to black with narrow paraxial stripes (Fig. 249). Legs brown to gray. First femur with light distal ring, second through fourth femora with light proximal and distal rings (proximal ring may be lacking in darker specimens). Tibiae with light proximal and median rings. First through third metatarsi and tarsi with narrow, light proximal ring, fourth metatarsus with narrow, light proximal and distal rings. Epigynal atrium 0.3 to 0.4 mm wide ($\bar{X}$ = 0.36, SD = 0.05, N = 55) and three-fifths as long as wide. Anterior rim of epigynum about as wide as posterior rim (Fig. 250). Epigynum in posterior view with a median depression (Fig. 251).

Male. Total length 2.4 to 3.4 mm ($\bar{X}$ = 2.93, SD = 0.35, N = 25), carapace length 1.0 to 1.4 mm ($\bar{X}$ = 1.21, SD = 0.10, N = 30), sternum length 0.6 to 0.8 mm ($\bar{X}$ = 0.70, SD = 0.05, N = 36). Carapace tan with a light median stripe beside which are brown, diverging stripes (Fig. 248). Sternum tan dusted with gray to solid gray in darker specimens. Dorsum of abdomen white with a pair of dark dots in the anterior third (Fig. 248) or, in darker specimens, with three to four dark gray chevrons. Venter of abdomen with a slightly darker median area. Legs tan, first femur reddish brown. The first tibia of most with eight or fewer dorsal spines. Length of central projection of median apophysis about 1.5 times the width of its base (Fig. 253). Bulb 0.3 to 0.4 mm wide ($\bar{X}$ = 0.37, SD = 0.05, N = 36).

Distribution. SE Texas through Central American and the Caribbean Islands (Map 4).

Philoponella oweni (Chamberlin), new combination
Table 6; Figures 255–258; Map 4

Uloborus oweni Chamberlin, 1924, Proc. Calif. Acad. Sci., 12(28): 579. Female holotype from Gulf of California, Carmen Island, Marquer Bay, collected 23 May 1921 by J. C. Chamberlin, V. Owen, and I. M. Johnston, in the California Academy of Sciences (specimen No. 1363), examined.

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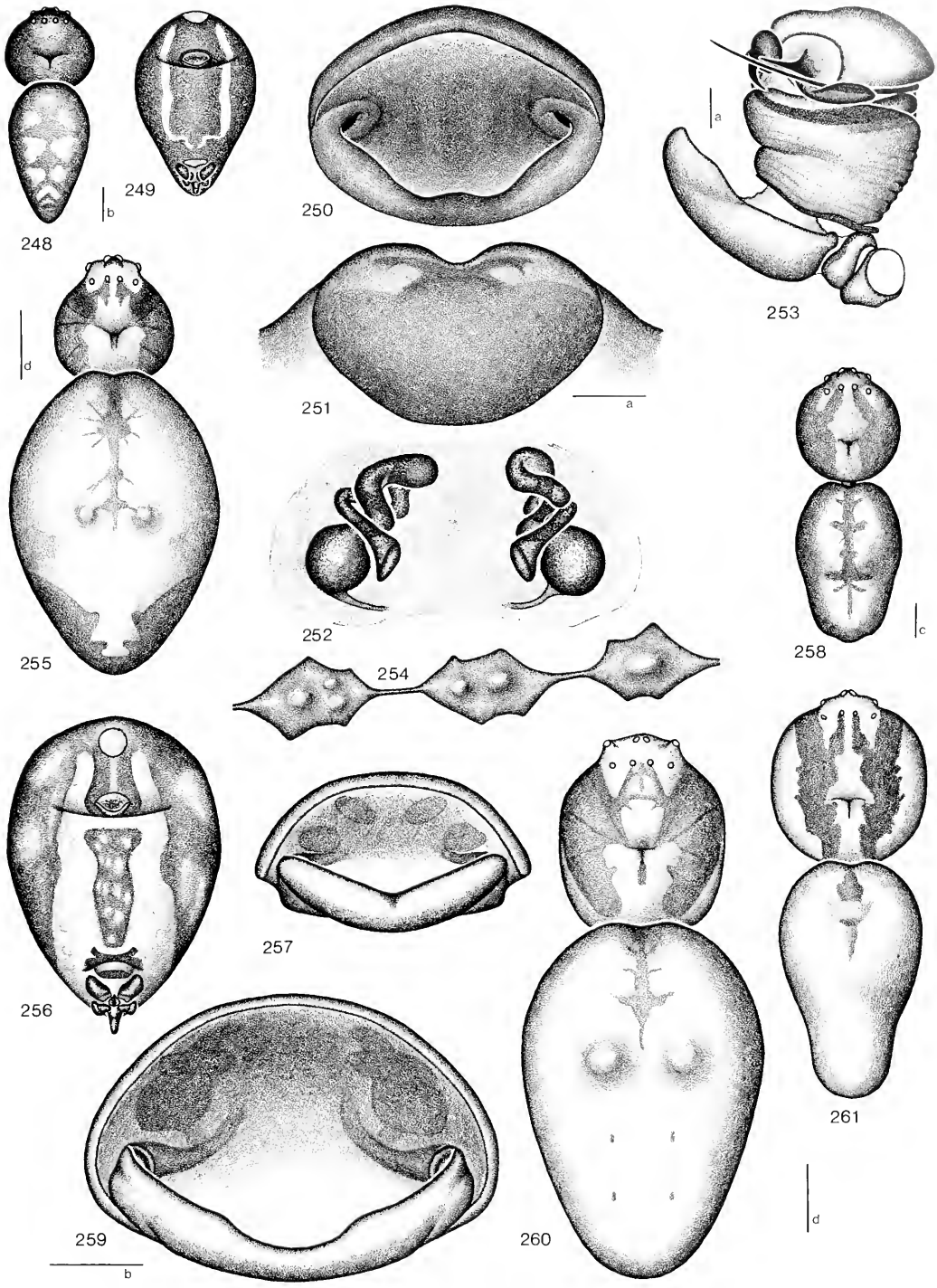
Figures 248–254. *Philoponella semiplumosa* (Simon). 248. Dorsal view of male. 249. Ventral view of female abdomen. 250. Ventral view of epigynum. 251. Posterior view of epigynum. 252. Dorsal view of cleared epigynum. 253. Retrolateral view of left male palpus. 254. Eggsacs. Figures 255–258. *Philoponella oweni* (Chamberlin). 255. Dorsal view of female. 256. Ventral view of female abdomen. 257. Ventral view of epigynum. 258. Dorsal view of male. Figures 259–261. *Philoponella arizonica* (Gertsch). 259. Ventral view of epigynum. 260. Dorsal view of female. 261. Dorsal view of male.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Muma and Gertsch, 1964, Amer. Mus. Novitates 2196: 34.

