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WEST INDIAN XENODONTINE COLUBRID SNAKES: THEIR PROBABLE ORIGIN, PHYLOGENY, AND ZOOGEOGRAPHY

VINCENT J. MAGLIO

CONTENTS

ABSTRACT

The relationships between the thirty-three species of xenodontine snakes in the West Indies are reviewed primarily on the basis of osteological and hemipenial morphology. Four species assemblages are recognized, distinguished by the shape of the frontal and prefrontal bones and by the structure of the hemipenis. Within the *cantherigerus* species assemblage three genera are recognized–*Alsophis*, *Hypsirhynchus*, and *Uromacer*. It is suggested that this group entered the West Indies from South or Central America, derived from a primitive form of *Alsophis*. The South American species *Alsophis chamissonis* appears to be a relict of that primitive stock. The mainland genera *Philodryas* and *Conophis* appear to be later specialized descendants from that same early stock. The three Galapagos species formerly referred to the genus *Dromicus* (*biserialis*, *dorsalis*, and *slevini*), are placed in the genus *Alsophis* and regarded as close to the primitive mainland forms.

The relationships of the genus *Ialtris* remain uncertain, but descent from West Indian *Alsophis* is reasonable.

The *melanotus* species assemblage has not progressed into the West Indies beyond the northern Lesser Antilles, and has almost certainly been derived from the mainland *Leimadophis*-*Liophis*-*Lygophis* complex. The generic name *Dromicus* is applied to these West Indian forms with the name *Leimadophis* as a junior synonym.

Two species, *andreae* and *parvifrons* from Cuba and Hispaniola, respectively, share a number of osteological characters with *Alsophis*, but are like *Dromicus* externally. The hemipenis is of the *Alsophis* type and unlike that of *Dromicus*. Because of their peculiar combination of characters these two species cannot readily be accommodated in any existing genus. The name *Antillophis* nov. gen. is proposed for them. It is suggested that they may be closely related to the mainland form *Lygophis boursieri* while the type species of that genus, *L. lineatus*, appears to be closer to *Dromicus*.

Eight species formerly placed in the genera *Arrhyton*, *Dromicus*, and *Darlingtonia*, are considered to form the *funereus* species assemblage. Except for the retention of *Darlingtonia* for *haetiana*, the species of this group are referred to the genus *Arrhyton*. A close relationship to the mainland genus *Rhadinaea* is postulated, and it is suggested that the two genera may have been derived from a common ancestor. The osteological similarities between these two groups are discussed in terms of general semiburrowing adaptations and are compared with other semiburrowing to burrowing New World colubrid snakes. It is concluded that these similarities represent a phylogenetic relationship rather than morphological convergence.

Four oversea colonizations from the mainland and numerous inter-island dispersals are required to explain the recent West Indian fauna and its present distribution.

INTRODUCTION

The West Indies today contain an endemic snake fauna of modest size. In the absence of an adequate fossil record, any

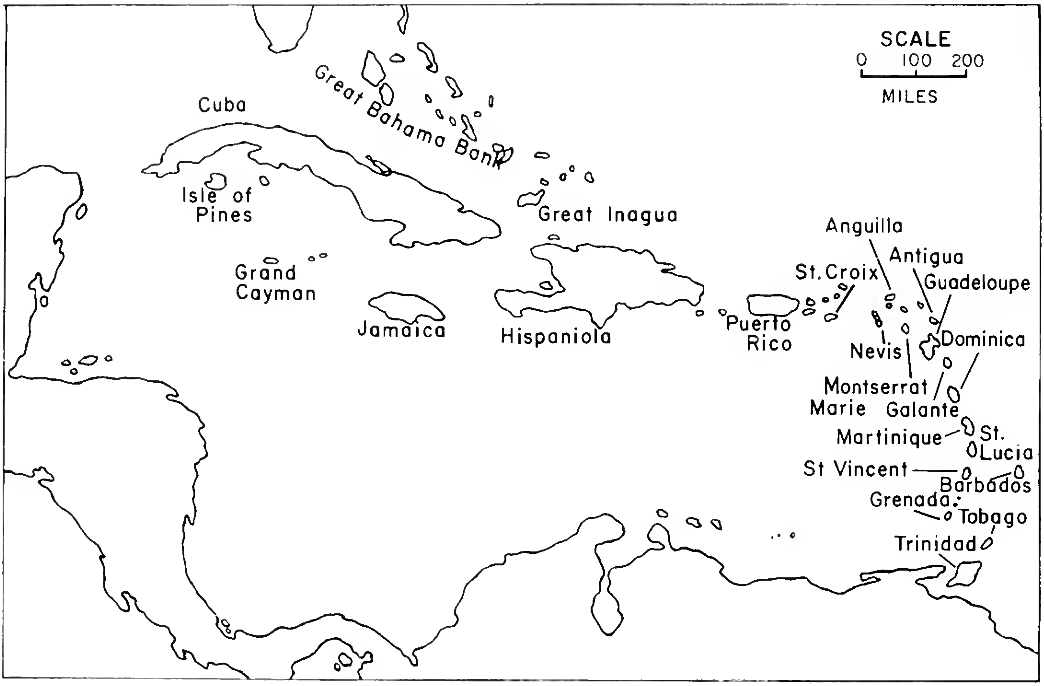

Fig. 1. Map of the West Indies in Mercator's projection.

discussion of relationships within this group and of its history must ultimately be based on the inferred relationships of living species. It is the purpose of the present study to examine the West Indian species of the subfamily Xenodontinae *(sensu* Dunn, 1928) of the family Colubridae, with reference to their origin, phylogeny, and zoogeography, so far as these can be deduced from their anatomy and distribution.

The only previous attempt to consider a large segment of this group was that by Dunn, 1932, but his work concerned only the Greater Antilles. Dunn relied heavily on the number of sensory pits present on each of the dorsal body scales and consequently recognized two basic generic groups in the West Indies; *Alsophis* was distinguished as having two pits per scale, and *Dromicus* only one pit. From these two groups Dunn derived all of the other endemic genera of the Greater Antilles. He also examined the dentition and hemipenis, concluding that these did not contradict his proposed relationships. However, examination of Lesser Antillean and mainland species in the present study, as well as a re-evaluation of all West Indian xenodontines, does contradict these conclusions. Dunn weighted his characters in such a way that several well-defined groups of species remained unrecognized.

The xenodontine fauna of the West Indies consists of the thirty-three species and their subspecies listed in Table 1. *Tretanorhinus variabilis* ssp. occurs on Cuba, and appears to be a recent immigrant from Central America where several closely related species occur; it will not be considered further here. The remaining thirty-two species—except for "*Leimadophis*" *melanotus* which occurs both on Trinidad and on the mainland (see Fig. 1 for map)—are endemic to the West Indies and form the basis of this work. All except *Ialtris parishi* have been examined. They

TABLE 1

CHECKLIST AND DISTRIBUTION OF WEST INDIAN AND SOME MAINLAND[1] AND GALAPAGOS[1] XENODONTINE COLUBRID SNAKES. GENERIC ASSIGNMENTS RECOGNIZED PREVIOUS TO THIS PAPER AND RECOGNIZED IN THE PRESENT STUDY ARE GIVEN FOR COMPARISON. SPECIES ARE ARRANGED IN ALPHABETICAL ORDER.

	Generic assignment		
Species	Previous	Present	Distribution
(*almadensis*)	*Leimadophis*	*Dromicus*	Brazil
andreae andreae	*Dromicus*	*Antillophis* nov. gen.	Cuba
andreae melophyrra			Cuba
andreae nebulatus			Isle of Pines
andreae orientalis			Cuba
andreae peninsulae			Cuba
(*angustilineatus*)	*Dromicus*	*Alsophis*	Peru
anomalus	*Alsophis*	*Alsophis*	Hispaniola
ater	*Alsophis*	*Alsophis*	Jamaica
antillensis antillensis	*Alsophis*	*Alsophis*	Guadeloupe
antillensis antiquae			Antigua
antillensis manselli			Montserrat
antillensis sanctorum			Les Saintes
antillensis sibonius			Dominica
(*biserialis*)	*Dromicus*	*Alsophis*	Galapagos
callilaemus	*Dromicus*	*Arrhyton*	Jamaica
cantherigerus cantherigerus	*Alsophis*	*Alsophis*	Cuba
cantherigerus adspersus			Cuba
cantherigerus brooksi			Swan Island
cantherigerus caymanus			Grand Cayman
cantherigerus fuscicauda			Cayman Brac
cantherigerus pepei			Cuba
cantherigerus ruttyi			Little Cayman
cantherigerus schwartzi			Cuba
catesbyi	*Uromacer*	*Uromacer*	Hispaniola, Tortue Island, Vache Island, Gonave Island
(*chamissonis*)	*Dromicus*	*Alsophis*	Chili, Argentina
cursor	*Dromicus*	*Dromicus*	Martinique
dolichurum	*Arrhyton*	*Arrhyton*	Cuba
dorsalis	*Ialtris*	*Ialtris*	Hispaniola
dorsalis	*Uromacer*	*Uromacer*	Gonave Island
(*dorsalis*)	*Dromicus*	*Alsophis*	Galapagos
exiguus exiguus	*Dromicus*	*Arrhyton*	American Virgin Islands
exiguus stahli			Puerto Rico
exiguus subspadix			Puerto Rico
ferox	*Hypsirhynchus*	*Hypsirhynchus*	Hispaniola
frenatus	*Uromacer*	*Uromacer*	Hispaniola, Beata Island
funereus	*Dromicus*	*Arrhyton*	Jamaica
haetiana haetiana	*Darlingtonia*	*Darlingtonia*	Hispaniola
haetiana perfector			Hispaniola
juliae juliae	*Dromicus*	*Dromicus*	Dominica
juliae copeae			Guadeloupe
juliae mariae			Marie Galante
melanichnus	*Alsophis*	*Alsophis*	Hispaniola
melanotus	*Leimadophis*	*Dromicus*	Trinidad, Tobago, South America
ornatus	*Dromicus*	*Dromicus*	St. Lucia
oxyrhynchus	*Uromacer*	*Uromacer*	Hispaniola
parishi	*Ialtris*	*Ialtris*	Hispaniola
parvifrons parvifrons	*Dromicus*	*Antillophis* nov. gen.	Hispaniola

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[1] Non-West Indian species are enclosed in parentheses.

TABLE 1 (Continued)

Species	Generic assignment		Distribution
	Previous	Present	
parvifrons alleni			Gonave Island
parvifrons lincolni			Hispaniola
parvifrons niger			Hispaniola
parvifrons paraniger			Hispaniola
parvifrons protenus			Hispaniola
parvifrons rosamondae			Vache Island
parvifrons stygius			Hispaniola
parvifrons tortugensis			Tortue Island
perfuscus	*Leimadophis*	*Dromicus*	Barbados
polylepis	*Dromicus*	*Arrhyton*	Jamaica
portoricensis portoricensis	*Alsophis*	*Alsophis*	Puerto Rico
portoricensis anegadae			Anegadae
portoricensis aphantus			Vieques
portoricensis nicholsi			Buck Island
portoricensis prymnus			Puerto Rico
portoricensis richardi			St. Thomas
portoricensis variegatus			Mona Island
rijgersmai	*Alsophis*	*Alsophis*	Anguilla Bank Islands
rufiventris	*Alsophis*	*Alsophis*	St. Kitts, Saba, St. Eustatius, Nevis
sanctierucis	*Alsophis*	*Alsophis*	St. Croix
(*slevini*)	*Dromicus*	*Alsophis*	Galapagos
(*tachymenoides*)	*Dromicus*	*Alsophis*	Peru
taeniatum	*Arrhyton*	*Arrhyton*	Cuba
variabilis	*Tretanorhinus*	(not considered)	Cuba
vittatum vittatum	*Arrhyton*	*Arrhyton*	Cuba
vittatum landoi			Cuba
vudii vudii	*Alsophis*	*Alsophis*	Great Bahama Bank Islands
vudii alterrinus			Grand Bahama Island
vudii picticeps			Bimini Island
vudii raineyi			Crooked Island
vudii utowanae			Great Inagua Island

are divided into four species assemblages on the basis of skull, hemipenial, and external characters, and will be treated within these groups in the following pages. All described subspecies except "*Dromicus*" *andreae peninsulae* and "*D.*" *a. melophyrrha* from Cuba, "*Dromicus*" *juliae copeae* from Guadeloupe, and "*D.*" *exiguus subspadix* from Puerto Rico, have been examined; but subspecies will not be discussed further unless the evidence suggests a change in taxonomic rank. The osteology of 70 mainland and Galapagos species was examined in order to determine possible relationships between Antillean and mainland forms.

Some previous generic allocations are here considered to be of questionable validity. I, therefore, as an initial procedure, will disregard current generic assignments and use only the specific names until probable relationships have been assessed and assemblages of probable generic value can be recognized. Changes in nomenclature are made only where

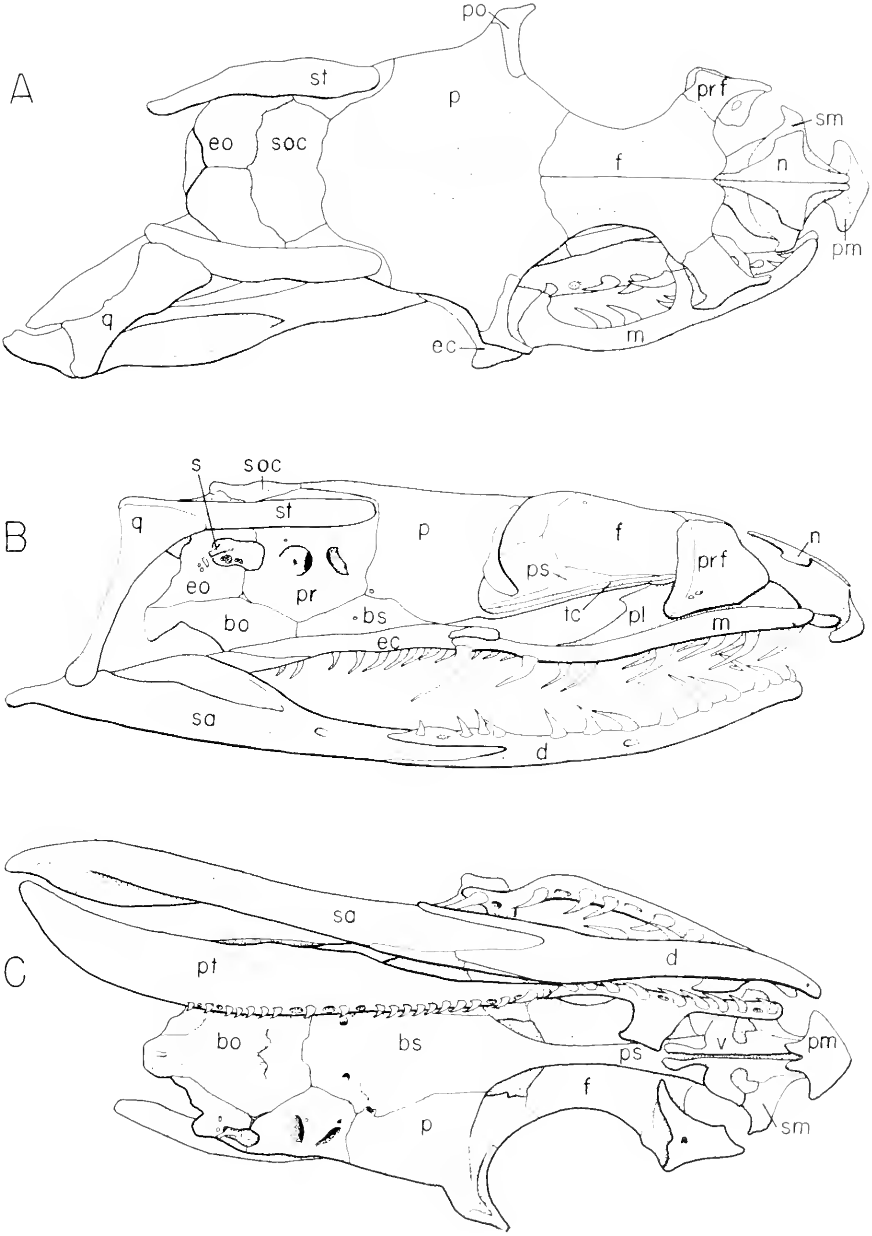


Fig. 2. Skull of *Alsaphis cantherigerus* (MCZ 44874) showing general relationships of bones in xenodontine colubrid snakes. A, dorsal view; B, lateral view; C, ventral view. Left tooth-bearing elements removed. Abbreviations: *bo*, basioccipital; *bs*, basisphenoid; *d*, dentary; *ec*, ectopterygoid; *eo*, exoccipital; *f*, frontal; *m*, maxilla; *n*, nasal; *p*, parietal; *pl*, palatine; *pm*, premaxilla; *po*, postorbital; *pr*, prootic; *prf*, prefrontal; *ps*, parasphenoid; *pt*, pterygoid; *q*, quadrate; *s*, stapes; *sa*, surangular; *sm*, septomaxilla; *soc*, supraoccipital; *st*, supratemporal; *tc*, trabecular canal; *v*, vomer. Approx. × 7.

necessary for consistency and for the logical implementation of generic concepts as developed here. In a final section I use the postulated relationships to suggest a possible interpretation of the zoogeographic history of what I consider to be the valid groups in the West Indies.

It is my feeling that snake genera are oversplit and not comparable to genera in other reptilian groups. This is a subjective judgment, however, and certainly not consistent with the philosophy and usage of the majority of herpetologists working on snakes. Since it is certainly desirable that taxonomic usage within the West Indies conform to that customary elsewhere, I have conservatively retained generic names (e.g., *Darlingtonia*) though I believe them to be of limited usefulness. In one case I have raised to generic rank a species group which, on current taxonomic usage, cannot be accommodated within any other existing genus.

As Darlington (1938) and Simpson (1956) have discussed, the islands of the Caribbean do not appear to have been connected with the mainland during the later Cenozoic and overseas migration best explains the available faunal evidence. This hypothesis seems best also to explain the present data.

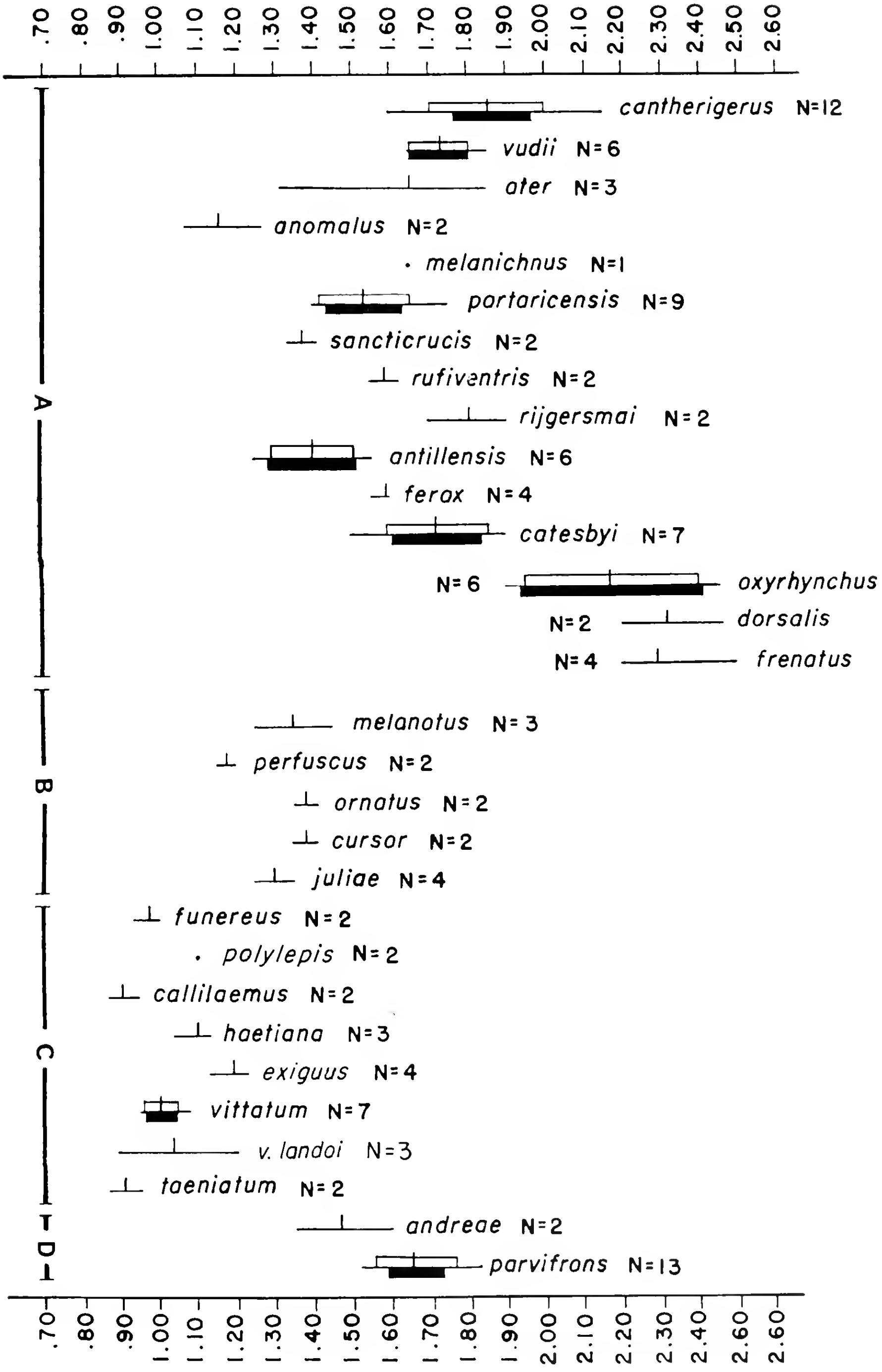
Characters utilized

The choice of specific skull characters was made only after more than 200 skulls of West Indian and mainland species had been examined to determine which characters were least variable within a species and to discover which ones could therefore be used to infer possible relationships with other species. The characters so chosen include the following:

1. The number of teeth which, in several of the species assemblages recognized here, show trends of reduction or increase from species to species (see Figs. 6, 20, and 29 below and the appendix).
2. The frontal bones (see Fig. 2 for labeled skull) also show considerable variation in shape within the West Indies, but prove to have distinctive proportions in certain assemblages, long and narrow on one group and nearly square in another. Figure 3 shows the distribution of length/width ratios for the frontal bones in 29 West Indian species. The four groups of species labeled A, B, C, and D represent the species assemblages recognized here on the basis of all characters combined. Nevertheless, even with respect to frontal shape alone, it is clear that assemblage C may be distinguished from assemblages A and D in having a frontal pair that is roughly as wide as it is long. In assemblage A, most of the species have a frontal pair that is one and one-half to two times as long as wide.
3. The shape of the prefrontal bone was found to be very reliable in separating assemblages in most cases, but quantification of this character was difficult. In Figure 4 the same 29 species as in Figure 3 are compared with respect to the length/width index for the prefrontal bone. Although assemblages B and C overlap completely, both exhibit a considerably longer and narrower prefrontal than in assemblage A (Fig. 5). Although there is a certain degree of variation with respect to shape of the prefrontal and other bones, they remain sufficiently distinctive in each group to be taxonomically useful. Other characters such as the parasphenoid width and skull proportions are discussed under each species assemblage.

→

Fig. 3. Length width indices for the frontal bone pair of 29 species of West Indian colubrid snakes. A, *cantherigerus* species assemblage; B, *melanotus* species assemblage; C, *funereus* species assemblage; D, *andreae* species assemblage. Horizontal line, observed range; vertical line, mean; open rectangle, ± one standard deviation from the mean; solid rectangle, 95 per cent confidence interval of the mean.


.70
.80
.90
1.00
1.10
1.20
1.30
1.40
1.50
1.60
1.70
1.80
1.90
2.00
2.10
2.20
2.30
2.40
2.50
2.60
A
cantherigerus N=12
vudii N=6
ater N=3
anomalus N=2
melanichnus N=1
portoricensis N=9
sancticrucis N=2
rufiventris N=2
rijgersmai N=2
antillensis N=6
ferox N=4
catesbyi N=7
N=6 oxyrhynchus
N=2 dorsalis
N=4 frenatus
B
melanotus N=3
perfuscus N=2
ornatus N=2
cursor N=2
juliae N=4
C
funereus N=2
polylepis N=2
callilaemus N=2
haetiana N=3
exiguus N=4
vittatum N=7
v. landoi N=3
taeniatum N=2
D
andreae N=2
parvifrons N=13
.70
.80
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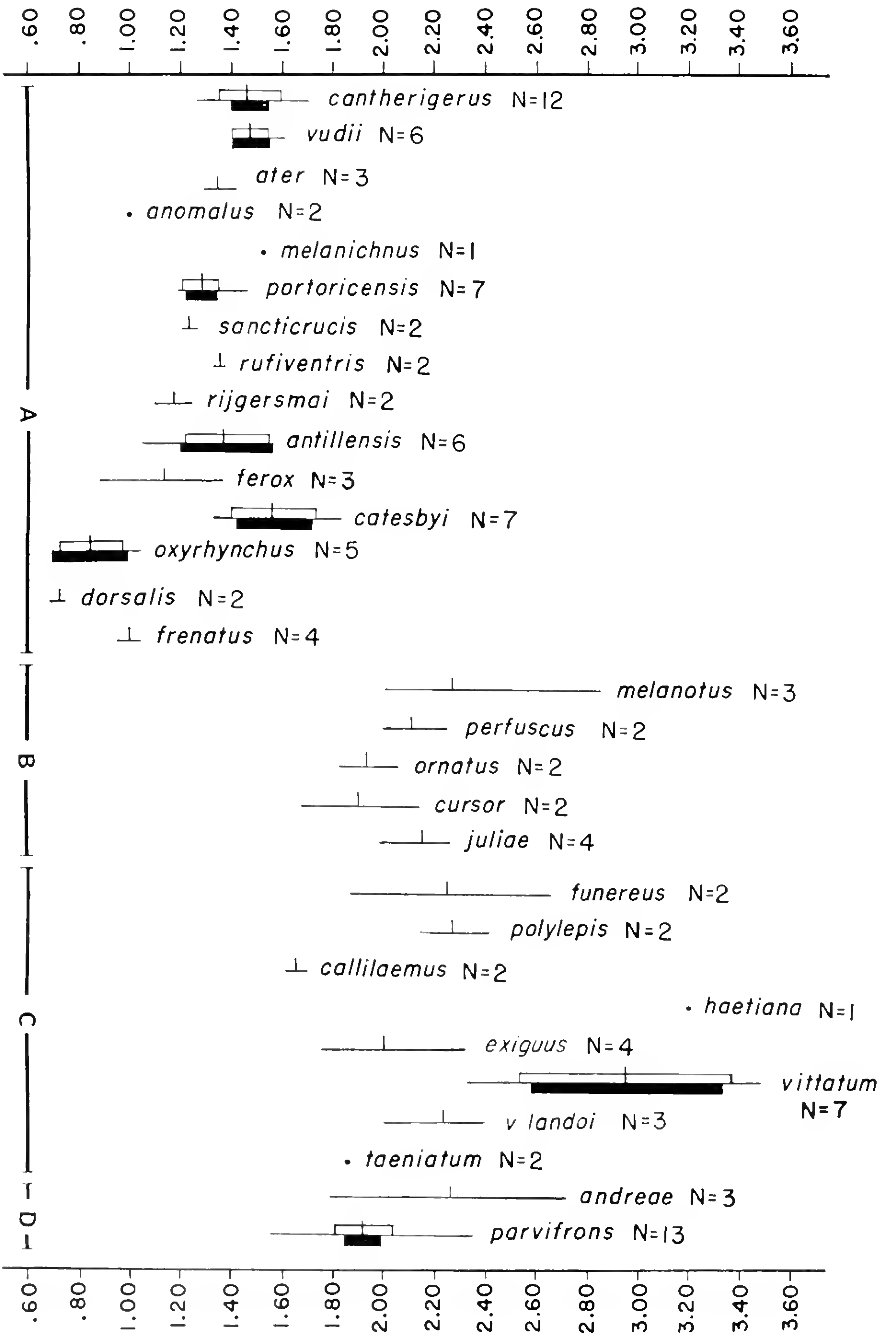

Fig. 4. Length width indices for the prefrontal bone of 29 species of West Indian colubrid snakes. Symbols as in Fig. 3.

The discussions of hemipenial morphology are based on dissections *in situ* of the uneverted organ. Terminology is after Dowling and Savage (1960).

It must be emphasized that in this study most measured parameters show various degrees of overlap in range for various species. This does not, however, lessen their value in attempting to recognize phylogenetic relationships through an analysis of morphological similarities. If an insular series of closely related species has been successively derived by island-hopping in a linear sequence, we might expect any two adjacent forms to show a greater similarity, barring extreme specialization, than the two geographically terminal species of the series.

The characters used here are those that combine relatively little intraspecific variability and enough variation between species to be useful in the study of intrageneric relationships. Certain characters such as an apical awn on the hemipenis, the shape of the prefrontal bone, or certain skull proportions appear to be constant within groups of species that show a close relationship in totality of characters combined, and are therefore considered to be of maximum value in indicating true affinities. Others, such as the number of pits on each dorsal body scale, have sometimes proved inconsistent with the majority of other traits and have therefore been considered unreliable at the level of major groups.

AGE VERSUS HABITUS

When attempting to establish relationships between extant forms based entirely on morphological considerations, it must be reasonably certain that differences are not the result of allometric phenomena. Likewise, it must be reasonably clear that apparent similarities are not the result of habitus rather than a close phylogenetic relationship.

Juvenile specimens, when available for comparison with the corresponding adult forms, show a number of consistent differences in the structure of the skull which appear to be related solely to size. The major differences may be summarized as follows:

Juvenile skull

Skull relatively wide
Quadrate thin and triangular
Supratemporal relatively short
Crests low and rounded
Postorbital small, non-projecting
Orbital foramen very large
Pterygoids short, not projecting beyond foramen magnum
Maxilla relatively lightly built
Bones of brain case thin

Adult skull

Skull relatively narrow
Quadrate with rodlike shaft
Supratemporal relatively long
Crests high and sharp
Postorbital large, projecting
Orbital foramen small
Pterygoids long, projecting far beyond foramen magnum
Maxilla relatively massive
Bones of brain case thick

It is clear that these characters should not ordinarily be given high taxonomic weight unless the comparison is between two species of comparable adult size.

Similarities resulting from habitus adaptations are more difficult to establish because the mode of life of these species is so poorly understood, and also because the adaptive significance of certain characters, such as scale pits, is at present unknown. Character convergence resulting from habitus similarity can, however, be inferred if a large number of characters are studied together. This point will be discussed in greater detail under the *funereus* species assemblage below.

THE SPECIES ASSEMBLAGES

Four species assemblages have been distinguished among the 32 species of West Indian xenodontine snakes here under study. These are characterized on the basis of a number of traits as follows:

	Prefrontal	*Frontals*	*Hemipenis*	*Size*
cantherigerus assemblage	long anteroposteriorly	long and narrow	no disk	large
melanotus assemblage	short anteroposteriorly	short and narrow	apical disk	medium
andreae assemblage	short anteroposteriorly	long and narrow	no disk	medium
funereus assemblage	short anteroposteriorly	square	no disk	small

CANTHERIGERUS SPECIES ASSEMBLAGE

Included West Indian species: *anomalus* Peters, Hispaniola; *antillensis* (= *leucomelas*)[1] Schlegel, Antigua, Montserrat, Guadeloupe, Les Saintes, Dominica; *ater* Gosse, Jamaica; *cantherigerus*[2] Bibron, Cuba, Isle of Pines, Swan Island, Grand Cayman, Little Cayman, Cayman Brac; *catesbyi* Schlegel, Hispaniola, Tortue Island, Vache Island, Gonave; *dorsalis* Dunn, Gonave; *ferox* Günther, Hispaniola; *frenatus* Günther, Hispaniola; *melanichnus* Cope, Hispaniola; *oxyrhynchus* Duméril and Bibron, Hispaniola; *portoricensis* Reinhardt and Lütken, Puerto Rico, Mona Island, Virgin Islands; *rijgersmai* Cope, Anguilla Bank Islands; *rufiventris* Duméril and Bibron, Saba, St. Eustatius, St. Kitts, Nevis; *sancticrucis* Cope, St. Croix; *vudii* Cope, Great Bahama Bank Islands, Great Inagua.

Osteology. The present group of species may be distinguished from other West Indian xenodontines by a number of skull features, the most characteristic of which is the shape of the prefrontal bone (see Fig. 5). Here this element is wide anteroposteriorly with a broad and strongly convex anterior edge. The lower margin of this anterior edge curves medially above the lacrimal foramen, so that the latter opens anteroventrally.

Within the assemblage, the species *cantherigerus* (Cuba) has the lowest number of teeth, with an average dental formula of about 12 + 2 maxillary, 10 palatine, 26 pterygoid, and 19 dentary teeth (see Fig. 6 and the Appendix for variation). The skull (Fig. 7) is long and the cranium is moderately deep dorsoventrally. The frontals are widest anteriorly where they make contact with the prefrontals and are strongly emarginated above the orbits. A short, stout postorbital bone is articulated in a deep notch on the parietal bone in such a way that a prominent flange or lateral extension of the parietal intervenes between the postorbital and the frontal bones (see Fig. 2). A weak, but clearly visible groove marks the dorsal midsagittal line of the parietal bone. The parasphenoid, forming the midventral surface of the skull, is narrow and has a deep trabecular canal on each lateral surface. This groove extends from the orbital foramen to the nasal capsule. A dorsal extension of the parasphenoid bone above the trabecular canals separates the two orbits, forming a thin interorbital partition.[1] The supratemporal is strong and curved, and extends some distance beyond the occiput. The quadrate is long and straight.

The species *vudii* on the islands of the Great Bahama Bank does not significantly differ osteologically from *cantherigerus.* The dental formula is about 12 + 2 maxillary, 10 palatine, 24 pterygoid, and 21 dentary teeth for *vudii vudii* and is roughly comparable to that of *cantherigerus.* A peculiar feature of *vudii* is the melanic

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[1] As discussed by Schwartz (1966: 178), Brongersma's (1937) analysis of Schlegel's cotypes and his choice of the Guadaloupe-like specimens as the lectotype of *Alsophis antillensis* have reduced the name *leucomelas* to the junior synonymy of *antillensis.*

[2] Senior synonym of *angulifer;* see Smith and Grant, 1958.

[1] Equals frontal crests of Underwood, 1967.

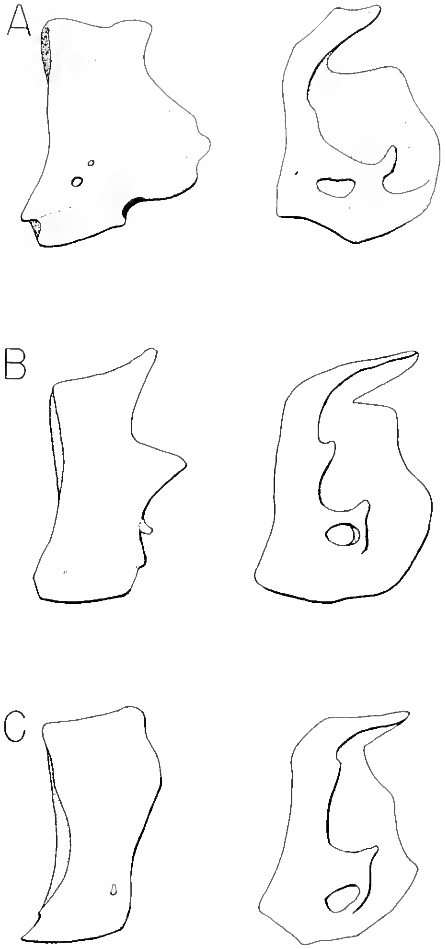

Fig. 5. Comparison of the three prefrontal bone types found in the four species assemblages of West Indian colubrid snakes as discussed in the text. A, *cantherigerus* assemblage type (*Alsophis cantherigerus*, MCZ 11200); B, *melanotus* and *andreae* assemblage type (*Antillophis parvifrons*, nov. gen., MCZ 77227); C, *funereus* assemblage type (*Arrhyton polylepis*, MCZ 81020). For each: left, lateral view; right, anterior view. Not to scale. Approx. × 10.

tissue lining the cranial cavity of every specimen examined. This tissue imparts a bluish gray color to the skull. A similar condition occurs occasionally in *cantherigerus*, and also in *catesbyi*, *dorsalis*, *frenatus*, and *oxyrhynchus* where it is the usual condition.

Although only two specimens including the type were available for study, *vudii utowanae* from Great Inagua differs from all the subspecies of *vudii* on the Great Bahama Bank in several characters. The nasal bone is distinctive in shape, but this character appears to be somewhat more variable than most skull characters and is therefore of uncertain significance. In its dentition, however, *vudii utowanae* is quite distinct from the other subspecies. The dental formula is about 15 + 2 maxillary, 13 palatine, 30 pterygoid, and 23 dentary teeth, and is greater for every tooth-bearing element. When additional specimens of *utowanae* become available, a greater degree of overlap with the Bahama Bank forms may become evident. However, *utowanae* still will largely lie outside the neatly clustered range for the other subspecies of *vudii*. As in *vudii vudii*, the skull of *utowanae* appears bluish gray due to the melanic tissue lining the cranial cavity.

On Jamaica the species *ater* has a dental formula higher than that of *cantherigerus*. The skull is generally flatter (Fig. 8) and, as a result of this flattening, the nasal bones are closer to the septomaxilla, and the frontal bones touch the trabecular canals ventrally so that the interorbital partition is very small, consisting only of that portion of the parasphenoid bearing the trabecular canals. The frontal bones are relatively shorter and wider (Fig. 9) in contrast to the long, narrow frontals of the Cuban species. In all other skull characters the two forms are very similar. The septomaxillae are expanded anteriorly and widen immediately behind the premaxilla (Fig. 10B).

The name *capistrata*, introduced by Gosse (1851: 373) for a patterned form from Jamaica, was synonymized with *ater* by Boulenger (1894) without comment. Two specimens of this form from the British Museum were made available to me for comparative purposes. Both are smaller than typical *ater* and differ from it in a number of osteological characters which in other species are related to

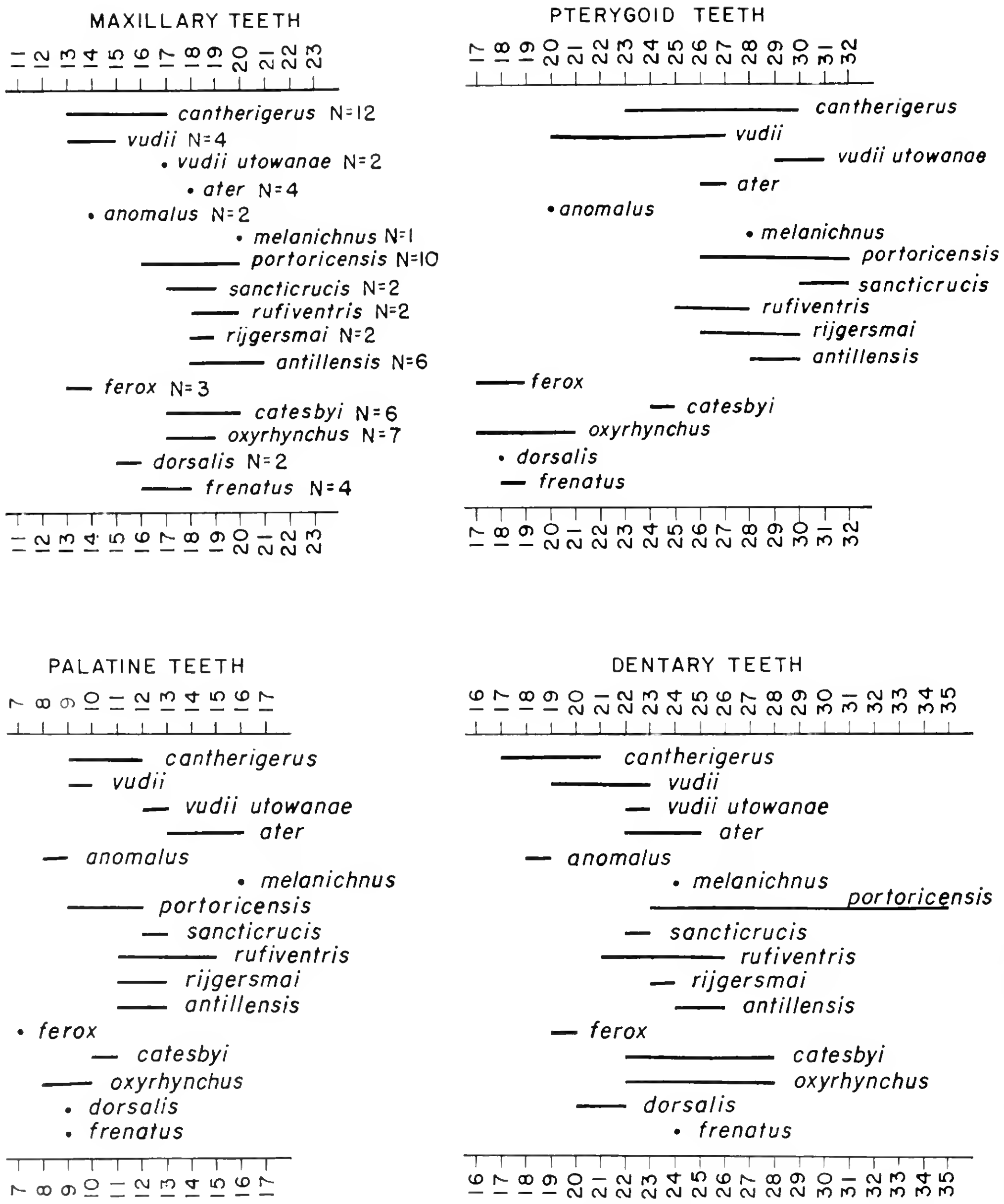

Fig. 6. Observed ranges of variation in numbers of teeth on each tooth-bearing element for the 15 West Indian species of the *cantherigerus* species assemblage.

ontogenetic changes. These include relatively narrower frontals, a broad rounded cranium, low crests and ridges, and thin cranial bones. It thus seems likely that *capistrata* represents a juvenile stage of *ater*, and we may follow Boulenger in regarding the two as synonymous.