Diagnosis. Females are similar to those of *P. semiplumosa* and *P. arizonica*, but are intermediate in size, having a carapace length of 1.5 to 2.0 mm and a sternum length of 1.0 to 1.5 mm. Like *P. arizonica* and unlike *P. semiplumosa*, the anterior epigynal rim is one-fourth as long as, rather than equal in length to, the posterior rim; some of the internal ducts show through the atrium's integument (Fig. 257), and broad, paraxial stripes set off a median gray area on the venter of the abdomen (Fig. 256). Females of *P. oweni* differ from those of *P. arizonica* by being more darkly pigmented, by having an epigynal atrium which is three rather than two times as wide as long (Fig. 257), and by lacking ventral lateral dark lines (Fig. 262) on the posterior face of the epigynum. Males of *P. oweni* are similar to those of *P. semiplumosa* and *P. arizonica* but are intermediate in size, having a carapace length of 1.6 to 1.8 mm, a sternum length of 0.9 to 1.1 mm, and a bulb width of 0.5 to 0.6 mm. *Philoponella oweni* has a median apophysis spine the length of whose central projection is 1.5 the width of its base rather than 2.5 as in *P. arizonica* (Fig. 245).

Description. Female. Total length 4.6 to 7.1 mm ($\bar{X}$ = 5.81, SD = 0.69, N = 27), carapace length 1.5 to 2.0 mm ($\bar{X}$ = 1.82, SD = 0.17, N = 27), sternum length 1.0 to 1.5 mm ($\bar{X}$ = 1.21, SD = 0.10, N = 46). Carapace brown with broad, median light area extending anteriorly to eyes (Fig. 255). Sternum tan at center with gray margins. Abdomen with small humps about midway along its length, dorsum entirely white or with white median area and gray sides (Fig. 255). Venter of abdomen white with narrow gray median longitudinal stripe (Fig. 256). Legs light brown. First femur with distal light ring, second through fourth femora with proximal and distal light rings. Tibiae with proximal and median light rings. First metatarsus without rings, second through fourth metatarsi with faint proximal and distal light rings. Tarsi with light narrow proximal rings. Epigynal atrium 0.4 to 0.5 mm wide ($\bar{X}$ = 0.46, SD = 0.05, N = 46) and about two-fifths as long as wide. Anterior rim of epigynum one-fourth the width of posterior rim (Fig. 257). Epigynum in posterior view without a proiment median depression.