On Hispaniola there are eight species

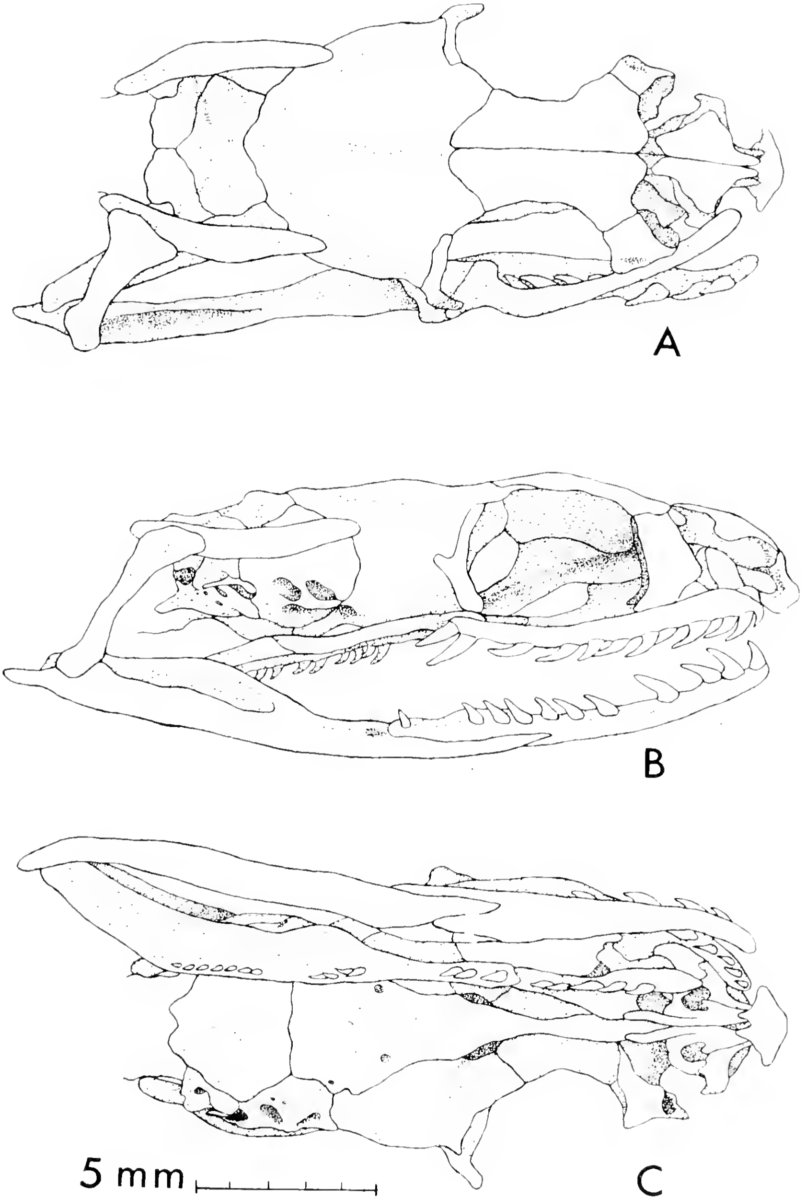

Fig. 7. Skull structure of *Alsophis cantherigerus*, MCZ 56429. A, dorsal view; B, lateral view; C, ventral view.

that may be placed in the present species assemblage. In the rare form *melanichnus*, the numbers of teeth are higher than in either *cantherigerus* or *ater;* the dental formula is 18 + 2 maxillary, 16 palatine, 28 pterygoid, and 24 dentary teeth. The posterior processes of the vomer are laterally expanded into flat plates, oval in shape when viewed from below. This character is not seen in any other West Indian

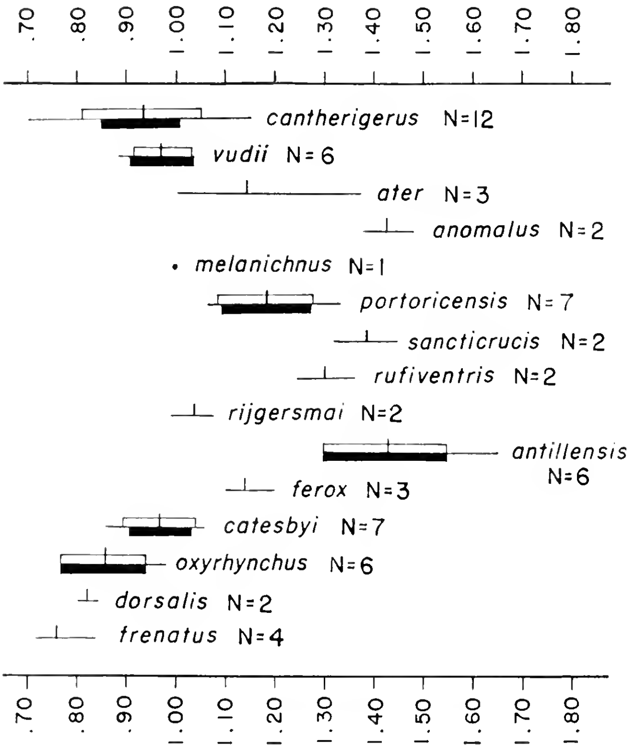

Fig. 8. Frontal bone width/preorbital skull depth indices for the 15 West Indian species of the *cantherigerus* species assemblage. Horizontal line, observed range; vertical line, mean; open rectangle, ± one standard deviation from the mean; solid rectangle, 95 per cent confidence interval of the mean.

xenodontine. In comparison to *cantherigerus*, the postorbital bone is wider in proportion to its length, and the frontal is relatively slightly shorter. The supratemporal is short and stout.

Another Hispaniolan species, *anomalus*, is closer in many ways to *cantherigerus* (Cuba) than it is to *melanichnus*, especially in the structure of the vomer, postorbital, and supratemporal. The skull is proportionately slightly wider and more dorsoventrally depressed, anterior to the orbit, than in the Cuban form. The premaxilla is a solid, heavy structure, semicircular in ventral view, and quite unlike that of other members of the assemblage. Ventrally, the parasphenoid is wider beneath the orbits than in *cantherigerus* and forms only a short interorbital partition (Fig. 11). The skull has numerous high crests and ridges for muscle attachment, but these crests appear to develop with positive allometry in most large specimens of xenodontines and are almost certainly related to the great size of this species. In its dentition, *anomalus* shows only slight modifications from the condition found in *cantherigerus* (Cuba), and has a formula of about 12+2 maxillary, 8 palatine, 20 pterygoid, and 19 dentary teeth.

Also found on Hispaniola is the well-defined species *ferox*. (I include specimens from the southwest peninsula of Haiti which consistently lack a loreal scale.) This form is remarkably like *ater* (Jamaica) in dorsoventral flattening of the skull, in the short, wide frontal, and

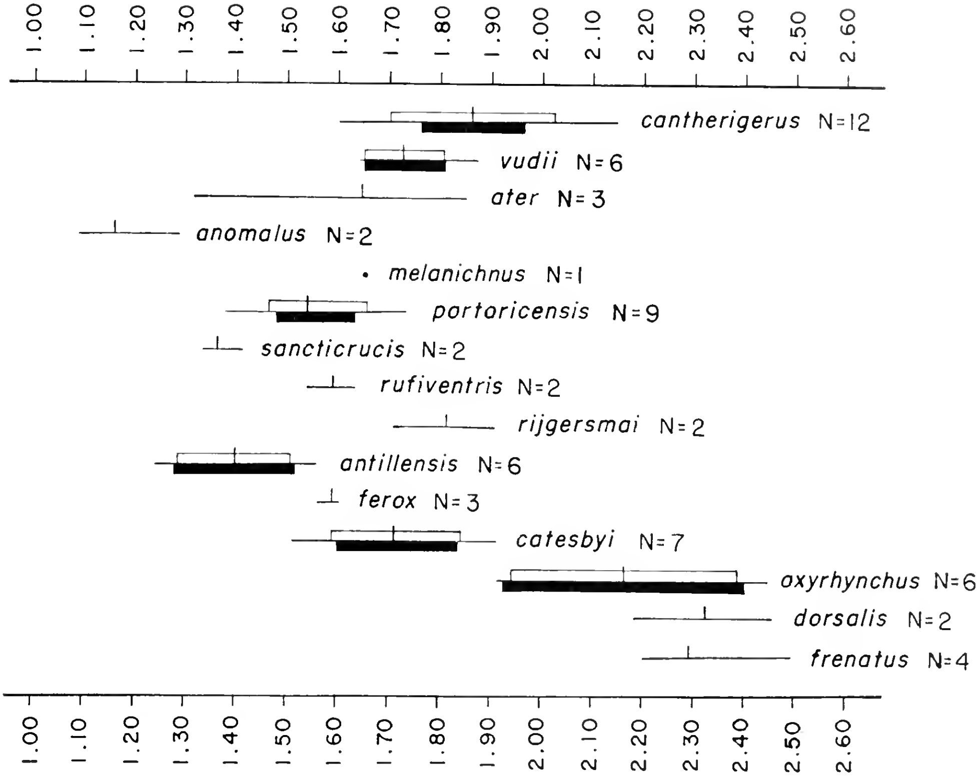

Fig. 9. Length/width indices for the frontal bone pair of the 15 West Indian species of the *cantherigerus* species assemblage. Symbols as in Fig. 8.

in the very small parasphenoid interorbital partition. The septomaxilla is even more expanded than in the Jamaica species (Fig. 10C), and the nasal area is depressed dorsoventrally as in that species so that the nasal bones lie close to the septomaxilla. In all of these characters this species is suggestive of *catesbyi* (discussed below). In its dental formula *ferox* shows a reduction in the number of teeth, as compared with *ater*. The teeth of *ferox* are larger than in *ater*, but this character is somewhat variable in specimens of equal size. In all other characters the similarity between *ferox* and *ater* is striking. The only notable osteological difference is in the shape of the nasal (Fig. 12), which in *ferox* is wide anteriorly and tapers off behind.

The four remaining Hispaniolan species are clearly united into a single subassemblage on the basis of external morphology (see below). Within the subassemblage, *catesbyi* is the least specialized and is very similar to *ferox* in skull structure; few cranial characters can adequately separate the two species. The major difference is in the higher dental formula in *catesbyi*. The teeth are enlarged as compared with *ater*, but not as much as in *ferox*, except for the palatine and pterygoid teeth which are as large as in that species. The most notable similarities between *ferox* and *catesbyi* are in the anteriorly expanded septomaxilla (Fig. 10), and in the dorsoventrally depressed preorbital portion of the skull. The nasal of *catesbyi*, although distinct in

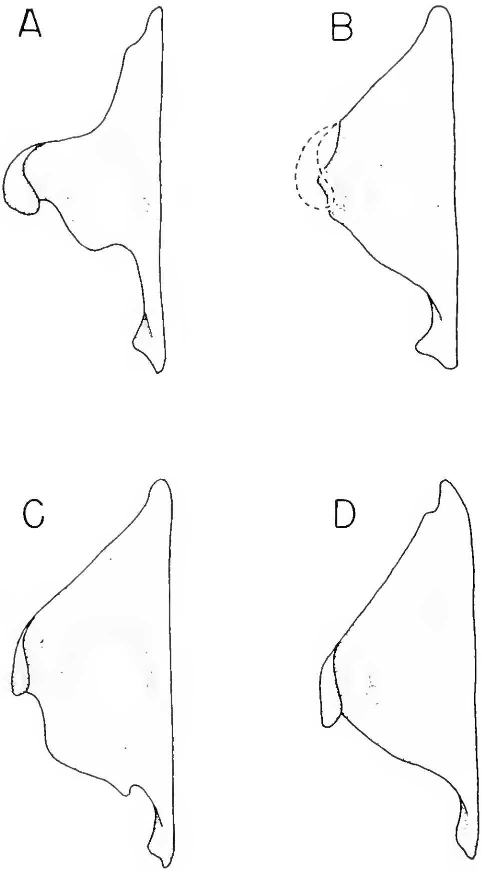

Fig. 10. Left septomaxilla of four species of the *cantherigerus* species assemblage. Dorsal view. A, *Alsophis cantherigerus*, MCZ 8611; B, *A. ater*, MCZ 6005; C, *Hypsirhynchus ferox*, MCZ 64785; D, *Uromacer catesbyi*, MCZ 3605. Not to scale. Approx. × 5.

shape, is not very different from that of *ferox*. The more highly specialized species of this subassemblage, *oxyrhynchus*, *dorsalis*, and *frenatus*, have greatly elongated nasals, vomers, and septomaxillae. The dentary, maxilla, and palatine are also elongated, thus extending the dental row forward. The species *oxyrhynchus* and *dorsalis* are the most highly specialized forms with an exaggeration of all these characters.

On Puerto Rico and the Virgin Islands the species *portoricensis* occurs. In the structure of its nasal, premaxilla, supratemporal, and quadrate (Fig. 13), it is more like *cantherigerus* (Cuba) and *anomalus* (Hispaniola) than like *melanichnus* (Hispaniola). The interorbital partition is small and the frontal is shorter anteroposteriorly than in the Cuban species. Ventrally the parasphenoid is wider than in either *cantherigerus* or *melanichnus*. The dental formula is higher than in *cantherigerus*, but there are fewer maxillary and palatine teeth than in *melanichnus*. The subspecies *portoricensis nicholsi* and *p. anegadae*, both from the Virgin Islands, are similar to each other in having a longer and narrower frontal bone than other subspecies of *portoricensis*. In *p. anegadae* the parasphenoid is very narrow, but in *p. nicholsi* this bone is as wide as in other subspecies of *portoricensis*.

On the northern islands of the Lesser Antilles there are four species that are osteologically very close to *portoricensis*. Most similar is *sanctecrucis* from St. Croix which is osteologically inseparable from that species. On Saba, St. Kitts, St. Eustatius, and Nevis, the species *rufiventris* is also very close to the Puerto Rican species in most osteological characters. The form on St. Barthelemy and Anguilla, *rijgersmai*, is another member of what may be called the *portoricensis* species group. In most characters of the skull and in the dentition, this form is like the Puerto Rican species. The nasal is like that of *rufiventris*, but the skull is narrower throughout, and the premaxilla reduced in size. The frontal is proportionately narrower than in other members of this subgroup. One other member of the group is *antillensis* (= *leucomelas*) which in most characters of skull morphology is like *rufiventris* (St. Kitts, etc.). Unlike *rijgersmai* the frontal is broad and the premaxilla is unreduced. The dentition in all of these species of the *portoricensis* species group is similar when the degree of variation in each is taken into account (see Fig. 6).

The species of the *portoricensis* species

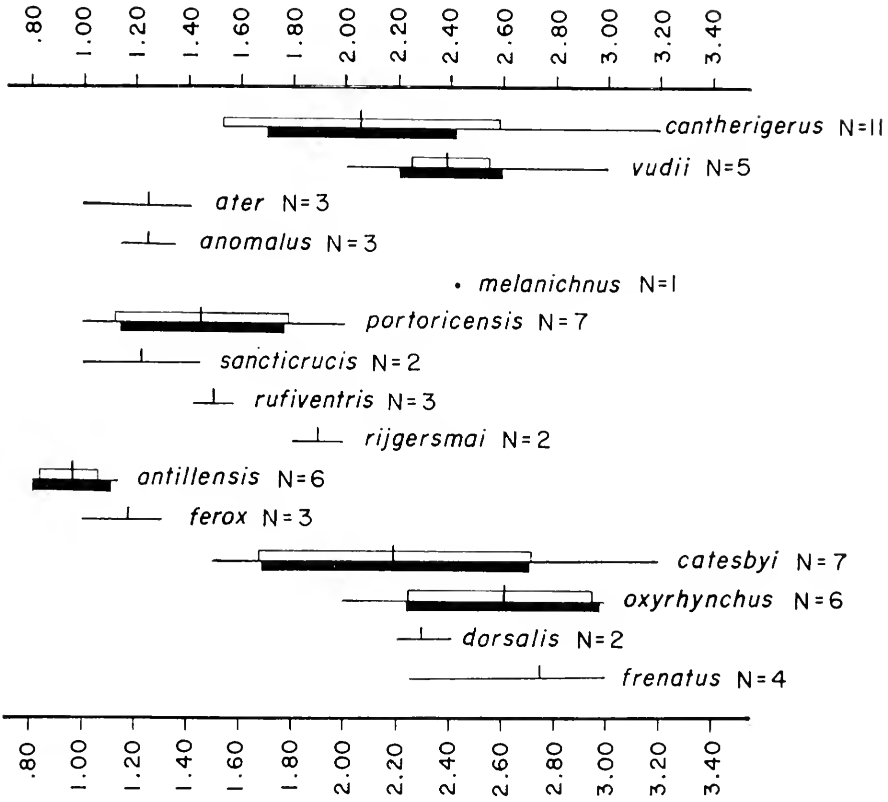

Fig. 11. Interorbital height/ventral width indices for the parasphenoid bone of the 15 West Indian species of the *cantherigerus* species assemblage. Symbols as in Fig. 8.

group show a far closer relationship among themselves than they do to any other species in the *cantherigerus* assemblage, although they are clearly part of that assemblage. The rather minor morphological distinctions which may be used to distinguish these species are shown diagrammatically in Figure 14 in relation to their geographic distribution. These five well-defined taxa may represent no more than geographic races within a morphologically variable species, but until additional data are available it is best to retain these forms as distinct species.

External morphology. Except for the specialized semiarboreal forms on Hispaniola, the members of the *cantherigerus* species assemblage are very similar to each other in most external characters. Several forms such as *ater* (Jamaica) and the *ferox* populations from the southwest peninsula of Haiti (for which the name *scalaris* Cope is available) have lost the loreal scale, but this has occurred repeatedly in many groups and cannot be considered more than a specific or subspecific difference. All the members of this group are similar in size, most falling between 800 and 1300 mm in total body length. There are always eight supralabials, usually with the third, fourth, and fifth entering the orbit. The number of dorsal scale rows ranges from 17 to 23. Ventral scale counts range approximately between 160 and 230, and caudal counts roughly between 100 and 150. The anal plate is usually divided, but may be

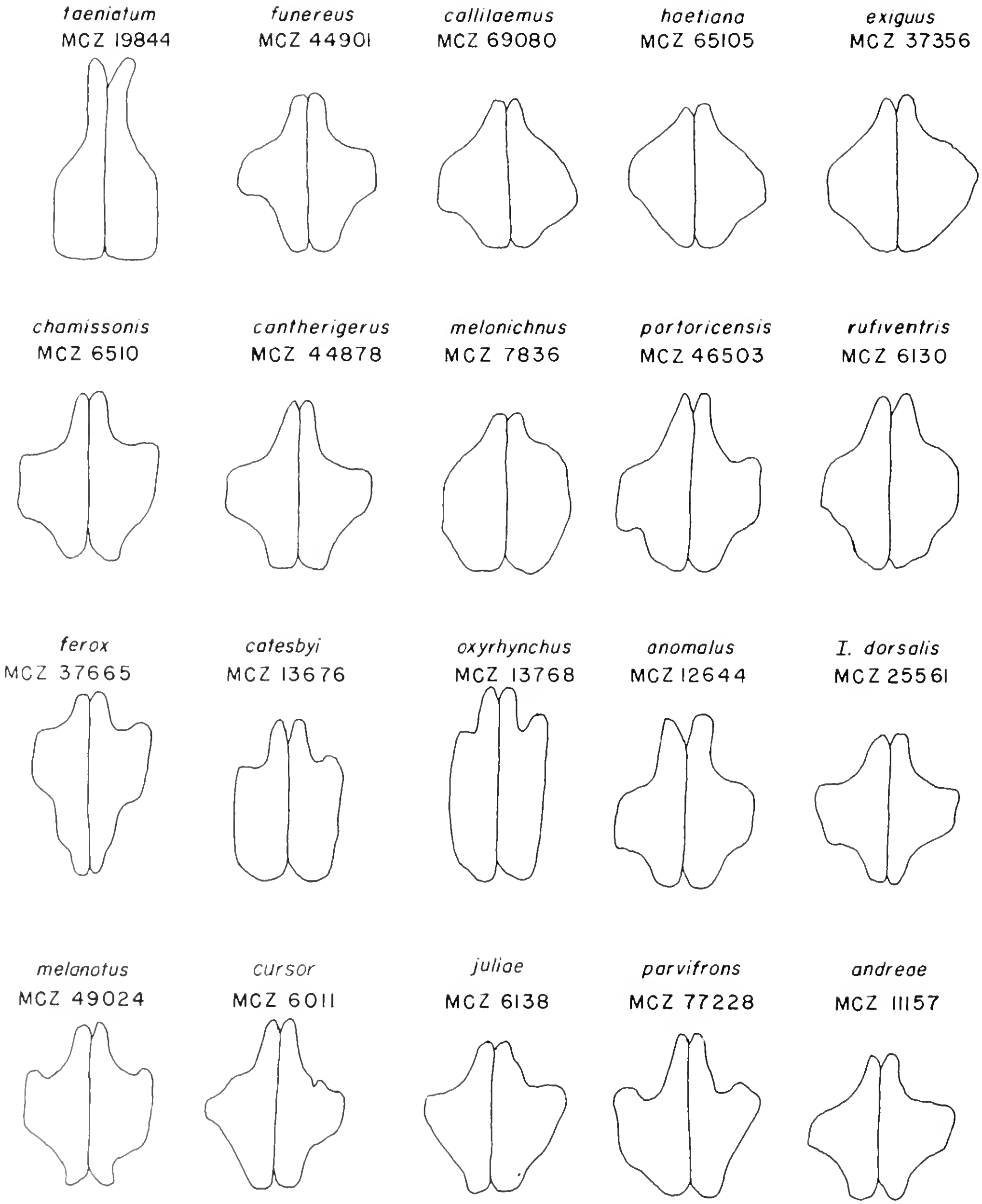

Fig. 12. Shape of the nasal bones for representative species of the four species assemblages of West Indian colubrid snakes as discussed in the text. Not to scale. Approx. × 7.

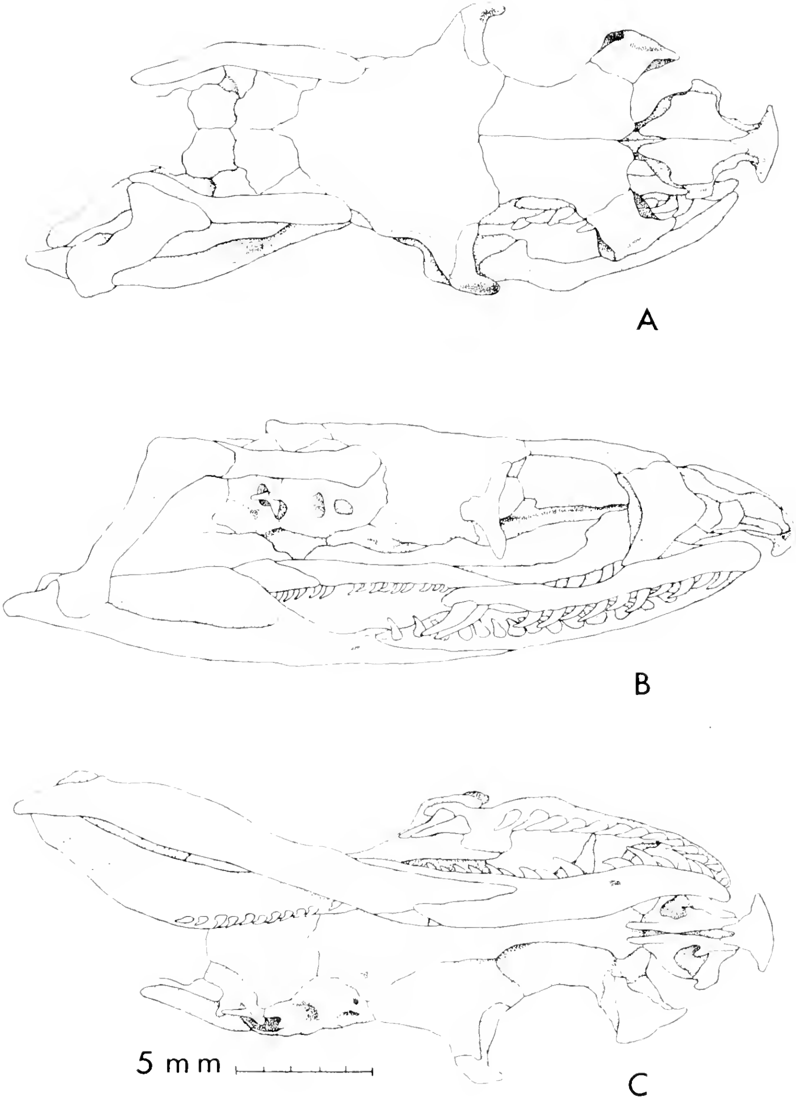

Fig. 13. Skull structure of *Alsaphis portoricensis*, MCZ 46503. A, dorsal view; B, lateral view; C, ventral view.

single in some specimens of *sancticrucis* (Schwartz, 1966). The Hispaniolan species *ferox* has a single apical pit on the dorsal body scales, whereas *catesbyi*, *oxyrhynchus*, *dorsalis*, and *frenatus* have none. The remaining species have two pits.

The species *ferox* differs externally from other members of the assemblage. The snout is elongated, the rostral scale forms an acute angle with the top of the head, and the eye is large and bulging. The pupil shape in *ferox* is usually oval, but out of 28 preserved specimens from the southwest population, 26 had round or irregularly rounded pupils, and only one individual had a distinctly oval pupil in both eyes.

The arboreal species of Hispaniola,

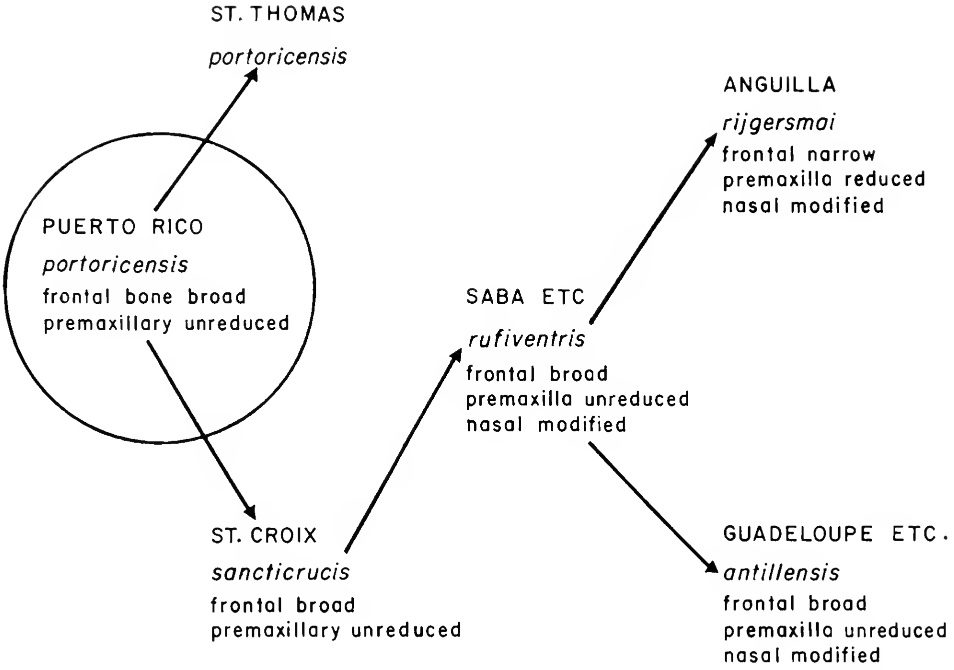

Fig. 14. Geographic distribution of several morphological characters within the *portoricensis* subgroup of the *cantherigerus* species assemblage. Circle represents the supposed center of dispersion of this group.

catesbyi, *oxyrhynchus*, *dorsalis*, and *frenatus*, are clearly united in a well-defined subgroup. All, except *catesbyi*, are long, slender, and clearly adapted for tree living. A recent study by Horn (1969) demonstrates the specific synonymy of "*wetmorei*" with *frenatus* and of "*scandax*" with *catesbyi*.

The subspecies *vudii utowanae* as described by Barbour and Shreve (1938) has a higher ventral and subcaudal scale count than other races of *vudii*.

Hemipenis. The structure of the hemipenis is remarkably uniform within the *cantherigerus* assemblage. The sulcus spermaticus is divided near the base of the organ and each branch extends to the tip of one lobe of the deeply bifurcated apex (Fig. 15). Several rows of longitudinally arranged stout spines are present along the middle one half of its length; these grade into numerous smaller spines basally. The base may also be nude or have long plicae. The sulcus is bordered by a fringe of folded tissue bearing modest sized, closely spaced spines that grade into smaller ones distally. On the apex of each lobe, a reticulate network of tissue surrounds the sulcus, with moderate to long filiform papillae (papillate calyces). These calyces usually grade into the surrounding tissue proximally, but may form a more or less well-defined capitate structure as in *protoricensis*, *rijgersmai*, and *antillensis*. The hemipenis in *ferox* does not differ from that of other species in this group except in having longer apical papillae. In *catesbyi* and the other arboreal snakes of Hispaniola the hemipenis is proportionately shorter than, but basically similar to, that of *cantherigerus*. It is more heavily spinose, and the apical papillae on the sulcate surface extend further basally to the point of division of the sulcus.

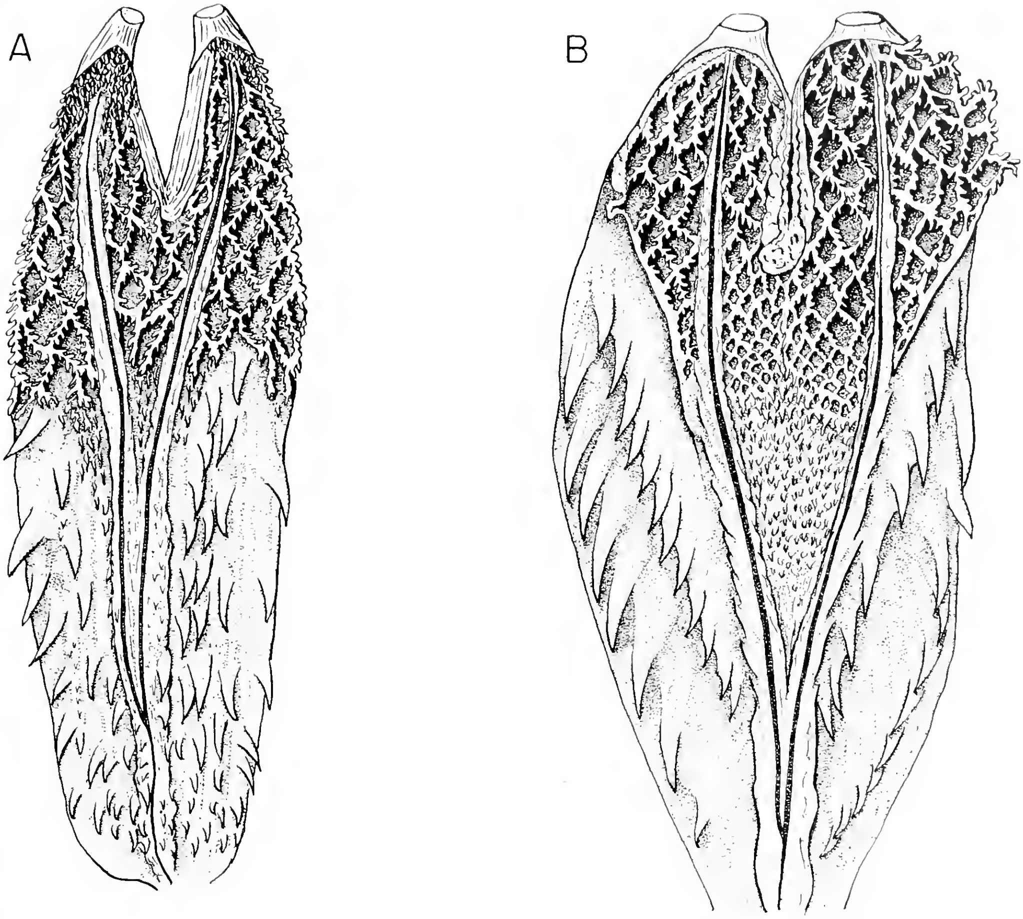

Fig. 15. Hemipenis morphology in the *cantherigerus* species assemblage; semidiagrammatic. Organ is uneverted and dissected *in situ*. A, *Alsophis ater*, MCZ 6005; B, *Alsophis portoricensis*, MCZ 58804. Approx. × 5.

Mainland relationships and origin of the group. Examination of South and Central American genera has revealed several that are morphologically very close to the *cantherigerus* species assemblage. Of the four mainland species customarily referred to the genus "*Dromicus*," three are clearly related to the present group; these are *chamissonis, tachymenoides*, and *angustilineatus*. The fourth species, "*Dromicus*" *amazonicus*, is allied to the *melanotus* species group to be discussed below.

The species *tachymenoides* (Peru) and *angustilineatus* (Peru) differ from *chamissonis* (Chile and Argentina) only in several minor characters, and what is said below about the latter will apply also to these two species. The major distinction between *chamissonis* and *cantherigerus* (Cuba) is the lower number of teeth in the former (see appendix); in all other skull characters the two are extremely close. Externally there are no differences which would argue against a close relationship, although the mainland species have only one pit on each dorsal body scale. In the structure of the hemipenis the sulcus spermaticus is less deeply divided in *chamissonis*, but the

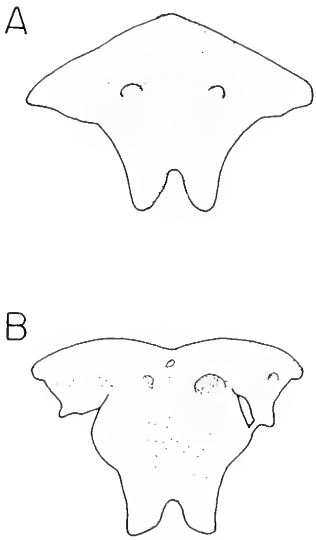

Fig. 16. Premaxilla in a typical West Indian species of the *cantherigerus* species assemblage compared with that bone characteristic of the Galapagos species of this group. A, *Alsophis cantherigerus*, MCZ 8611; B, *Alsophis slevini*, MCZ 28470. Ventral view. Approx. × 12.

arrangement of spines and the nature of the apical differentiation is similar to that of the Cuban form. As a whole, *chamissonis* must be considered as a mainland representative of the *cantherigerus* assemblage.

Two other mainland genera showing a close relationship to the *cantherigerus* group are *Philodryas* from South America and *Conophis* from Central America. Osteologically these genera are very close to *chamissonis*, except that both have well-developed grooves on the posterior maxillary teeth. Externally *Philodryas* may have one or two apical pits per dorsal body scale, and *Conophis* has none, but in size, scale pattern, and scale count they do not differ significantly from *chamissonis*. The structure of the hemipenis in both genera is of the *cantherigerus* type, with a deeply forked sulcus, lateral spines, and an apical ornament of papillate calyces arranged as in that group.

The present distribution of *chamissonis*, *tachymenoides*, and *angustilineatus* makes it difficult to derive any part of the West Indian fauna from them unless we postulate a former widespread distribution for an ancestral group. *Philodryas* and *Conophis* now occupy the geographic areas which the ancestral genus must have inhabited if the West Indian representatives of this group were derived by waif dispersal from the mainland. However, the presence of rear fangs in these two genera would appear to preclude them from any direct ancestry to the nonfanged Antillean group. The morphological relationships between *Philodryas*, *Conophis*, and *chamissonis*, etc., as well as their present distributions, suggest a widespread ancestral group common to all three. The species *chamissonis*, *tachymenoides*, and *angustilineatus* may represent relatively undifferentiated relicts of that ancestral group, and *Philodryas* and *Conophis* specialized rear-fanged descendants. The development of rear fangs has occurred repeatedly in a number of unrelated groups and is no bar to the relationship here suggested. If such a specialization was of selective advantage over the nonfanged condition, we might expect these forms to have displaced the ancestral type from much of its former range.

Taxonomy. The *cantherigerus* species assemblage as defined above on the basis of osteological and hemipenial characters may be expanded to include *chamissonis*, *tachymenoides*, and *angustilineatus* from South America. The three species from the Galapagos referred to the genus "*Dromicus*" must also be placed here. These three species–*biserialis*, *dorsalis*, and *slevini*–are very much like the present assemblage in external characters, osteology, and hemipenial morphology. However, they are clearly closer to each other, and represent products of speciation on the Galapagos. The dental formula is similar in all three forms and is as low as in their mainland relatives (appendix). A minor but distinctive character which sets these forms apart

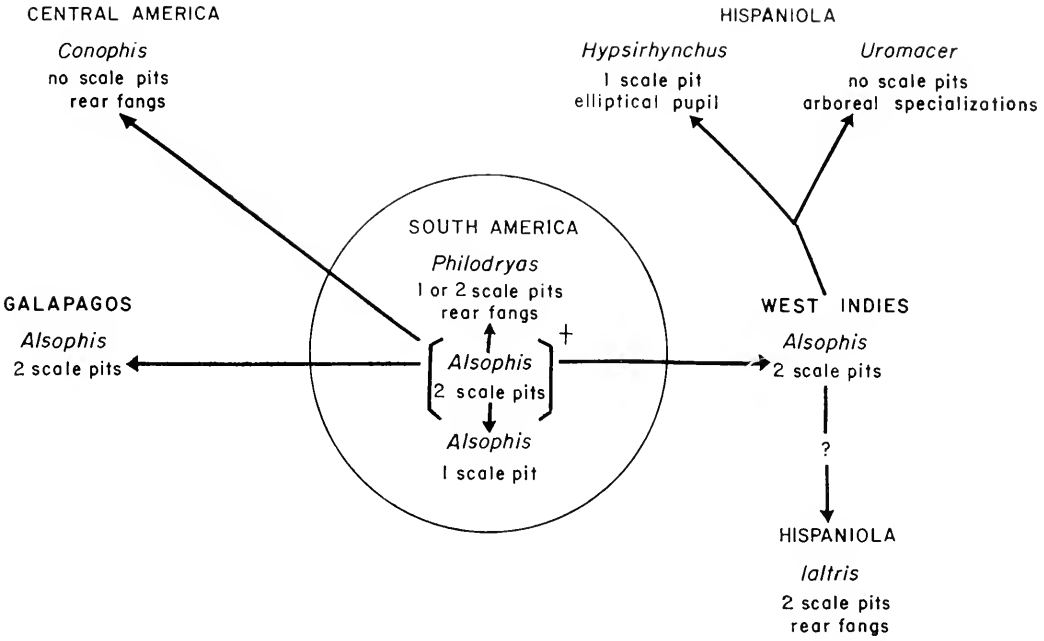

Fig. 17. Geographic distribution of several morphological characters in the genus *Alsophis* and in two related mainland genera. The circle represents the supposed center of dispersion for this group. The † symbol indicates that the ancestral form of *Alsophis* is extinct on the mainland.

from other members of the *cantherigerus* group is the shape of the premaxilla (Fig. 16); here this element is depressed anteriorly in the midline so that the lateral processes appear to curve forward and then back in a winglike fashion.

Within the West Indies as discussed above, *utowanae* from Great Inagua is somewhat distinct from other subspecies of *vudii*. At the time of writing only two specimens including the type were available for study. Although the differences of these two specimens from *vudii vudii* appear to be more than subspecific, it seems advisable to retain *utowanae* as a subspecies of *vudii* until additional specimens are available and the range of variation better known.

The four arboreal species on Hispaniola –*catesbyi*, *oxyrhynchus*, *dorsalis*, and *frenatus*–are unquestionably closely related and united morphologically; they form the well-defined genus *Uromacer*. The Hispaniolan species *ferox* is osteologically undifferentiated from other members of the group except for its enlarged teeth, and in many ways it is intermediate between *ater* (Jamaica) and *Uromacer catesbyi*. Mertens (1939) favored retention of *ferox* in a distinct genus (*Hypsirhynchus*) because of its elliptical pupil in contrast to the rounded pupil of "*Dromicus*." However, variation between *ferox* from the southwest population and *ferox* from other areas on Hispaniola with respect to pupil shape makes this character suspect for use on the generic level in this group until more is known concerning postmortem effects on this structure. Nevertheless, the other peculiarities of *ferox*, such as its enlarged teeth and unusual head shape, probably warrant retention of the currently recognized genus *Hypsirhynchus*. The consistent absence of a loreal scale in the populations from the southwest peninsula of Haiti, plus the suggestion of a distinction in pupil shape, justify the use of the subspecific name *ferox scalaris* for them.

Dunn (1932) divided the remaining species of the present *cantherigerus* assemblage into two additional genera based on the number of apical pits on the dorsal body scales: *Alsophis* was distinguished as having two pits and *Dromicus* one pit.

An examination of the relationships within the *cantherigerus* assemblage in the present study indicates that scale pit number may or may not be consistent with other characters at the generic level, and therefore cannot always be used to define major taxa. The genus *Hypsirhynchus* has one pit and the six species of *Uromacer* have none. The remaining West Indian species have two pits side by side at the tip of the dorsal body scales, whereas on the mainland, *chamissonis*, *angustilineatus*, and *tachymenoides* have a single apical pit. The three Galapagos species have two pits. The distinction between *Philodryas* and *Conophis* made by Boulenger (1896) was based on the presence of one apical pit in the former and none in the latter. Osteologically these two genera are very close but, since a detailed analysis of these groups was not made as part of the present study, they are here considered provisionally distinct genera. The geographic distribution of scale pits and their suggested phyletic relationships are shown in Figure 17, along with several other characters. From the evidence one might reasonably infer a primitive condition of two scale pits with reduction as indicated in the figure.

Scale pits have served, in the past, to diagnose groups based on this feature alone. However, it is clear from other characters that the use of scale pits to define major groups may result in oversplitting of otherwise closely related assemblages. With the recognition that scale pits by themselves are useful as taxonomic characters within this group only at the species or species-group level, the West Indian species of the *cantherigerus* assemblage (excluding *Hypsirhynchus* and *Uromacer*) may be considered congeneric with *chamissonis*, *angustilineatus*, and *tachymenoides* from South America, and with *dorsalis*, *biserialis*, and *slevini* on the Galapagos archipelago.

Smith and Grant (1958) have shown that Bibron's (1843) type of *Dromicus* was *cursor* from Martinique. This is a form unrelated to South American "*Dromicus*," as I will show below. With the name *Dromicus* thus unavailable, the present assemblage of species is referred to *Alsophis* with the type *antillensis* (= *leucomelas*) Fitzinger. (See Brongersma, already cited above, for the identity of the name *antillensis*.)

The suggested phyletic relationships between the genera and species of the *cantherigerus* assemblage are shown in Figure 18.