Male. Total length 3.2 to 4.4 pm ($\bar{X}$ = 4.00, SD = 0.33, N = 14), carapace length 1.6 to 1.8 mm ($\bar{X}$ = 1.69, SD = 0.09, N = 14), sternum length 0.9 to 1.1 mm ($\bar{X}$ = 1.01, SD = 0.07, N = 30). Carapace brown dusted with gray, light median longitudinal stripe extends anteriorly to eyes (Fig. 258). Sternum with gray margins and tan center. Dorsum of abdomen all white or with a white median area and gray sides (Fig. 258). Venter of abdomen light or with a narrow median gray area set off by broad paraxial white stripes. Legs reddish brown and, in most specimens, with no prominent markings. First tibia of most with nine or ten dorsal macrosetae. Length of central projection of median apophysis about 1.5 the width of its base. Bulb 0.5 to 0.6 mm wide ($\bar{X}$ = 0.52, SD = 0.03, N = 30).

Distribution. SW Texas, SW United States, and NW Mexico (Map 4).

Philononella arizonica (Gertsch), new combination

Table 6; Figures 259–263; Map 4

Uloborus arizonicus Gertsch, 1936, Amer. Mus. Novitates, 852: 2. Male holotype from Sabino Basin, Santa Catalina Mountains, Arizona (elevation 1280 m), collected 8 to 12 July 1916 by F. E. Lutz, in the American Museum of Natural History, examined. Muma and Gertsch, 1964, Amer. Mus. Novitates, 2196: 35.

Diagnosis. Males and females are similar to those of *P. oweni* but are usually larger, males being at least 4.0 mm long and females being at least 6.7 mm. Females of *P. arizonica* are more light colored. See *P. oweni* diagnosis for ad-

ditional distinguishing characters of these two species.

Description. Female. Total length 6.7 to 8.0 mm ($\bar{X}$ = 7.26, SD = 0.50, N = 11), carapace length 2.3 to 3.2 mm ($\bar{X}$ = 2.48, SD = 0.21, N = 16), sternum length 1.5 to 1.7 mm ($\bar{X}$ = 1.52, SD = 0.05, N = 16). Carapace brown with broad, light median longitudinal stripe extending anteriorly to eyes (Fig. 260). Sternum tan, often dusted with gray. Abdomen with small humps in anterior two-fifths, dorsum all white or with light gray sides (Fig. 260). Venter of abdomen all white or with a narrow median gray stripe. Legs light tan with no prominent markings. Epigynal atrium 0.6 to 0.8 mm wide ($\bar{X}$ = 0.68, SD = 0.04, N = 16), and four-sevenths as long as wide (Fig. 259). Anterior rim of epigynum one-fourth the width of the posterior rim. Epigynum in posterior view without a prominent median depression and with ventral lateral dark lines showing through the integument (Fig. 262).

Male. Total length 4.0 to 6.4 mm ($\bar{X}$ = 5.34, SD = 1.03, N = 11), carapace length 2.0 to 3.8 mm ($\bar{X}$ = 2.56, SD = 0.50, N = 11), sternum length 1.1 to 1.4 mm ($\bar{X}$ = 1.27, SD = 0.12, N = 11). Carapace tan with two brown paraxial stripes extending to anterior margin (Fig. 261). Sternum tan, in some dusted with gray. Dorsum of abdomen all white or with gray sides and cardiac area (Fig. 261). Venter of abdomen all white or with narrow gray median longitudinal stripe. Legs tan with no prominent markings. First tibia of most with 12 dorsal macrosetae. Length of central projection of median apophysis about 2.5 times the width of its base. Bulb of median apophysis 0.6 to 0.7 mm wide ($\bar{X}$ = 0.66, SD = 0.04, N = 10).

Distribution. Arizona (Map 4).

Philoponella vittata (Keyserling), new combination

Figures 264–271; Map 5

Uloborus vittatus Keyserling, 1882, Verh. zool.-bot. Ges. Wien, 31: 279. Three female and one male syntypes from Peru, in British Museum (Natural History), examined.

Uloborus servulus Simon, 1892 [1893], Ann. Soc. ent. France, 61: 424. Male, three female, and three immature female syntypes from San Esteban (6 km S of Puerto Cabello) in the Venezuelan state of Caracas, collected 29 February to 27 March by E. Simon, in Muséum National d'Histoire Naturelle, Paris, examined, NEW SYNONYMY.

Uloborus semiargenteus Simon, 1893, Ann. Soc. ent. France, 62: 299. Six female, two male, and five immature syntypes from le Pará (presently Belém), Brazil, collected by M. de Mathan, in Muséum National d'Histoire Naturelle, Paris, examined, NEW SYNONYMY.

Uloborus amazonicus Mello-Leitão, 1949, Boletim do Museu Nacional, Rio de Janeiro, 92: 2. Female holotype from the vicinity of Rio Xingu in northwestern Brazil, collected by J. C. Carvalho, in the Museu Nacional, Rio de Janeiro, examined, NEW SYNONYMY.

Note. Keyserling lists female and male syntypes from "Peru: Amable Maria and Junin" and mentions that numerous examples are in the University of Warsaw collection. These specimens were not received with other requested material from the Polska Akademia Nauk and appear to be lost. Specimens in the British Museum (Natural History) marked "type" appear to be part of Keyserling's type series.

Diagnosis. Females are most similar to those of *P. republicana* and *P. vicina*, but may be distinguished by their color pattern (Fig. 264), by having a broad, convex anterior epigynal border (Fig. 266) rather than a narrow, precipitous margin; by having openings in the posterior sixth rather than posterior third or half of the atrium (Fig. 266), and by having these openings separated by a third the atrial width. Epigynal ducts loop twice before connecting with the spermathecae (Fig. 268). Males are similar to those of the other members of this species group, but may be distinguished by the presence of a light chevron on the abdomen's venter (Fig. 265), by having a median apophysis bulb which is dome-shaped rather than flat in lateral view, and by having a more extensive conductor lobe (Fig. 270).

Description. Female. Total length

4.7 to 6.3 mm ($\bar{X}$ = 5.29, SD = 0.46, N = 16), carapace length 1.4 to 1.7 mm ($\bar{X}$ = 1.58, SD = 0.10), sternum length 0.9 to 1.1 m ($\bar{X}$ = 1.02, SD = 0.07). Carapace uniformly tan to dark brown or with a light central area which may be trilobed (Fig. 264). The AMEs often surrounded by a small, light area, never by a black area. Clypeus height 0.5 to 0.6 AME diameter. Sternum brown to dark gray. Abdomen half as wide as long with a slight raised area in the anterior quarter. Dorsum white to dark gray with a light median longitudinal stripe a third to half the abdomen's width, within which are three pairs of darkly bordered white spots or three medially divided chevrons (Fig. 264). Anterior lateral margins of abdomen each with a white oval patch, posterior tip of abdomen with a white chevron. Abdomen's venter with an hourglass-shaped median light area set off by a narrow white line. Booklung covers unpigmented. Legs uniformly light in color or with dark proximal and distal rings of femora and tibiae. Epigynum with a shallow central depression bordered anteriorly and laterally by broad, convex margins and posteriorly by a narrow, overhanging rim (Fig. 266). Openings in posterior sixth of epigynum, separated by a third the epigynal width. Ducts loop twice before entering spherical spermatheca (Fig. 268).

Male. Total length 3.6 to 4.2 mm ($\bar{X}$ = 3.91, SD = 0.19, N = 16), carapace length 1.5 to 1.8 mm ($\bar{X}$ = 1.63, SD = 0.09, sternum length 0.9 to 1.0 mm ($\bar{X}$ = 0.96, SD = 0.04). Carapace light tan, often with a light median stripe and lateral markings (Fig. 265). All eyes with a narrow black rim. Clypeus height equal to AME diameter. Sternum light tan. Abdomen's dorsum light tan, often with light gray sides, four medially divided white chevrons, and two anterolateral white patches (Fig. 265). Abdominal venter with a gray median longitudinal stripe about half the abdomen's width and with a light chevron midway between the spinnerets and epigastric furrow. Legs all light or faintly colored as in females. Palpal femur with two small, equal-sized proximal ventral tubercles. Median apophysis bulb large and dome-shaped, conductor spike long and conductor blade large, three times as long as wide (Fig. 270).

Distribution. South America (Map 5).

The *Philoponella fasciata* Species Group

This group contains *P. fasciata*, *P. para*, and *P. bella*. Females of these species and males of *P. para* have a clypeus height equal to the AME diameter and male *P. fasciata* a clypeus height twice the AME diameter. Epigynal openings are found in the anterior third (Fig. 287) or posterior half of the atrium (Fig. 275, 284) and are separated by a distance equal to 0.6 to 0.8 the atrial width. The duct leading from each opening coils once (Figs. 275, 285) before connecting to the spermatheca and in the region of this coil its walls are thickened. Anterior epigynal rim precipitous, its anterior border is broad and convex (Figs. 275, 284, 287). Anterior and posterior rims are not separated by conspicuous troughs and the posterior rim is not indented (Figs. 276, 286, 288). The male palpus has a short, square conductor blade, but unlike the other species groups, has a long, thin,