Zoogeography. Two lines of evidence indicate a western origin for the *cantherigerus* species assemblage into the West Indies. First, *Alsophis cantherigerus* from Cuba is the Antillean species most similar to *A. chamissonis* of the mainland; this similarity is most notable in osteological characters and especially in the dental formula, which in these two species is the lowest of the whole assemblage. The Galapagos forms, likewise, have relatively few teeth, as do the suggested mainland derivatives *Philodryas* and *Conophis*. Within the West Indies a general trend toward increased number of teeth is evident, especially in the specialized arboreal species of *Uromacer*, and in the *portoricensis* species group. From the geographic distribution of dental formulae, it would appear that a low number of teeth is primitive for the mainland ancestor of this assemblage. In other characters also, the more easterly distributed species show a greater divergence from the mainland forms, thus tending to support the view that the group entered from the west.

The second line of evidence indicating a western origin is that no member of this

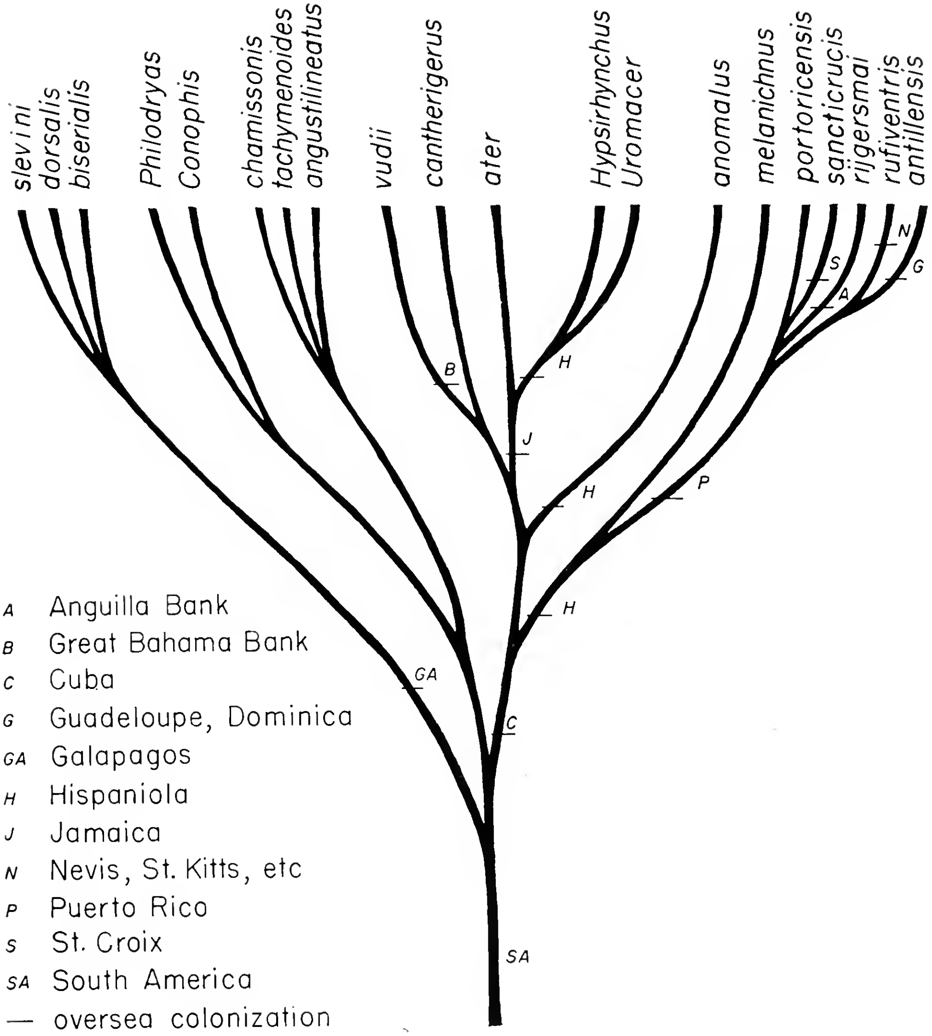

Fig. 18. Suggested phyletic relationships between species of the *cantherigerus* species assemblage and related genera. Short horizontal lines indicate proposed oversea colonizations. Geographic distributions as indicated by lettered symbols.

species assemblage occurs on the Lesser Antilles south of Dominica. This in itself is not significant since, as Gorman and Atkins (1969) have shown for *Anolis*, colonization does not necessarily proceed sequentially island by island along the chain of the Lesser Antilles. Nevertheless, taken with the first line of evidence, this assumes more importance.

The following zoogeographical history for the genus *Alsophis* may be suggested. The assemblage appears to have been derived from an ancestral species probably not unlike *Alsophis cantherigerus* in its osteological, hemipenial, and external morphology. From this widely distributed ancestral group in South America (and probably Central America as well), a single trans-Caribbean colonization could have resulted in the establishment of this group

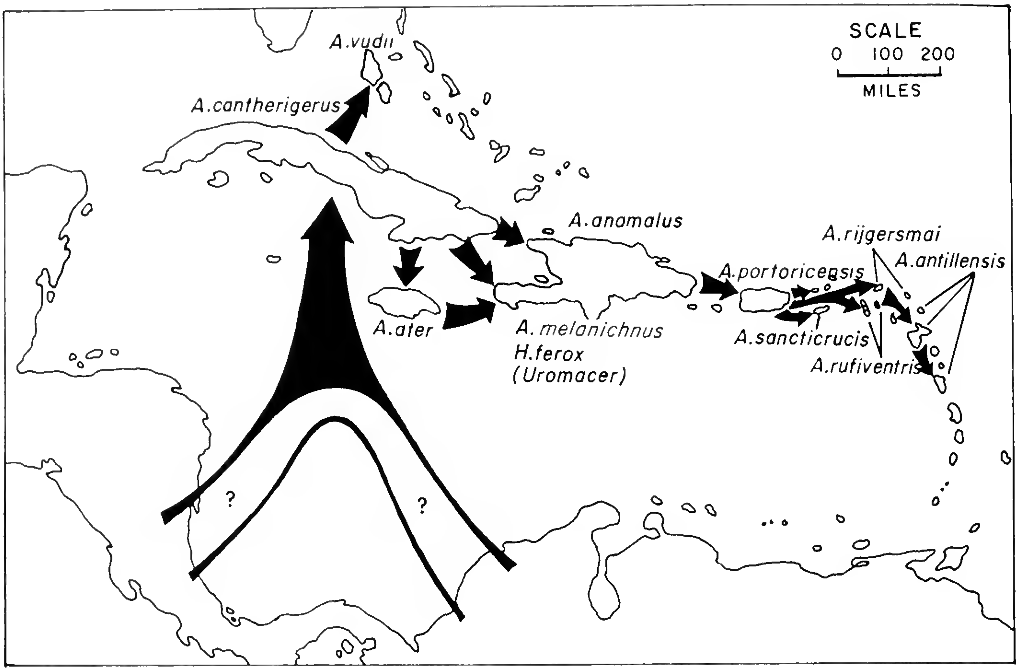

Fig. 19. Proposed routes of colonization of the West Indies by the *cantherigerus* species assemblage. The arrows are not intended to represent exact paths. The distribution of extant species and genera is as indicated. It is not certain whether this group entered from Central or South America.

on Cuba. This was followed by a subsequent dispersion and radiation to Jamaica *(ater)*, the Little and Great Bahama banks *(vudii)*, and Hispaniola *(melanichnus)* (Fig. 19). From Hispaniola an early stage of *melanichnus* gave rise to *portoricensis* on Puerto Rico. The four species of the Virgin Islands and Lesser Antilles, *sancticrucis*, *rufiventris*, *rijgersmai*, and *antillensis*, appear to be part of a relatively recent radiation of *portoricensis*, with differentiation on these geographically isolated islands. The remaining history of the group involves a series of inter-island colonizations to centrally placed Hispaniola from the more peripheral islands of the Greater Antilles. A second migration from Cuba by an early stage of *cantherigerus* seems best to account for *anomalus*, which shows a closer affinity to the Cuban species than to *melanichnus* (Hispaniola). Alternatively, a back colonziation from Puerto Rico may have resulted in *anomalus*. The rather peculiar *Hypsirhynchus ferox* is close to *ater* (Jamaica) with respect to its skull and hemipenis and possibly represents a Jamaica-Hispaniola migration, with subsequent specialization of *Hypsirhynchus* resulting in its external differences. Another endemic genus on Hispaniola, *Uromacer*, may have been derived from an early form of *H. ferox* before the latter achieved its peculiar specializations.

Because of its central location, Hispaniola has received a greater number of species than any of the other islands, and it may have been competition between these species that led to the specializations of some of them. The giant form *anomalus*, the arboreal species of the genus *Uromacer*, and *Hypsirhynchus* may have differentiated as a means of dividing up the habitat more efficiently. Competition among closely related and overlapping species

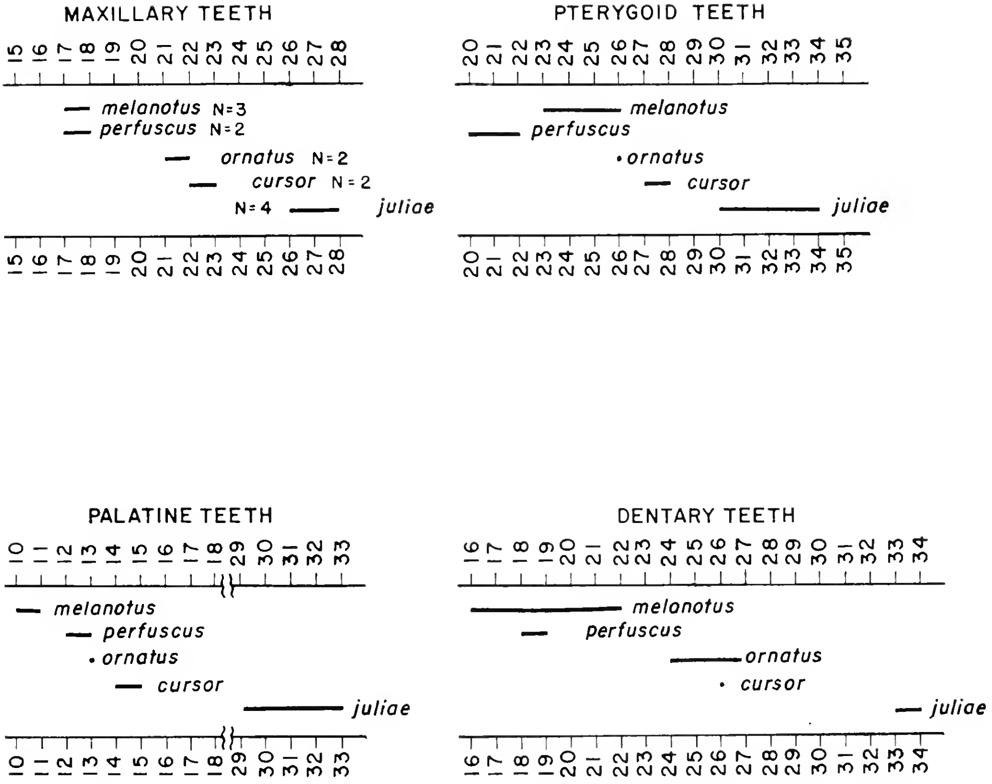

Fig. 20. Observed ranges of variation in numbers of teeth on each tooth-bearing element for the five West Indian species of the *melanotus* species assemblage.

often results in the well-known phenomenon of character divergence whereby the competing forms become adapted (first ecologically, then morphologically) to somewhat different aspects of the environment, thus reducing competition. It is interesting to note that, even in the relatively less specialized Hispaniolan species *anomalus* and *melanichnus*, character divergence has progressed to a remarkable degree, so that these forms lie near the two extremes of variation for the entire assemblage in many of their characters (see Figs. 6, 8, 9, and 11).

Another waif dispersal from the mainland to the Galapagos almost certainly resulted in the differentiation of *biserialis*, *dorsalis*, and *slevini* on these islands. Later, rear-fanged specialization within the ancestral mainland genus possibly led to *Philodryas* and *Conophis* which displaced their antecedent from much of its former range. The three closely related species, *chamissonis*, *tachymenoides*, and *angustilineatus*, have remained as relatively unmodified relicts of the original mainland stock, except for reduction in the number of scale pits.

MELANOTUS SPECIES ASSEMBLAGE

Included West Indian species: *cursor* Lacépède, Martinique; *juliae* (including *mariae*) Cope, Guadeloupe, Marie Galante, Dominica; *melanotus* Shaw, South America, Trinidad, ? Grenada; *ornatus* Garman, St. Lucia; *perfuscus* Cope, Barbados.

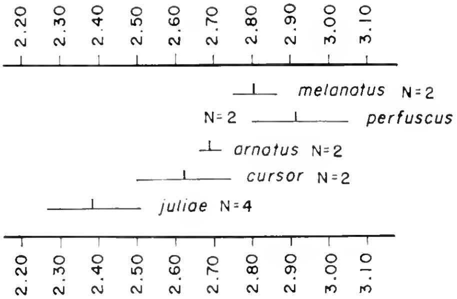

Fig. 21. Skull length/width indices for the five West Indian species of the *melanotus* species assemblage. Widths are taken at the otic region of the skull.

Osteology. This assemblage of species is distributed from the island of Guadeloupe south to Trinidad. It is distinguished from the *Alsophis cantherigerus* species assemblage and other Antillean xenodontines primarily by the shape of the prefrontal bone and by the structure of the hemipenis (discussed below). The prefrontal is long dorsoventrally and narrow anteroposteriorly with a sharply pointed anterior projection at about midlength (see Fig. 5).

The species for which this group is named, *melanotus*, occurs on Trinidad and Tobago and has been questionably reported from Grenada. It also occurs in Venezuela and Colombia. Like all members of this group *melanotus* is about half the size of *A. cantherigerus* and contrasts with it in the following skull characters: the postorbital region is proportionately longer; the frontal bone is relatively shorter anteroposteriorly with very little emargination above the orbits; the skull is considerably more flattened dorsoventrally as compared with its width; as a result of the latter character, the interorbital partition formed by the parasphenoid bone is shorter in its dorsoventral extension; long, thin lateral processes extend back from the premaxilla in contrast to the short, wide based processes of *A. cantherigerus.* The dental formula for *melanotus* is about 15 + 2 maxillary, 10 palatine, 24 pterygoid, and 19 dentary teeth (Fig. 20 for variation).

The skull of the endemic species *perfuscus* on the island of Barbados is proportionately longer and narrower than that of *melanotus* (Fig. 21). The supratemporal and quadrate bones are more elongated and comparatively narrower. The orbit is small. The postorbital bone lies far forward on the parietal and is nearly in contact with the frontal. In this last character *perfuscus* is distinct from other members of the present group; in the latter, a wide expansion of the parietal bone separates the postorbital from the frontal. In general skull proportions and in its low dental formula, *perfuscus* is closer to *melanotus* and other mainland representatives of this assemblage than it is to other Antillean species on adjacent islands.

The species *ornatus* from St. Lucia is slightly larger than *melanotus* (Trinidad) and has a somewhat broader skull. The prefrontal bone is of the *melanotus* type, but is wider than in that species. In most other skull characters the two forms are very similar except for the dental formula, which is higher in *ornatus.* Clearly related to the latter is the species *cursor* from Martinique (Fig. 22), which differs only in the smaller size of the nasal bone. On Guadeloupe, Dominica, and Marie Galante the species *juliae* has a higher dental formula than *cursor*, and the supratemporal, quadrate, and premaxilla are greatly reduced in relative size. A similar reduction is seen in some related mainland species such as *bimaculatus*, but this probably represents parallelism rather than an independent derivation from one of these mainland forms.

It is surprising that no member of this group has been reported from St. Vincent. This island forms an important intermediate stepping stone between Grenada and St. Lucia. The mongoose is widespread on this island, and it is possible that a formerly present species, endemic or not, has become extinct.

External morphology. Externally the *melanotus* species assemblage is a homo-

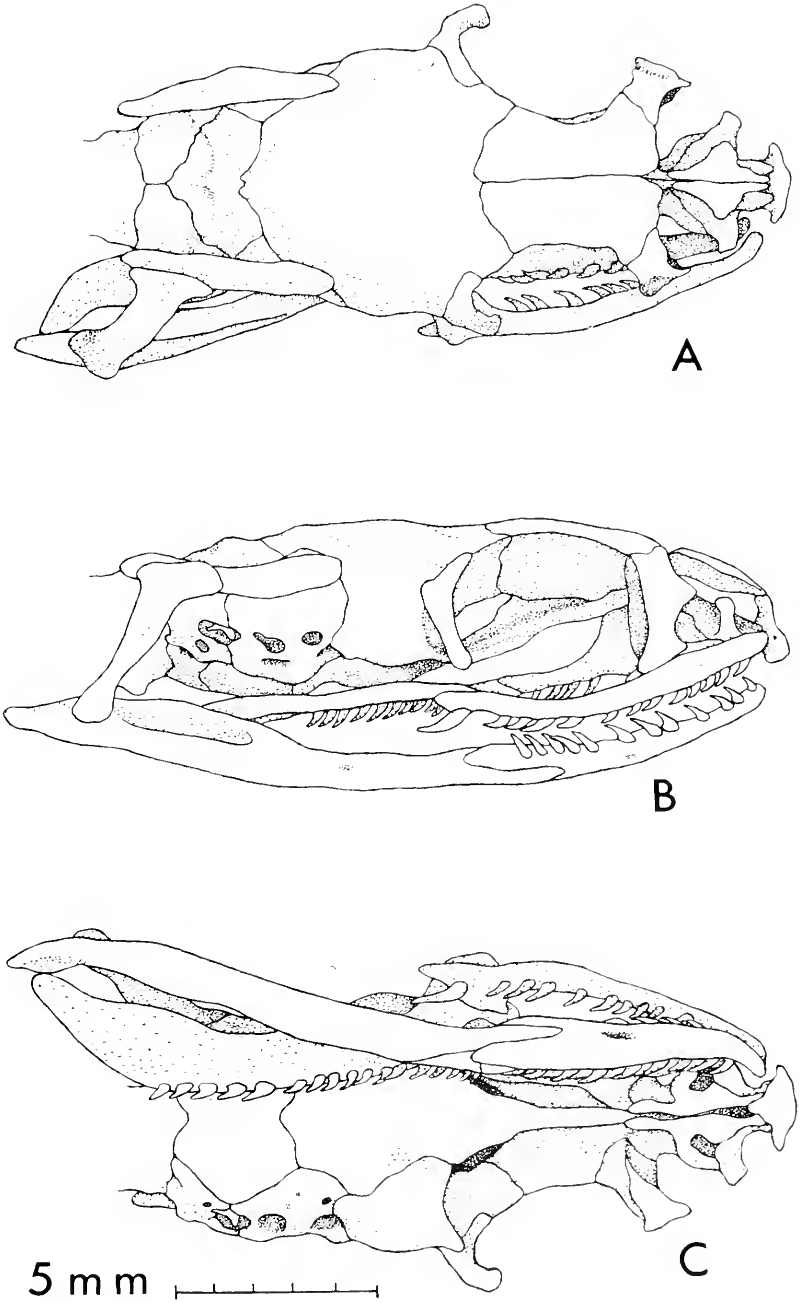

Fig. 22. Skull structure of *Dromicus cursor*, MCZ 6011a reversed). A, dorsal view; B, lateral view; C, ventral view.

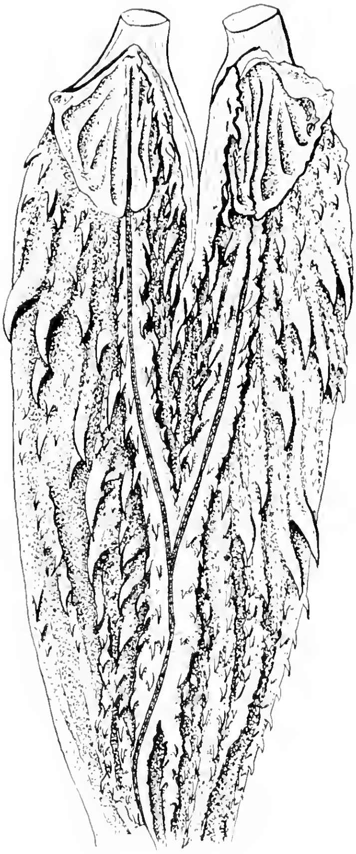

Fig. 23. Hemipenis morphology in *Dromicus cursor* (MCZ 6011) showing the typical apical own of the *melanotus* species assemblage; semidiagrammatic. The organ is uneverted and dissected *in situ*. Approx. × 5.

geneous one and in many respects is similar to the *cantherigerus* assemblage. As in the latter group there are eight supralabials, but here only the fourth and fifth enter the orbit. The number of scale rows may be 17 or 19, and the ventral scales number approximately between 150 and 200. In contrast to *Alsophis*, the number of subcaudals is rarely over 100. The anal plate is divided. All of these snakes are moderate in size and are roughly between 600 and 1000 millimeters in total body length. A single apical pit is usually present on the dorsal body scales, but may be absent as in *juliae mariae*.

Hemipenis. The hemipenis of *cursor* (Fig. 23) is shorter proportionately than in *Alsophis cantherigerus*, and the sulcus spermaticus is less deeply divided. As in that species, several rows of stout spines extend along the sides of the organ but, in contrast to it, small spines are also present between the diverging branches of the sulcus. The organ is generally weakly bifurcated and the apical ornament is distinct from all other West Indian xenodontines. Here papillae are never present; instead, a series of membranous folds radiate from the apex and terminate in a transverse fold of tissue which encircles the tip of each lobe. This fold forms a well-defined apical disk on each lobe when the organ is everted. The sulcus forks and proceeds onto the disk and to the tip of each lobe.

The structure of the hemipenis in the other species in this assemblage is essentially like that of *cursor.*

Origin and Zoogeography. The *melanotus* group offers no problem of origin. This well-defined and closely related assemblage is morphologically continuous with the widespread series of species currently referred to the genus *Leimadophis*, common on the mainland.[1] In both its osteology and hemipenial morphology the type species of *Leimadophis*—*L. almadensis*—is clearly allied to the present group, and there are no external characters which would preclude such a relationship. It seems probable that a northward colonization of the Lesser

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[1] *Dromicus amazonicus* is known only from the type specimen, MCZ 2820, and may also be referred to the present group. Its prefrontal bone is essentially of the *melanotus* type and the hemipenis has a weak apical disk. In all its osteological characters this specimen may be distinguished from other members of the present group only in having those features, such as broad skull, thin cranial bones, low, rounded crests, etc., which normally characterize juvenile specimens. Even the relatively weak disk on the hemipenis probably reflects the youthful condition of the specimen. It is thus quite possible that this form represents an immature specimen of a previously described South American species of the present assemblage.

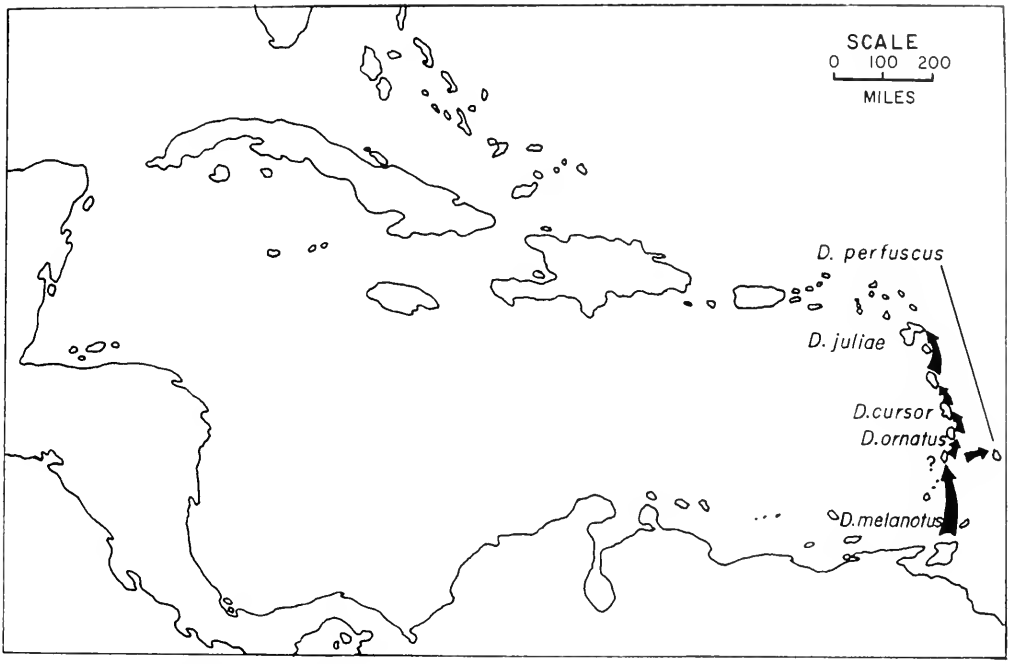

Fig. 24. Proposed routes of colonization of the West Indies by the *melanotus* species assemblage. Distribution of extant species is as indicated.

Antilles by a mainland species similar to *melanotus* occurred in relatively recent times. From this species or its ancestor, *ornatus* (St. Lucia) was almost certainly derived, possibly via a now extinct intermediate species on St. Vincent. Successive overseas migration (Fig. 24) probably resulted in *cursor* on Martinique and *juliae* on Guadeloupe, Dominica, and Marie Galante. The Barbados species, *perfuscus*, appears to have been derived from one of the islands to the west, perhaps from St. Vincent or Grenada.

Taxonomy. As mentioned above, Smith and Grant (1958) have shown that Bibron's (1843) type of *Dromicus* was *cursor*. With *cursor* and *almadensis* here considered as congeneric, *Dromicus* Bibron 1843 and *Leimadophis* Fitzinger 1843 become synonymic names for this assemblage. Although the actual dates of publication of these two names remain in question, December 31, 1843, is now to be taken as the official publication date of Fitzinger's *Systema Reptilium* (Smith and Grant, 1958), and Bibron's *Dromicus* thus becomes the senior synonym for the present assemblage with *Dromicus cursor* as the type species.[1]

The genus *Dromicus* is very similar to the South American genus *Liophis* Wagler 1830. In all of the characters studied, Wagler's type of *Liophis*—*L. cobella*—is close to the present assemblage. The prefrontal is like that of *D. melanotus*, the frontal is short with very little emargination above the orbits, and the interorbital partition is very small. The hemipenis of *Liophis* has a pair of well-developed apical disks as in *D. melanotus*, but differs in the presence of basal hooks (Roze, 1964). Body

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[1] After the present paper was in manuscript form, it was brought to my attention that Drs. Albert Schwartz and Richard Thomas reached the conclusion of "*Dromicus*" cf. *cursor* – *Leimadophis* synonymy independently of the present author. Their conclusion was reported in a letter to Dr. E. E. Williams.

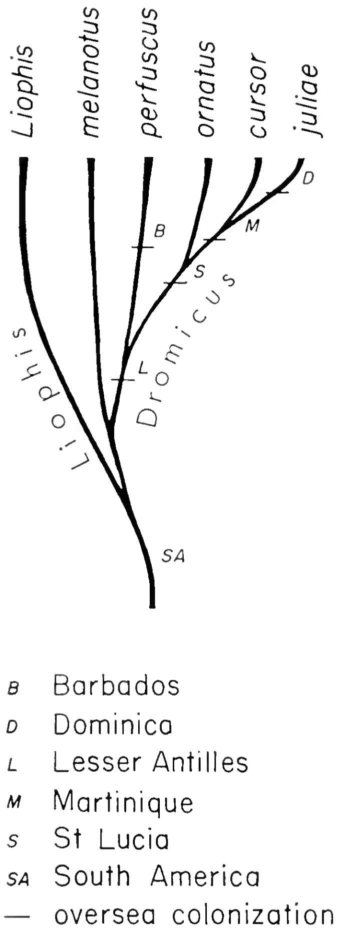

Fig. 25. Suggested phyletic relationships between species of the *melanotus* species assemblage and the genus *Liophis*. Short horizontal lines indicate proposed oversea colonizations.

size and scale counts are within the range of *Dromicus* (present concept).

The question arises as to the validity of the generic distinctions between "*Leimadophis*" (i.e., *Dromicus*) and *Liophis* made by Roze (1964: 535). As we have seen, the presence or absence of scale pits may not be as important a distinction as formerly believed. Thus, the only major difference between these two genera is in the maxillary dentition in which "*Leimadophis*" has a diastema with much enlarged posterior teeth, whereas *Liophis* lacks a diastema and the posterior teeth are little enlarged (Roze, 1964). I suspect that these two groups will be considered as congeneric when better known, but on present evidence I here treat them as valid genera.

The inferred phyletic relationships between *Liophis* and the West Indian species of *Dromicus* are presented in Figure 25.

ANDREAE SPECIES ASSEMBLAGE

Included West Indian species: *andreae* REINHARDT AND LÜTKEN, Cuba; *parvifrons* COPE, Hispaniola.

Osteology. Only two species of this assemblage are extant in the West Indies, *andreae* on Cuba and *parvifrons* on Hispaniola and nearby islands. They are generally considerably smaller in size than *Alsophis* and are about the size of *Dromicus melanotus*. In cranial osteology *andreae* and *parvifrons* show features characteristic of both *Alsophis* and *Dromicus* (Fig. 26). The frontal bones are very long and narrow with a deep emargination above the orbits as in *Alsophis*, but unlike the proportionately shorter and wider frontals of *Dromicus* (see Fig. 3). On the contrary, in the structure of the prefrontal bone, the present assemblage is close to *Dromicus* with a long and narrow prefrontal bearing a sharply rounded anterior process. This is quite distinct from the relatively wider prefrontal of *Alsophis* in which the anterior surface is broadly rounded and the bone is proportionately wider (see Fig. 5). In general skull proportions *andreae* and *parvifrons* are closer to *Alsophis* than to *Dromicus*. The parasphenoid bone is very narrow as in *A. cantherigerus* and other westerly distributed species of *Alsophis*, as well as mainland forms, but unlike the rather broad shape of that bone in the *A. portoricensis* species group or in *Dromicus*. The parasphenoid partition between the orbits extends high above the trabecular canals, as in most species of *Alsophis* except

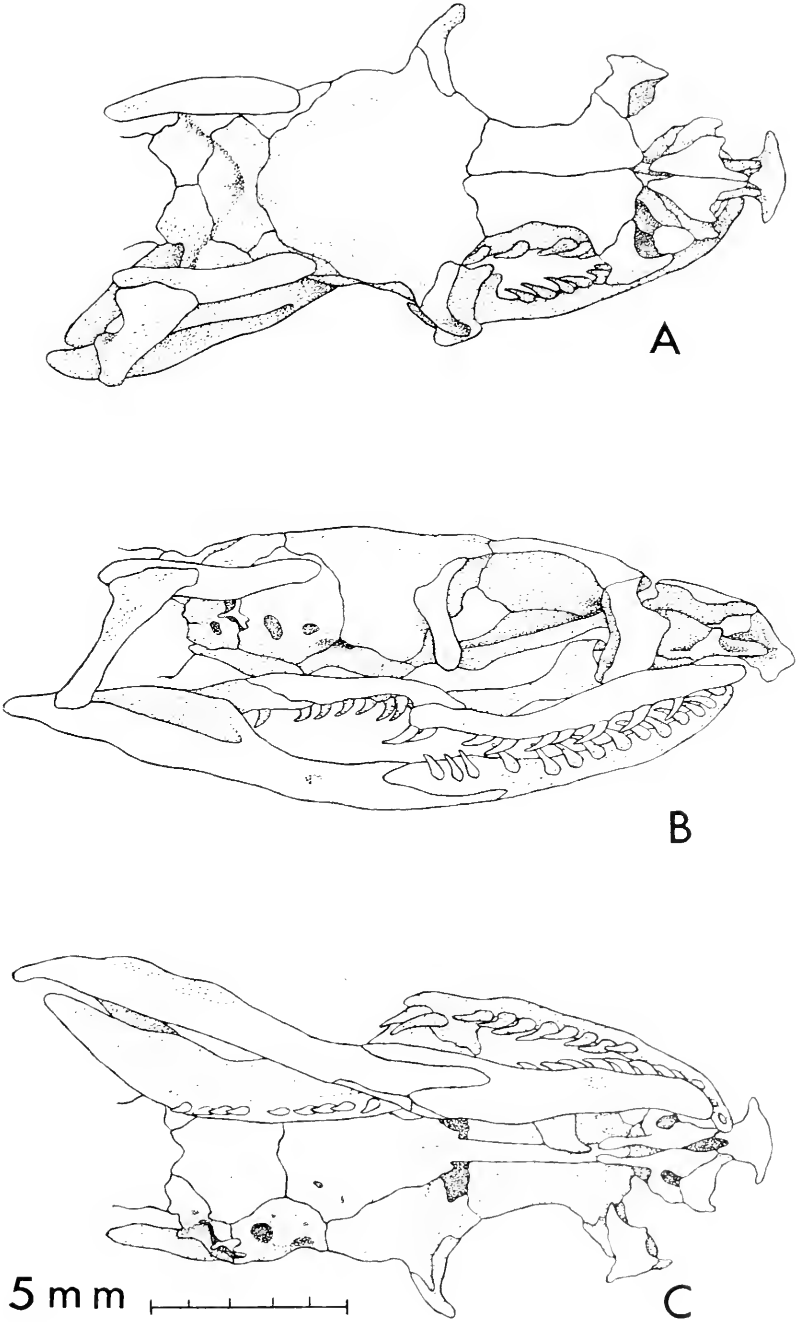

Fig. 26. Skull structure of *Antillaphis parvifrons* nov. gen., MCZ 77228. A, dorsal view; B, lateral view; C, ventral view.

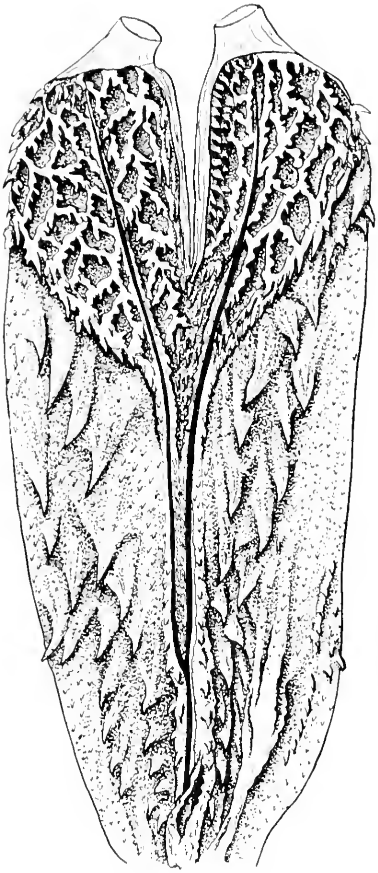

Fig. 27. Hemipenis morphology in *Antillophis parvifrons* nov. gen., MCZ 60064; semidiagrammatic. The organ is uneverted and dissected *in situ*. Approx. × 5.

portoricensis and related species. The premaxillary bones in *andreae* and *parvifrons* lack the long lateral process as in *Dromicus*.

The dental formulae in these two species is comparable to that of both *Alsophis* and *Dromicus;* that is, about 16 + 2 maxillary, 12 palatine, 26 pterygoid, and 21 dentary teeth in *parvifrons*, and 21 + 2 maxillary, 16 palatine, 35 pterygoid, and 26 dentary teeth in *andreae*.

Nonosteological characters. In external characters *andreae* and *parvifrons* are similar to *Dromicus*. The number of ventral scales is generally lower for these species than in *Alsophis* and about the same as in *Dromicus*. The subcaudal scale number in *parvifrons* is higher than that of *andreae* and of species of *Dromicus*, while it is within the normal range for species of *Alsophis*.

In the present assemblage, each dorsal body scale bears a single sensory pit in contrast to the two pits in all West Indian species of *Alsophis*, and in this respect is like most species of *Dromicus*.

It is in the structure of the hemipenis, however, that *andreae* and *parvifrons* depart radically from *Dromicus*. Here the organ has a deeply divided sulcus spermaticus, bordered by a thick fold of spinose tissue. Several rows of stout spines parallel the sulcus, each branch of which terminates on a diskless apex bearing long filiform calyces (Fig. 27). There are no basal hooks, neither are there spines between the branches of the sulcus spermaticus as in *Dromicus*. This structure is basically like that of *Alsophis* and is quite unlike that of *Dromicus* in which strong apical disks are present.

Taxonomy and Origin. As noted above, the two species of the *andreae* group exhibit osteological features characteristic of both *Alsophis* and *Dromicus*, though closer to the former. In most external characters they seem closer to *Dromicus*, but in the structure of the hemipenis they differ markedly from that group, being extremely close to *Alsophis*. Taken as a whole, this group cannot easily be referred to either genus. With regard to both skull and hemipenial characters, these two species resemble certain members of the South American genus *Lygophis*. The hemipenis in members of the latter genus, as currently recognized, is very heterogeneous. The organ may possess well-differentiated apical disks as in *L. lineatus* (Fig. 28A), the type species, and *L. flavifrenatus*, or it may be essentially of the *Alsophis* type, as in *L. boursieri* (Fig. 28B), in which the apical calyces are more spinulate along their margins than in the *Alsophis* type. Of these three species, *Lygophis boursieri* (Ecuador

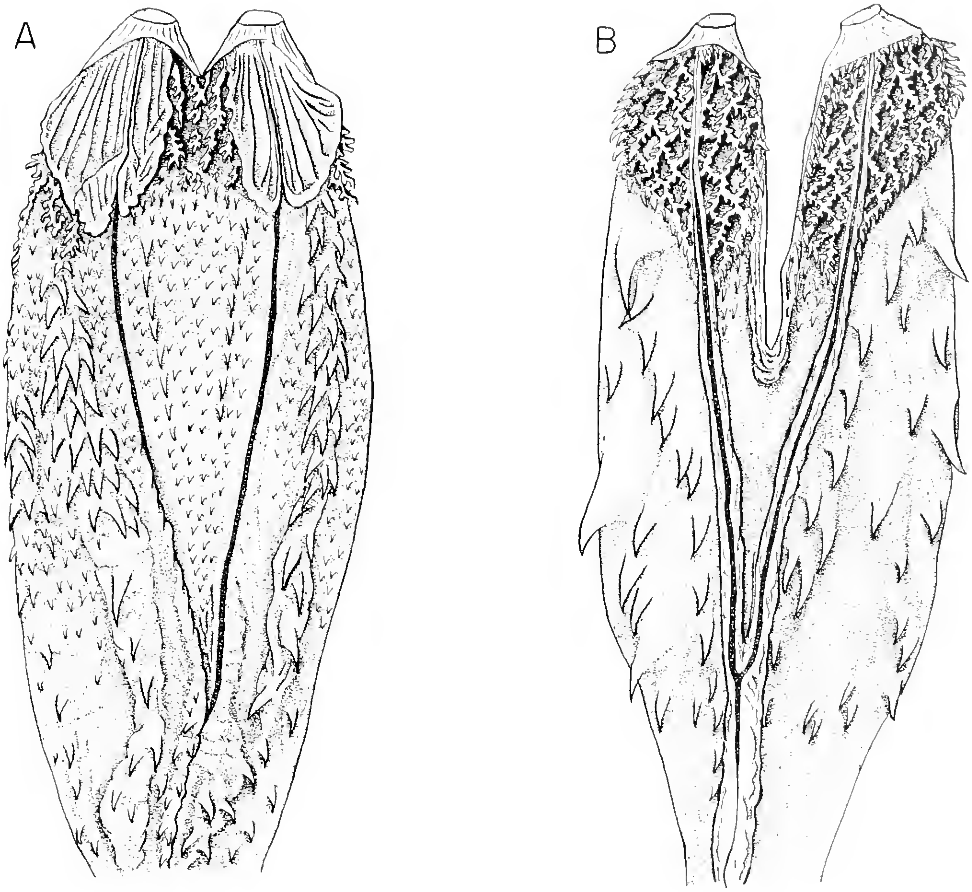

Fig. 28. Hemipenis morphology in the South American genus *Lygophis*; semidiagrammatic. The organ is uneverted and dissected *in situ*. A, *Lygophis lineatus*, MCZ 80994; B, *Lygophis boursieri*, MCZ 36948. Approx. × 5.

and Colombia) is very close to *andreae* and *parvifrons* in both skull and hemipenial characters, as well as in external scale pattern.

From this incomplete study of *Lygophis*, it seems possible that we may be dealing with a compound genus of distantly related forms. The evidence seems to suggest that *L. boursieri* might be placed in a separate genus with *andreae* and *parvifrons* as a specialized radiation, perhaps derived from mainland *Alsophis;* and that the type of *Lygophis*, *L. lineatus*, may need to be synonymized with *Dromicus* from which it differs primarily in the lack of scale pits and the presence of basal hooks on the hemipenis (Roze, 1964). However, we must await more detailed taxonomic work to clarify these issues.[1] Nevertheless, it seems clear that generic distinctions between *Dromicus* (present concept) and

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[1] In a reappraisal of South American snakes related to *Lygophis boursieri*, Myers (1969) established the *boursieri* species group including *Rhadinaea antioquiensis*, *R. tristriata*, and *L. boursieri*. The group is placed in *Lygophis* "... simply because *boursieri* already resides there." But the artificiality of the resulting genus is clearly pointed out, and the necessity of generic reassignment is affirmed.

Lygophis (see Roze, 1964) rest on slim evidence.

Since on present generic concepts it is not possible to accommodate the species of the *andreae* group in any existing genus, it seems best to propose a new generic name. Though close similarities exist between *andreae* and *parvifrons* and at least part of what is now called *Lygophis*, the type species, as stated above, is certainly distinct from them on the generic level. The solution adopted here, though not completely satisfactory, seems the most desirable one until a complete revision of the mainland forms is undertaken.

Antillophis nov. gen.

Type species: *Dromicus parvifrons* Cope 1862. Proc. Acad. Nat. Sci., Philadelphia, 1862, p. 79.

Distribution of genus: Hispaniola, Gonave Island, Vache Island, Tortue Island, Cuba, Isle of Pines.

Diagnosis: Small to medium-sized xenodontine snakes having generally long and narrow frontal bones as in *Alsophis*, but narrow prefrontal bones as in *Dromicus*; scale rows 17–19; 9–10 lower labials, 8 upper labials with nos. 3, 4, and 5 bordering the orbit as in *Alsophis*, but unlike *Dromicus* in which only nos. 3 and 4 generally border the orbit; one sensory pit on each dorsal body scale as usual in *Dromicus*, but unlike the usual condition in West Indian *Alsophis* or in *Lygophis*; hemipenis like that in *Alsophis*, lacking the apical disks of *Dromicus* and the disks and basal hooks of *Lygophis*.