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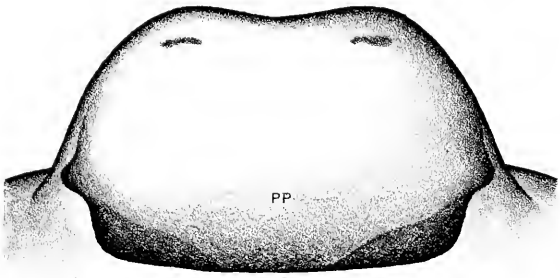
Figures 262–263. *Philoponella arizonica* (Gertsch). 262. Posterior view of epigynum. 263. Dorsal view of cleared epigynum. Figures 264–271. *Philoponella vittata* (Keyserling). 264. Dorsal view of female. 265. Dorsal view of male. 266. Ventral view of epigynum. 267. Posterior view of epigynum. 268. Dorsal view of cleared epigynum. 269. Ventral view of male palpal femur. 270. Retrolateral view of male left palpus. 271. Apical view of left male palpus. Figure 272. Apical views of male left median apophysis spurs of *Philoponella fasciata* species group. Figures 273–274. *Philoponella fasciata* (Mello-Leitão). 273. Female carapace. 274. Dorsal view of female holotype abdomen.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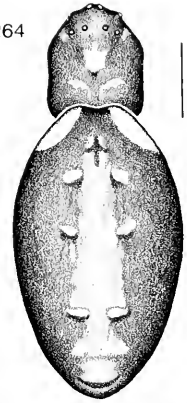
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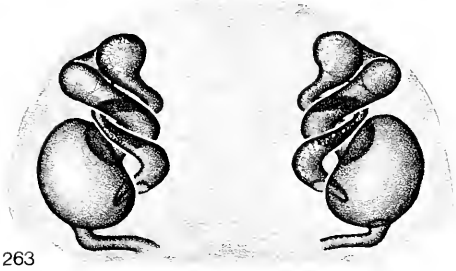
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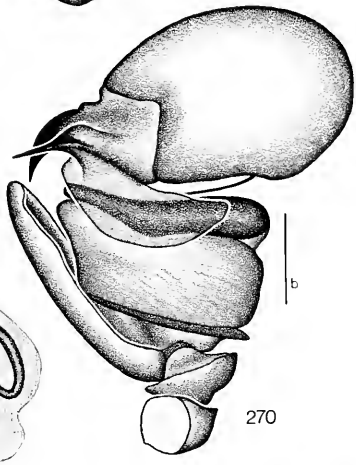
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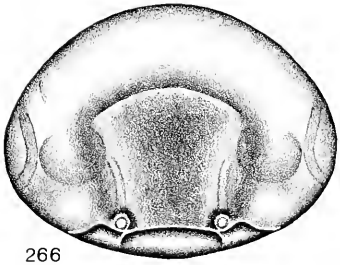
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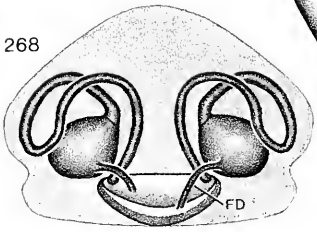
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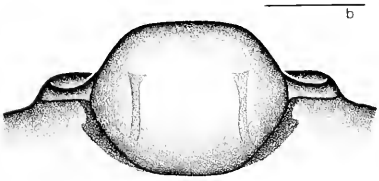
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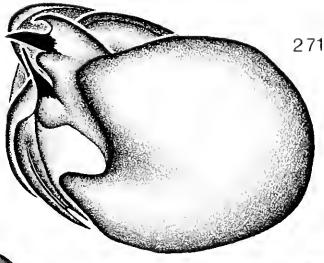
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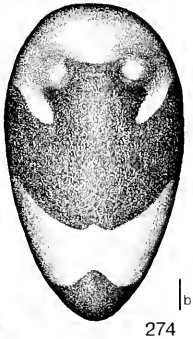
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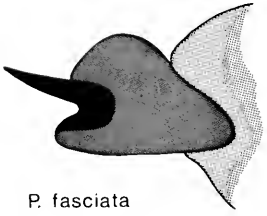
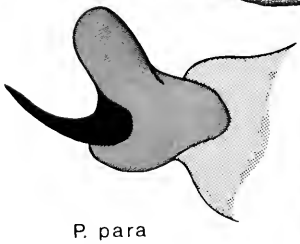
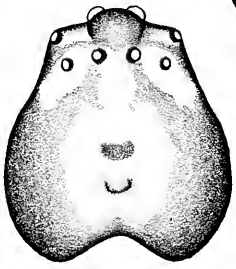

P. fasciata


P. para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Map. 5. Distribution of *Philoponella vittata* and *P. fasciata*.

distal prong which runs nearly parallel to the conductor spike (Figs. 280, 283). The conductor spike is as long as or longer than the median apophysis spur's slender apical region.

Philoponella fasciata (Mello-Leitão), new combination
Figures 272–281; Map 5

Uloborus fasciatus Mello-Leitão, 1917, Esc. Sup. Agric. Medic. Vet., 1(1): 4. Female holotype from Nova-Iguacú in the Brazilian state of Rio de Janeiro, collected by Blanc de Freitas, in Museu Nacional, Rio de Janeiro, examined.

Diagnosis. Females are distinguished from other members of the *variegata* species group by having: 1. a total length of less than 3.5 mm, 2. a sternum length of 0.7 mm or less, 3. long, longitudinal epigynal openings located in the posterior half of the epigynal crypt and bordered laterally by a broad, flat inclined region (Fig. 275), and 4. a gray spot just anterior to the carapace's thoracic depression. Males are distinguished from others of the genus by their high, nearly cylindrical carapace (Figs. 278, 279), long lateral palpal femoral tubercle (Fig. 281), and coloration (Figs. 278, 279). They are distinguished from other members of the *variegata* species group by their short basal conductor lobe and its long, thin extension (Fig. 280).

Description. Female. Total length 2.4 to 3.2 mm ($\bar{X}$ = 2.76, SD = 0.30, N = 10), carapace length 1.0 to 1.1 mm ($\bar{X}$ = 1.00, SD = 0.05), sternum length 0.6 to 0.7 mm ($\bar{X}$ = 0.64, SD = 0.04). Abdomen three-fourths as wide and high as long and peaked in the anterior third of its length. Carapace light tan to black, all but the darkest specimens having color markings similar to those shown in Fig. 273. Sternum tan to dark brown. Abdomen coloration of holotype (Fig. 274) differs from that of other specimens examined. In these it ranges from white to black, but in most specimens has a wide white dorsomedian stripe, gray sides, and a gray venter with a pair of thin, widely separated paraxial stripes extending from booklungs to spinnerets. In ventral view epigynal atrium is 0.1 to 0.2 mm long ($\bar{X}$ = 0.15, SD = 0.02) and 0.2 to 0.3 mm wide ($\bar{X}$ = 0.26, SD = 0.02). Its long openings lie just posterior to the atrium's center, medial to wide lateral borders, and sep-