Zoogeography. On present evidence it is not possible to determine the zoogeographic history of this assemblage, and it seems fruitless to indulge in speculation at this time. If, as suggested, *andreae* and *parvifrons* are derivatives of a mainland stock close to *L. boursieri*, then their entrance into the West Indies must have involved a colonization independent of that of *Alsophis*. It is possible, however, that further evidence will suggest a West Indian origin for these two species from the genus *Alsophis*.

FUNEREUS SPECIES ASSEMBLAGE

Included West Indian species: *callilaemus* Gosse, Jamaica; *dolichurum* Werner, Cuba; *funereus* Cope, Jamaica; *haetiana* Cochran, Hispaniola; *polylepis* Buden, Jamaica; *exiguus* Cope, Puerto Rico, Virgin Islands; *taeniatum* Günther, Cuba; *vittatum* Gundlach, Cuba.

Osteology. This group of eight species is very distinctive and is clearly separable from other West Indian xenodontines. They are all very small in size. The prefrontal bone is unlike that of *Alsophis* or *Dromicus* (Fig. 5). It is moderately long dorsoventrally, narrow and gently curving with nearly parallel anterior and posterior edges. The two frontal bones together form a square plate above the orbits, unlike the condition in other West Indian groups. Ventrally the parasphenoid is proportionately wider along its entire length, especially posteriorly. The skull is proportionately flatter, and thus the interorbital partition formed by the dorsal extension of the parasphenoid does not extend above the trabecular grooves. Rather, the frontal bone on each side covers the entire lateral aspect of the parasphenoid. The supratemporal and quadrate are reduced in size, and the latter is flat and triangular in shape.

On Jamaica there are three species of this group, *funereus*, *polylepis*, and *callilaemus*. The specific distinction between *funereus* and *polylepis* has recently been demonstrated by Buden (1966), but osteologically they are very similar. They have the highest dental formulae of the group (Fig. 29) with about 19 + 2 maxillary, 11 palatine, 19 pterygoid, and 24 dentary teeth in *funereus*, and 17 + 2 maxillary, 11 palatine, 24 pterygoid, and 27 dentary teeth in *polylepis*. The parasphenoid bone beneath the orbits is broad throughout its

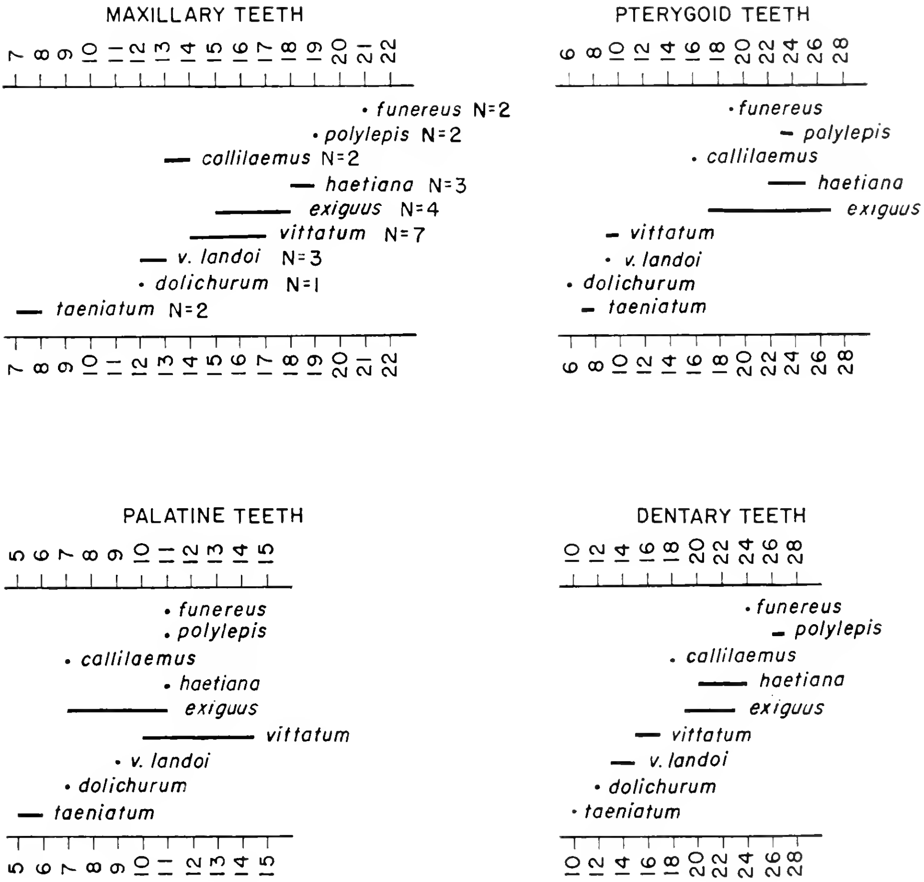

Fig. 29. Observed ranges of variation in numbers of teeth on each tooth-bearing element for the eight species of the *funereus* species assemblage.

length, being wider anteriorly, and bears a deep midventral groove along its entire length (Fig. 30). The postorbital bone is short and stout and is separated from the frontal only by a small spur of the parietal. The juxtastapedial fossa leading to the fenestra ovalis is variable in the degree of closure around the columella; it may be widely open and rounded, formed equally by the prootic and exoccipital bones as in most other West Indian xenodontines (Fig. 31A), or it may be constricted dorsoventrally by a ventral extension of the prootic portion of the fossa.

Also on Jamaica is the species *callilaemus* which is clearly related to *funereus*. The premaxilla and nasal are more solid and compact. The supratemporal and quadrate are further reduced, but this is probably a result of the smaller size of this species. The juxtastapedial fossa tends to be even more constricted than in *funereus*, and it may be nearly divided into two separate openings (Fig. 31B). The columella extends out of the posterior opening and is directed more posteriorly than laterally. The parasphenoid is wider than in *funererus*, and the midventral groove is

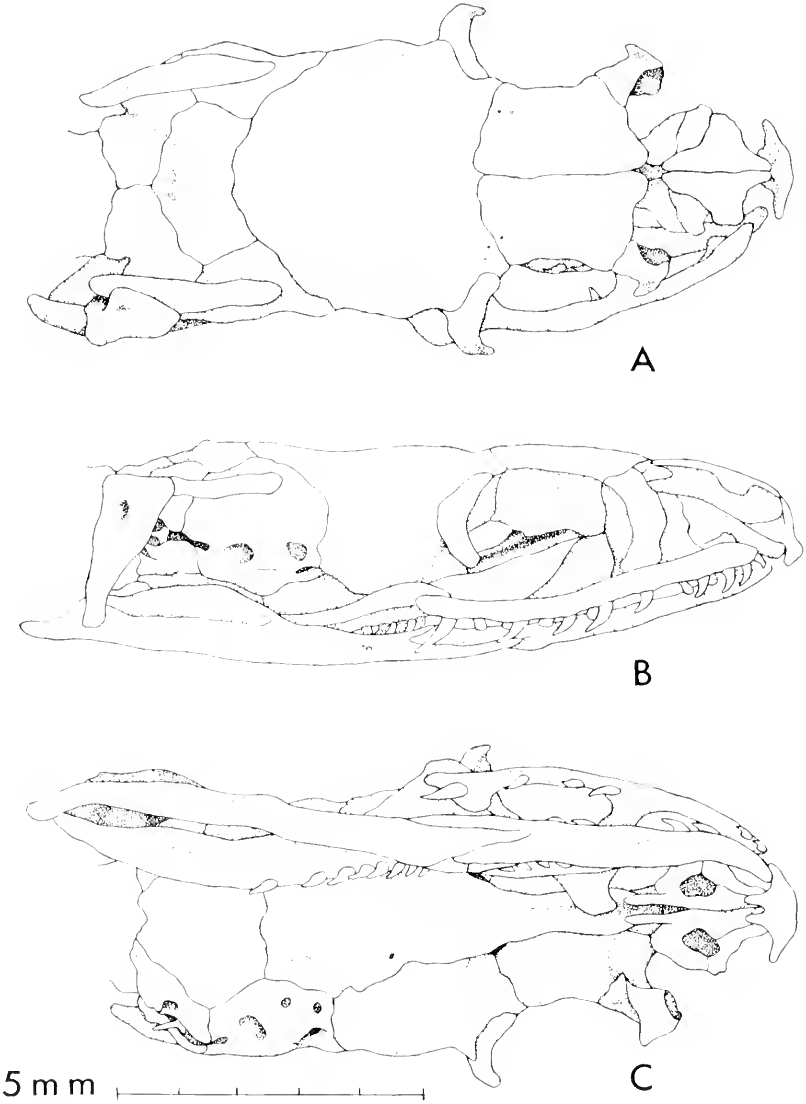

Fig. 30. Skull structure in *Arrhyton funereus*, MCZ 44901. A, dorsal view; B, lateral view; C, ventral view.

more conspicuous. The dental formula is lower with about 12 + 2 maxillary, 7 palatine, 16 pterygoid, and 18 dentary teeth.

At least three species found on Cuba may be referred to this assemblage. Of these *vittatum* is closest to *callilaemus*. The dentition is not strikingly different; there are approximately 14 + 2 maxillary, 12 palatine, 10 pterygoid, and 16 dentary teeth. The parasphenoid is variable in width as is the degree of closure of the juxtastapedial fossa. The premaxilla and nasal are massive elements which approach the type found in some burrowing forms. The orbit is small, and the postorbital bone is slender and in contact with the frontal bone; there is no intervening parietal spur. The supratemporal and quadrate are even more reduced than in the Jamaican form. The otic region is expanded so that it is the widest part of the brain case. The subspecies *vittatum landoi* is like *vittatum vittatum* in skull structure, but the dentition is somewhat reduced; there are about 11 + 2 maxillary, 9 palatine, 9 pterygoid, and 14 dentary teeth.

In another Cuban species, *dolichurum*, the parasphenoid bone is even broader than in *vittatum* and the premaxilla is more robust. The supratemporal is reduced to a mere splint, and further reduction in the postorbital bone is evident. In its dental formula *dolichurum* shows a reduction over *vittatum landoi* and has about 10 + 2 maxillary, 7 palatine, 6 pterygoid, and 12 dentary teeth.

It is in *taeniatum* (Cuba) that we find the greatest development of the trends observed in the series leading from *funereus* and *callilaemus* on Jamaica to *vittatum* and *dolichurum* on Cuba. The parasphenoid is very broad with a very wide but shallow midventral groove. The skull (Fig. 32) is proportionately longer than in *dolichurum*, and the orbit is relatively smaller (see Fig. 33). Reduction of the supratemporal is not quite so great as in that species. The nasal is an elongated solid bone, and the premaxilla is massive and in firm contact with the nasals. The dental formula is the lowest of the entire assemblage with approximately 6 + 2 maxillary, 5 palatine, 8 pterygoid, and 10 dentary teeth. The constriction of the juxtastapedial fossa is complete; bony dorsal and ventral growths from the prootic and exoccipital bones close off the center of the fossa, leaving two openings to the outside. The columella extends nearly straight backwards out of the posterior opening, and the newly formed anterior opening lies close to the foramen for the mandibular nerve (Fig. 31C).

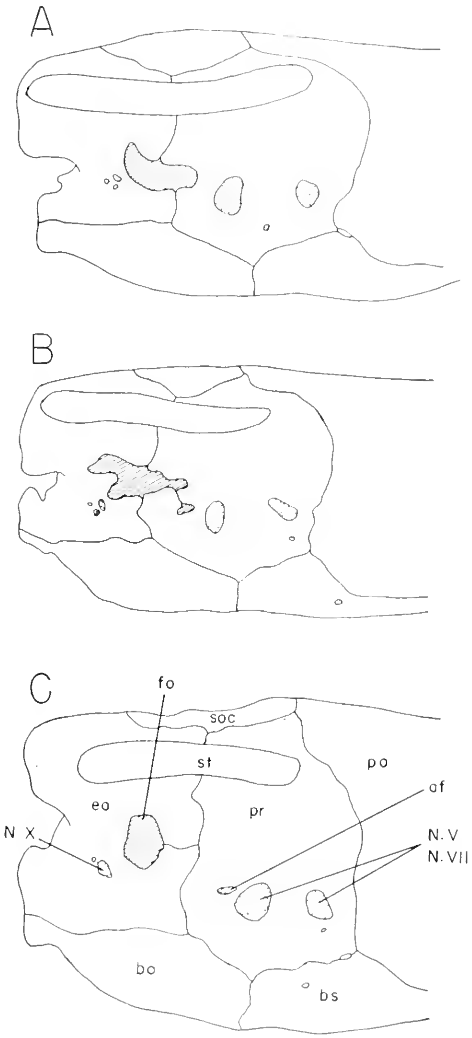

Fig. 31. Variation in the structure of the juxtastapedial fossa and foramen ovalis in the *funereus* species assemblage. A, *Arrhyton funereus*, MCZ 13294; B, *A. callilaemus*, MCZ 69078; C, *A. taeniatum*, MCZ 19874. Roman numerals, foramina for cranial nerves. Abbreviations: *af*, "anterior foramen," see text; *fo*, foramen ovalis. Other abbreviations as in Fig. 2. Approx. × 12.

The Hispaniolan species of this assemblage is *haetiana*, a montane form somewhat differentiated externally, but osteologically close to the other members of the group. The shape of the frontal bone is the same as in *funereus* (Jamaica), and the prefrontal and postorbital are similar. As in the latter, the parietal spur between the frontal and postorbital is very small. In the degree of reduction in the supratemporal and quadrate, and in general skull

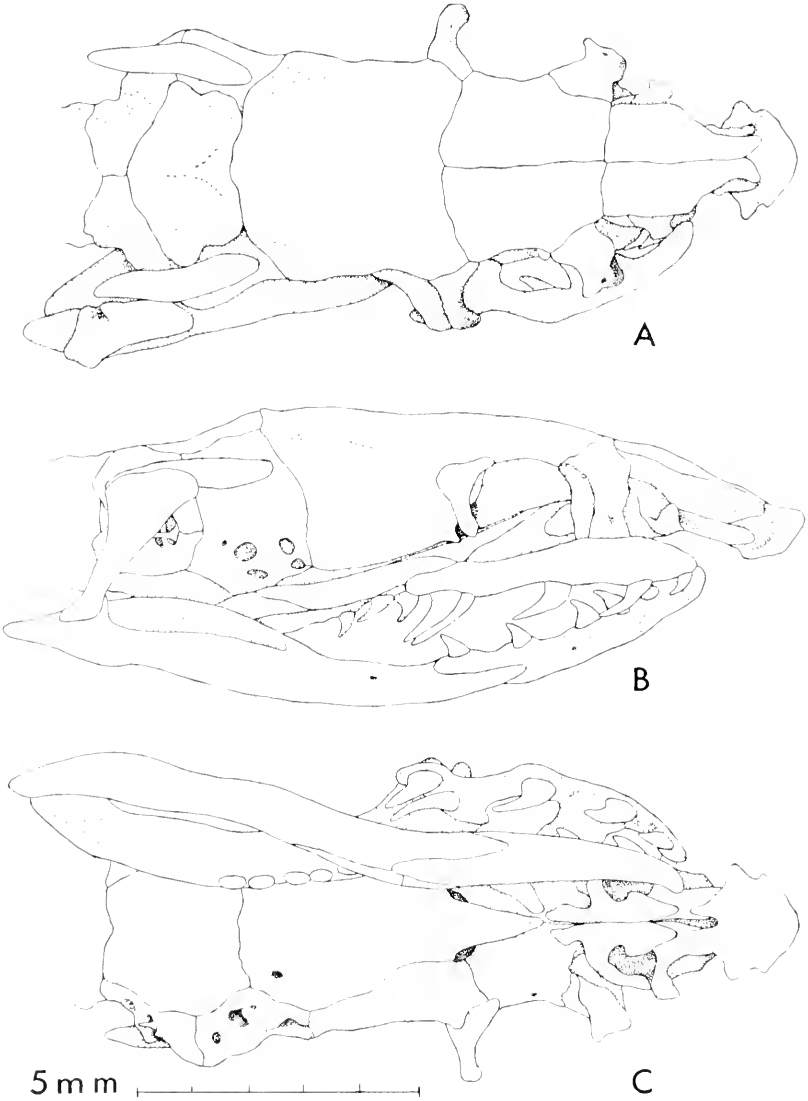

Fig. 32. Skull structure of *Arrhyton taeniatum*, MCZ 44901. A, dorsal view; B, lateral view; C, ventral view.

proportions, *haetiana* is similar to *funereus*. The orbits are reduced in size nearly as much as in *taeniatum*. The otic region is expanded as in the Jamaican species and the juxtastapedial fossa varies from widely open to completely closed. In *haetiana* may be seen the beginning of a trend in a direction opposite from that seen in the *callilaemus-taeniatum* series. Here the parasphenoid is narrower than in *funereus*, and the dental formula is unreduced, with about 17 + 2 maxillary, 11 palatine, 24 pterygoid, and 22 dentary teeth.

The Puerto Rican species, *exiguus stahli*, is considerably larger than *haetiana*. The skull is proportionately narrower and as a consequence the frontals are relatively longer. The orbits are small as in other

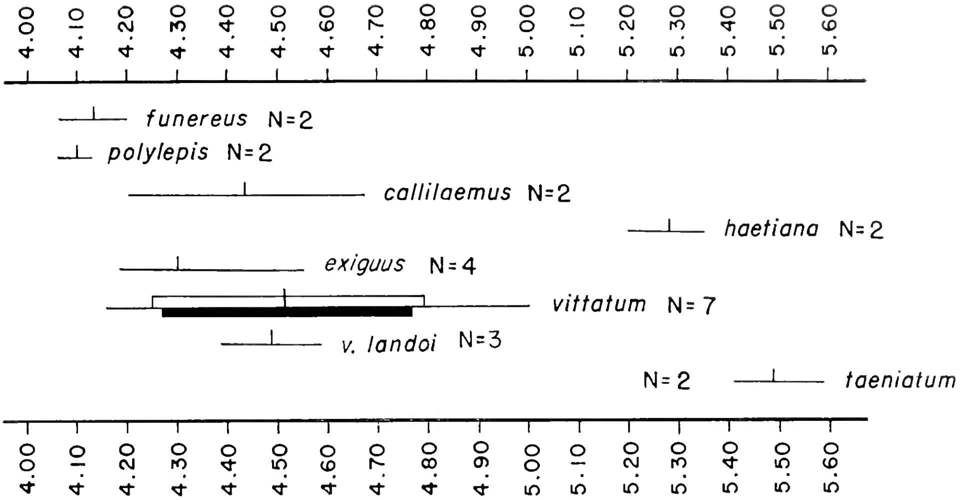

Fig. 33. Skull length/orbit length indices for seven of the eight species of the *funereus* species assemblage (*Arrhyton dolichurum* is not included). Horizontal line, observed range; vertical line, mean; open rectangle, ± one standard deviation from the mean; solid rectangle, 95 per cent confidence interval of the mean.

members of the group, but not as small relatively as in *haetiana*. The parasphenoid is as wide as in the Hispaniolan species. The dental formula is approximately 15 + 2 maxillary, 9 palatine, 23 pterygoid, and 22 dentary teeth, and is nearly the same as in *haetiana*. On the Virgin Islands the subspecies *exiguus exiguus* is very similar to *exiguus stahli* in osteological characters except for the lower dental formula (about 13 + 2 maxillary, 7 palatine, 17 pterygoid, and 19 dentary teeth), and the more reduced supratemporal. The species *exiguus* is superficially similar to *Dromicus juliae* (Dominica); the latter is small with a wide skull, short frontals, and reduced supratemporals. However, several important differences suggest that *exiguus* is not closely related to *Dromicus*, but that it is allied with the *funereus* assemblage. In *juliae* the parasphenoid is narrow and the interorbital partition is very prominent, as in *Dromicus*. The prefrontal is of the *Dromicus* type and is unlike that of *exiguus*. The orbit is large and the quadrate is relatively long. In all of these characters *D. juliae* contrasts with *exiguus*. On these grounds (and on external and hemipenial evidence), *exiguus* is placed in the *funereus* group close to *haetiana*.

External morphology. Externally the *funereus* species group is more diverse than the three other West Indian groups discussed above. The usual number of supralabials is seven, but may be seven or eight in *haetiana* and six or seven in *dolichurum*. In *exiguus* the usual number is eight. The infralabials number eight in the Jamaican species (*funereus*, *polylepis*, and *callilaemus*), eight or nine in the Cuban forms (*taeniatum*, *vittatum*, and *dolichurum*), usually eight and more rarely nine in *haetiana*, and nine in *exiguus*. The number of scale rows is 17 in all of the Cuban species and 19 in the remainder of the group. Ventral scale number may vary from a median of about 118 in *vittatum* to about 181 in *taeniatum*; caudal counts vary from a median of about 45 in *haetiana* to one of about 119 in *dolichurum*. The loreal is absent in *haetiana* and *taeniatum*, but the method of scale loss in the two species was different. In *taeniatum* the prefrontal scale has either extended downward later-

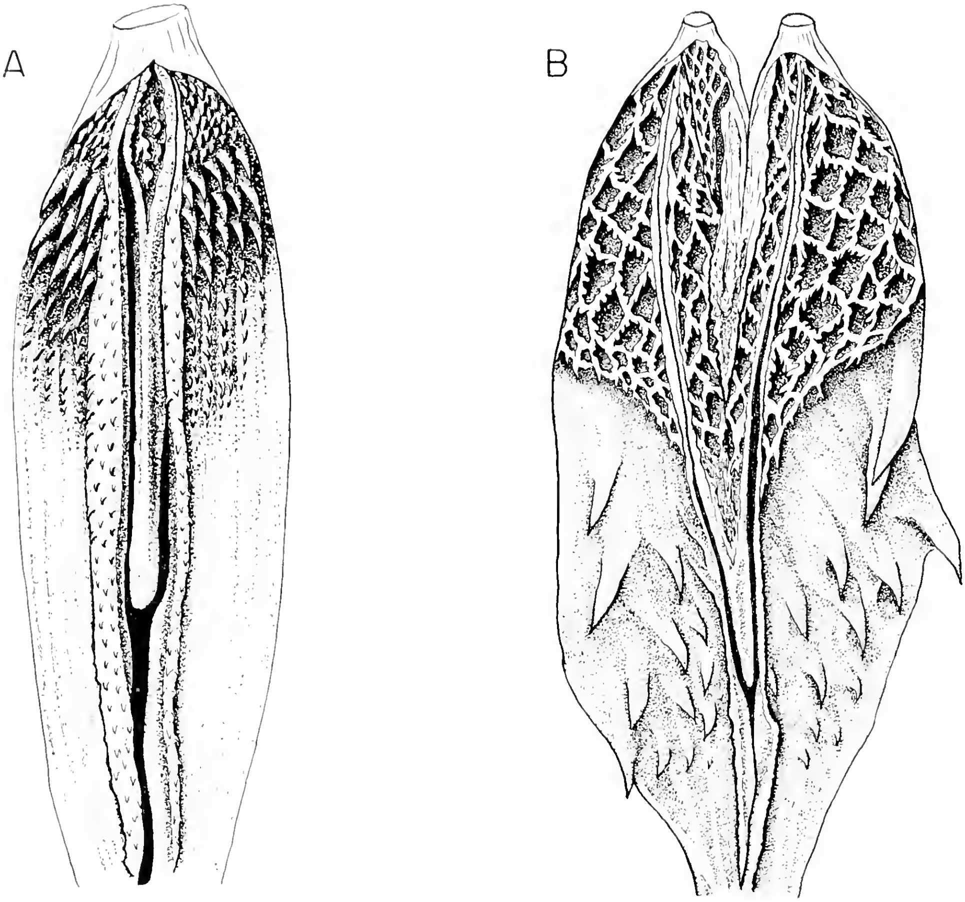

Fig. 34. Hemipenis morphology in the *funereus* species assemblage; semidiagrammatic. The organ is uneverted and dissected *in situ*. A, *Arrhyton funereus*, MCZ 13295; B, *A. vittatum*, MCZ 42505. Approx. × 5.

ally to take the place of the loreal and thus lies between the nasal and the preocular, or else the loreal has fused with the frontal, giving the same result. In *haetiana* the nasal has either replaced the loreal by being extended backward to contact the preocular, or has fused with the loreal.

Of the diagnostic characters used by Cochran (1941) in her description of *Darlingtonia haetiana*, only two set this species apart from the other members of the present species assemblage. These are: the single anal plate in contrast to the divided plate of the other species; and the first pair of lower labials not meeting in the midventral line. In view of the scale variations already noted for this group, these characters are only doubtfully of generic value in this assemblage.

With respect to scale pits, *funereus* and *polylepis* have two pits per dorsal body scale, *callilaemus* has only one. The pit in the latter is asymmetrical and suggests its derivation from a two-pit condition by the loss of one pit. The Cuban species lack scale pits, as does *haetiana*. On Puerto Rico *exiguus stahli* has no pits on most of the body scales, but may have two pits on the scales of the dorsal side of the neck. The subspecies *exiguus exiguus* has no pits. In view of the numerous other characters indicating close relationship, scale pits do not appear to be reliable as a taxonomic character above the species level in this group of snakes. Roze (1958) came to the same conclusion with reference to "Urotheca," and I have suggested the same for *Alsophis*, above.

Hemipenis. As seems to be the case with other characters, the structure of the hemipenis is considerably more variable here than in other West Indian groups. In *funereus* and *polylepis* the organ is undivided although the sulcus spermaticus is deeply forked (Fig. 34A). Small spines are situated along the sulcus from the base to somewhat beyond the point of branching, whereupon lateral bands of spines encircle the organ. In *funereus*, spinose folds of tissue border the sulcus for much of its length, and fine spinose papillae cover the apex. In *callilaemus*, the hemipenis is weakly bifurcated and bears several rows of relatively large spines along the sides of the sulcus. These grade into fine spines basally. The apex of each lobe is covered with soft spinose calyces. The hemipenis in *taeniatum* and *vittatum* (Fig. 34B) is of the *callilaemus* type, but the lateral spines extend further towards the apex; the latter is covered with calyces of fine papillae instead of soft spines. This distinction, however, is very slight and the two forms are essentially the same. In *haetiana* the organ is essentially like that of *callilaemus*, but as in the Cuban species the spines extend more distally, and the apical ornament consists of papillate calyces. The Puerto Rican and Virgin Island species *exiguus* has a more deeply bifurcated hemipenis than does *haetiana*, and the area of strongly reticulated apical papillae is sharply demarcated around its edge.

Figure 35 summarizes the geographic distribution of some of the more important morphological characters.

Origin. The *funereus* species assemblage cannot easily be derived from any other West Indian group. Turning to the mainland, the genus *Rhadinaea*[1] shows a remarkable similarity to the *funereus* group as a whole.[2]

The external scale pattern in species of *Rhadinaea* shows a variation equal to that of the *funereus* group. The supralabials are usually eight in number, except in *R. flavilata* and *R. calligaster* in which there are seven. The number of infralabials may be eight, nine, or ten. The fifth infralabial is the largest of the series in the *funereus* group, but in *Rhadinaea* the largest may be the fourth, fifth, or sixth scale. Considerable variation is seen in the structure of the hemipenis also. In most species of *Rhadinaea*, such as *R. flavilata* and *R. decorata*, the organ is not bifurcated and the sulcus spermaticus is only very weakly divided near the apex. Very large lateral spines are arranged in several rows along the sides of the sulcus. The apex is capitate with spinulate calyces arranged in several thick folds. In *R. calligaster* the sulcus is more deeply divided. The apex is only weakly capitate and the thick folds are lacking; the hemipenis is similar to that of *vittatum* (Cuba), with papillate calyces rather than spinulate ones.

In its osteology *Rhadinaea* is basically like the *funereus* group. The shape of the prefrontal bone is distinct from the Antillean forms for the most part; the ventral half is greatly constricted anteroposteriorly. However, this is variable and in some species this bone approaches the condition found in the *funereus* assemblage. The skull is short and the supratemporal bone is reduced. In some forms, such as *R.*

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[1] This generic name is used here in the sense of Myers (1967) and is considered equivalent to *Urotheca sensu* Roze (1958).

[2] *Rhadinaea dumerillii*, the type species, was unavailable for study, but from Bibron's (1843) figure and description it appears to be close to Central American species of *Rhadinaea* and unlike any Cuban species. *R. dumerillii* now appears not to be a Cuban form as originally described, but almost certainly a mainland form (Roze, 1958).

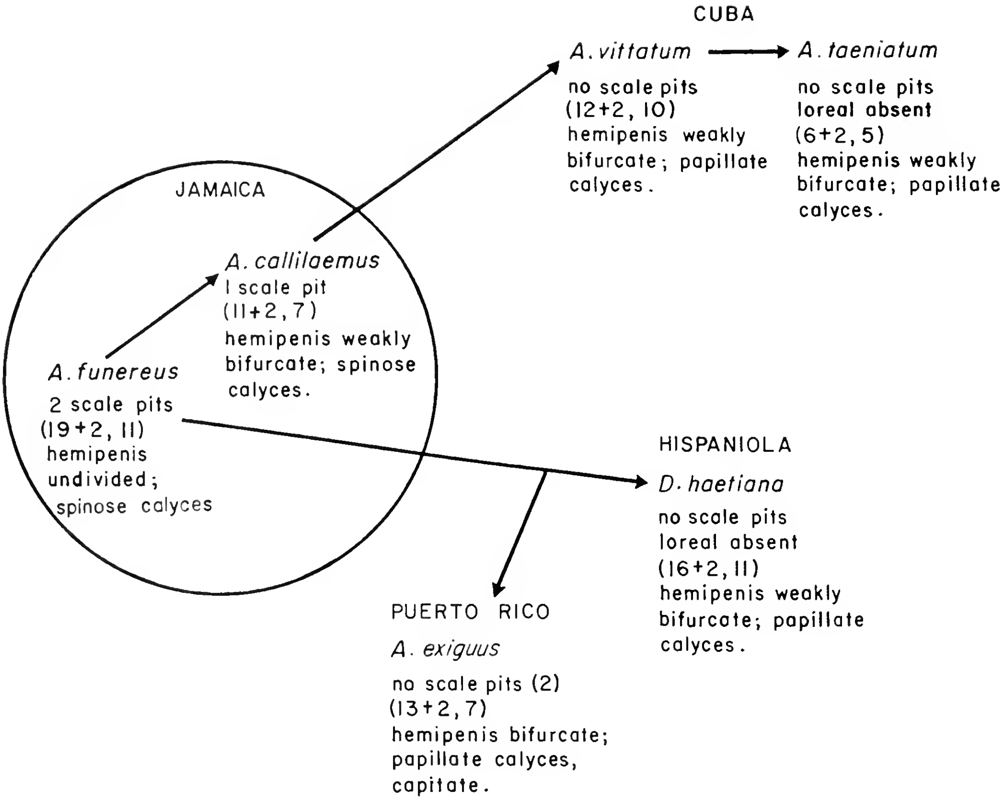

Fig. 35. Geographic distribution of several morphological characters in the *funereus* species assemblage. The circle represents the supposed center of dispersion for this group.

decorata, the parietal spur between the frontal and the postorbital is short as in *funereus*. In *R. serperaster* and *R. lateristriga* the parasphenoid bone is very wide and bears a deep midventral groove. All of the characters that distinguish the *funereus* assemblage from other West Indian xenodontines also occur within *Rhadinaea*, although no one of the species examined possesses all of these characters. Although it seems likely that no one living species of *Rhadinaea* can now be considered as the ancestor of the West Indian *funereus* group, it is not unreasonable to suggest a common descent for both groups from an ancestral form combining the requisite characters, all of which occur in various combinations throughout this morphologically broad genus as presently defined.

It is, of course, possible that the morphological similarities between *Rhadinaea* and the *funereus* group are the result of habitus rather than heritage characters, and that both groups have evolved in parallel fashion with respect to those characters related to a semiburrowing mode of life. There appear to be certain features common to most semiburrowing xenodontines, and these almost certainly evolved independently in many groups under the influence of similar habitus selection. But the exact way in which parallel characters are achieved, even under identical selection pressures, depends upon raw materials in the form of existing morphological structures, and upon genetic variability. The more distantly related any two forms are, the more likely it is that they will achieve functionally similar adaptations in a divergent way.

An examination of semiburrowing adaptations in xenodontine snakes of the New World shows similar osteological trends common to all of them, but, as expected, they differ from each other in details. In most osteological characters studied, *Rhadinaea* and the *funereus* group exhibit a similarity of form which suggests more than morphological parallelism with respect to semiburrowing adaptations.

The osteological modifications which generally appear to be associated with semiburrowing adaptations are: small body size; reduction in relative orbit size; shortening of the parietal region of the skull; enlargement and consolidation of the preorbital bones to form firm contacts with each other; broadening of the parasphenoid bone associated with the reduced orbits; relative broadening of the otic region so that it becomes the widest part of the skull (probably associated with general streamlining); reduction of the supratemporal and quadrate bones; and, a relatively low number of teeth.

With respect to all of these characters, as well as others not obviously correlated with burrowing, the *funereus* group and *Rhadinaea* show a close correspondence, differing only in the structure of the prefrontal bone. The frontal bones form a nearly square plate above the orbits and contact the parietals in a broad, nearly straight suture. In contrast, the parietals of *Geophis mutitorquis* extend lateral to the posterior half of the frontals, occupying a deep groove in the latter. A similar condition exists in *Apostolepis ambinigra*, where the frontals are trapezoidal in shape, being wider anteriorly. In *Atractus latifrons* the frontals are oval in shape, with their long axis in the transverse direction.

In the *funereus* group and *Rhadinaea* the parietal retains the shape normal for nonburrowing xenodontines. In *Geophis mutitorquis* a posterior process extends into the deeply divided interparietal, and in *Atractus latifrons* and *Rhinostoma guianense* the parietals are so shortened that they are broader than long.

The reduced quadrate in the *funereus* group and *Rhadinaea* is thin and triangular in shape. In *Rhinostoma guianense* and *Drepanoides eatoni* the quadrate retains its normal rodlike shape. It should be emphasized that in xenodontine snakes generally, the quadrate and supratemporal appear to increase allometrically with body size and, therefore, the reduced size of these elements in most semiburrowing forms may, in part, be the result of their small size.

The *funereus* group and *Rhadinaea* have retained more or less normal skull proportions, except for *A. taeniatum* in which the skull is somewhat elongated. In *Rhinostoma guianense* the skull is much shortened, whereas in *Apostolepis ambinigra* it is greatly elongated.

In the *funereus* group and in *Rhadinaea* only *taeniatum* shows some enlargement of the nasals and premaxilla and a definite trend towards consolidation of the preorbital region of the skull. In *Carphophis amoena* and *Apostolepis ambinigra* the nasals are greatly enlarged and form a firm contact with the frontals and premaxilla.

In general skull details, *Rhadinaea* and the *funereus* group approximate each other in numerous ways and contrast with most other semiburrowing xenodontines from the mainland, although they show a closer resemblance to forms like *Drepanoides* than to others like *Rhinostoma*, *Apostolepis*, and *Carphophis*. The close similarity between *Rhadinaea* and the *funereus* group in osteological and other characters (excepting the hemipenis) suggests a phylogenetic relationship rather than morphological convergence, though additional evidence is needed. The differences in the hemipenis between these two groups rests primarily in the capitation of the organ in *Rhadinaea* and the lack of capitation in the *funereus* assemblage. I do not, however, feel that this difference is so significant as to preclude their belonging to a phylogenetically related group of genera.

It was stated above that *vittatum landoi* was distinct from *vittatum vittatum* in its dentition. In this respect *v. landoi* is intermediate between *vittatum vittatum* and *dolichurum*. Schwartz (1965) discussed the differences in ventral and subcaudal scale count and body length between the two subspecies of *vittatum*. These characters, together with the clear difference in dentition, indicate a distinction worthy of specific recognition, and the taxon *landoi* should probably be raised to the rank of full species. However, since the present sample of *v. landoi* was too small (three specimens) to determine the degree of variation, it is here, for the present, retained as a subspecies of *vittatum*.[1]

Despite the morphological variation within the *funereus* group, it is difficult to divide these species into distinct genera. Although usually placed in different genera, *vittatum* (Cuba) is closer to *callilaemus* (Jamaica) in dentition, osteology, and external scale pattern than it is to *taeniatum*. Both *vittatum* and *callilaemus* form intermediate grades between *funereus* and *taeniatum*, and a generic boundary within this group cannot be distinguished adequately. As discussed above, *exiguus* (Puerto Rico) shows certain similarities to species of the genus *Dromicus*. However, its totality of characters, especially the hemipenis, makes a close relationship between the two unlikely. On present evidence *exiguus* seems allied to the present assemblage. The three species, *funereus*, *haetiana*, and *exiguus*, form a morphological series distinct from that leading to *taeniatum*, although *haetiana* appears to have diverged from both *funereus* and *exiguus* in certain external characters. These characters have been used to separate *haetiana* from other West Indian species on the generic level (see above). It is my feeling that generic splitting within the present species assemblage will obscure the clear relationships between all of these species which (except possibly for *exiguus*) certainly represent a phylogenetically related group. However, constancy in classification makes the retention of the genus *Darlingtonia* for *haetiana* desirable at this time.

The exact phyletic relationships between *exiguus* and other West Indian species is, as indicated above, not completely certain. Although open to question, I feel that this species could be considered congeneric with the *funereus* group without unduly broadening the limits of that assemblage.

Although the morphological similarities between the genus *Rhadinaea* and the *funereus* assemblage possibly suggest an ancestor-descendant relationship (or perhaps a more distant common ancestry), the *funereus* group is generically distinct from *Rhadinaea* on present evidence. The *funereus* assemblage, then, should be referred to the genus *Arrhyton*, which has priority, and the type species, unfortunately, is *A. taeniatum*, the most specialized form. The proposed phyletic relationships between *Rhadinaea* and the species of the genus *Arrhyton* are summarized in Figure 36.

Zoogeography. In terms of species diversity the center of distribution of *Rhadinaea* today is Central America. Beginning from a closely related stock, we may suggest the following zoogeographic history for this group. From an early stock of this (or an ancestral) genus a single oversea colonization presumably resulted in the establishment of the *Arrhyton funereus* prototype on Jamaica. *Arrhyton polylepis* is extremely close to *A. funereus* and the two forms appear to be relatively

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[1] After the present paper was sent to press, Lando and Williams (1970) formally raised *landoi* to the rank of full species.

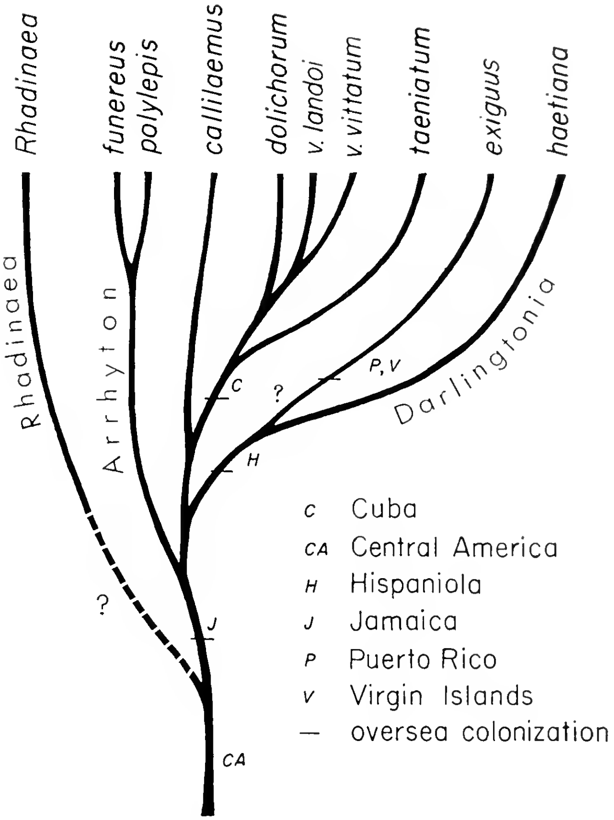

Fig. 36. Suggested phyletic relationships between the species of the *funereus* species assemblage and the genus *Rhadinaea*. Short horizontal lines indicate proposed oversea colonizations.

recent products of speciation on that island. The most primitive member of the genus is *A. funereus* which forms the base of both the *A. funereus–A. taeniatum* series and the *A. funereus–A. exiguus* series. It is the only Antillean species (except for *A. polylepis*) with a nonbifurcated hemipenis and in this respect is closest to species of *Rhadinaea*. Within the *A. funereus–A. taeniatum* series it is the least specialized in terms of the reduction of skull bones and other semiburrowing adaptations. From this early *A. funereus* stock two basic lines appear to have been established; *A. callilaemus* (Jamaica) began a trend toward reduction of the posterior skull bones and in the dentition, and a widening of the parasphenoid bone. A colonization of Cuba from this early *A. callilaemus* stock led to the Cuban forms which, through repeated speciation, continued the trend, with *A. taeniatum* as the most highly specialized species of the group. The second line resulted from a migration to Hispaniola and tended toward a narrower parasphenoid, larger size, and in many ways a general convergence toward other West Indian xenodontine groups, especially *Dromicus*. This may have been related to a general tendency away from semiburrowing adaptations. In order to derive *A. exiguus* from this early Hispaniolan form we must postulate a widespread distribution for this latter form before (or concurrent with) its differ-

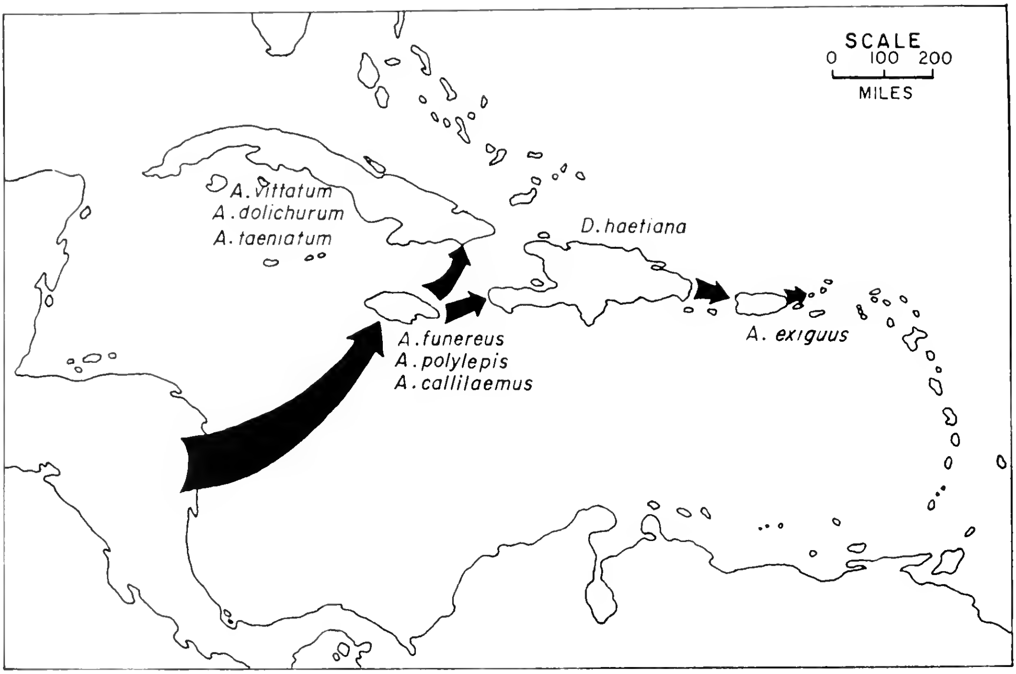

Fig. 37. Proposed routes of colonization of the West Indies by the *funereus* species assemblage. The arrows are not intended to represent exact paths. The distribution of extant species is as indicated.

entiation into the morphologically somewhat specialized and ecologically restricted species *Darlingtonia haetiana.* Today *D. haetiana* occurs only in the montane massifs of the southwestern and Barahona peninsulas at altitudes ranging from 1000 to 5600 feet. One possible explanation for the peculiar distribution of this species is an ecological replacement of the former widespread species (possibly by *parvifrons?*) with *D. haetiana* remaining as a montane relict. This zoogeographic pattern is summarized in Figure 37.