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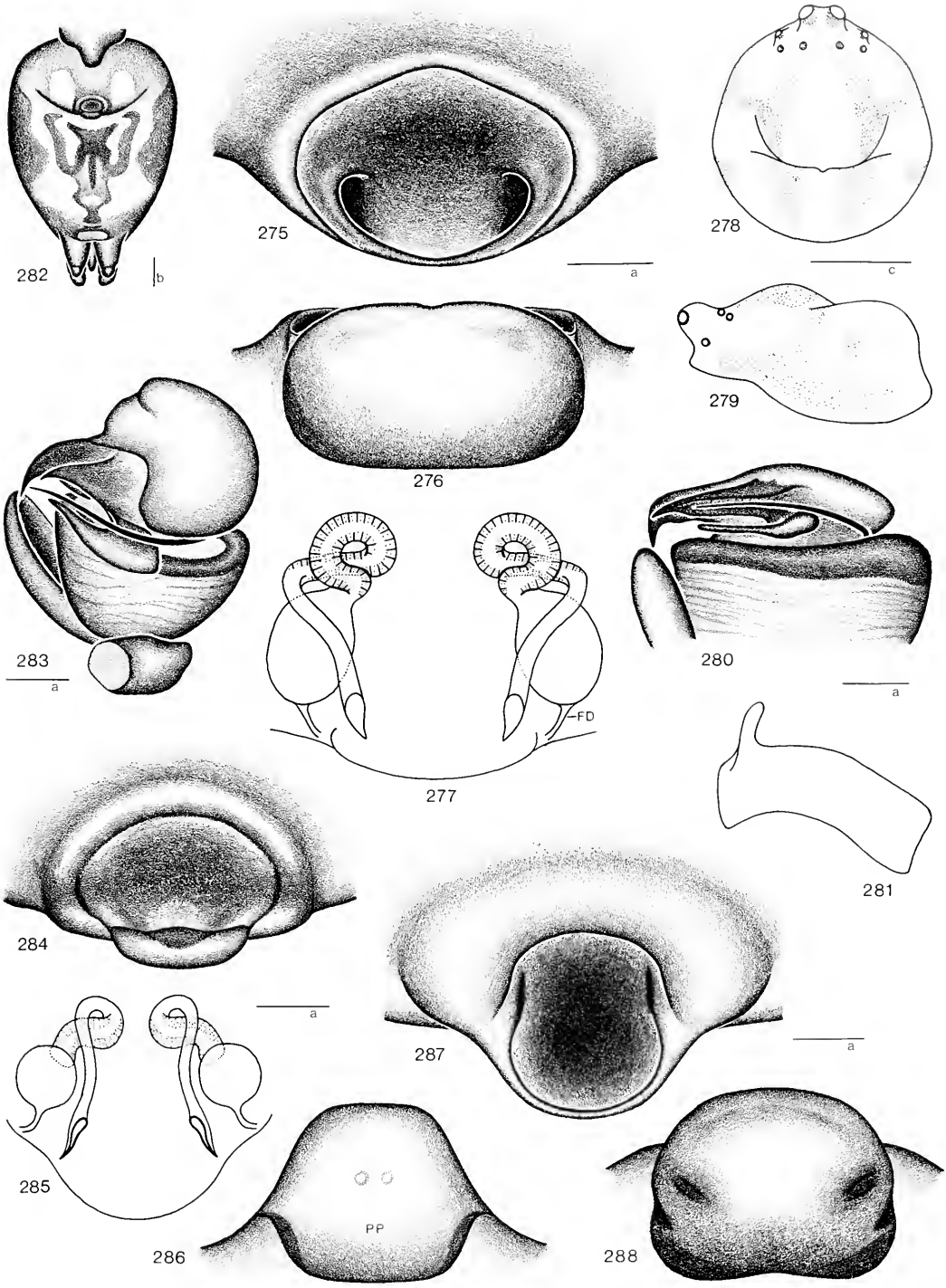
Figures 275–281. *Philoponella fasciata* (Mello-Leitão). 275. Ventral view of holotype's epigynum. 276. Posterior view of epigynum. 277. Dorsal view of cleared epigynum. 278. Dorsal view of male carapace. 279. Lateral view of male carapace. 280. Retrolateral view of apical region of male left palpus. 281. Retrolateral view of male left palpal femur. Figures 282–286. *Philoponella para* n. sp. 282. Ventral view of female abdomen. 283. Retrolateral view of male palpus. 284. Ventral view of epigynum. 285. Dorsal view of cleared epigynum. 286. Posterior view of epigynum. Figures 287–288. *Philoponella bella* n. sp. 287. Ventral view of epigynum. 288. Posterior view of epigynum.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288

arated by a distance equal to 0.8 the atrium's width (Fig. 275). In posterior view posterior plate twice as wide as high and with a slight median indentation (Fig. 276). A duct leading from each opening loops once around itself before connecting with a spherical spermatheca (Fig. 277).

Male. The male of this species is described here for the first time. Total length 2.2 to 2.6 mm, carapace length 1.1 to 1.3 mm, sternum length 0.6 to 0.7 mm. Carapace high with nearly straight sides, a deep and wide transverse thoracic groove, and a more prominent AME tubercle than present in other *Philoponella* males (Figs. 278, 279). Length of retrolateral palpal femoral tubercle twice the width of its base (Fig. 281). First femur with two or three prolateral, one retrolateral, one dorsal, and no ventral macrosetae. First tibial prolateral, retrolateral, and dorsal surfaces each with four spines, venter without spines. Carapace tan to black and in most specimens with color markings similar to those shown in Figs. 278, 279. Sternum tan to gray. Abdomen tan with irregular white spots and a gray posterodorsal tip. Median apophysis bulb very flat (Fig. 280), 0.3 mm long and 0.2 to 0.3 mm wide. Conductor spur long and concave (Fig. 280). Conductor basal lobe shorter than other known members of the *variegata* species group and with a long, thin, nearly transparent projection which extends parallel to the conductor spur and is about as long as the latter (Fig. 280).

Distribution. Southeastern Brazil and Paraguay (Map 5).

Philoponella para n. sp.
Figures 282–286

Types. Female holotype, one male and two female paratypes from Taguaraiapa [cannot be located in gazeteteers] in the Paraguay department of Alto Paraná, in the American Museum of Natural History. The specific epithet is an arbitrary combination of letters.