A PROBLEMATICAL GENUS

Two species remain to be discussed: *Ialtris dorsalis* and *I. parishi* from Hispaniola. *Ialtris dorsalis* (I have not seen *I. parishi*) is a large species and is most similar to *Alsophis* in many skull characters, but distinct in many external and hemipenial characters. The skull is narrower, especially in the otic region. In its dentition this species is unique among West Indian xenodontines in having prominent grooves on the enlarged posterior maxillary teeth. The bilobed hemipenis is very long, ridged with numerous folds, and has an apical ornament of weakly developed flounces. Externally there are seven upper labials as in *Arrhyton* generally, but the ventral and subcaudal scale counts are similar to those of *Alsophis. Ialtris dorsalis* (and presumably *I. parishi* also) is not very close to any other Antillean species as far as can be determined from its present morphological specializations and therefore certainly should be retained in a distinct genus. In most characters *Ialtris* shows its greatest similarity to *Alsophis,* and it may have been derived from that genus on Hispaniola.

CONCLUSIONS

The use of skull and hemipenial characters, in addition to those of external

TABLE 2

DISTINGUISHING CHARACTERISTICS OF THE EIGHT GENERA OF XENODONTINE COLUBRID SNAKES IN THE WEST INDIES AS DISCUSSED IN THE TEXT.

Genus	prefrontal	frontal	hemipenis	size	supra-labials	grooved max. teeth	anal scale	no. sensory pits	loreal scale
Alsophis	*cantherigerus* type	long and narrow	no disk	large	8	no	divided	2(1)	present
Dromicus	*melanotus* type	short and narrow	apical disk	medium	8	no	divided	1(0)	present
Antillophis	*melanotus* type	long and narrow	no disk	medium	8	no	divided	1	present
Arrhyton	*funereus* type	square	no disk	small	7–8	no	divided	0–1	present (absent in *A. taeniatum*)
Darlingtonia	*funereus* type	square	no disk	small	7–8	no	complete	0	absent
Hypsirhynchus	*cantherigerus* type	long and narrow	no disk	large	8	no	divided	1	present
Uromacer	*cantherigerus* type	long and narrow	no disk	large, arboreal	8	no	divided	0	present
Ialtris	*cantherigerus* type	long and narrow	no disk	large	7	yes	divided	0	present

morphology, appears to be of significant aid in suggesting relationships between species of West Indian xenodontine colubrid snakes. They not only provide data for a proposed redefinition of generic concepts, but suggest certain phylogenetic relationships with mainland groups. Such relationships are of considerable interest, since they allow a tentative reconstruction of the possible origin and history of these snakes in the Antilles. The generic groups of xenodontine snakes here recognized in the West Indies and listed in Table 1 may be distinguished as in Table 2.

The present xenodontine fauna of the West Indies was possibly wholly derived from Central and South American stocks through at least four oversea colonizations. Based on present evidence, a summary of the postulated historical events follows: 1) From the formerly widespread South American genus *Alsophis*, a waif colonization established this group on Cuba. Subsequent radiation into a number of species and endemic genera led to its present distribution throughout the Greater Antilles and the northern Lesser Antilles. A minimum of three separate inter-island migrations of this group is required to explain the peculiar faunal assemblage of Hispaniola. 2) The specialized genus *Ialtris* possibly emerged from *Alsophis* on Hispaniola. 3) Using Jamaica as a port of entry and center of dispersion, a single stock, possibly derived from the Central American genus *Rhadinaea*, successfully spread through the Greater Antilles in two distinct but closely related lines and established the genera *Arrhyton* and *Darlingtonia*. 4) Possibly derived from part of what is now called *Lygophis* in South America, the species *andreae* and *parvifrons* may have reached Cuba and Hispaniola by a direct oversea colonization. 5) A relatively recent invasion of the Lesser Antilles by a species of *Dromicus* (= *Leimadophis*) almost certainly entered via Trinidad, but has not yet progressed beyond Guadeloupe.

The chronological sequence of colonizations cannot definitely be established on present evidence. However, a sequence roughly similar to that above is not unreasonable. It, of course, cannot be assumed that the West Indies were devoid of a xenodontine ophifauna before the series of colonizations that established the present fauna, but our knowledge of earlier xenodontine colonizers is nonexistent because of the lack of a significant fossil record.

From the patterns of dispersion discussed in this paper it would appear that numerous combinations of inter-island migrations have occurred. The main sequences have progressed from one island to the next adjacent island and in this sense were for the most part linear. The following series have been proposed: mainland-Cuba-Hispaniola-Puerto Rico-Lesser Antilles; mainland-Cuba-Jamaica-Hispaniola; mainland-Cuba-Bahamas; mainland-Jamaica-Cuba; mainland-Jamaica-Hispaniola-Puerto Rico; mainland-Trinidad-Lesser Antilles.

Inter-island migration, especially to centrally located Hispaniola, seems to have been more frequent than mainland-island migrations. This was certainly the result of the greater cross-water distance between the mainland and any island than between the various islands themselves, as Simpson (1956) and Darlington (1957) have suggested. The greatest diversity in species and genera occurs on Hispaniola; this is to be expected in view of its central position and consequently greater number of colonizations. Its large size, varied habitats, complex physiography and history have provided an excellent opportunity for immigrants to differentiate into noncompeting forms.

The zoogeographical patterns here proposed are based on limited evidence and are in large measure speculative. It is hoped that they offer a workable contribution toward the continued study of this group. However, only when adequate information about the comparative anatomy, karyotypes, ecology, physiology, and biochemistry of all Antillean snakes and their mainland relatives is available will we be able to draw firmer conclusions concerning the origin and zoogeography of xenodontine snakes in the West Indies.

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APPENDIX

Dental formulae and variation for West Indian and some related mainland and Galapagos xenodontine colubrid snakes. Variation includes ranges of subspecies.[1]

	N[2]	maxillary	palatine	pterygoid	dentary
Alsophis					
angustilineatus	1	11+2	11	17	18
anomalus	1	12+2	8–9	20	18–19
antillensis	6	16–19+2	11–13	28–30	24–26
ater	4	16+2	13–16	26–27	22–25
biserialis	1	12+2	7	16	17
cantherigerus	12	11–15+2	9–12	23–30	17–21
chamissonis	2	9+2	7–8	10–14	15–16
dorsalis	1	12+2	7	16	17
melanichnus	1	18+2	16	28	24
portoricensis	10	14–18+2	9–12	26–32	23–35
rijgersmai	2	16–17+2	11–13	26–30	23–24
rufiventris	3	16–18+2	11–15	25–28	21–26
sancticrucis	2	17–19+2	12–13	30–32	22–23
slevini	1	11+2	8	18	19
tachymenoides	1	11+2	10	16	21
rudii rudii	4	11–13+2	9–10	20–27	19–23
rudii utowanae	2	15+2	12–13	29–31	22–23
Antillophis gen. nov.					
andreae	4	18–21+2	15–16	34–35	25–28
parvifrons	13	13–16+2	10–13	25–27	19–24
Arrhyton					
callilaemus	2	11–12+2	7	16	18
dolichurum	1	10+2	7	16	12
exiguus	4	13–16+2	7–11	17–27	19–23
funereus	2	19+2	11	19	24
polylepis	2	17+2	11	23–24	26–27
taeniatum	2	6+2	5	7–8	10
vittatum vittatum	7	12–15+2	10–14	9–10	15–17
vittatum landoi	3	10–11+2	9	9	14–15
Conophis					
lineatus	1	10+2	7	17–18	18
Darlingtonia					
haetiana	3	16–17+2	11	22–25	20–24
Dromicus					
almadensis	2	18–19+2	15–16	27–28	26–29
amazonicus	1	18+2	12	22	23
bimaculatus	1	21+2	14	28	26
cursor	2	20–21+2	14–15	27–28	26
epinephalus	2	22–24+2	16–18	27–32	32
juliae	1	24–26+2	29–33	30–34	33–34
melanotus	3	15–16+2	10–11	23–26	16–22
ornatus	2	19–20	13	26	24–27
perfuscus	2	15–16+2	12–13	20–22	18–19
pseudocobella	1	18+2	13	23	19
reginae	1	16+2	12	27	20
taeniurus	1	19+2	11	25	25
Hypsirhynchus					
ferox	3	11–12+2	7	17–19	19–20

Appendix (Continued)

	N[2]	maxillary	palatine	pterygoid	dentary
Ialtris					
dorsalis	2	16+2	7	21	20
Liophis					
anomala	1	12+2	10	19	17
cobella	3	19–20+2	13–14	26–29	24–30
jaegeri	1	21+2	18	27	—
merremi	1	18+2	14	26	22
Lygophis					
boursieri	1	22+2	14	28	25
flavifrenatus	1	26+2	23	35	35
lineatus	2	19–20+2	14–15	29–32	27–29
Philodryas					
aestivus	1	14+2	11	20	19
burmeisteri	1	12+2	9	16	19
olfersii	1	10+2	9	17	13–14
Uromacer					
catesbyi	7	15–18+2	10–11	24–25	22–28
dorsalis	2	13–14+2	9	18	20–22
frenatus	4	14–16+2	9	18–19	24
oxyrhynchus	7	15–17+2	8–10	17–21	22–28
Rhadinaea					
brevirostris	1	14+2	9	21	18
decorata	1	22+2	14	34	24
flavilata	1	24+2	11	24	20
serperaster	1	17+2	9	14–16	14

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[1] Problematical subspecies which may be full species are listed separately.
[2] Number of specimens examined.

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The Milliped Family Conotylidae in North America, with A Description of the New Family Adritylidae (Diplopoda: Chordeumida)

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THE MILLIPED FAMILY CONOTYLIDAE IN NORTH AMERICA, WITH A DESCRIPTION OF THE NEW FAMILY ADRITYLIDAE (DIPLOPODA: CHORDEUMIDA)

WILLIAM A. SHEAR

ABSTRACT

The milliped family Conotylidae in North America is revised; figures and descriptions of all known species are given. The new family Adritylidae is proposed for the genus *Adrityla* Causey.

Two new genera of conotylids are described: *Achemenides* (type species, *Conotyla pectinata* Causey) and *Plumatyla* (type species, *Conotyla humerosa* Loomis). Twelve new species of conotylids are described: *Conotyla extorris*, *C. personata*, *C. elpenor*, *C. smilax*, *C. ocypetes*, *C. aeto*, *C. vista*, *C. celeno*, *Taiyutyla napa*, *T. francisca*, *Austrotyla borealis*, and *A. chihuahua*. Three new synonymies in the genus *Conotyla* are recognized.

The biology and zoogeography of the group is briefly discussed.

INTRODUCTION

The small millipeds of the family Conotylidae are poorly represented in most collections, though species are fairly common in the northern parts of the United States, and at higher elevations elsewhere. That the distribution of this interesting group is a relict of a previous, colder age seems beyond question. Several species occur in caves, and many are characteristic of high altitudes, reaching near the timberline in the Rocky Mountains of Colorado and Alberta and in the White Mountains of New Hampshire, while adjacent lowlands are poor in species and in individuals. In the middle Appalachians, a pattern of highly localized, rare, endemic species is now emerging. The importance of millipeds to zoogeographers was repeatedly emphasized by O. F. Cook, but attempts to use them have been few, probably due to the chaotic state of diplopod taxonomy. It is hoped that studies like this one will encourage zoogeographers and paleoecologists to utilize the excellent zoogeographic information presented in many groups of millipeds.

The family name Conotylidae was proposed by O. F. Cook in 1896 for the milliped genera *Conotyla*, *Trichopetalum*, *Scoterpes* and *Zygonopus*, first described in detail by Cook and Collins in 1895. Since its establishment, little revisionary work has been done on the taxonomy of this family despite the large number of additional names that have accumulated under it. Verhoeff (1932) realized that the Conotylidae, in the sense of previous work, was an unnatural assemblage, and removed some genera to his new family, Trichopetalidae; his paper was not noticed by American students. Chamberlin (1952) established the genus *Taiyutyla*, and several new species were added to *Conotyla* by Loomis (1939, 1943) and by Causey (1952).

Hoffman (1961), aware of Verhoeff's assignment of the genera *Trichopetalum*, *Scoterpes*, and *Zygonopus* to the Trichopetalidae, studied the gonopods of several species of *Conotyla* in detail. He reviewed previous studies of the conotylids, and placed a number of the forms then in *Conotyla* into a new genus, *Sonoratyla*. *Taiyutyla* was also discussed, as well as Chamberlin's enigmatic genera *Zygotyla* (1951), *Cookella*, and *Bollmanella* (1941). Hoffman made no attempt under the circumstances (see section below on dubious names) to clarify the status of these latter three genera. At the same time, Causey (1961a) carried out a similar study, published earlier than Hoffman's, and proposed the genus *Austrotyla* for some of the species later included in Hoffman's *Sonoratyla*. Later in the same year, Causey (1961b) published the new genus, *Adrityla*, based on *Conotyla deseretae*. Although further papers on conotylid genera have been announced (Causey, 1961a), they have not as yet been published.

I wish to thank Dr. Richard Hoffman, Radford, Virginia, for suggesting this study and providing numerous specimens and much unpublished data. His advice has been greatly appreciated. Dr. Nell Causey, Baton Rouge, Louisiana, loaned her collection of Conotylidae, probably the largest and most representative in existence, and made many helpful suggestions. H. F. Loomis, Miami, Florida, loaned unpublished drawings of new related taxa. Dr. Herbert W. Levi, Museum of Comparative Zoology, Cambridge, Massachusetts, read and edited the manuscript and loaned material from the collections under his care. Dr. Ralph Crabill, U. S. National Museum, loaned important type specimens. Dr. Andrew A. Weaver, Wooster, Ohio; Mr. Robin Leech, Edmonton, Alberta, Canada; Mr. Michael Gardner, Davis, California; and, Mr. Erik Thorn of the British Columbia Provincial Museum, Victoria, British Columbia, Canada, also loaned or donated important specimens. Mr. Stewart Peck of the Museum of Comparative Zoology loaned specimens and unpublished data, and contributed much to my understanding of the biology and evolution of the cave forms in the Conotylidae. All types of new species described herein are deposited in the Museum of Comparative Zoology.

TAXONOMIC POSITION OF THE FAMILY CONOTYLIDAE

The affinities of the Conotylidae lie primarily with three North American families (one briefly described as new, below) and with a poorly known group of Asian and South American species. Verhoeff (1913) placed *Japanosoma* (Japan) in the monotypic subfamily Japanosominae, and *Eudigona* (Chile) in the subfamily Eudigoninae of the Conotylidae. Neither of these subfamilies has been restudied since their original proposal, and their position remains in doubt. However, judging from the published data, they seem to be typical conotylids. The Asian family Diplomaragnidae is somewhat more distantly related to the Conotylidae (Verhoeff, 1942; Hoffman, 1963). Recently, Buckett and Gardner (1967) have described a new monotypic family, Idagonidae, type genus *Idagona*, from caves in Idaho. They stated that the new family was related to both the Conotylidae and the Cleidogonidae, but as I have earlier pointed out (Shear, 1969), the Conotylidae and the Cleidogonidae are not at all closely related to each other. The single major distinction between the Conotylidae and the Idagonidae lies in the loss of the telopodite articles of the posterior gonopods (ninth legs) in the Idagonidae; except for this, *Idagona* might be considered as an aberrant conotylid genus.

The relationship of the Conotylidae to the Trichopetalidae is somewhat problematic. The two families are quite similar in general body plan, but there is a distinct morphological gap in gonopod structure. The anterior gonopods of the conotylids are fused into a single article; those of the trichopetalids are two-articled, with a prominent coxite. A colpocoxite is lacking in the posterior gonopods of trichopetalids, which are two- or three-articled in all known forms; conotylids have a large colpocoxite on the three-articled posterior gonopods.

Milliped gonopods are developed from walking legs, and there is a well-recognized tendency for more primitive forms to have the gonopods more closely resembling legs; reduction and fusion of segments is considered a specialized character. Thus, the Trichopetalidae seem a more primitive stock than the Conotylidae. Moreover, the conotylids have relatives in Asia and in South America, indicating possible dispersal routes into North America from either of these regions (or the reverse), while the trichopetalids, like the cleidogonids, are peculiarly North American. My own feeling is that judgment should be reserved pending a study of the Trichopetalidae; it is quite likely that the resemblance between them and the conotylids is due in great part to parallelism, or that trichopetalids are nearer an ancestral stock than conotylids. The problem is aggravated by the obviously derived trichopetalid characters of reduction in segment number, loss of at least some ocelli, and minute size, all of which contrast with the seemingly more primitive gonopod plan.

The following key will serve to separate the North American milliped families that may be confused with the Conotylidae. All of the families have in common swollen lateral segmental shoulders and greatly enlarged segmental setae; the male gonopods superficially resemble each other.

KEY TO CONOTYLIDAE AND RELATED FAMILIES IN NORTH AMERICA

1a. Telopodites of ninth legs of males absent, ninth leg represented by the simple, subtriangular colpocoxite, which curves around the larger telopodites of the anterior gonopods; caves in Idaho .... Family IDAGONIDAE

1b. Telopodites of ninth legs of males present but reduced, distal articles enlarged and turned dorsally 2

2a. Tenth legs of males with the coxae greatly enlarged and lobed, tenth telopodite reduced to two or three segments; anterior gonopods a pair of cheirites formed by fusion of telopodites, sternites, and tracheal apodemes .... Family ADRITYLIDAE, new

2b. Tenth legs with the coxae only slightly enlarged, not lobed; anterior gonopods with telopodites free from the sternites 3

3a. Ninth male legs with a conspicuous colpocoxite, telopodites two-articled, the distal article oval and enlarged; anterior gonopods a single article; segmental setae usually less than one half the body width .... Family CONOTYLIDAE

3b. Ninth male legs without colpocoxites, telopodites usually a single article often with conspicuous constrictions, often with a claw; telopodite of anterior gonopods two-articled; segmental setae frequently more than one half the body width .... Family TRICHOPETALIDAE

A detailed study of the gonopod structure of *Adrityla deseretae* (Chamberlin) has convinced me that it should not be retained in the Conotylidae, as to retain it would make the family obviously polyphyletic. The new family Adritylidae, briefly characterized below, is probably related to the Conotylidae to about the same degree as is the Trichopetalidae. By even the most conservative criteria, the structure of the gonopods of *Adrityla* excludes it from any known chordeumoid family, though there is a vague resemblance to *Marquetia* (Opisthocheiridae; Brölemann, 1935: 278); I have not seen specimens of *Marquetia*.

Family ADRITYLIDAE new family

Type genus. Adrityla Causey, 1961; type species *Conotyla deseretae* Chamberlin, by original designation and monotypy.

Diagnosis. Large chordeumid millipeds (to 25 mm long) with 30 postcephalic segments, segmental setae and paranota prominent, head not covered by collum. Male gonopods modified from three interlocking pairs of legs; anterior gonopods (eighth legs) consisting of pair of cheirites formed from fusion of telopodite, sternite and trachael apodeme of each side; posterior gonopods (ninth legs) three-segmented, coxae with large colpocoxite, partially fused to sternites and tracheal apodemes, distal telopodite article inflated, turned dorsally. Tenth legs with coxae greatly enlarged and lobed, coxal gland present, coxae fused to sternites, telopodites reduced. Eleventh legs without coxal glands.

Notes. The single known species, *A. deseretae*, is common in canyons of the Wasatch Mts., Utah. The reader is referred to the paper of Causey (1961b) for further details.

Family CONOTYLIDAE Cook

Conotylidae Cook, 1896, Brandtia, No. 2, p. 8. Verhoeff, 1932, Zool. Jahrb. Abt. Syst., Vol. 62, p. 500. Hoffman, 1961, Trans. Amer. Ent. Soc., Vol. 87, p. 263.

Type genus. Conotyla Cook and Collins, 1895.

Diagnosis. Small to medium-sized (9–25 mm) chordeumid millipeds with 30 post-cephalic segments. Head not covered by collum. Eyes present, in triangular patch, sometimes reduced in size and number from maximum of 22–24. Antennae with third article longest, proportions of other articles variable; not markedly clavate; long and slender. Sensory cones four or five. Mouthparts typical. Mentum not divided, mandibles with about 12 pectinate lamellae. Post-collum segments with prominent lateral swellings bearing outer two segmental setae on each side. Segmental setae large, prominent, movable. Epiproct and periprocts truncate; spinnerets two. Legs long, slender, claws prominent, basal segments heavily setose-pilose. Legs one and two of males reduced in size, six-segmented; legs three through seven longer than post-gonopodal legs, usually thickened and crassate, often with strong knobs on some of the segments. Gonopods modified from eighth and ninth legs; anterior gonopods consisting of single article, sternum variable. Posterior gonopods three-jointed, coxa free from sternum, with large colpocoxite, distal telopodite article inflated, turned dorsad, without a claw. Coxae of tenth legs with large coxal glands, coxae sometimes lobed. Coxae of eleventh legs without glands, sometimes with prominent hooks. Prefemur of eleventh legs with prominent hooks. Remaining legs unmodified. Female cyphopods of two valves opening anteriorly at rest, pore of oviduct covered by single receptacle.

Distribution. North America, Japan, Chile.

BIOLOGY OF THE CONOTYLIDAE

Little is known of the biology and ecology of the Conotylidae. In southeastern West Virginia, immature specimens were frequently taken from leaf litter and rotted wood by Tullgren funnel sampling during the summer and early fall. However, nearly 90 percent of all examined collections of mature specimens, including those from caves and high altitudes, were taken between the months of November and April. Cook and Collins (1895) commented on the surprising activity of *Conotyla* during the winter, and I have seen mature specimens of *Conotyla* walking briskly over frozen logs and ice crystals. In addition, most of the records known to me from the eastern part of the continent are either from caves, high altitudes, or cool microclimates supporting such trees as hemlock, spruce, and fir. In the Rocky Mountains of Colorado, all but a few records of *Austrotyla coloradensis* are from coniferous forest above 7000 ft. (2300 m) elevation. *Conotyla albertana* has been collected in Alberta in alpine meadows above 6500 ft. (2150 m), and no records below 4200 ft. are known. *Austrotyla specus, Conotyla blakei*, and *C. bollmani* are found at low elevations in the interior of the continent, but most reliable records are from caves. *Achemenides pectinatus* and *Plumatyla humerosa* are known only from caves, and the latter is the only conotylid showing well-marked cave adaptations.

Howden (1963) has pointed out that animal species populations may adjust to a warming climate by persisting in cooler microhabitats (caves, mountain-tops), or by adjusting their major period of activity to the cooler part of the year. The evidence above seems to indicate that, following Quaternary glaciations, both adjustments may have been made by various species of conotylids.

The distributions of *Conotyla blakei* (Map 2) and of *Austrotyla specus* (Map 3) may reflect a current period of cave invasion and northward movement following the Wisconsin glaciation and subsequent retreat. Barr (1968), in an excellent summary of the evolution of troglobitic animals, points out that the isolation and evolution of a troglobite usually is preceded by a stage during which an ancestral species is troglophilic. The small cave populations are occasionally swamped genetically by invasions from the surface population. Isolation and subsequent speciation occurs when the surface populations are eliminated by some (usually climatic) change that does not significantly affect the environmental conditions in the caves. Because populations in caves are small, genetic drift and founder phenomena play a great part in their evolution (Barr, 1968: 82–84). Although present *Conotyla* and *Austrotyla* cave populations seem to be geographically isolated from large surface populations, no appreciable differentiation has taken place. Perhaps more thorough surface collection in the regions of cave records will produce evidence of populations that can produce the swamping effect.

However, it must not be overlooked that it is the maxima and minima of climatic parameters, not the average, that usually restrict the range of a species. In the case of *Achemenides pectinatus*, caves may have served as refugia from the severe periglacial climate during the glacial maxima. A further difficulty is posed by the wide distribution in California of *Plumatyla humerosa*, a true troglobite. More than one species may be represented in the numerous collections of immature specimens.

I have made extensive personal observations on the ecology of only a single species, *Conotyla blakei*. About 20 specimens of both sexes were observed and collected on Mt. Equinox, Bennington Co., Vermont, and Mt. Greylock, Berkshire Co., Massachusetts. All specimens were taken from above 3000 ft. (1000 m) in elevation, in dense fir forests. The Mt. Equinox populations were observed in October, 1968, and May, 1969; those on Mt. Greylock in May, 1969. Without exception, the animals were found under the bark of dead standing trees or fallen logs. The bark was loosened to the extent that it could easily be peeled off in large slabs, and the wood underneath, on which the animals were usually resting, was saturated and soft—water could easily be squeezed from it by the fingers. Held in the hand or exposed to sunlight, the millipeds reacted by curling the head and first few segments under the body and withdrawing the legs into a position parallel with the long axis. After a few seconds, a period of rapid running and searching followed. If not allowed to find shelter from the sun, or if not released from the hand, the millipeds became immobile and moribund in a matter of 30 seconds. Similarly, an attempt to keep *C. blakei* in the laboratory resulted in the death within 24 hours of all individuals collected, even though high humidity was maintained. Presumably, temperature was a major factor in the laboratory and field deaths.

A single mating was observed in May, 1969, on Mt. Equinox, at an elevation of about 3800 ft.; there were numerous persistent snowbanks in the fir thicket where the mating pair was found. The female held onto the wood of the rotted tree-trunk with the last 10 or 12 segments, while the male coiled about her body, using the crassate first seven pairs of legs to embrace her head and anterior segments. No thrusting movements of any sort were observed, but the pair experienced difficulty in separating after being disturbed.

Schubart (1934) reported spermatophore

formation and transfer in some European chordeumids. In these forms, the male secretes sperm from the seminal pores on the coxae of the second legs into coxal sacs on the postgonopodal legs (in the case of the conotylids, these sacs are found on the tenth legs only). The secretions from these glandular sacs then form the seminal fluid into a spermatophore (Fig. 34) which, during mating, is transferred to the female cyphopods (Fig. 15) at the bases of the second legs by the gonopod complex (Fig. 14) of the male. In preserved male specimens of conotylids, these coxal sacs on the tenth legs are often extruded. In several cases, two large globular objects were attached to the extruded ends of the coxal sacs. These were easily detached, and examination under a compound microscope showed that each consisted of a cemented mass of small cells. This structure may represent a spermatophore. If this is the type of mating behavior that occurs in the family, then the distinction in gonopod function pointed out for other families by Brölemann (1935) and referred to by Hoffman (1961) may be applicable to conotylids.[1]

Feeding presumably takes place as in other chilognath millipeds, material being scraped or picked up from the substrate by a combination of movements of the gnathochilarium and mandibles, and ground by the dentate and pectinate lamellae of the mandibles. The finely triturated material in the foreguts of several *C. blakei* was composed of wood tracheids and fungal hyphae.

Molting and oviposition have not been observed, but some North American chordeumids make silk chambers for these purposes.

TAXONOMIC CHARACTERS AND GONOPOD STRUCTURE

Unfortunately, as is true of many milliped groups, nonsexual characters are of very little use in separating species, and even genera. Causey (1961a) attempted to use the relative lengths of the antennal segments in some species of *Austrotyla*, but such meristic characters must be used with caution when few specimens are available. In species that occur both in and out of caves, ocelli number and arrangement is variable, or it is the same in related epigean species, so that this character is usually of little value. Nonetheless, since such characters may at some time be useful, I have described them for all the species mentioned here. I have, however, omitted much of the usual detail from the species descriptions, particularly description of structures which are common to all members of a family or genus.

Also, female specimens are difficult to assign to species, and even genus. The cyphopods, useful in other chordeumid groups, are virtually identical in different species of Conotylidae. In addition, they are generally so poorly sclerotized that they shrivel when preserved, further reducing their utility in taxonomy. The best taxonomic characters are to be found in the male gonopods. In addition, the modifications of some of the pregonopodal legs of the males, usually taking the form of mesal lobes on one or two segments, are quite important in separating species.

Conotyla melinda (Figs. 1, 2) has gonopods typical in many respects of the large group of Appalachian species which are highly endemic in their distribution. In lateral view (Fig. 1) the anterior gonopods are seen to curve laterad of the colpocoxites *(c)* of the posterior gonopods (telopodite articles of posterior gonopod not shown). The apex of the anterior gonopod is divided into two branches, an anterior branch *(ab)* and a posterior branch *(pb)*, and there is a prominent lateral shoulder *(ls)* on

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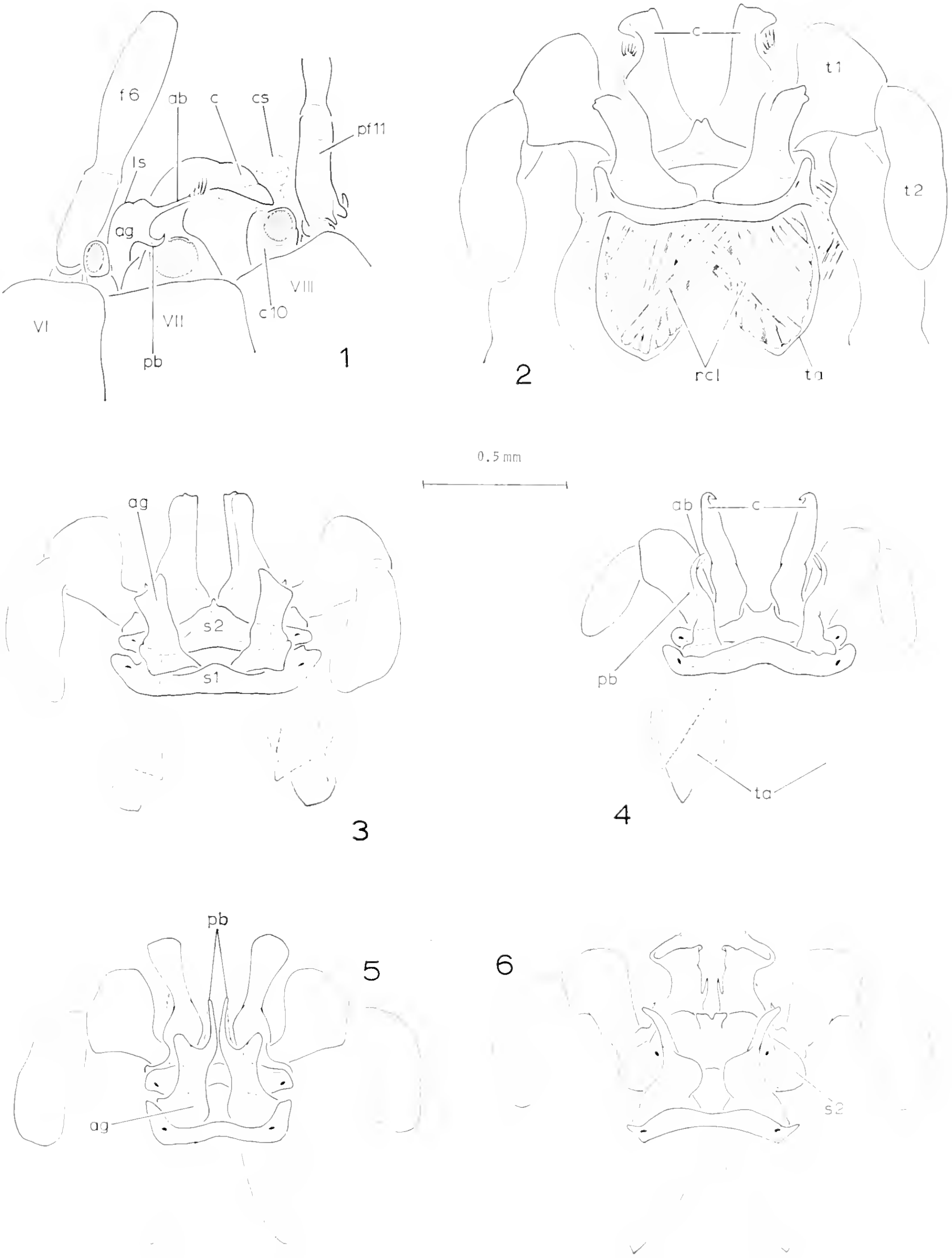
[1] Because of some uncertainty, I have not used the terms *paragonopod* and *peltogonopod* (see Hoffman, 1961) but have used the more understandable, though less specific, terms *anterior gonopods* to indicate those modified from the eighth legs, and *posterior gonopods* to indicate those modified from the ninth legs.



igures 1–6. Anotomy of conotylid male gonopods. Fig. 1. *Conotyla melinda*, lateral view. Fig. 2. *C. melinda*, anterior iew. Fig. 3. *C. fischeri*, anterior view. Fig. 4. *C. blakei*, anterior view. Fig. 5. *C. smilax*, anterior view. Fig. 6. *C. trolineata*, anterior view.

which, in some species, the process of the femur of the seventh leg rests (*Conotyla vista*, Fig. 41). Note also the coxal sac of leg ten (*cs*) and the modified prefemur of leg eleven (*pf 11*). In an anterior semi-diagrammatic view (Fig. 2), the narrow, bandlike sternum of the anterior gonopods is visible, as well as the telopodite articles of the posterior gonopods. Hoffman (1961) showed that the narrow muscle (*rcl*) known as the remotor coxae longus, extending from the distal part of the tracheal apodeme (*ta*) to the base of the anterior gonopod, can be used to establish the homology between that portion and the coxa of a walking leg. Thus, the anterior gonopod is a coxotelopodite articulating directly with its sternum. In *Conotyla fischeri* (Fig. 3), a similar pattern is repeated, but the anterior branch of the anterior gonopod (*ag*) is usually not developed. This branch is typically plumose when present. *Conotyla blakei* (Fig. 4) is representative of a group of species with somewhat simpler gonopod construction. The anterior branch (*ab*) of the anterior gonopod is reduced to a poorly sclerotized plumose rod that is broken off in many specimens, and the posterior branch (*pb*) is a smooth continuation of the gonopod mass. There is no lateral shoulder. The colpocoxites (*c*) are likewise simpler in form (Fig. 17). The sterna are somewhat broader in this species than in the central Appalachian group. *Conotyla similax* (Fig. 5) is a slightly aberrant Appalachian form in which the anterior gonopods (*ag*) do not pass laterad of the colpocoxites (*c*), and bear no posterior branch. The colpocoxites (Fig. 31) are complex on the posterior surface, with a terminal process (*tp*), mesal tooth (*mt*), lateral notch (*ln*), and pilose area (*pa*).

Conotyla atrolineata (Fig. 6) differs from the eastern North American species of *Conotyla* in the simplification and reduction of the anterior gonopods, the broadening of the sternum of the posterior gonopods (*s*), and the much greater complexity of the colpocoxites (Figs. 48, 49, 50). This trend culminates in the related species, *C. albertana*, with an exceptionally broad posterior gonopod sternum (Fig. 7).

In *Taiyutyla corvallis* (Fig. 8), the anterior gonopod sternum (*s*) is heavily sclerotized and not bandlike, completely encircling the simple, platelike anterior gonopods (*ag*), which are larger than the colpocoxites (*c*).

In *Austrotyla coloradensis* (Fig. 9), the sternum of the anterior gonopods (*s*) may, in certain preparations, appear divided, though it is in reality a single piece encircling the gonopods and nearly meeting posteriorly. Lateral extensions of this sternum articulate with the lateral surface of the gonopod, which is simple and leaflike and larger than the colpocoxite. The colpocoxite (*c*) is usually cupped anteriad and may have two parts. The tracheal apodemes are reduced in size.

Plumatyla humerosa (Fig. 10) is a unique form somewhat intermediate between *Taiyutyla* and *Austrotyla*, but the lateral extensions of the solidly constructed sternum (*s*) are more firmly fused to the gonopod than they are in either of the preceding. The anterior gonopod (*ag*) is complex (Fig. 80), with two branches perhaps homologous to the two branches found in many *Conotyla* species. The colpocoxites (*c*) are remotely similar to those of *Austrotyla*.

Achemenides pectinatus (Fig. 11) differs in most respects from the other members of the family. The anterior gonopod sternum (*s*) is truly divided, and each sternite is doubled over longitudinally (Figs. 54, 55). The anterior gonopods (*ag*) are fused at the base, and are much larger than the colpocoxites (*c*), which are widely separated on a thin, bandlike sternum. The tracheal apodemes of the posterior gonopods are small and bifurcate.

PROBLEMATICAL NAMES IN THE CONOTYLIDAE

Due to the fact that the male genitalia are the only reliable specific characters in this family, names based on females and on immature specimens are extremely difficult to assign, particularly if more than one species of conotylid occurs in the region. In two cases, *Conotyla wyandotte* (Bollman) and *Conotyla jonesi* Chamberlin, I have made some attempt to place names attached to females or lost specimens in the proper synonymy.

Listed below are the problematical names, with brief discussions of their original proposals and histories.

Cookella leibergi (Cook and Collins)

Conotyla leibergi Cook and Collins, 1895, J. New York Acad. Sci., 9(1): 77, figs. 102–104.
Cookella leibergi, Chamberlin, 1941, Bull. Univ. Utah, Biol. Ser., 6(5): 13.

This species was originally described from a female (holotype in U. S. National Museum, examined), which was supposed to have a small, broadly triangular promentum. This mistaken original observation of Cook and Collins (1895) was used by Chamberlin (1941) as a pretext for erecting the completely unnecessary genus *Cookella*. The type locality, [the shore of] Lake Pend d'Oreille, Idaho, could be within the range of either *Conotyla atrolineata* or *C. albertana*, and *leibergi* would thus be treated either as a junior synonym of *atrolineata* or the correct name for *albertana*. Loomis (personal communication, 1968) has in preparation descriptions of new taxa from the Idaho-Montana area; *leibergi* males may conceivably be represented among them. As neither the generic or specific name can be properly dealt with in the absence of males, I consider *Cookella leibergi* a *nomen dubium*.

Trichopetalum glomeratum Harger

Trichopetalum glomeratum Harger, 1872, Amer. J. Sci. Arts, 4: 118.
Conotyla glomerata, Cook and Collins, 1895, J. New York Acad. Sci., 9(1): 78.

The holotype, from the John Day Valley, Oregon, has been lost, and as Cook and Collins (1895) stated, the original description is too vague to allow definite placement, though a certain similarity to *Taiyutyla* emerges. It is probably neither a *Trichopetalum* nor a *Conotyla*. I consider it a *nomen dubium*.

Bollmanella oregona Chamberlin

Bollmanella oregona Chamberlin, 1941, Bull. Univ. Utah, Biol. Ser., 6(5): 12.

The male holotype, from John Day Creek, Douglas Co., Oregon, is reputedly in the Chamberlin collection at the University of Utah, but it could not be located by the curator there. There is nothing diagnostic about the description of the genus or of the type and only species, which even contradict one another in the matter of a lobe on the fourth article of the fifth legs. No illustrations were presented. I consider it a *nomen dubium*.

Zygotyla phana Chamberlin

Zygotyla phana Chamberlin, 1951, Nat. Hist. Misc. No. 87: 7–8, fig. 14.

The holotype, from Blue River, British Columbia, Canada, is obviously immature, having only 28 segments and undeveloped gonopods ["The gonopods seem to have been broken off in the type (Chamberlin, 1951)."] Though the type was to have been placed in the Provincial Museum of British Columbia, they have never received it, and it could not be located in the Chamberlin collection at the University of Utah. Geographically, this species could possibly be a synonym of *C. atrolineata*, but it may also represent an undescribed species. *Nomen dubium*.

Conotyla jonesi Chamberlin

Conotyla jonesi Chamberlin, 1951, Nat. Hist. Misc. No. 87: 7, fig. 13.

The drawing given by Chamberlin (1951) for *C. jonesi* is very much like *Taiyutyla corvallis* when properly oriented; the type localities (type of *T. corvallis* from Corvallis, Oregon) are only about 25 miles apart and both are in the Willamette River valley. None of the characters given in the original description of *C. jonesi* are in the least diagnostic; they could apply to almost any conotyloid of the region. See Hoffman (1961) for a full discussion of Chamberlin's errors of observation in the description of *T. corvallis*. The type of *jonesi* was supposedly placed in the Provincial Museum of British Columbia, but they have no record of ever having received it, and it could not be located in Chamberlin's collection at Salt Lake City. At any rate, if specimens from the type locality of *jonesi* prove to be identical to *corvallis*, the name may have to be changed to *jonesi*, which has a year's priority. For the present, *jonesi* is best regarded as a *nomen dubium*.