Diagnosis. Females are distinguished by having a posterior epigynal margin which protrudes conspicuously ventrally and in posterior view is as high as broad (Figs. 284, 286). The atrium is twice as wide as long and openings situated in its posterior quarter are hidden in ventral view (Fig. 284). The abdomen's light venter has a dark W-shaped mark (Fig. 282). Males of *P. para* and *P. fasciata* are characterized by having a small conductor lobe with a long, thin extension projecting nearly parallel to the conductor spike (Figs. 280, 283). The median apophysis bulb of *P. para* is dome-shaped and has a small apical lobe (Fig. 283); whereas the bulb of *P. fasciata* males is flat (Fig. 280).

Description. Female. Total length 2.4 to 2.8 mm, carapace length 0.9 to 1.0 mm, sternum length 0.7 mm. Carapace and sternum mottled gray. Abdomen width and height two-thirds its length. Abdominal dorsum white with irregular patches of gray, lateral surface white to gray, venter white with a more or less distinct, upright gray "W" (Fig. 282). Legs white. First and fourth femora with proximal, central and distal gray rings; second and third femora with median and distal gray rings. First tibia with proximal and distal gray rings; first metatarsus and tarsus gray. Second through fourth tibiae and metatarsi with median and distal gray rings. Second through fourth tarsi white. In ventral view epigynal atrium about twice as wide as long (length 0.1 mm, width 0.2 mm) and has a concave, ventrally directed median lobe which is three-fourths as wide as the atrium and has a straight ventral margin (Fig. 284). The epigynal atrium's anterior rim is rounded (Fig. 284). In posterior view the epigynum is as high as wide (Fig. 286). An indistinct epigynal opening is located at each centrolateral margin of the atrium and the duct leading from it loops once before connecting to a small spherical spermatheca which lies at the level of the anterior atrial rim (Fig. 285).

Male. Total length 2.2 mm, carapace length 1.0 mm, sternum length 0.6 mm. Carapace and sternum light tan; lateral

regions of carapace lightly mottled with gray; sternum with narrow gray lateral borders. Abdomen tan, overlain with white patches; dorsal tip gray, venter with two widely separated, paraxial gray stripes. Legs tan with a faint, distal gray ring on first femur. First femur with three prolateral, one retrolateral, and no dorsal and ventral macrosetae. First tibia with three prolateral, four retrolateral, four dorsal and no ventral spines. Proximal, ventral surface of palpal femur with two small, nearly equal-sized tubercles. Median apophysis bulb dome-shaped, 0.2 mm long, and 0.2 mm wide, and with a small apical lobe (Fig. 283). Median apophysis spur's basal region two-thirds as long as wide, with a prominent apical lobe and a spike equal to the latter's length (Fig. 272). Conductor's basal lobe (Fig. 283) longer than that of *P. fasciata*. Like *P. fasciata*, the basal conductor lobe has an extension which runs nearly parallel to the conductor spike. In *P. para* this extension is about two-thirds the spike's length.

Distribution. Known only from the type locality in Paraguay.

Philoponella bella n. sp.
Figures 287–288

Types. Female holotype and female paratype from Río Domachui trail, elev. 2700 to 3000 m, near Santa Marta in the Colombian state of Magdalena, collected 2 February 1973 by J. A. Kochalka, in the Museum of Comparative Zoology. The specific epithet is an arbitrary combination of letters.

Diagnosis. Female *P. bella* are distinguished from other members of the genus by having an epigynal atrium whose length and width are equal and whose protruding posterior surface has two lateral grooves (Figs. 287, 288).

Description. Only females are known. Total length 3.5 to 3.6 mm, carapace length 1.3 to 1.4 mm, sternum length 0.8 mm. Carapace and sternum mottled gray; carapace with white lateral rim. Abdomen tan, mottled with dark gray and with a pair of large dark dorsal spots in the anterior quarter and a cluster of five narrow, transverse, gray dorsal stripes in the posterior third. First femur gray with a distal white ring. Second through fourth femora white, each with a proximal, central, and distal gray ring. Proximal half of tibiae white with a gray ring, distal half gray-brown. Metatarsi white with dark central and distal rings. Tarsi white proximally and gray distally. In ventral view length and width of epigynal atrium are equal; half of the atrium's length projecting posterior to the epigastric furrow (Fig. 287). The atrium's posterior region forms a deep pocket and is bordered by a thin posterior rim. Openings are situated slightly anterior to the rim's center at the atrium's lateral margins. In posterior view the epigynum has two lateral grooves (Fig. 288). From each epigynal opening a duct loops once before connecting with a small, spherical spermatheca from whose posterior median surface a fertilization duct arises.

Distribution. Known only from the type locality in northeastern Colombia.

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