KEY TO GENERA OF CONOTYLIDAE OF NORTH AMERICA

1a. Anterior gonopod sternum divided; anterior gonopods fused to each other at base, much larger than colpocoxites of posterior gonopods (Fig. 10); northern Illinois, northeastern Iowa, southwestern Wisconsin .... *Achemenides*

1b. Anterior gonopod sternum not divided (Figs. 1–9); anterior gonopods not fused to each other, though they may be closely appressed, smaller or larger than colpocoxites of posterior gonopods 2

2a. Anterior gonopods flattened, platelike, often appressed in the midline (Figs. 8, 9), larger than or subequal to colpocoxites of posterior gonopods 3

2b. Anterior gonopods never flattened, often with complex or plumose branches (Figs. 1, 32–34), smaller than or subequal to colpocoxites of posterior gonopods 4

3a. Anterior gonopod sternum with lateral processes partially fused to lateral sides of coxotelopodites (Fig. 69); coxotelopodites complex on posterior surface (Fig. 78); colpocoxites small, cupped anteriad; Illinois and Missouri, and Rocky Mountains from Alberta to Chihuahua .... *Austrotyla*

3b. Anterior gonopod sternum without such processes, heavily sclerotized, completely surrounding bases of coxotelopodites (Figs. 59, 61, 63); colpocoxites subequal to anterior gonopods, frequently complex and branched (Fig. 61), not cupped anteriad; Pacific Coast from central Oregon to San Francisco Bay region .... *Taiyutyla*

4a. Anterior gonopod sternum with lateral process partially fused to lateral edge of gonopod; gonopod two-branched, mesal edge of major branch heavily laciniate (Figs. 80, 81); colpocoxite two-branched; animals without pigment, ocelli irregular; caves in northern California .... *Plumatyla*

4b. Anterior gonopod sternum simple and bandlike (Figs. 1–7); gonopod with one or two small branches, usually not laciniated, colpocoxites with complex posterior surface (Fig. 52), but not two-branched; animals usually pigmented, ocelli round, black; eastern North America from Maine to North Carolina, Rocky Mts. of Alberta and British Columbia, Sierra Nevada Mts. of California .... *Conotyla*

Genus *Conotyla* Cook and Collins, 1895

Craspedosoma, Bollman (in part, not of Leach, 1815), 1893, U. S. Nat. Mus. Bull. No. 46, pp. 35, 183.

Trichopetalum, McNeill (in part, not of Harger, 1872), 1887, Proc. U. S. Nat. Mus., Vol. 10, p. 330; Bull. Brookville Soc., Vol. 3, p. 8.

Scoterpes, Bollman (in part, not of Cope, 1872), 1893, Bull. U. S. Nat. Mus. No. 46, p. 106.

Conotyla Cook and Collins, 1895, Ann. New York Acad. Sci., Vol. 9, No. 1, pp. 70–71. Hoffman, 1961, Trans. Amer. Ent. Soc., Vol. 87, p. 265.

Proconotyla Verhoeff, 1932, Zool. Jahrb. Abt. Syst., Vol. 62, p. 501. NEW SYNONYMY.

Type species of *Conotyla*, *Conotyla fischeri* Cook and Collins, of *Proconotyla*, *P. blakei* Verhoeff. The generic name is a feminine Greek noun, "a cone-shaped lump," and refers to the segmental shoulders.

Diagnosis. Anterior gonopod sternum simple and bandlike, not divided. Anterior gonopods variously branched or simple and acuminate, smaller than or subequal in size to colpocoxites of posterior gonopods. Anterior gonopods usually curved posteriad of colpocoxites. Colpocoxites of posterior gonopods large, complex to simple on posterior surface. Sternum of posterior gonopods bandlike or conspicuously broadened and ovate, spiracles large and prominent, tracheal apodemes fused to sterna. Progonopodal legs of males frequently with femoral knobs, appearing on all legs in one case, and on none in another extreme. Species usually pigmented; ocelli 14–23,

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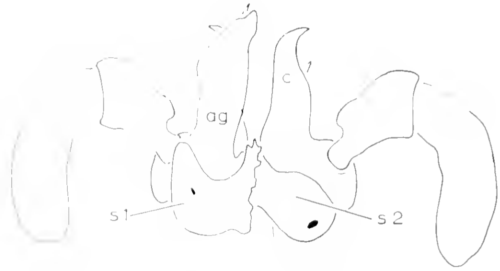

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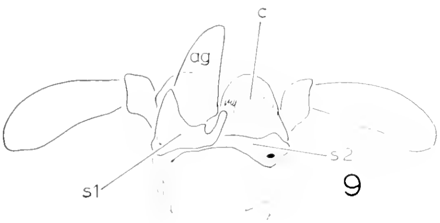

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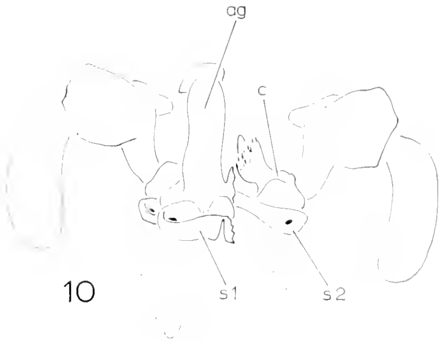

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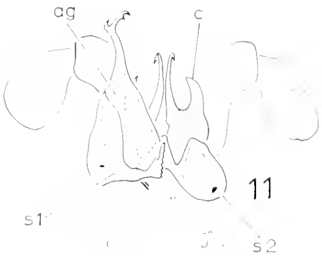

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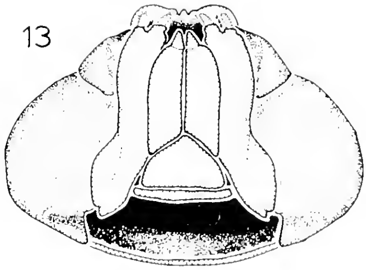

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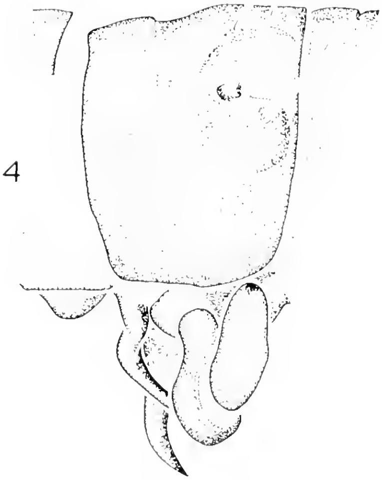

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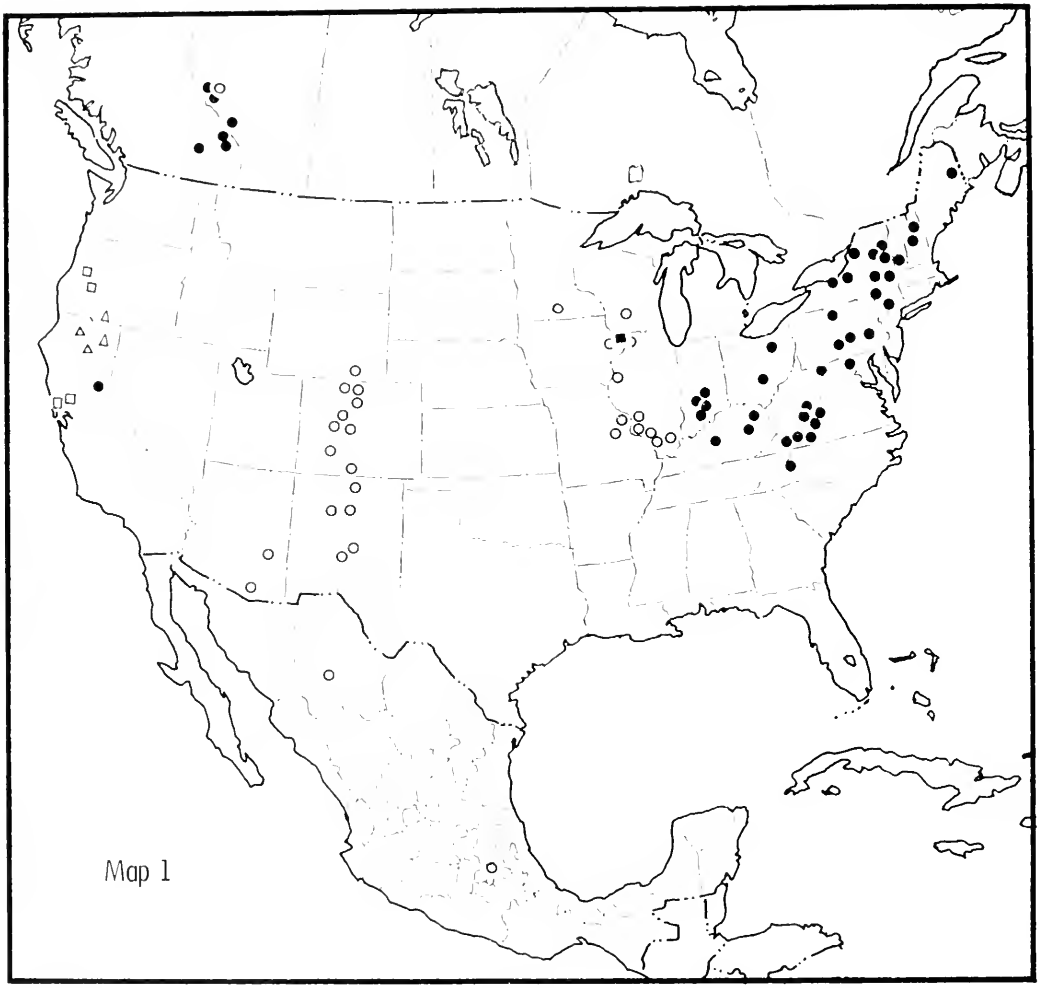
igures 7–14. Anatomy of conotylid male gonopods and of *Conotyla blakei.* Fig. 7. *Conotyla albertana* gonopods, anerior view. Fig. 8. *Taiyutyla corvallis* gonopods, anterior view. Fig. 9. *Austrotyla coloradensis* gonopods, anterior view. ig. 10. *Achemenides pectinatus* gonopods, anterior view. Fig. 11. *Plumatyla humerosa* gonopods, anterior view. Figs. 12–14. *Conotyla blakei.* Fig. 12. Leg 7, posterior view. Fig. 13. Gnathochilarium, ventral view. Fig. 14. Segment 7 of male, lateral view (anterior to the left).



Map 1. North America, showing distribution of conotylid genera (some records of immature specimens included); dots, *Conotyla* spp.; circles, *Austrotyla* spp.; triangles, *Plumatyla* spp.; solid square, *Achemenides pectinatus;* open squares, *Taiyutyla* spp.

usually round, black, arranged in triangular eyepatch in four or five rows. Coxae of tenth legs with large coxal glands, not lobed; coxae of eleventh legs normal; prefemur of eleventh legs with prominent posterior hooks.

Species. Fifteen known.

Distribution. See Map 1. Eastern North America from Maine through Vermont, New Hampshire and New York to Ohio and Indiana in the west and to North Carolina in the east; center of diversity is apparently in eastern West Virginia and southwestern Virginia; Rocky Mountains of the Alberta-British Columbia border; Sierra Nevada Mts. of California.

KEY TO SPECIES (MALES)

1a. Pregonopodal legs only slightly more crassate than postgonopodal legs, without knobs; Nevada Co., California ...... *extorris*

1b. Pregonopodal legs strongly crassate (Fig.

12), at least leg 4 or 7 with a femoral knob 2
2a. Leg 4 with a femoral knob 3
2b. Leg 4 without a femoral knob, leg 7 with strong femoral knob (Fig. 12); Vermont, New York, Pennsylvania, Maryland, and West Virginia, often in caves .... *blakei*
3a. Leg 7 without a femoral knob 4
3b. Leg 7 with a strong femoral knob 6
4a. Legs 2 and 3 with femoral knobs; Virginia .... *celeno*
4b. Legs 2 and 3 without femoral knobs 5
5a. Leg 5 without a femoral knob; Indiana .... *bollmani*
5b. Leg 5 with a femoral knob; Virginia .... *venetia*
6a. Leg 6 without a femoral knob; British Columbia .... *atrolineata*
6b. Leg 6 with a femoral knob 7
7a. Leg 2 with a femoral knob 8
7b. Leg 2 without a femoral knob 9
8a. Leg 1 with a femoral knob; West Virginia .... *vista*
8b. Leg 1 without a femoral knob; Virginia .... *melinda*
9a. Leg 3 with a strong femoral knob 10
9b. Leg 3 with a weak femoral knob, or lacking a knob 11
10a. Posterior surface of colpocoxite (Fig. 52) with several branches; Alberta .... *albertana*
10b. Posterior surface of colpocoxite (Fig. 29) with a single plumose branch; Kentucky .... *elpenor*
11a. Leg 3 with a weak femoral knob 12
11b. Leg 3 without a femoral knob 13
12a. Colpocoxite (Fig. 38) with an attenuate apical hook; Virginia .... *acto*
12b. Colpocoxite (Fig. 31) blunt apically; West Virginia .... *smilax*
13a. Femoral knob of leg 4 weakly developed; Ohio .... *personata*
13b. Femoral knob of leg 4 strong 14
14a. Colpocoxite (Fig. 36) with an attenuate distal process; Ohio .... *ocypetes*
14b. Colpocoxite (Fig. 25) apically blunt; New York .... *fischeri*

The following arrangement into species groups is not wholly a natural one, but serves the purpose of making the task of writing abbreviated species diagnoses easier. The arrangement is based primarily on the form of the anterior gonopods.

THE *BLAKEI* GROUP

This group is characterized by simple, usually acuminate anterior gonopods in which the anterior branch is reduced to a poorly sclerotized plumose rod (Figs. 4, 19, 22). *Conotyla blakei* and *C. bollmani* are clearly related, but the resemblance of *C. extorris* to these species is probably a result of parallelism.

Conotyla blakei (Verhoeff)
Figures 12–18

Proconotyla blakei Verhoeff, 1932, Zool. Jahrb. Abt. Syst., Vol. 62, p. 501, figs. 33–37. Hoffman and Chamberlin, 1958, U. S. Nat. Mus. Bull. 212, p. 101. Hoffman, 1961, Trans. Amer. Ent. Soc., Vol. 87, p. 271.

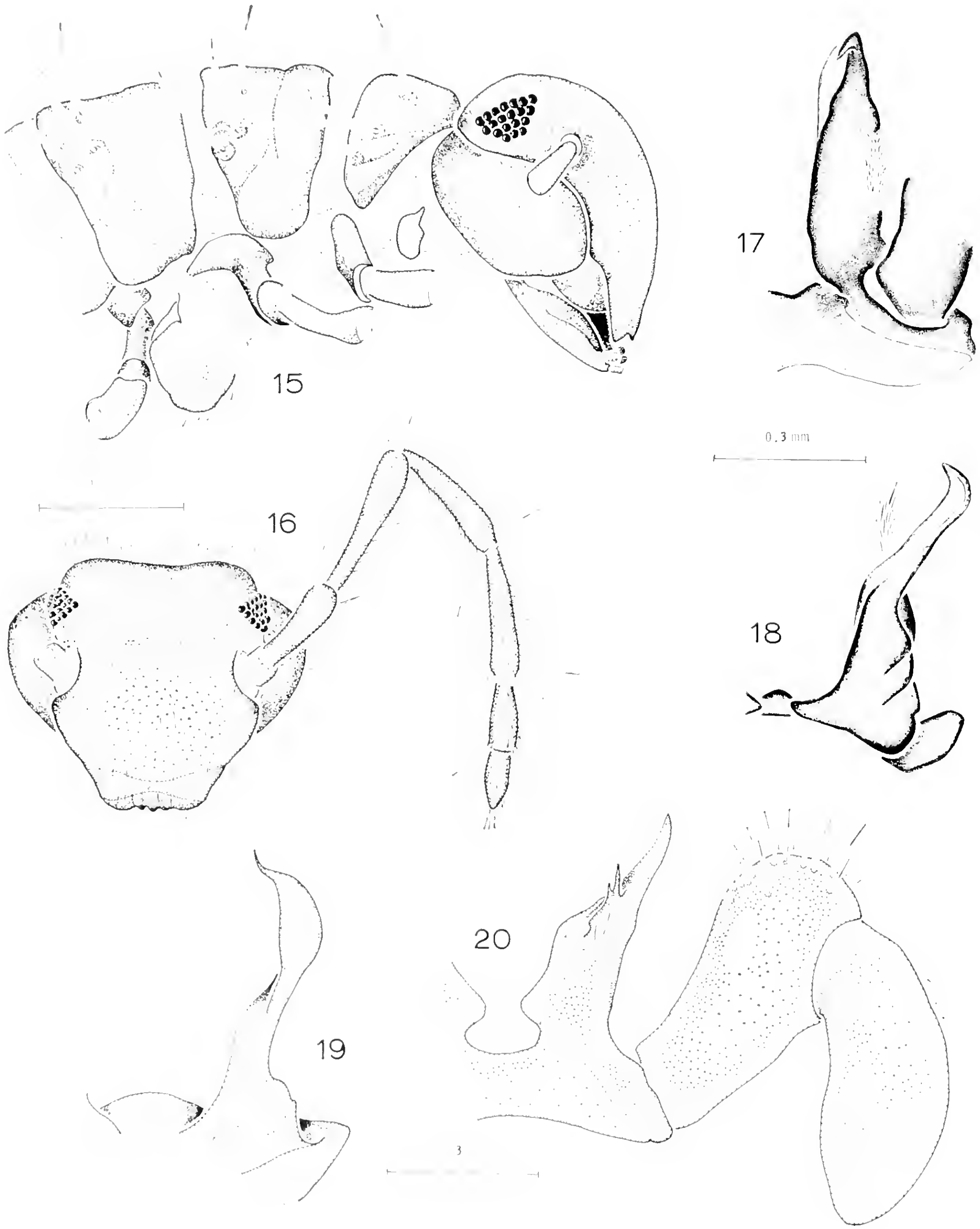
Conotyla vaga Loomis, 1939, Bull. Mus. Comp. Zool., Vol. 86, pp. 182–183, fig. 10. Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull. 212, p. 99. NEW SYNONYMY.

Types. Male holotype of *P. blakei*, Mt. Adams, Essex Co., N. Y., whereabouts unknown; of *C. vaga*, South Temple Cave, Berks Co., Pennsylvania; in the M. C. Z., examined.

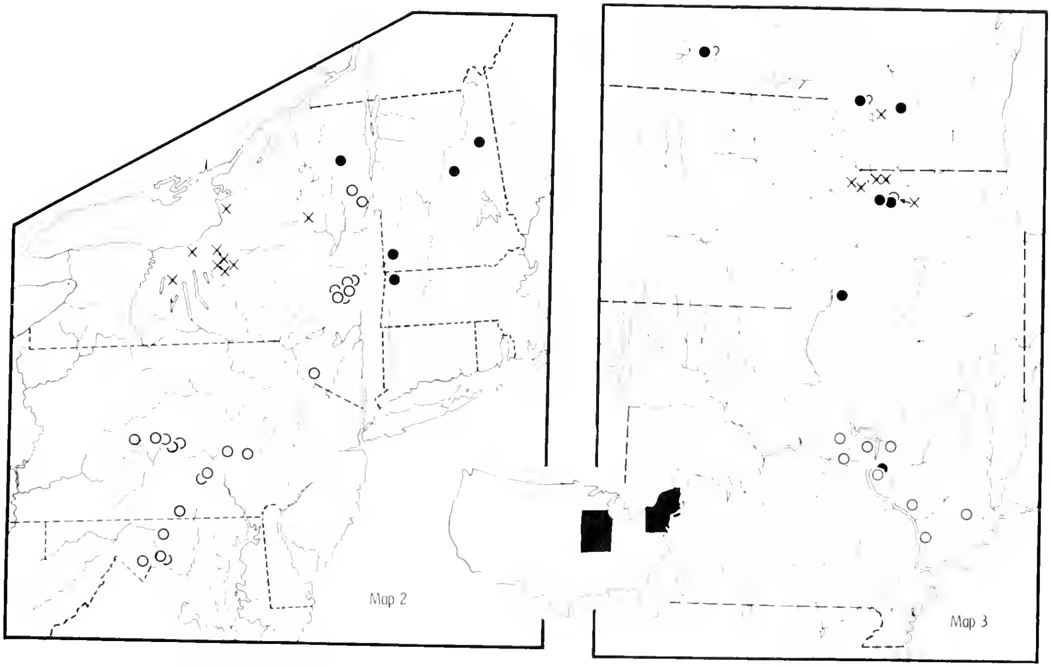
Diagnosis. Distinct from other species of the *blakei* group in having an apophysis on leg 7 (Fig. 12); *bollmani* has an apophysis only on leg 4, and *extorris*, besides occurring in California, has no pregonopodal leg modifications at all.

Description of male from Mt. Equinox, Bennington Co., Vermont. Length, 18.0 mm. Eyepatches (Figs. 15, 16) triangular, 18 ocelli in 4 rows on both sides. Antennal articles (Fig. 16) in order of length: 3, 5, 4, 2 = 6, 7, 1. Leg 7 (Fig. 12) with large, capitate, proximal apophysis on femur, pregonopodal legs otherwise unmodified. Anterior gonopods (Fig. 18) prolonged directly into posterior branch, anterior branch single, inconspicuous plumose rod; posterior branch narrowing at tip, curving around lateral side of colpocoxites of posterior gonopods. Colpocoxites of posterior gonopods (Fig. 17) acuminate, drawn out smoothly into decurved terminal process; just below origin of terminal process is a mesal transparent plate; pilose area limited to lateral surface, without branches; mesal tooth and lateral notch not present.

Remarks. This species is widely distributed (Map 2). It has been collected



Figures 15–20. Anatomy of *Conotyla blakei* and gonopods of *Conotyla* spp. Figs. 15–18. *Conotyla blakei*. Fig. 15. Head and anterior trunk segments of female, lateral view. Fig. 16. Head of female, anterior view. Fig. 17. Colpocoxite of left posterior gonopod, posterior view. Fig. 18. Left anterior gonopod of male, posterior view. Figs. 19–20. *C. bollmani*. Fig. 19. Left anterior gonopod of male, posterior view. Fig. 20. Left posterior gonopod, posterior view.



Map 2. Part of northeastern United States, showing distribution of some *Conotyla* spp.; dots, epigean records of *C. blakei*; circles, cave records of *C. blakei*; crosses, records of *C. fischeri*. Question mark indicates a dubious identification.

Map 3. Part of central United States, showing distribution of *Austrotyla* and *Achemenides*; dots, epigean records of *Austrotyla specus*; circles, cave records of *A. specus*; crosses, records of *Achemenides pectinatus* (all cave records). Question mark indicates a dubious identification.

in the Adirondack counties of New York in Canadian Zone Forests and in caves; in caves in Sullivan, Orange, and Schoharie counties, and in numerous caves in central Pennsylvania and Maryland, and a single case in Jefferson Co., West Virginia. I have personally collected *blakei* in a scrubby fir forest at 3800 feet on the summit of Big Equinox Mountain, Bennington Co., Vermont, where it was abundant under the bark of both standing and fallen dead trees. The distribution of *blakei* follows exposures of limestone and marble up to the Adirondacks, where it is also found on other substrates. This distributional pattern seems to clearly indicate that *blakei* followed the boreal forests north with the retreat of the Wisconsin ice at the end of the Pleistocene, leaving behind relict populations in suitable habitats, such as limestone caves.

The cave populations described by Loomis (1939) as *vaga* differ hardly at all from the typical form of *blakei*, except that the pigmentation is much weaker in some specimens and the arrangement and size of the ocelli is somewhat irregular.

Conotyla bollmani (McNeill)

Figures 19, 20

Trichopetalum bollmani McNeill, 1887, Proc. U. S. Nat. Mus., Vol 10, p. 330.

Scotherpes wyandotte Bollman, 1889, Proc. U. S. Nat. Mus., Vol. 11, p. 405. Misspelling of *Scoterpes wyandotte*. NEW SYNONYMY.

Conotyla bollmani, Cook and Collins, 1895, Ann. New York Acad. Sci., Vol. 9, p. 76, figs. 79–94. Loomis, 1943, Bull. Mus. Comp. Zool., Vol. 92, p. 381 (key). Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull. 212, p. 98 (list).

Conotyla wyandotte, Cook and Collins, 1895, Ann. New York Acad. Sci., Vol. 9, p. 78, fig. 101; Chamberlin and Hoffman, 1958, U. S. Nat.

Mus. Bull. 212, p. 100 (list). NEW SYNONYMY.

Types. Male types of *T. bollmani* from Mayfield's Cave, Bloomington, Monroe Co., Indiana; type in U. S. National Museum (?); of *C. wyandotte*, near Wyandotte cave, Crawford Co., Ind.; type in U. S. National Museum.

Diagnosis. Differs from the other species of the *blakei* group in having an apophysis on the fourth article of the fourth leg; *blakei* and *extorris* both lack such an apophysis.

Description of male from Boone Cave, Owen Co., Indiana. Length, 14.0 mm. Ocelli 22 in four rows plus single ocellus on the right side, 20 ocelli in four rows on left side. Antennal articles in order of length, 3, 4, 5, 2, 6, 7, 1. Body white, ocelli somewhat irregular in shape and arrangement. Leg 4 with large capitate apophysis on femur. Anterior gonopods (Fig. 19) simple, acuminate to tip of posterior branch, anterior branch a simple, inconspicuous plumose rod; lateral shoulder low, rugose. Anterior gonopods passing around lateral side of colpocoxites of posterior gonopods *in situ*. Colpocoxites of posterior gonopods (Fig. 20) bluntly pointed, without definite terminal process; mesal tooth bifid; pilose area small, restricted to part of posterior surface.

Notes. Known primarily from caves and a few surface records in south-central Indiana. Surface specimens are normally pigmented, while cave populations are usually white and have rather irregular ocelli. The identity of immature and female specimens from adjacent regions of Kentucky is unclear. Map 7 shows the boundaries of the supposed glacial maxima of Wisconsin and of Illinois time (from Wayne and Zumberge, 1965), but since the availability of a suitable substrate also affects the distribution of cave animals, and surface records are scarce, I would rather not speculate on the possible history of this species.

Conotyla extorris n. sp.

Figures 22, 23

Type. Male holotype from 1 mile south of Grass Valley, Nevada Co., California, collected January 5, 1968, by D. E. Bragg and R. F. Denno. The specific epithet is a Latin adjective meaning "banished, exiled," and refers to the distance separating this species from the others of its genus.

Diagnosis. Distinct from others of the *blakei* group in having no modifications at all on the pregonopodal legs, which are of normal size and lacking apophyses. The gonopods (Figs. 22, 23) are only about a third the size of those of *bollmani* and *blakei*.

Description of holotype male. Length, 12.6 mm, the smallest known species of *Conotyla*. Eyepatches triangular, 20 ocelli in four rows on the right side, 19 ocelli in four rows on the left side. Antennal joints in order of length: 3, 5, 4, 6, 2, 7, 1. Pregonopodal legs unmodified. Anterior gonopods (Fig. 22) with posterior branch large, broadened near the tip and recurved, passing laterad of the colpocoxites of the posterior gonopods; anterior branch a single, inconspicuous plumose rod. Colpocoxites of the posterior gonopods (Fig. 23) with terminal process sharply curved dorsad and slightly laterad; mesal tooth (?) a long rod reaching to the tip of the colpocoxite; lateral notch and pilose area absent.

→

Figures 21–29. Male gonopods of *Conotyla* spp. Fig. 21. *Conotyla bollmani,* left anterior gonopod, lateral view. Figs. 22–23. *C. extorris.* Fig. 22. Right gonopods, anterior view. Fig. 23. Right gonopods, posterior view. Figs. 24–25. *C. fischeri.* Fig. 24. Left anterior gonopod, posterior view. Fig. 25. Left posterior gonopod colpocoxite, posterior view. Figs. 26–27. *C. personata.* Fig. 26. Left anterior gonopod, posterior view. Figs. 28–29. *C. elpenor.* Fig. 28. Left anterior gonopod, posterior view. Fig. 29. Colpocoxite of left posterior gonopod, posterior view.

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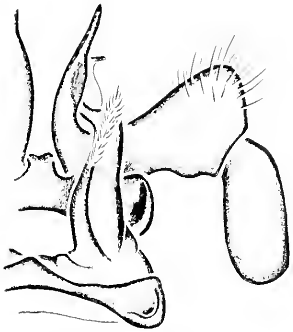

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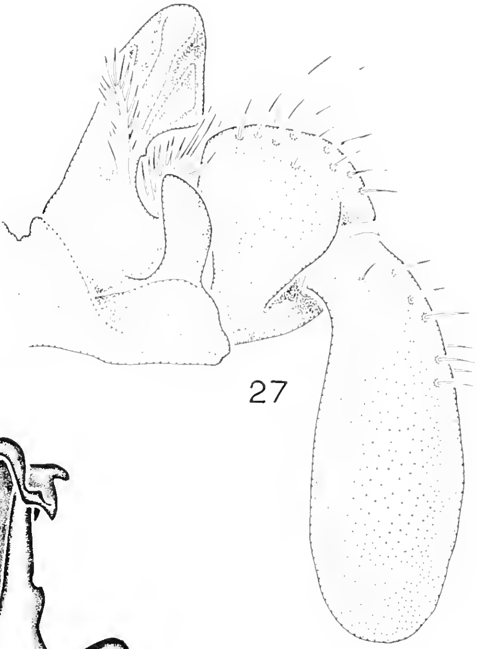

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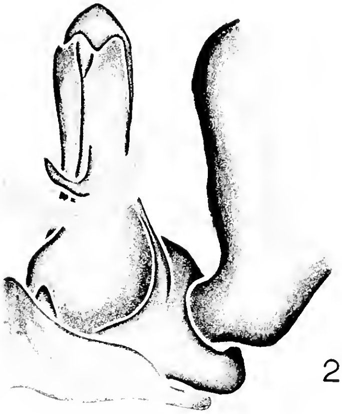

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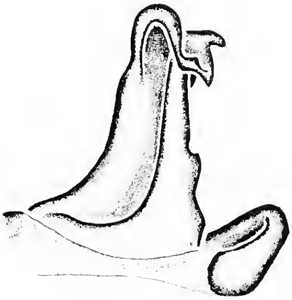

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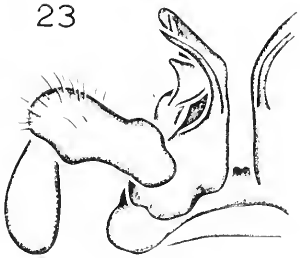

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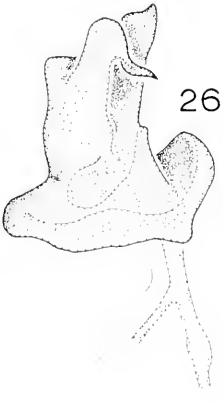

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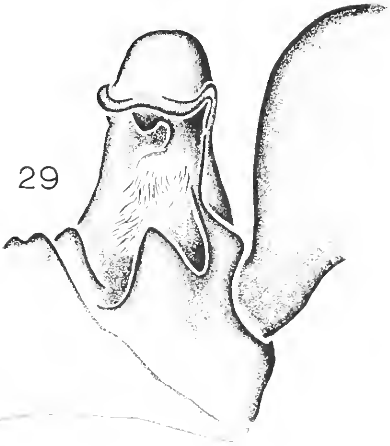

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Notes. The type locality (Map 6) is near the Boyce Thompson Institute of Forest Studies, at about 2400 ft. elevation. The area is forested primarily with pine, *Arctostaphylos*, and oaks. Michael Gardner (personal communication) has recorded the millipeds *Brachycybe producta*, *Wamokia sierra*, *Buzonium crassipes*, and *Placerna dorada*, among others, from Grass Valley.

The assignment of this species to *Conotyla* may prove to be controversial. It has many of the characters of *Taiyutyla*, a genus geographically closer. However, the form of the gonopods and especially the anterior gonopod sternum favor the present placement. If more new species with a similar combination of characters are collected, a new genus may be justified.

THE *FISCHERI* GROUP

This is a compact, closely related group of three species from New York, Ohio, and Kentucky, characterized by the reduction of the anterior branch of the anterior gonopods, and by their similar colpocoxites.

Conotyla fischeri Cook and Collins
Figures 3, 24, 25

Conotyla fischeri Cook and Collins, 1895, Ann. New York Acad. Sci., Vol. 9, pp. 71–74, figs. 55–78. Loomis, 1943, Bull. Mus. Comp. Zool., Vol. 92, p. 382 (key). Hoffman, 1961, Trans. Amer. Ent. Soc., Vol. 82, pp. 265–266, fig. 7. Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull. 212, pp. 98–99 (list).

Types. None designated by original authors; type locality restricted by Chamberlin and Hoffman (1958) to Syracuse, Onondaga Co., New York.

Diagnosis. Distinct in the form of the gonopods from all other species except the closely related *personata;* differing from *personata* in the gonopods as described under that species, and also in having a much more pronounced apophysis on the femur of leg 4.

Description of male from Skaneateles, Onondaga Co., New York. Length, 19.4 mm. Eyepatches triangular, 20 ocelli in four rows on left side, 21 ocelli in four rows on right side. Antennal segments in order of length: 3, 4 = 5, 2, 6, 7, 1. Pregonopodal legs somewhat less enlarged than usual, legs 4–7 usually with apophyses on femur; distal on leg 4, mesal on legs 5 and 6; large, proximal and toothed, if present, on leg 7, but not resting on anterior gonopod *in situ.* Anterior gonopods (Fig. 24) short, subquadrate, posterior branch absent, anterior branch short, not curving around colpocoxites of posterior gonopods; lateral shoulder poorly developed. Colpocoxites of posterior gonopods (Fig. 25) without a terminal process, but with a prominent ridge on the posterior surface, bearing near its proximal end a long, rather flattened rod; lateral notch absent; pilose area with one or two pilose branches.

Notes. Cook and Collins (1895) had over 100 specimens from Onondaga, Ontario, and Wayne counties, New York (Map 2). They were collected primarily from rotting litter in woods, and under the moist, rotting bark of fallen trees. Hoffman (1961) reported the species from Hamilton Co., 2 miles west of Morehouseville, but gave no additional ecological data. His material, which I re-examined for this study, differs from the Cook and Collins series and from other Onondaga Co. specimens in having the apophysis of the seventh legs very small, or absent; the other apophyses are normally developed. The species is evidently limited to the rolling hills south and east of Lake Ontario (Map 2), but extension of its range into areas bordering on Lake Erie would be most interesting, as it might indicate the exact nature of this species' relationship to *personata*, which occurs in similar terrain just south of Lake Erie in Ohio. Several intriguing immature specimens from Ontario, northern New York, and from Potter Co., Pennsylvania, this latter locality near the southern limit of Pleistocene glaciation, may belong to this species.

Conotyla personata n. sp.
Figures 26, 27

Type. Holotype male collected by A. A. Weaver, May 5, 1960, Funk's Hollow, Wooster, Wayne Co., Ohio. The specific epithet is a Latin adjective, meaning "masked, hidden," and refers to my original confusion between this species and *fischeri.*

Diagnosis. Very similar to *fischeri*, but distinct in details of the gonopods. The lateral shoulder of the anterior gonopod is much higher (Fig. 26) than in *fischeri*, and the posterior branch is longer and more pronounced; the lateral notch of the colpocoxite is almost obsolete in *fischeri;* in *personata* it is the deepest and broadest of any species in the genus.

Description of male holotype. Length, 14 mm. Ocelli in four irregular rows on each side, 21 on right side and 23 on left side. Antennal segments in order of length: 3, 4, 5, 6 = 2, 7, 1. Fourth joints of legs 4, 5, and 6 with small, distal knob; fourth joint of leg 7 with long, apically toothed proximal process that *in situ* rests on the lateral shoulder of anterior gonopod. Sternum of anterior gonopods as described for genus, but lateral edge not visible in posterior view. Anterior gonopods (Fig. 26) short, subrectangular in posterior view; lateral shoulder prominent; anterior branch absent, posterior branch curved dorsad slightly. Colpocoxite of posterior gonopod (Fig. 27) bluntly subtriangular, all processes and teeth undeveloped; pilose area extended into at least one pilose branch; lateral notch deep, extending nearly halfway up colpocoxite.

Notes. The male holotype was taken in a deep, heavily wooded, mesic ravine surrounded by rolling cultivated land. The north-facing slope of the ravine supports a heavy mixed forest with much hemlock; the south-facing slope is forested with oak and pine. A study of the humus fauna of these slopes produced several immature and female *Conotyla* in early fall. This species is possibly widespread in northern and central Ohio, but the only males are from the type locality, and nearby.

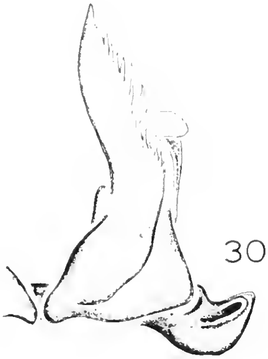
Conotyla elpenor n. sp.
Figures 28, 29

Type. Male holotype collected with another male and two females on 26 February 1966 by Branley A. Branson, nine miles northwest of Pine Ridge, elevation 800 ft. (250 m), Wolfe County, Kentucky. The specific epithet refers to one of the companions of Odysseus, changed into a swine by Circe's witchcraft.

Diagnosis. With the characters of the *fischeri* group; distinct in the form of the anterior gonopods, with two well-defined branches (Fig. 28), and in the colpocoxites of the posterior gonopods having an exceptionally deep lateral notch and coxal pocket.

Description of holotype male. Length, 18 mm. Eyepatches subtriangular, 20 ocelli in four rows on each side. Antennal articles in order of length: 3, 4 = 5, 6, 2, 7, 1. Pregonopodal legs 3 through 7 with apophyses on femur; apophysis of leg 3 small, distal; of legs 4 and 5 mesodistal, larger; of leg 6, proximal and blunt, of leg 7 proximal and greatly elongated, coarsely toothed distally, resting *in situ* posterior of lateral shoulder of anterior gonopod. Anterior gonopod (Fig. 28) with lateral shoulder, large, lamellate; two branches of gonopod may represent a bifurcation of the posterior branch, *in situ* they extend laterally around colpocoxites of posterior gonopods. Colpocoxites of posterior gonopods (Fig. 29) closely resembling those of *personata;* but somewhat longer, bent sharply posteriad, blunt; lateral notch deep, pilose area with two indistinct branches.

Notes. The holotype and the other known specimens were taken from beneath a rotting log in mixed hardwood forest. Though the specimens were labelled as being from Wolfe Co., the distance north-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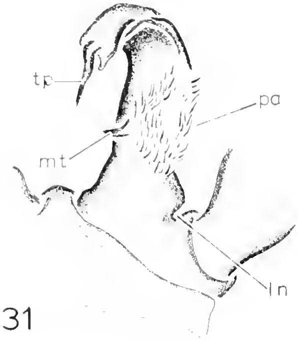

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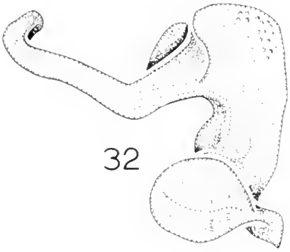
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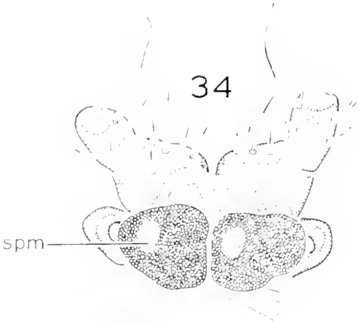

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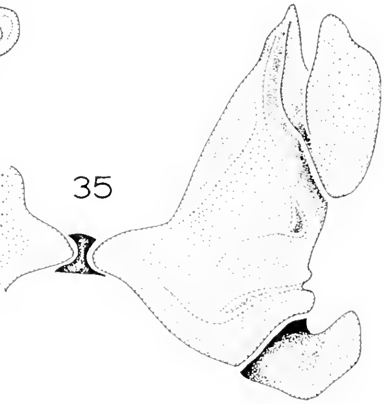
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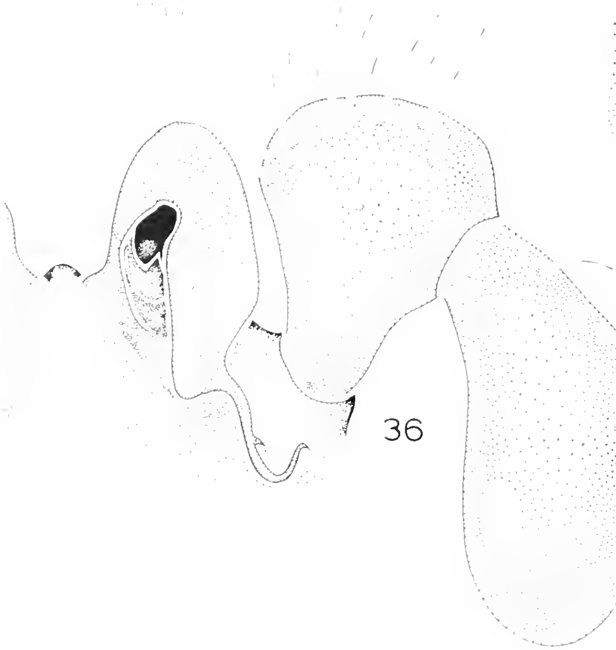
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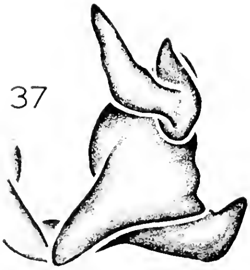
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west of Pine Ridge indicated on the label would place the locality in Powell Co. This species is known only from the type locality. A female from Carter Co., Kentucky (MCZ), may belong to *elpenor* (Map 5).

THE *SMILAX* GROUP

The single species of this group, *C. smilax*, is unique in several ways, but may be related to the preceding group.

Conotyla smilax n. sp.
Figures 30, 31

Type. Holotype male collected ca. elev. 3000 ft. (1000 m), Kate's Mt., above White Sulphur Springs, Greenbriar Co., West Virginia, April 1, 1967, by W. A. Shear. The specific epithet is a Latin noun in apposition and refers to *Smilax*, the greenbriar, abundant at the type locality.

Diagnosis. Distinct from all other related species of *Conotyla* in lacking the posterior branch of the anterior gonopods (Fig. 30). The anterior branch is well developed and had a deeply laciniated membrane running the length of its posterolateral edge.

Description of male holotype. Length, 13.3 mm. Ocelli in four rows on each side, 20 ocelli in each eyepatch. Legs 3 through 7 enlarged and crassate, knob present on femur of legs 3 through 7. Antennal articles in order of length: 3, 4 = 5, 6 = 2, 7, 1. Sternum of anterior gonopods as described for genus. Anterior gonopods (Fig. 30) with conspicuous lateral shoulder, but knob of fourth segment of leg 7 does not rest on shoulder when gonopod is *in situ;* posterior branch absent, anterior branch large, thin, nearly half as long as remainder of coxotelopodite, extending straight ventrad, with a deeply laciniated membrane on posterolateral surface. Colpocoxites of posterior gonopods with terminal process long, aciculate; mesal tooth inconspicuous, pilose area with definite branches, extensive (Fig. 31).

Notes. The male holotype, the only known specimen, was collected after a light rain, crawling about on dead twigs under a *Rhododendron.* The type locality (Map 5) is an unusual area, dissected into adjacent areas of very mesic forest of mixed hardwoods and hemlock and "shale barrens," with a hot, dry microclimate and sparse vegetation of scrub oak and Virginia pine. *Apheloria trimaculata* and *Cleidogona major* were taken in abundance.

THE *VENETIA* GROUP

These species have similar anterior gonopods in which the anterior branch is absent and the posterior branch long, giving a right-angled appearance to the gonopod (Fig. 33).

Conotyla venetia Hoffman
Figures 32–34

Conotyla venetia Hoffman, 1961, Trans. Amer. Ent. Soc., Vol. 87, p. 267, Pl. IX, figs. 1–3.

Type. Male holotype from three miles north of Clifton Forge, Alleghany Co., Virginia; type in U. S. National Museum, examined.

Diagnosis. Distinct from all other species of *Conotyla* in bearing apophyses on the fourth article of legs 4 and 5 only; distinct in details of the gonopods from others of the *venetia* group.

Description of male from Warm Spring Mt., Alleghany Co., Virginia. Length, 14.5 mm. Ocelli 20 on each side, in four rows. Antennal segments in order of length: 3, 4, 5, 2, 6, 7, 1. Legs 4 and 5 with small

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Figures 30–37. Male gonopods of *Conotyla* spp. Figs. 30–31. *Conotyla smilax.* Fig. 30. Left anterior gonopod, posterior view. Fig. 31. Left posterior gonopod, posterior view. Figs. 32–34. *C. venetia.* Fig. 32. Left anterior gonopod, lateral view. Fig. 33. Colpocoxite of left posterior gonopod, posterior view. Fig. 34. Coxae of 10th legs of male, ventral view. Figs. 35–36. *C. ocypetes.* Fig. 35. Left anterior gonopod, posterior view. Fig. 36. Left posterior gonopod, posterior view. Fig. 37. *C. aeto,* left anterior gonopod, posterior view.

apophyses on femora, distal in position. Anterior gonopods (Figs. 32, 33) with posterior branch extending at right angle posteriad from telopodite, anterior branch absent; lateral shoulder well developed, heavily rugose on lateral surface; posterior branch extending *in situ* well around lateral surface of colpocoxite of posterior gonopod. Colpocoxite of posterior gonopod (Fig. 34) subrectangular in outline; terminal process definitely set off by prominent shoulders at its base; mesal tooth reduced to small knob; pilose area lateral; lateral notch present, but small.

Notes. This species is known only from two localities in Alleghany Co., Virginia (Map 5), separated by nearly 3000 ft. (1000 m) of altitude (400–3400 ft.). Hoffman (1961) implies that the species may be widespread in central western Virginia.

Conotyla ocypetes n. sp.
Figures 35, 36

Type. Male holotype from Sugar Grove, Fairfield Co., Ohio, collected by J. H. Emerton, December 26, 1915. The specific epithet is a noun in apposition, the Greek name of one of the three Harpies of mythology.

Diagnosis. Distinct from others of the *venetia* group in details of the gonopods and in the apophyses of the pregonopodal legs; from *aeto* in having a strong apophysis on the third joint of leg 2 and none on leg 3, and from *venetia* by having apophyses on legs 6 and 7.

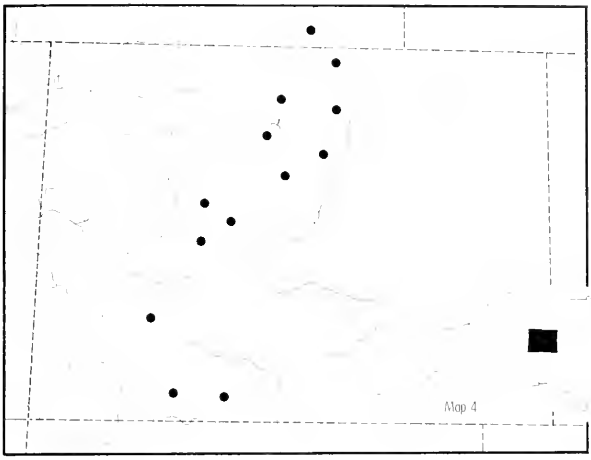
Description of holotype male. Length, 20.0 mm. Eyepatch of right side triangular-truncate, 20 ocelli in four rows; eyepatch of left side probably anomalous, five large ocelli in two rows. Antennae missing. Leg 2 with strong distal apophysis on third joint; legs 4 through 6 with apophyses on femora becoming smaller and mesal; leg 7 with small proximal apophysis on femur that does not touch anterior gonopod *in situ*. Anterior gonopod (Fig. 35) typical of *venetia* group, anterior branch absent, posterior branch large, becoming spatulate distally, curving around lateral side of colpocoxites of posterior gonopods; lateral shoulder not at all developed, instead gonopod is highly ridged mesally. Colpocoxites of posterior gonopods (Fig. 36) unusually long, but arched dorsad; terminal process very long and irregularly sinuate, with a small triangular tooth about half its length from the origin; mesal tooth present; lateral notch absent; pilose area small, limited to lateral margin.

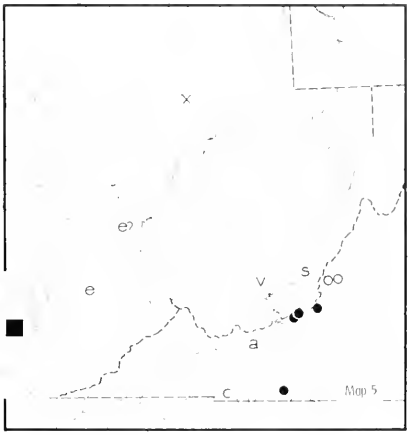
Notes. The male holotype was collected with a female and an immature specimen; probably all are of the same species. The southern section of Fairfield County (Map 5) is in the valley of the Hocking River, a region of low hills highly dissected into deep gorges with abrupt sandstone walls. Most of these gorges are very moist; the vegetation is mostly hemlock and beech. Emerton unfortunately failed to indicate exactly where the type specimen was obtained, but it seems likely that such a gorge as the ones described above would provide the most favorable habitat. However, several years of extensive collecting in the Hocking area by Dr. A. A. Weaver and others has resulted in the collection of no conotylids.

Conotyla aeto n. sp.
Figures 37, 38

Type. Male holotype from top of Clinch Mt., ca. 4500 ft. (1500 m), Burke's Garden, Tazewell Co., Virginia, collected November 14, 1965, by Radford College Biology Club. The specific epithet, like *celeno* and *ocypetes*, is a Greek noun in apposition, the name of one of the Harpies of mythology.

Diagnosis. Distinct from other species of the *venetia* group in the modifications of the pregonopodal legs and in details of the gonopods; from *venetia* in having apophyses on legs 6 and 7, and from *ocypetes* in having a slight apophysis on leg 3 and none on leg 2.





Map 4. Colorado, dots showing distribution of *Austrotyla coloradensis*.
Map 5. North central Appalachian region and part of Ohio, showing distribution of *Conotyla* spp.; dots, *C. melinda*; circles, *C. venetia*; cross, *C. ocypetes*; o, *C. aeto*; c, *C. celeno*; e, *C. elpenor*; v, *C. vista*; s, *C. smilax*. Question mark indicates a dubious identification.

Description of holotype male. Length, 15 mm. Eyepatch triangular, 21 ocelli in four rows and single ocellus on right side; 20 ocelli with same arrangement on left side. Antennal articles in order of length: 3, 4, 5, 2 = 6, 7, 1. Legs 3 through 7 with apophyses on femora, that of leg 3 small, becoming stronger to leg 6, all distal in position; apophysis of leg 7 proximal in position, capitate and toothed, but not resting on shoulder of anterior gonopod *in situ*. Prefemoral hooks of leg 11 particularly large. Anterior gonopods (Fig. 37) typical of *venetia* group, anterior branch absent, posterior branch large, broadened towards tip, extending well around lateral side of colpocoxites of posterior gonopods in undissected animal; lateral shoulder poorly developed. Colpocoxites of posterior gonopods (Fig. 38) distinct; terminal process flattened dorsoventrally, hooked dorsad; subterminal process expanded laterad into a large plate that in natural position covers apical end of posterior branch of anterior gonopod and is heavily ridged on posterior side, the distal ends of the ridges drawn out into prominent teeth (Fig. 38); mesal tooth absent; pilose area with single pilose branch; lateral notch absent.

Notes. The northeastern part of Clinch Mountain, which extends from southwest to northeast across western Virginia, forms the southern and western wall of Burke's Garden, an unusual semicircular anticlinal valley, the floor of which is at nearly 3000 ft. (1000 m) elevation, surrounded by mountains up to 4800 ft. (1600 m), with their tops in well-developed Canadian Zone forests.

THE *MELINDA* GROUP

Both branches of the anterior gonopod are nearly equal in this group. The posterior branch is distally plumose, but strong and heavy.

Conotyla melinda Hoffman
Figures 1, 2, 39, 40

Conotyla melinda Hoffman, 1961, Trans. Amer. Ent. Soc., Vol. 87, p. 266, Pl. IX, figs. 4–6.

Type. Male holotype from Brush Mt., 2 miles west of Blacksburg, Montgomery Co., Virginia; type in U. S. National Museum, examined.

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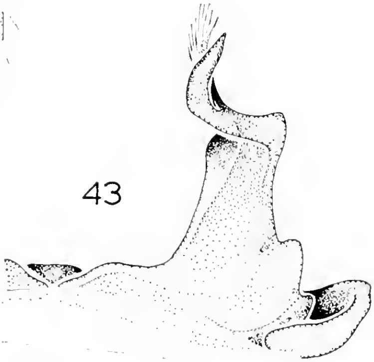

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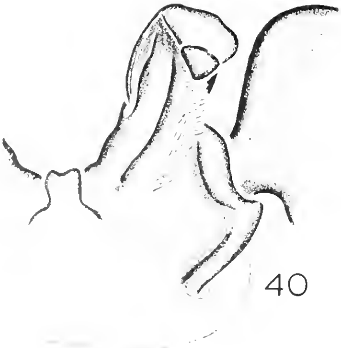

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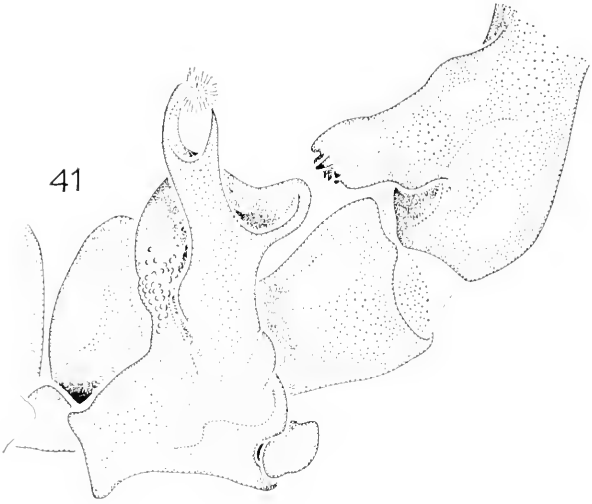

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Diagnosis. Distinct from others of the *melinda* group in details of the gonopods and the distribution of apophyses on the pregonopodal legs; *vista* has apophyses on all the pregonopodal legs, *celeno* lacks them on leg 6.

Description of male from type locality. Length, 18.5 mm. Ocelli 20 in triangular eyepatch of four rows on right side, 19 ocelli in four rows on left side. Antennal articles in order of length: 3, 5, 4, 2, 6, 7, 1. Leg 2 with large apophysis on third joint; legs 3 through 6 with similar apophyses on femora, largest on legs 4 and 5, distal in position. Anterior gonopods (Fig. 39) with anterior branch larger than posterior, twisted and deeply laciniate at the end; posterior branch a short hook; lateral shoulder with prominent knobs. Colpocoxites (Fig. 40) of posterior gonopods with terminal process bluntly triangular, curved posteriad, pilose area extensive; mesal tooth absent, lateral notch inconspicuous.

Notes. Hoffman's original description overlooked the posterior branch of the anterior gonopod. Reported from Craig, Montgomery, Giles and Patrick counties in southwest Virginia (Map 5). All records are for November and December, except for a pair taken *in copula* on March 15, 1956, in oak woods. Other records are from *Rhododendron* thickets and a sinkhole (Hoffman, 1961).

Conotyla vista n. sp.
Figures 41, 42

Type. Male holotype collected by W. A. Shear and David Bard, January 25, 1967, Natural Tunnel No. 1, Grandview State Park, 13 miles northeast of Beckley, Raleigh Co., West Virginia, elevation 2250 ft. (710 m). The specific epithet is a Latin noun in apposition and refers to the sweeping view of the New River canyon visible from the type locality.

Diagnosis. Distinct from the other species of the *melinda* group, and from all other known *Conotyla* species, in having prominent apophyses on all the pregonopodal legs, including the first.

Description of holotype male. Length, 26 mm, the largest known species of the family. Nineteen ocelli in four rows in a triangular eyepatch on left side, 16 ocelli in four rows on right side. Antennal joints in order of length: 3, 4, 5, 2, 6, 7, 1. Joint 3 of legs 1 and 2 with mesal apophyses of moderate size; similar apophyses on the femora of legs 3 through 6, becoming largest on leg 4; femur of leg 7 with an exceptionally large, apically toothed, sinuate process on proximal end, that *in situ* rests in pocket, on anterior gonopod of each side (Fig. 41). Anterior gonopods with lateral shoulder prominent and rimmed; mesal to shoulder apical region of gonopod is depressed, forming a pocket in which apophysis of leg 7 fits when gonopods are *in situ;* posterior branch somewhat larger than anterior, somewhat laciniate apically, both branches pass laterally around the colpocoxites *in situ.* Colpocoxites of posterior gonopods (Fig. 42) with a long, sigmoid and aciculate apical process, pilose area occupying the lateral margin; lateral notch and mesal tooth absent. Colpocoxite distinctly thickened on mesal margin.

Notes. The male holotype is the only known specimen. The type locality (Map 5) is a ridge of heavily faulted, coarse sandstone overlooking the 1200 foot deep gorge of the New River. The Natural Tunnels are roofed crevices formed by down-

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Figures 38–43. Male gonopods of *Conotyla* spp. Fig. 38. *Conotyla aeto*, colpocoxite of left posterior gonopod, posterior view. Figs. 39–40. *C. melinda.* Fig. 39. Left anterior gonopod, posterior view. Fig. 40. Colpocoxite of left posterior gonopod, posterior view. Figs. 41–42. *C. vista.* Fig. 41. Left anterior gonopod and basal segments of leg 7, posterior view. Fig. 42. Left posterior gonopod, posterior view. Fig. 43. *C. celeno*, left anterior gonopod, posterior view.

slope creeping of sandstone blocks, and are long enough to have totally dark areas and at least some troglophilic species (*Meta menardii* and *Calymmaria cavicola*, both spiders), but *C. vista* shows no cave modifications. Folding-door spiders (*Antrodiaetus* sp.) are very common in the immediate area.

Conotyla celeno n. sp.
Figures 43–45

Type. Holotype male collected December 12, 1965, by R. L. Hoffman, in vicinity of Comer's Rock, Iron Mt., ca. 4000 ft. (1300 m), Grayson-Wythe cos., Virginia. The specific epithet is a noun in apposition, and is the Greek name of one of the three Harpies of ancient mythology.

Diagnosis. Distinct from the other species of the *melinda* group in details of the gonopods, but is most easily separated from *vista* by the absence in *celeno* of an apophysis on the third joint of the first leg, and from *melinda* by the absence of apophyses on legs 6 and 7.

Description of holotype male. Length, 23.8 mm. Ocelli in triangular patch, in four rows plus single ocellus on right side, total of 19; in five rows on left side, total of 21. Antennal joints in order of length: 3, 4, 5, 2, 6, 7, 1. Leg 2 with distinct distal apophysis on the third joint; apophyses mesal in position on the femora of 3 and 4, apophyses of leg 4 the largest, distinctly capitate; apophysis of femur of leg 5 very small; legs 6 and 7 unmodified. Anterior gonopods (Figs. 43, 44) with lateral shoulder of normal size, lateral surface of lateral shoulder heavily pebbled; anterior and posterior branches subequal in size, anterior branch *in situ* curved around colpocoxite of posterior gonopod, anterior branch extending straight ventrad, heavily laciniated. Colpocoxites of posterior gonopods (Fig. 45) with terminal process thick, curved dorsal; lateral margin flared out as large, thin plate, lateral notch not at all developed; plumose area with a single branch; mesal tooth large, curved.

The *Atrolineata* Group

This group of two species may be generically distinct from *Conotyla*, but in my opinion are not sufficiently differentiated, although they have obviously had a long separate history—perhaps since the Pliocene droughts brought the Great Plains into being. They are characterized by reduced anterior gonopods, complex colpocoxites, and broadened posterior gonopod sterna.

Conotyla atrolineata (Bollman)
Figures 6, 46–50

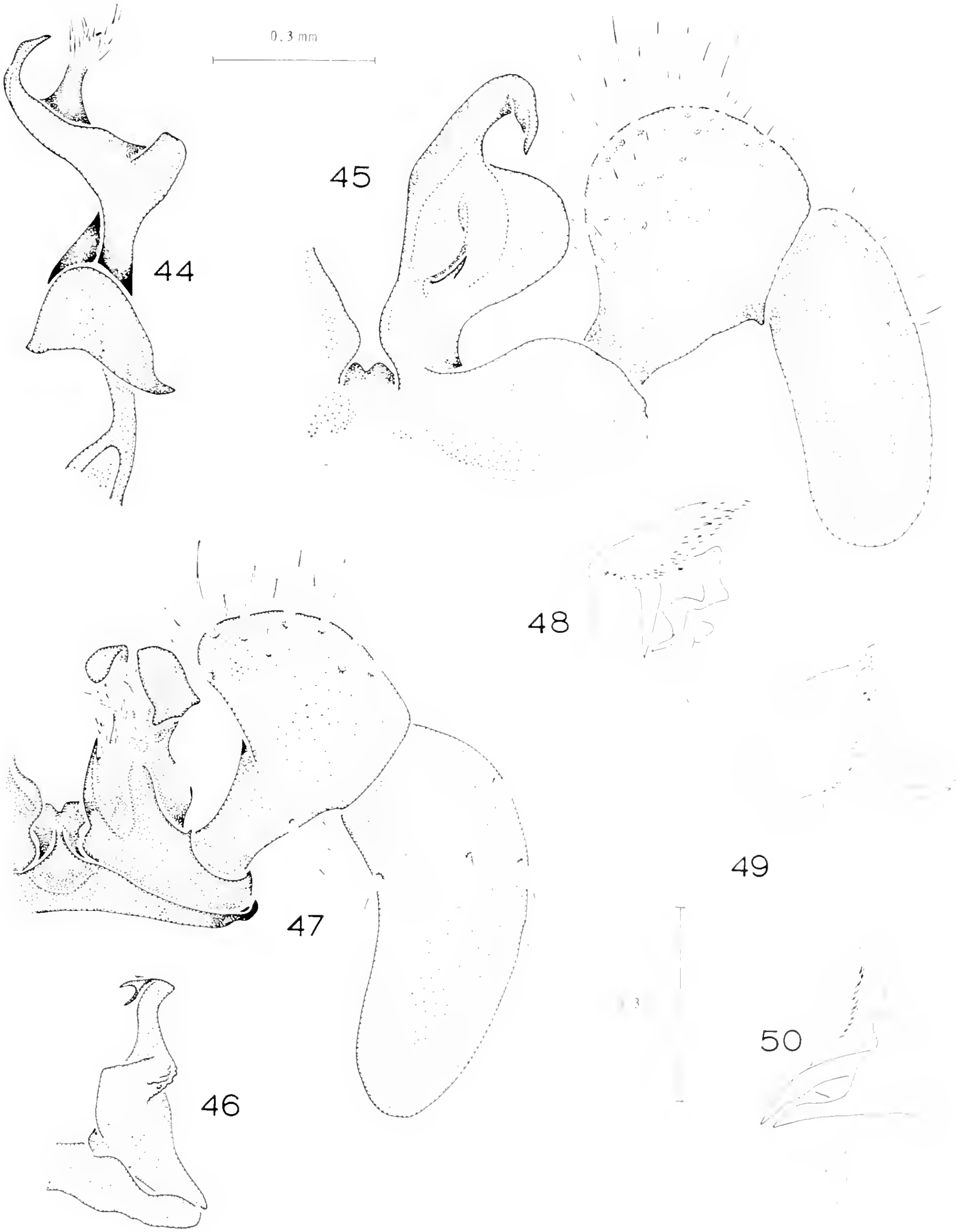
Craspedosoma atrolineatum Bollman, 1893, Bull. U. S. Nat. Mus., Vol. 46, pp. 35–36.

Conotyla atrolineata, Cook and Collins, 1895, Ann. New York Acad. Sci., Vol. 9, p. 75, figs. 95–100. Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull. 212, p. 98 (list).

Type. Male specimen from Glacier, British Columbia; assumed to be Glacier National Park, although the park was not established at the time the paper by Bollman was written (1887, 1893 dates the posthumous commemorative collection of Bollman's work). There is a Glacier post office in the park on the Canadian Pacific Railroad at the head of the Illecillewaet River. Type in U. S. National Museum, examined.

Diagnosis. Differing in the expanded sternum of the posterior gonopods from all species except *albertana*; from *albertana* in the much larger anterior gonopods and details of the colpocoxites of the posterior gonopods.

Description of male from Yoho National Park, B. C. Length, 15.5 mm. Eyepatches triangular, 20 ocelli in four rows on each side. Antennal segments in order of length: 3, 4 = 5, 2, 6, 7, 1. Leg 4 with large apophysis on femur, pregonopodal legs otherwise unmodified. Anterior gonopods



Figures 44–50. Male gonopods of *Conotyla* spp. Fig. 44–45. *Conotyla celeno*. Fig. 44. Left anterior gonopod, lateral view. Fig. 45. Left posterior gonopod, posterior view. Figs. 46–50. *C. atrolineata*. Fig. 46. Right anterior gonopod, anterior view. Fig. 47. Left posterior gonopod, posterior view. Figs. 48–50. Apical region of colpocoxite of posterior gonopod. Fig. 48. Posterior view. Fig. 49. Lateral view. Fig. 50. Mesal view.

(Fig. 46) with lateral shoulder lacking; large mesal lamella (posterior branch?) present; anterior branch curving around lateral surface of posterior gonopods *in situ*, tip three-pointed. Colpocoxites (Figs. 47–50) deeply cleft apically, posterior surface with two decurved lamellae and two prominent pointed branches; lateral pilose area present; mesal tooth sharp, pointed.

Notes. Known from several localities in the Rocky Mountains of eastern British Columbia; elevations between 4000 ft. and 5000 ft. in Yoho National Park, and from Robson Creek, Mt. Robson National Park (elevation unknown), in addition to the type locality. The continental divide separates this species from *C. albertana*, and it seems likely that they took refuge from the Cordilleran ice sheets on their present sides of the mountains, although there is no evidence of glacial refugia, other than possible isolated nunataks, in British Columbia.

Conotyla albertana Chamberlin
Figures 51–53

Conotyla albertana Chamberlin, 1920, Canadian Ent., Vol. 52, p. 167, fig. 17. Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull. 212, p. 98 (list).

Type. Male holotype from Bow River, Alberta, Canada; in Mus. Comp. Zool., examined. The Bow River flows from Bow Lake, just south of Bow Pass (6878 ft.) through Calgary, Alta., and joins the Oldman River to form the South Saskatchewan just north of Bow Island, Alta., a total course of more than 300 miles. Since most other known records for *C. albertana* are some 250 miles to the north of the river, it seems wise to here restrict the type locality to the banks of the Bow River in the vicinity of Lake Louise, Banff National Park, Alberta.

Diagnosis. Distinct from all but *atrolineata* in having the posterior gonopod sternum large, expanded and suboval, with prominent spiracles on the anterior surface, and in having the colpocoxites of the posterior gonopods with complex posterior surfaces. From *atrolineata*, *albertana* is distinct in the two-branched anterior gonopods, as described below.

Description of male from Jasper National Park, Alberta. Length, 11.0 mm. Eyepatches subhexagonal (truncate-triangular), five rows containing 18 ocelli on right side, 20 ocelli in five rows on left side. Antennal articles in order of length: 3, 4 = 5, 2, 6, 7, 1. Pregonopodal legs with slight apophyses on the femora of legs 3, 4, 5, 6; all mesal in position, heaviest on leg 4; apophysis of leg 6 very small. Anterior gonopods (Fig. 53) with lateral shoulder so well developed as to appear sigmoid; lateral shoulder rugose; anterior branch a heavy lamella, pressed against lateral side of sternum of posterior gonopod *in situ;* posterior branch curved, rodlike, sharply pointed. Posterior gonopods (Figs. 51, 52) with colpocoxites truncate, slightly curved posteriad, posterior surface with a complex group of smooth and plumose branches.

Notes. Aside from the type locality, this species is known from numerous specimens from several localities on Mt. Edith Cavell, including an alpine meadow, in Jasper National Park, Alberta, and Sulphur Mt. in Banff National Park. Unfortunately, the exact locality of some of the Jasper specimens was not indicated on the labels, only the altitudes (4500, 5000, and 5300 ft.). Since the tree line in western Alberta at the latitude of the park is from 7000–7500

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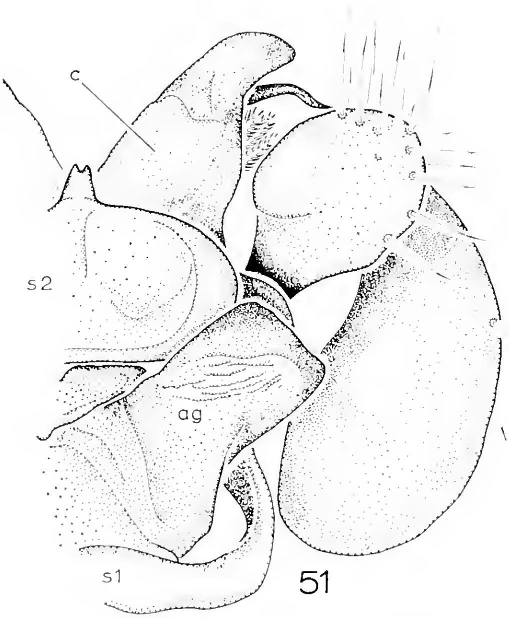
Figures 51–55. Male gonopods of *Conotyla* and *Achemenides*. Figs. 51–53. *Conotyla albertana*. Fig. 51. Right gonopods, anterior view. Fig. 52. Left gonopods, posterior view. Fig. 53. Right anterior gonopod, anteromesal view. Figs. 54–55. *Achemenides pectinatus*. Fig. 54. Right anterior gonopod and sternum, lateral view. Fig. 55. Basal region of anterior gonopods, anterior view.



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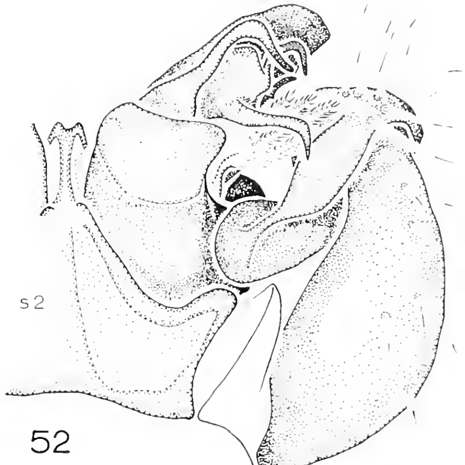

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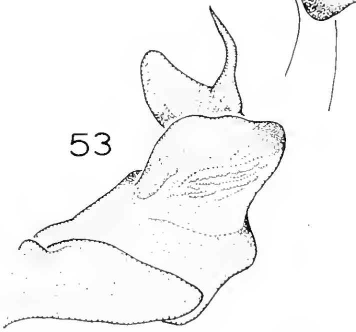

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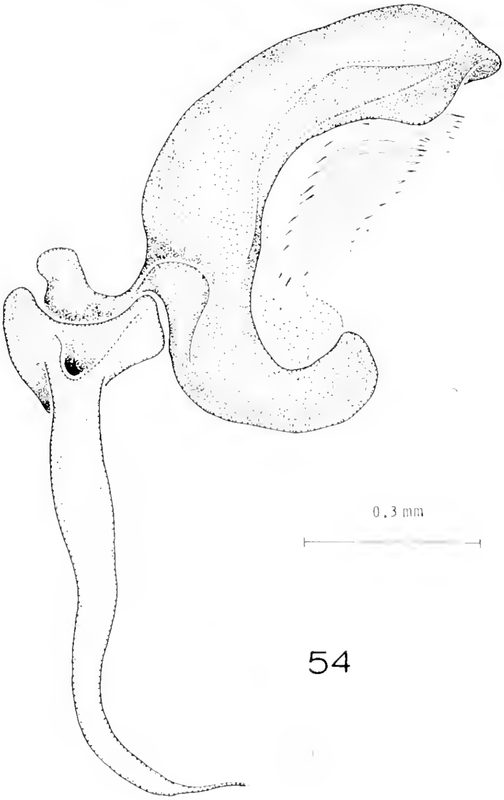

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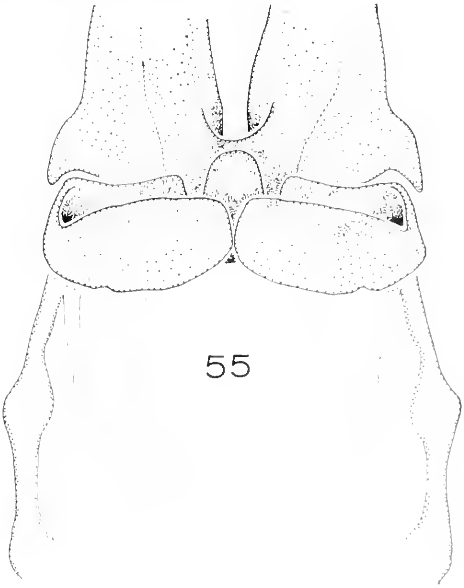

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ft., depending on local conditions, it seems safe to assume that *albertana* inhabits the Canadian and Hudsonian Zones. During the Wisconsin glaciation, there may have been an ice-free refugial corridor between the Cordilleran and Keewatin ice sheets (Moss, 1955), into which *albertana* or its ancestral form may have retreated, but little is known of the vegetation of this corridor. From such a refugium, *albertana* may have re-invaded the montane regions.

Chamberlin's male holotype lacks the seventh legs; he failed to see the apophysis of leg 6. The posterior branch of the anterior gonopods is also missing in the holotype.

Genus *Achemenides* new genus

Type species. Conotyla pectinata Causey. The generic name (Greek, masculine) refers to a Greek marooned in a cave after the Trojan War.

Diagnosis. Medium-sized conotylids with somewhat reduced ocelli (14–17 in the single known species). Antennal segment 5 nearly twice as long as segment 4. Pregonopodal legs of male with apophyses on either third or fourth segments or both. Anterior gonopods fused at the base, drawn anteriad as a knob articulating with both lateral sternal plates. Sternum of the anterior gonopods divided, joined by a lightly sclerotized membrane; each sternal plate deeply cupped mesally, spiracle at lateral margin of cup, tracheal apodeme somewhat reduced. Posterior gonopods with the telopodite articles subequal; colpocoxites with two branches, the anterior laminate, the posterior rodlike. Sternum of posterior gonopods much reduced, bandlike, deeply curved posteriad between coxae; spiracle lateral, tracheal apodemes much reduced, bifurcate.

Distribution. Upper Mississippi River Valley, presently known only from caves and mines.

Species. One, the type species.

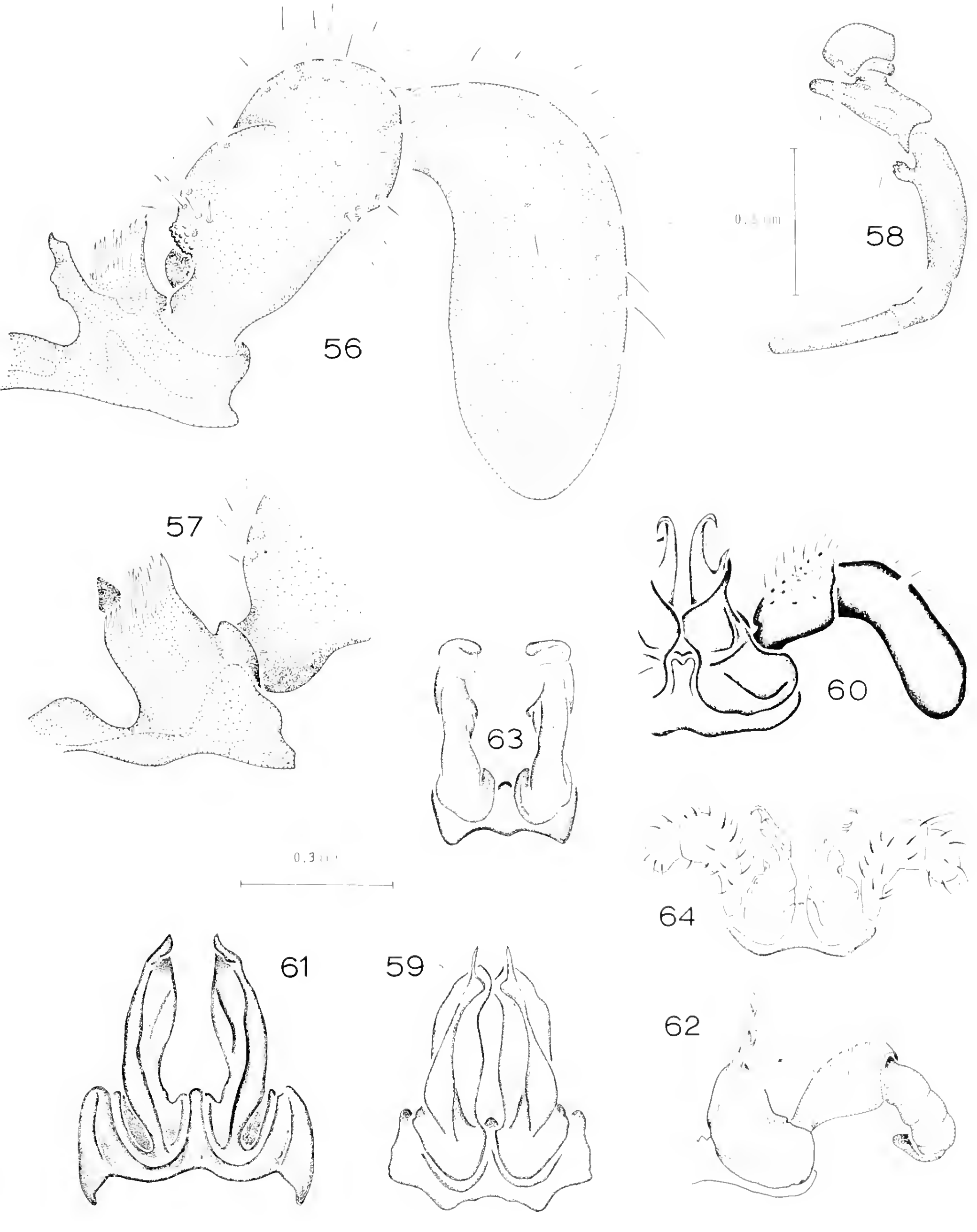
Achemenides pectinatus (Causey)
Figures 10, 54–58

Conotyla pectinata Causey, 1952, Proc. Biol. Soc. Wash., Vol. 65, pp. 112–113, figs. 4, 5. Chamberlin and Hoffman, 1958, U. S. National Mus. Bull. 212, p. 99 (list).

Sonoratyla pectinata Hoffman, 1961, Proc. Ent. Soc. Amer., Vol. 87, p. 268.

Type. Male holotype from "Smith Park, Mt. Carroll, Carroll Co., Illinois"; in collection of Illinois Natural History Survey, examined. Mr. Stewart Peck, who has had access to the field notes of H. H. Ross and M. W. Sanderson, collectors of the holotype male, informed me that the type locality was actually Smith Park Cave. As the type consists of only a dozen legless midbody segments, badly stained, and slide-mounted gonopods that could not be located, the description below is based on a specimen from the type locality identified by Causey and placed in the Illinois Natural History Survey Collection. The specific epithet is a Latin adjective referring to the comblike appearance of the anterior gonopods.

Description of male from Mt. Carroll, Illinois. Length, about 22 mm (specimen fragmented). Ocelli in three rows on each side, 14 in each triangular eyepatch. Antennal segments in order of length: 3, 5, 4, 2, 6, 7, 1. Legs 1 and 2 with slight swellings on the third joint, leg 4 with a weak apophysis (sometimes lacking) on the femur; legs 5 and 6 with strong distal apophyses on the femora; leg 7 with a capitate, toothed apophysis on the femur and a long, proximal lobe on the prefemur (Fig. 58). Anterior gonopods (Figs. 54, 55) very large, joined at base to form an anteriorly projecting curved knob; posterior surfaces with a thin, deeply laciniated ridge. Colpocoxites of posterior gonopods (Figs. 56, 57) with two divisions; an anterior deeply laciniated lamella and a posterior sagittiform branch; first telop-



igures 56–64. Gonopods and associated structures of *Achemenides* and *Taiyutyla*. Figs. 56–58. *Achemenides pectinatus*. ig. 56. Left posterior gonopod, posterior view. Fig. 57. Colpocoxite of right posterior gonopod, anterior view. Fig. 58. ight leg 7, posterior view. Figs. 59–60. *Taiyutyla corvallis*. Fig. 59. Anterior gonopods, posterior view. Fig. 60. Left osterior gonopods, posterior view. Figs. 61–62. *T. francisco*. Fig. 61. Anterior gonopods, posterior view. Fig. 62. Left pos- erior gonopod, posterior view. Figs. 63–64. *T. napa*. Fig. 63. Anterior gonopods, posterior view. Fig. 64. Posterior gono- ods, posterior view.

odite joint with a low, rugose swelling on posterior mesal side.

Notes. I find the following discrepancies between the original description and the topotype specimen: the apophysis of leg 5 is on the fourth, not the third joint; leg 6 has a single lobe on the fourth joint, not two lobes on the third; leg 7 (Fig. 58) has apophyses on both the third and fourth joints, not just the third; there is no evidence of a "dorsal" (anterior) branch of the anterior gonopods; the deeply laciniate lamellae of the posterior gonopods are coxal, not sternal.

The reduced ocelli and fairly large size of this species indicate that it is somewhat adapted for a subterranean existence. *Austrotyla specus*, on the other hand, is troglophilic and shows no strong adaptations for cave life. Thus both could possibly occur in Smith Park Cave without competing directly. The locality needs to be recollected to confirm this, and to provide more specimens. The presence of this species at the edge of the classical Driftless Area, and in caves, is of great potential significance, especially since it shows a combination of conotyloid-austrotyloid features. But the problems associated with defining this area (Frye, 1965) limit speculation. Cushing (1965) found evidence of many disjunct arctic-alpine plants in the Driftless Area, and other plants that occur only south of the Wisconsin maximum farther east. It is not unlikely, therefore, that the region escaped glaciation, while the extreme climate drove *A. pectinatus* or its ancestor to seek refuge in the moderated climate of caves. In view of this unusual interest, I present a detailed list of new records below (see also Map 3).

Records. ILLINOIS: Jo Daviess Co., mines in North California Diggings, 7 mi. NW of Hanover, 31 October 1965, S. Peck, ♂ ♀ ♀; South Nicholsen Mine, 31 October 1965, S. Peck, ♂ ♂ ♀; Hutchings Mine, 5 mi. E of Galena, 30 October 1965, S. Peck, ♂ ♀. IOWA: Jackson Co., Hunter's Cave, 5 mi. N of Andrew, January–February 1966, S. Peck, ♂ ♂ ♀ ♀. WISCONSIN: Richland Co., John Gray Cave, 5.5 mi. NNE of Richland Center, no date, C. Krekeler, ♂.

Genus *Taiyutyla* Chamberlin, 1952

Taiyutyla Chamberlin, 1952, Nat. Hist. Misc., Chicago Acad. Sci. No. 113, p. 1. Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull. 212, p. 102. Hoffman, 1961, Trans. Amer. Ent. Soc., Vol. 87, p. 270.

Type species. Taiyutyla corvallis Chamberlin, by original designation. The origin of the generic name, a neologism, is obscure. The gender is believed to be feminine.

Diagnosis. Small (8–11 mm in length) conotylids with the fifth antennal segment longer than the fourth, 20 ocelli or less in each eyepatch. Pregonopodal legs with apophyses on third or fourth article. Eleventh legs with prefemoral hooks. Anterior gonopods platelike, sometimes with terminal and subterminal processes or lamellae; sternum of anterior gonopods completely surrounding coxotelopodites, which articulate primarily on its posterior surface; spiracle prominent, in lateral depression. Posterior gonopods large, but slightly smaller to distinctly smaller than anterior gonopods, platelike or with two major branches, subterminal branch usually flattened, but sometimes spikelike, subtending or bearing a plumose-hirsute area; terminal branch or process short, or long and spirally curved, often bearing accessory teeth; no coxal depression, coxal bases swollen posteriorly. Sternum of posterior gonopods broad and deep anteriorly, thin and ribbonlike posteriorly; spiracles at proximolateral margins of broad, semicircular depressions. Telopodite articles of posterior gonopods variable, in some cases subequal and with second showing signs of segmentation, or with the first twice as long as the second, which is reduced to a small knob.

Species and distribution (Map 1). Three species in southern Oregon and northern California.

KEY TO SPECIES

1a. Second telopodite joint of male posterior gonopods only half the length of the first (Fig. 64); leg 3 with an apophysis on the fourth joint, other pregonopodal legs unmodified .... *napa*
1b. Second telopodite joint of male posterior gonopods (Figs. 60, 62) at least as long as the first; legs 4 through 7 and sometimes leg 3 with femoral apophyses 2
2a. Third leg of male with an apophysis on the femur; gonopods as in Figs. 61, 62; Marin Co., California .... *francisca*
2b. Third leg of male unmodified; southern Oregon .... *corvallis*

Taiyutyla corvallis Chamberlin
Figures 8, 59, 60

Taiyutyla corvallis Chamberlin, 1952, Nat. Hist. Misc., Chicago Acad. Sci. No. 113, pp. 1–2, figs. 1, 2. Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull. 212, p. 102 (list). Hoffman, 1961, Trans. Amer. Ent. Soc., Vol. 87, p. 270, pl. 10, figs. 8, 9.

Type. Holotype from Corvallis, Linn Co., Oregon; in Chamberlin collection, Salt Lake City, Utah, could not be located.

Diagnosis. Unique in lacking an apophysis on the fourth joint of leg 3.

Description of male from Corvallis, Oregon. Length, 10.5 mm. Eyepatches triangular, three rows plus single ocellus, totaling 17, on right side; 20 ocelli in four rows on left side. Antennal articles in order of length: 3, 5, 4, 2, 6 = 7, 1. Legs 4 through 7 with apophyses on femora; apophyses on legs 4 and 5 very small, distal; apophysis of leg 6 strong, capitate, mesal; apophysis of leg 7 strong, capitate and toothed, promixal. Anterior gonopods (Fig. 59) larger than colpocoxites of posterior gonopods, subrectangular, flattened antero-posteriorly, slightly bent mesad, with aciculate subterminal process arising from a longitudinal ridge; lateral edges vaguely serrate. Sternum of anterior gonopods completely encircling coxotelopodites, produced between them as bilobed or trilobed condyle. Colpocoxites of posterior gonopods (Fig. 60) large and bulbous at base, ending in pointed terminal process, below which is a pilose area and a pointed subterminal process. Second joint of posterior gonopod with a distinct basal shoulder; third joint nearly twice as long as second.

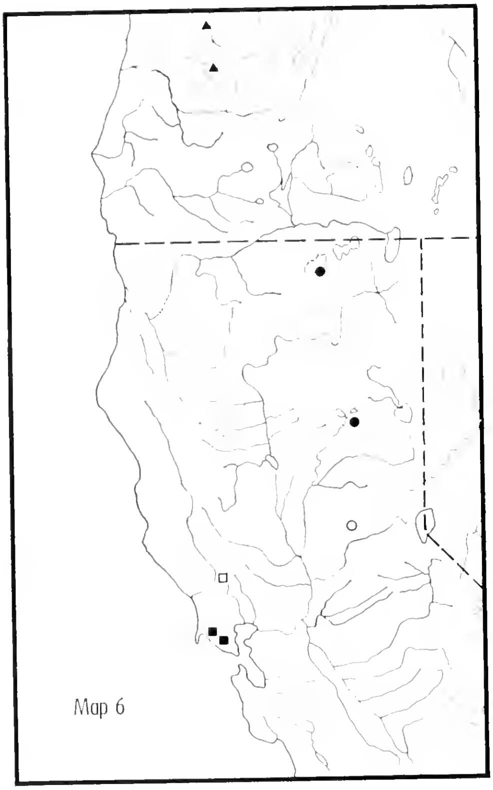
Notes. Nothing is known of the ecology and biology of this species, which is known only from the type locality (Map 6).

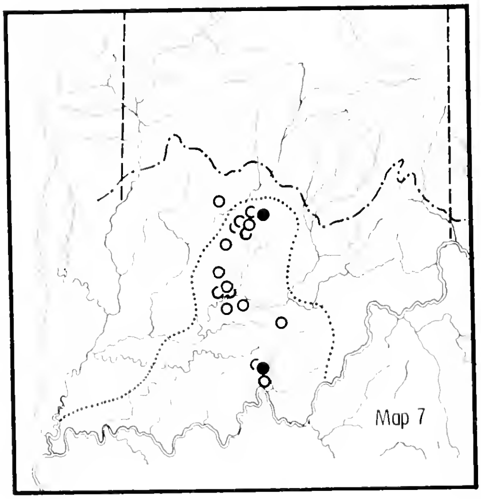
Taiyutyla napa n. sp.
Figures 63, 64

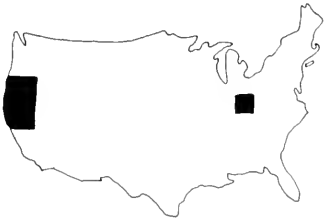
Type. Holotype male collected with two females and an immature specimen by Vincent Roth, 31 December 1953, Mt. St. Helena, Napa and Sonoma cos., California. The specific epithet refers to the type locality.

Diagnosis. In both *corvallis* and *francisca*, the second telopodite article of the posterior gonopods is longer than or as long as the first; in *napa* the second joint is less than half as long as the first. Only leg 3 has an apophysis on the fourth joint in *napa; corvallis* has leg 3 unmodified and *francisca* has apophyses on legs 4 through 7, as well as 3. The low swelling on the third joint of leg 2 present in *napa* is absent in the other two species.

Description of holotype male. Length, 8 mm. Eyepatches irregularly triangular, 3 irregular rows with a single ocellus totalling 18 on right side; 18 ocelli in four rows on left side. Antennal joints in order of length: 3, 5, 4, 2 = 6, 7, 1; joint 5 about twice as long as joint 4. Leg 3 with large distal apophysis on femur; leg 2 with a low, longitudinal swelling on the mesal side of third joint. Anterior gonopods (Fig. 63) curved posteriad distally, with prominent mesal shoulder about midway in their length, and with a thin, membranous subterminal lamina extending mesally. Colpocoxites of posterior gonopods (Fig. 64) intermediate between *corvallis* and *francisca*, subterminal process short, pointed; terminal process long, curved posteriad, with single accessory tooth. First telop-







Map 6. Northern California and southern Oregon, showing distribution of various conotylids; dots, *Plumatyla humerosa*, circle, *Conotyla extorris*; solid squares, *Taiyutyla francisca*; open squares, *T. nopa*; triangles, *T. corvallis*, including *T. jonesi*.

Map 7. Southern Indiana, showing distribution of *Conotyla bollmani*; dots, epigean records; circles, cave records; dotted line, limit of Illinoisan glacial drift; broken line with dots, limit of Wisconsin glacial drift.

odite joint more than twice as long as second.

Notes. Nothing is known of the biology of this species, which is known only from the type locality (Map 6). Mt. St. Helena has a maximum elevation of 4344 feet.

Taiyutyla francisca n. sp.

Figures 61, 62

Type. Holotype male collected by C. W. O'Brien, 7 January 1962, one mile SE of Inverness, Marin Co., California. The specific epithet, a noun in apposition, refers to the proximity of the type locality to San Francisco Bay.

Diagnosis. Distinct from *corvallis* primarily in the form of the colpocoxites of the posterior gonopods, which bear spirally curved apical processes with several accessory teeth, also in the stronger modifications of legs 4 and 5 of the males.

Description of holotype male. Length 9.5 mm. Eyepatches triangular, 20 ocell in four rows on left side, 20 ocelli in four rows and single ocellus on right side. Antennal segments in order of length: 3, 5, 4, 2, 6, 7, 1. Apophyses of legs 3 through 7 approximately same size, distal on leg 3 slowly becoming mesal on succeeding legs and proximal on leg 7. Anterior gonopods

(Fig. 61) large, flattened, terminal process blunt, slightly curved; large, thin mesal flange present. Colpocoxites of posterior gonopods (Fig. 62) smaller than anterior gonopods, complex; terminal process curved in a spiral of two turns, with four accessory processes as shown (Fig. 62); subterminal process a twisted, horizontal lamella finely laciniate on the posterior side. Second telopodite joint of posterior gonopod slightly longer than first, vaguely annulated.

Notes. Little is known of the biology of this species; the holotype was taken in a Berlese sample of *Pinus muricata* duff. See Map 6.

Genus *Austrotyla* Causey, 1961

Austrotyla Causey, 1961, Proc. Biol. Soc. Washington, Vol. 74, p. 260 (in part).

Sonoratyla Hoffman, 1961, Trans. Ent. Soc. Amer., Vol. 87, p. 269.

Type species. Of *Austrotyla*, *Conotyla specus* Loomis, by original designation; of *Sonoratyla*, *Conotyla montivaga* Loomis. The generic name is a feminine Latin-Greek neologism referring to the southerly distribution of the genus with respect to *Conotyla*.

Diagnosis. With the characters of the family. Anterior gonopod sternum appearing divided in some cases, but usually contiguous in the anterior and posterior midlines, or joined by sclerotic membrane. Anterior gonopods flattened, platelike, but with complex posterior surfaces; anterior gonopods covering colpocoxites of posterior gonopods *in situ*. Colpocoxites of posterior gonopods much smaller than anterior gonopods, usually with a single cupped lamella and a rodlike or platelike mesal branch, sometimes plumose. Pregonopodal legs with femoral lobes on legs 3 and 4 in all known species. Capitate lobes present on coxae of legs 10 and 11 in some species. Species usually pigmented, 20–24 ocelli in triangular patch.

Species. Five; distributed (Map 1) through Missouri and Illinois, Rocky Mountains from Alberta to Chihuahua (and possibly Queretaro). Separation of *specus* or its ancestors from the Rocky Mountain species may have occurred as early as the Pliocene, at the time of the formation of the Great Plains.

Key to Species

1a. Coxae 10 and 11 of males without lobes .... *borealis*
1b. Coxae of legs 10 and 11 with lobes, or either coxa 10 or 11 lobed 2
2a. Lobe on coxa 11 only .... *coloradensis*
2b. Lobe on coxa 10 3
3a. Lobe on coxa 10 only 4
3b. Lobes on both coxae 10 and 11 .... *specus*
4a. Gonopods as in Figs. 68–70 .... *montivaga*
4b. Gonopods as in Figs. 77–79 .... *chihuahua*

Austrotyla specus (Loomis)
Figures 65–67

Conotyla specus Loomis, 1939, Bull. Mus. Comp. Zool., Vol. 86, p. 184, figs. 11a–c. Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull. 212, p. 99 (list).

Austrotylus specus specus, Causey, 1961, Proc. Biol. Soc. Wash., Vol. 74, pp. 260–264, figs. 5–10.

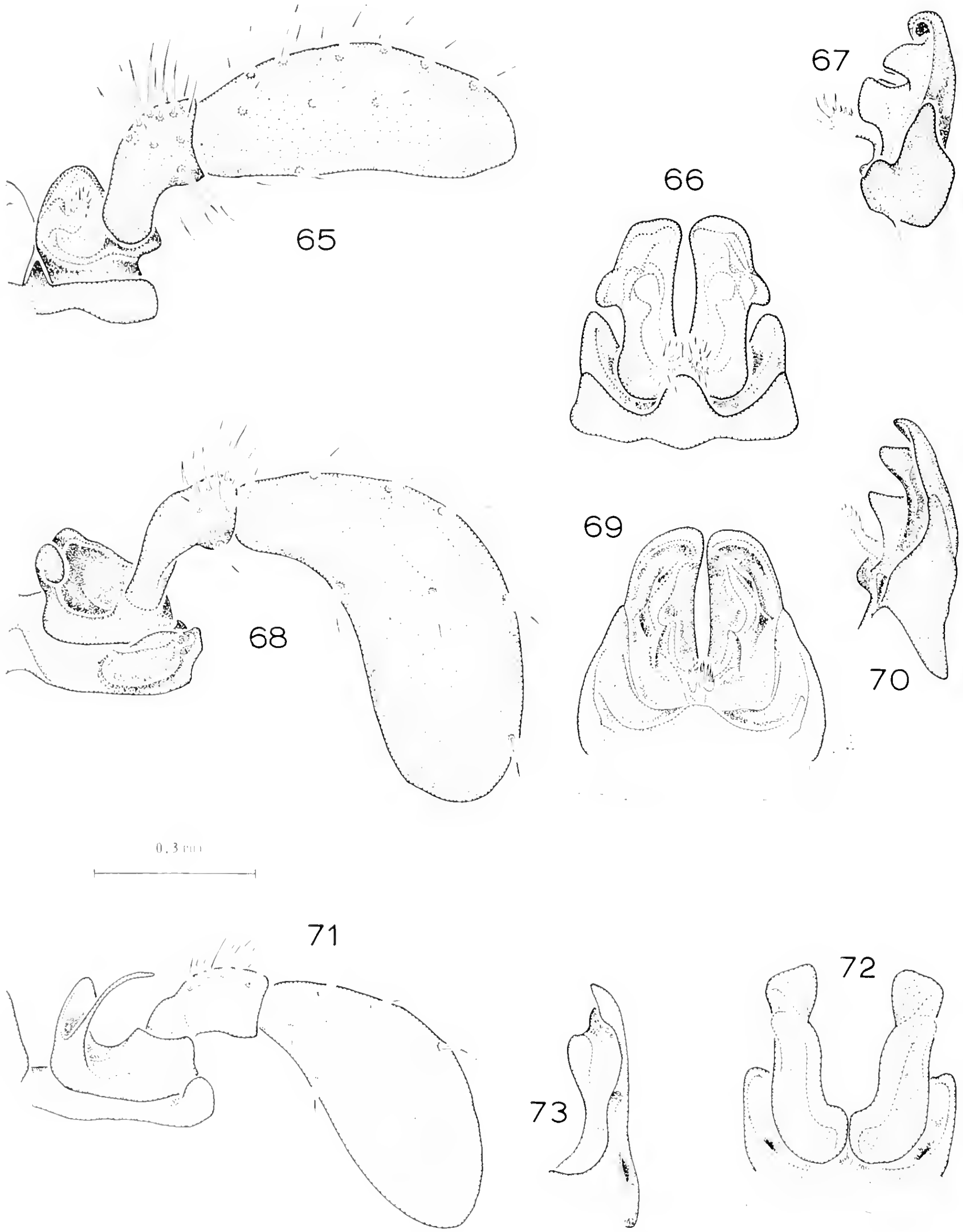
Austrotyla specus montivaga, (in part) Causey, 1961, Proc. Biol. Soc. Wash., Vol. 74, pp. 264–265.

Sonoratyla specus, Hoffman, 1961, Trans. Ent. Soc. Amer., Vol. 87, p. 269.

Type. Male holotype from Rice's Cave, 3 miles northeast of Goldman, Jefferson Co., Missouri, in Museum of Comparative Zoology, examined. The specific epithet is a noun in apposition (Latin: "cave") referring to the habitat of the type series.

Diagnosis. This species has much less complex anterior gonopods than *coloradensis* or *chihuahua*, and those of *borealis* are much simpler. In addition, the coxal processes of legs 10 and 11 are unique. See under *montivaga* for a discussion of differences between that species and *specus*.

Description of holotype male. Length, 11.5 mm. Eyepatches quadrangular, ocelli of both sides in three rows, 21 on the left side, 23 on the right, ocelli fully pigmented, not irregular in shape. Antennal articles in



Figures 65–73. Gonopods of *Austrotyla*. Figs. 65–67. *Austrotyla specus*. Fig. 65. Right posterior gonopod, anterior view. Fig. 66. Anterior gonopods, posterior view. Fig. 67. Left anterior gonopod, lateral view. Figs. 68–70. *A. montivaga*. Fig. 68. Right posterior gonopod, anterior view. Fig. 69. Anterior gonopods, posterior view. Fig. 70. Left anterior gonopod, lateral view. Figs. 71–73. *A. borealis*. Fig. 71. Right posterior gonopod, anterior view. Fig. 72. Anterior gonopods, posterior view. Fig. 73. Left anterior gonopod, lateral view.

order of length: 3, 5, 4, 6, 2, 7, 1. Pregonopodal legs modified as described for the genus, legs 10 and 11 with anteriorly directed capitate lobes on the coxae. Anterior gonopods (Figs. 66, 67) with the sternal lobes evenly and heavily sclerotized, coxotelopodites with a lateral lobe above the sternal lobes; proximal laciniated branches large, prominent. Colpocoxites (Fig. 65) with the posterior lamella cupped and rounded distally, anterior branch sigmoid, laciniated distally; third telopodite joint twice the length of the second.

Notes. Both Causey and Loomis overlooked the lobes on the coxae of the 11th legs. Causey noted the variation in coloration and ocelli of this species, and a study of other populations indicates that both pigmented and unpigmented individuals occur in the same caves. Epigean specimens are rare; Causey reported them as *A. s. montivaga* from northern Illinois and Wisconsin. It seems likely that the same situation holds in this species as in *Conotyla blakei*, with troglophilic populations in the southern, lowland part of the range and epigean populations in the northern part. The absence of epigean records of either species in the regions of the cave populations may be due to a lack of collecting at the proper time, late fall, winter, and early spring, when these animals mature and are most active. Unpublished records kindly given to me by Stewart Peck include caves in Jackson Co., Iowa, and in the following Illinois counties: Jackson, Jo Daviess, Monroe, Saline, Henderson, and Union. Causey (1961) reported it from Franklin, Jefferson, and St. Clair cos., Missouri, and Sauk Co., Wisconsin (Map 3). An immature specimen in the Museum of Comparative Zoology from Blue Earth Co., Minnesota, strongly resembles *A. specus.*

Austrotyla montivaga (Loomis)
Figures 68–70

Conotyla montivaga Loomis, 1943, Bull. Mus. Comp. Zool., Vol. 92, pp. 383–384, figs. 4a–d. Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull. 212, p. 98 (list).

Sonoratyla montivaga, Hoffman, 1961, Trans. Ent. Soc. Amer., Vol. 87, p. 268, pl. 10, figs. 10–11.

Austrotyla specus montivaga, (in part) Causey, 1961, Proc. Biol. Soc. Washington, Vol. 74, p. 264.

Type. Male holotype from Santa Rita Mts., elevation 7500 ft., Pima Co., Arizona, in Museum of Comparative Zoology, examined.

Diagnosis. This species is much smaller than *coloradensis*, and the posterior surface of the anterior gonopods is much less complex; there is no clear area on the lateral sternal lobes as there is in *coloradensis* and *chihuahua*. Distinct from *specus*, which it closely resembles, in the details of the gonopods; in specimens I have examined, the third telopodite article is nearly three times as long as the second in *montivaga*, while in *specus* it is only slightly more than twice as long; there is no coxal lobe on leg 11 in *montivaga*, and one is present in *specus*.

Description of holotype male. Length, 9.0 mm. Causey (1961) described in detail the nonsexual characters of this species, but stated that the gonopods (Figs. 68, 69) were identical to those of *specus*. This is not the case. In posterior view (Fig. 69), the proximal laciniated lobes of *montivaga* are smaller, the ridges and lobes are less developed, and there is no lateral extension on the coxotelopodite above the insertion of the sternal lobes. The colpocoxites (Fig. 68) are less developed in *montivaga*, and the anterior branch is thicker and blunter. Otherwise, the description given by Causey (1961) is accurate.

Notes. Known from numerous specimens collected in the Santa Rita and Santa Catalina Mts., north and south of Tucson, Pima Co., Arizona. The type is from an elevation of 7500 ft., probably in or just below the *Pinus ponderosa* zone at the latitude of Tucson. The identity of specimens from Mescalero, New Mexico, could not be checked, as they were not available for study, but Chamberlin reported *colora-*

densis from Ruidosa, in the same mountains and only about 20 miles to the northeast. Which species (or an undescribed one) actually occurs in southern New Mexico awaits clarification. Both Loomis and Chamberlin might have assumed that their species was the only one in the Rocky Mountains; *coloradensis* males were not described until 1961. The records reported by Causey (1961) from Illinois and Wisconsin refer to epigean populations of *specus;* she stated that the gonopods were identical with *specus*, and placed *montivaga* as a subspecies of *specus*. A comparison of my figures of the holotypes of both species should establish their distinctness, besides the geographic difficulties of having a single subspecies with two populations separated by nearly a thousand miles of uninhabitable terrain.

Austrotyla borealis n. sp.
Figures 71–73

Type. Male holotype collected by D. Whitehead, 2–4 October, 1967, Jasper National Park, Alberta, "Sta. 5," 5300 ft. The specific epithet is an adjective indicating that it is the extreme northerly representative of its genus.

Diagnosis. This species is smaller than the other representatives of the genus, being about 9 mm long in mature males. The sterna of the anterior gonopods show very distinct angular shoulders while still attached to the telopodites, as in *specus*. The posterior surface of the coxotelopodites is simpler than in any other species, and there are no lobes on the coxae of legs 10 and 11.

Description of holotype male. Length, 9.8 mm. Eyepatches triangular; 24 ocelli on left side, in four rows plus single ocellus; four rows plus single ocellus totalling 22 ocelli on right side. Antennal segments in order of length: 3, 5, 4, 6, 2, 7, 1. Legs 3 and 4 modified as described for genus. Lateral lobes of the sterna of the anterior gonopods forming a distinct angular shoulder with the telopodites (Figs. 72, 73), with a distal area of very thin cuticle; spiracle on anterior surface, easily seen. Coxotelopodites of anterior gonopods simple, with single thickened ridge on posterior surface, ending in somewhat swollen knob. Colpocoxites of posterior gonopods (Fig. 71) with anterior branch long, filiform, branched. First telopodite joint is less than one third length of second telopodite joint. Coxae 10 and 11 without lobes.

Notes. Known only from the type locality. See notes on *Conotyla albertana* for further details on type locality.

Austrotyla coloradensis (Chamberlin)
Figures 74–76

Conotyla coloradensis Chamberlin, 1910, Ann. Ent. Soc. Amer., Vol. 3, p. 237, pl. 32, figs. 7–9, pl. 33, figs. 1–3. Chamberlin and Hoffman, 1958, U. S. Nat. Mus. Bull. 212, p. 98 (list).

Austrotyla coloradensis, Causey, 1961, Proc. Biol. Soc. Washington, Vol. 74, pp. 254–260, figs. 2–4.

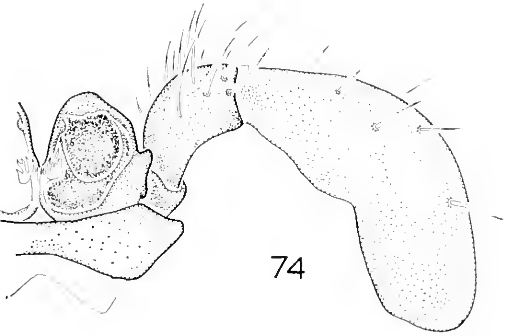
Type locality. Colorado. Causey (1961) designated a male neotype from Allen's Park, Boulder Co., Colorado, which is deposited in the Museum of Comparative Zoology, examined.

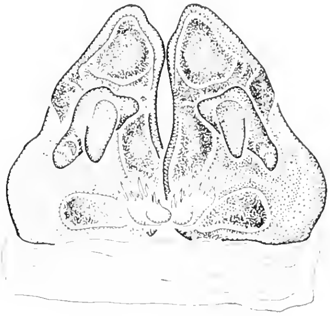
Diagnosis. Distinct in size and complexity of gonopods from all except *chihuahua*, but *coloradensis* has no anterior lobe on the coxa of leg 10. Distinct from *montivaga* by the larger size and much more prominent lateral shoulders.

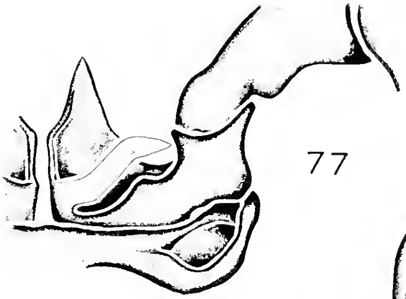
Description of neotype male. Length, 15.7 mm. Eyepatches triangular, 23 ocelli on each side in four rows plus single ocellus. Antennal articles in order of length: 3, 5, 4, 6, 2, 7, 1. Pregonopodal legs modi-

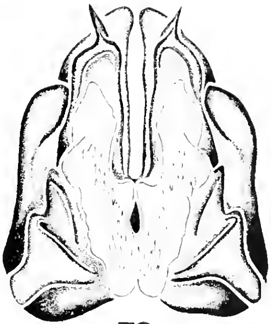
→

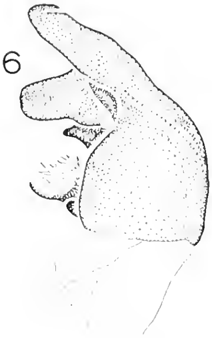
Figures 74–81. Gonopods of *Austrotyla* and *Plumatyla*. Figs. 74–76. *Austrotyla coloradensis*. Fig. 74. Right posterior gonopod, anterior view. Fig. 75. Anterior gonopods, posterior view. Fig. 76. Left anterior gonopod, lateral view. Figs. 77–79.

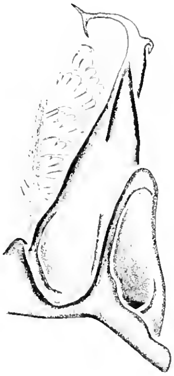


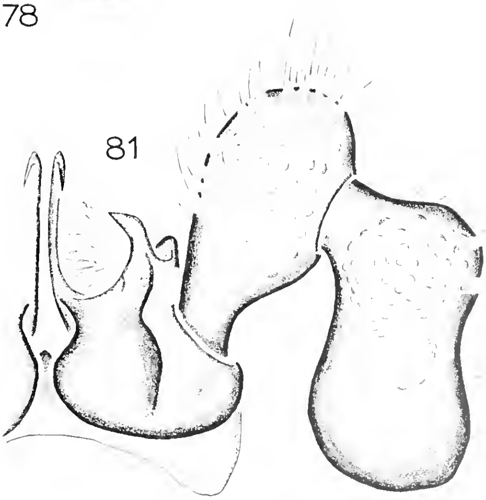












A. *chihuahua*. Fig. 77. Colpocoxite of right posterior gonopod, anterior view. Fig. 78. Anterior gonopods, posterior view. Fig. 79. Left anterior gonopod, lateral view. Figs. 80–81. *Plumatyla humerosa*. Fig. 80. Right anterior gonopod, anterior view. Fig. 81. Left posterior gonopod, posterior view.

fied as described for genus, apophysis of leg 3 somewhat larger than that of leg 4. Anterior gonopods (Figs. 75, 76) thin, lamellate, bearing posteriorly a prominent knob near the midline of each telopodite and a mesal laciniated branch; sternal lobes with a semicircular area of very thin cuticle that appears to be a hole at low magnification. Colpocoxites of the posterior gonopods (Fig. 74) relatively large, deeply cupped, posterior lamella deeply notched laterally, anterior branch small, lightly laciniated; second telopodite joint twice the length of first.

Notes. Causey's (1961a) drawings of the gonopods, made from cleared, slide-mounted material, leave something to be desired. The thin area on the sternal lobes is represented as an open space, and the tracheal apodeme is shown as being coalesced with the sternal lobe high up on the coxotelopodite. In actuality, the tracheal spiracle, not seen by Causey, is easily visible on uncleared preparations and is at the lateroanterior corner of the sternum, whence it leads normally into the tracheal apodeme. The horizontal portions of the sternites meet in the anterior midline as well as the posterior, rather than being represented entirely by a membranous area. The colpocoxites of the posterior gonopods in Causey's illustration show neither the deep lateral cleft in the posterior lamella, nor the short, mesal plumose branch. See Causey (1961a) for emendations in Chamberlin's original description, based on a female.

There is some variability in size in this species, but it could not be connected with any geographical trend. The smallest specimens were about 16 mm long and the longest were close to 23 mm long.

Known from numerous specimens from the following Colorado counties (Map 4): Larimer, Jackson, Eagle, Pitkin, Chaffee, Gunnison, Hinsdale, Mineral, and Conejos. Probably also occurs in southern Wyoming and northern New Mexico. The majority of records are from coniferous forests above 7000 ft. elevation.

Austrotyla chihuahua n. sp.
Figures 77–79

Type. Male holotype from 100 m above Rio Urique, 84 km south of Creel, Chihuahua, Mexico, collected February 28, 1966, by J. Reddell and W. Bell. The specific epithet is a noun in apposition, referring to the type locality.

Diagnosis. The posterior surface of the anterior gonopods is complex, as in *coloradensis*, but the colpocoxites of the posterior gonopods of *chihuahua* have the posterior lamella angular and the anterior branch large, flattened and reflexed; *chihuahua* has a coxal lobe on leg 10, while *coloradensis* has none.

Description of holotype male. Length, 14.0 mm. Eyepatches truncate-triangular, 23 ocelli in four rows on left side, 21 ocelli in four rows on right side. Antennal articles in order of length: 3, 5, 4, 2 = 6, 7, 1. Legs 3 and 4 modified as described for genus, apophyses slightly larger than in other species. Sterna of anterior gonopods as in *coloradensis;* gonopods (Figs. 78, 79) almost contiguous in midline, distinctly depressed mesally on anterior surface; posterior surface with complex knobs and plumose branches. Colpocoxites of posterior gonopods (Fig. 77) with posterior lamella triangular; anterior branch flattened, reflexed. Coxa of leg 10 with an anterior lobe.

Notes. Nothing is known of the biology of this species, which is known only from the type locality.

Genus *Plumatyla*, new genus

Austrotyla Causey, (in part) 1961, Proc. Biol. Soc., Washington, Vol. 74, p. 260.

Sonoratyla Hoffman (in part) 1961, Trans. Amer. Ent. Soc., Vol. 87, p. 269.

Type species. Conotyla humerosa Loomis; the generic name is a Latinized

Spanish-Greek neologism derived from the related genus *Conotyla* and Plumas Co., California, type locality of the type species. The gender is feminine.

Diagnosis. With the characters of the family. Anterior gonopod sternum intermediate between *Taiyutyla* and *Austrotyla*, heavily sclerotic throughout, with lateral obes extending laterad to coxotelopodites, but incomplete posteriorly, as in *Conotyla*. Anterior gonopods with two major branches, the anterior largest and set mesally with small laciniate processes; posterior branch a simple hirsute rod. Posterior gonopod sternum broadened and depressed laterally. Colpocoxites of posterior gonopods with a large mesal branch bearing laciniations as in anterior gonopod; lateroposterior lamella heavily sclerotized. Femoral lobes on some pregonopodal legs. Species troglobitic, without pigment, ocelli about 10, in two rows.

Species. One, found in mines and caves n northern California.

Plumatyla humerosa (Loomis)

Figures 80, 81

Conotyla humerosa Loomis, 1943, Bull. Mus. Comp. Zool., Vol. 92, pp. 384–385, figs. 5a–d.

Type. Male holotype and other specimens collected Sunnyside Mine, 3 mi. SW of Seneca, Plumas Co., California, January 22, 1923, by H. S. Barber; deposited in U. S. National Museum, examined; immature male paratype in Museum of Comparative Zoology.

Diagnosis. See generic diagnosis.

Description of topotype male. Length, 6.0 mm. Ocelli in two rows, 9 ocelli on left side, 8 ocelli on right side. Antennal segments in order of length: 3, 5, 4, 2, 6, , 1. Legs 5, 6, and 7 with prominent femoral lobes. Anterior gonopods (Fig. 0) larger than colpocoxites; posterior branch bears a subterminal lateral hook nd is distally bifid; posterior branch rodke, densely pilose. Posterior basal knob ts into sternal cavity of posterior gonopods. Colpocoxites of posterior gonopods (Fig. 81) with two branches, anterior mesal branch hooked posteriad, small laciniated branches on lateral surface; posterior lateral branch a subtriangular, curved, well-sclerotized lamella. Tracheal apodemes of both gonopods reduced in size.

Notes. The only other mature specimens known to me, excepting the specimens from the type locality kindly lent to me by N. B. Causey, are from Indian Wells Ice Cave, Lava Beds National Monument, Siskiyou Co., California. They differ from the holotype and paratype by being smaller (13–14 mm), lacking a lobe on the femur of leg 5, and having the anterior branch of the anterior gonopod slightly more attenuate. Otherwise, the gonopod structure is identical to the Sunnyside Mine specimens. For this reason, I hesitate to describe it as a distinct species. Immature representatives of *Plumatyla* are known from a number of mines, limestone caves, and lava tubes in northern California and adjacent Oregon. Only the collection of mature specimens can indicate the range of variation and the number of species in this genus. The lava tubes in Lava Beds National Monument may be as old as 60,000 years (Gale, 1959). The local glaciation of the northern California area during the late Pleistocene (Detling, 1968) may have been responsible for the cave habitat of these animals.

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Valid generic and species names in italics; only major discussions listed for species.

Bulletin OF THE
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Monograph of the Cuban Genera *Emoda* and *Glyptemoda* (Mollusca: Archaeogastropoda: Helicinidae)

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MONOGRAPH OF THE CUBAN GENERA *EMODA* AND *GLYPTEMODA* (MOLLUSCA: ARCHAEOGASTROPODA: HELICINIDAE)

WILLIAM J. CLENCH AND MORRIS K. JACOBSON

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ABSTRACT

The present paper is the third in a series dealing with the Cuban representatives of the land prosobranch family Helicinidae. The studies on the genus *Viana* (1968) and *Priotrochatella* (1970) have already appeared. The genus *Emoda* is assumed to have originated in Oriente Province, probably from some form of the West Indian genus *Alcadia*. From there it spread westward across the island into Pinar del Río Province. It occurs in each of the six provinces, but is absent from the Isle of Pines. The specific and subspecific taxa assigned to *Emoda* were investigated. Of the 27 taxa proposed, it is concluded that 16 are valid. In addition, one new species, *Emoda caledoniensis*, is described and the subgenus *Glyptemoda* Clench & Aguayo 1950 is raised to generic rank.

INTRODUCTION

The family Helicinidae appears in two widely disjunct areas of distribution centered in the Caribbean in the western hemisphere and in Southeast Asia and the Philippine Islands in the eastern hemisphere. The island of Cuba has an especially rich helicinid fauna, possessing no fewer than four endemic genera with numerous species. In a previous study (1968), the present authors have monographed the endemic genus *Viana*, and in 1970, their monograph on *Priotrochatella* was published. In this work we take up two more such genera, *Emoda* and *Glyptemoda*. In this series of studies, we also plan to complete the examination of all Cuban helicinids and to investigate the Cuban species of the genera *Helicina sensu stricto*, *Eutrochatella*, *Alcadia*, *Lucidella*, *Ceratodiscus*, and *Proserpina*.

Lea (1834b: 161) described the first *Emoda* as *Helicina pulcherrima* and until the appearance of Wagner's work (1907–1908), most other new species were included in the genus *Helicina*. The name

Emoda was given by H. and A. Adams in 1856 to a conglomerate of species which had few cohesive affinities. Because of this, the name was disregarded by later students of Cuban mollusks (Arango, 1878–1880; Crosse, 1888), and it first entered into general use after Wagner (1907–1908) published his extensive monograph. Although this author used only conchological and opercular characteristics, and in spite of serious defects in his work, he defined the taxon, which he considered a subgenus of *Alcadia* Gray, so successfully that all the species he considered to belong to *Emoda* are still considered to do so today. He confined the group to Cuba. H. B. Baker (1922), placing *Emoda* as a subgenus of *Schasicheila* Shuttleworth, examined the radulae of several species and chose *Helicina silacea* Morelet 1849 as the type. (See below for a further discussion of the generic and subgeneric placement of *Emoda*.) Aguayo & Jaume (1954) introduced several new taxa and briefly reviewed some of the older ones. Twenty-seven taxa have been proposed for the members of this genus; of these we recognize 16 and add one new taxon. Of the 17, 11 occur only in Oriente Province, 3 or possibly 4 in Las Villas, 3 in Camagüey, and 2 in Pinar del Río. Havana and Matanzas have only the widely ranging *E. submarginata*, which is also the only species occurring in more than one province. We have records of its occurrence in each of the six provinces of Cuba. All the other forms are found in only a single province and most of them in narrowly limited localities (Pls. 4, 5; Table 1).

Emoda is confined to the mainland of Cuba and to at least one of its satellite cayos or keys (Pl. 4). No species is known to occur on the Isle of Pines or elsewhere in the West Indies. *Emoda* probably had its origin in the eastern end of Cuba and especially in Oriente Province, since many more species exist in that area than elsewhere on the island. The most widely spread species in Oriente is *E. pulcherrima* and, with no opposing fossil records, it might be viewed as an early, if not the earliest, form of the genus. *E. submarginata*, which, with little difficulty, can be derived from *pulcherrima*, was in all likelihood the form which, because of its ability to populate lowland as well as hilly areas, spread the genus to other parts of the island. *Emoda bermudezi* and *E. najazaensis*, two forms found in Camagüey, the province immediately adjacent to Oriente, can be easily derived from *submarginata* and probably resulted from isolation in the mountain ranges of Cubitas and Najaza respectively.

The species found in Oriente occupy calcareous areas isolated by intervening volcanic rock. The isolation in the more western parts of the island results from mountain areas separated by noncalcareous lowlands. This isolation must have occurred during the late Tertiary, probably dating from the early Pliocene when Cuba more or less attained its present form. Only in this way can we account for such sharp differentiation as that shown, for example, between the two neighboring species *ciliata* and *briarea* in southern Las Villas Province.

The only area of clear overlap appears to be in the eastern part of Pinar del Río Province at the Sierra del Rosaria area of the Sierra de los Organos. Here *E. submarginata* and *sagraiana* both occur. The small form of typical *sagraiana* (see below, p. 105) is more easily derived from *submarginata* than is the larger form called "*percrassa*." It may be assumed that the former then is ancestral to the latter. As will be shown, however, isolation of the two *sagraiana* forms did not take place, and both, with numerous degrees of intergradation, occur throughout the range.

Species of *Emoda*, unlike *Viana*, are found in each of the six provinces of Cuba and occur from the eastern tip near Cabo Maisí in Oriente Province to the western limits of the Sierra de los Organos in Pinar del Río. They are largely confined to the mountain areas, except for one species with the widest distribution, *E. submarginata* (Gray), which also occurs in the lowlands. Though *Emoda* is for the most part an upland group, it is not as closely confined to a limestone substrate as *Viana*, and it is found on the ground under rotting leaves, and on branches and vines, as well as on calcareous rocks.

Alcadia striatura (Lamarck) from Puerto Rico, the type-species of the subgenus *Striatemoda* H. B. Baker 1940, is obviously not an *Emoda*, despite Baker's doubts on this point (1940: 71). Among other differences such as size, operculum, and color, it also lacks the diagonal, slightly curved axial furrows on the protoconch. The fact that it has no spiral sculpture is not significant, since most species of *Emoda* also lack this feature.

We have not been able to examine or at least confirm the location of some pertinent type material. Dance (1966) reported that the nonmarine shells of Pfeiffer, among which were many types of Cuban land shells, became part of the Dohrn collection in the Stettin (Szczecin) Museum, Poland, where it was totally destroyed during World War II. A personal communication (July 1968) from the museum director, Dr. W. Filipowiak, confirmed this fact. The words "type destroyed" in the text of this study reflect this situation.

The types of the species described by Poey and some described by Gundlach are presumably in the Museo Poey[1] in the University of Havana. In spite of repeated requests, we have failed to obtain permission from the museum authorities to examine the collection, nor has it been possible for us to have the presence of this material in the collection verified. Nevertheless, we suppose that the material is there and indicate this assumption by writing "Type, probably MP" in the body of the text.

The specimens examined are in the collection of the MCZ, unless otherwise noted.

ABBREVIATIONS USED:

MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts.
USNM	United States National Museum, Washington, D. C.
MP	Museo Poey, University of Havana, Havana.
BM(NH)	British Museum (Natural History), London.

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Genus *Emoda* H. and A. Adams

Emoda H. and A. Adams 1856, the Genera of Recent Mollusca, London, 2: 304 [as a subgenus of *Helicina* Lamarck 1799], (type-species, *Helicina silacea* Morelet 1849, subsequent designation H. B. Baker 1922: 56).

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[1] A new public museum has been established recently, with exhibits housed in the former Capitol building in Havana. This museum is called the Museo Felipe Poey and should not be confused with the older Museo Poey in the University of Havana.

Description. Shell generally about 15 to 30 mm in diameter, imperforate, depressed to moderately depressed, to subglobose, dull or moderately glossy and generally solid. Color brown, green, yellow, or reddish purple, banded in occasional populations or individual specimens. Outer lip simple to considerably thickened, generally with basal notch and or protuberance. Axial sculpture variable: smooth or with faint, irregular growth lines or with regular, irregular, or wrinkled ribs. Spiral sculpture generally wanting, or when present, consisting of rather faint incised lines or rows of small pits. Periostracum weak to strong, shining or lusterless, wanting in occasional species, sometimes raised in somewhat hirsute spiral ridges. Operculum auriculate, concave, thickest at columellar margin, thinning rapidly and becoming bladelike at outer margin. External calcareous layer of operculum nearly smooth, microscopically pitted, white, light brown, or reddish; internal chitinous layer reddish or brownish, marked by irregular, semicircular growth lines. Columellar edge raised in narrow ridge, generally straight but bent inward at top, forming a short, oblique furrow internally. Nucleus lateral and central on columellar edge.

Remarks. Emoda has at various times been regarded as a subgenus, either of *Schasicheila* Shuttleworth 1852 (Baker 1922; Thiele, 1929) or of *Alcadia* Gray 1840 (Wagner, 1907–1908; Keen, 1960). In this study, we follow Baker (1926) and Wenz (1938) and accord *Emoda* full generic rank in the subfamily Helicininae.

Although the shells of *Emoda* have several features in common with those of *Alcadia*, especially with the subgenus *Analcadia* Wagner, they are readily distinguishable. In *Emoda* the shells are generally larger, frequently considerably so, than the *Alcadia* from Cuba; the smallest *Emoda* shells are about 15 mm in diameter, whereas many species of *Alcadia* have shells considerably smaller. *Emoda* generally has a far more vivid coloration and at times is strongly sculptured. *Alcadia* is generally smooth, unicolored, or white with shades of brown or pink; these various colors are never arranged in bands. There are also constant differences in the opercula, especially at the raised columellar edge, which in *Alcadia* has the upper portion extended internally as a low, narrowly triangular protuberance, a condition not found in *Emoda*. Finally, *Alcadia* is primarily a Jamaican genus with some forms in Cuba and elsewhere, whereas *Emoda* occurs only on the main island of Cuba. The *Alcadia* closest to *Emoda* in appearance is the species *nuda* Pfeiffer 1866, and its subspecies, *E. n. bagaensis* Aguayo 1953, from Oriente. Here, however, an examination of the operculum will immediately reveal the true relationship.

The differences between *Schasicheila* and *Emoda* in shell and opercular structure are even more pronounced. The shells of *Schasicheila* are colorless and much more fragile, and the roundly inflated base gives it a shape that is never seen in *Emoda*. (See below for further discussion.) It also differs in the nature of the peristome at its insertions in the basal angle and the notch in the upper columellar angle. The wide parietal callus, found in all species of *Emoda*, is wanting in *Schasicheila*. Finally, the operculum, though superficially similar, differs as follows: in *Emoda* it always presents some color, either in the corneous layer alone or in both calcareous and corneous layers, whereas the operculum of *Schasicheila* is always white, with occasionally only a small area of light brown near the columellar ridge. The columellar margin of the *Emoda* operculum, as viewed from the side, is relatively straight or only very weakly sinuous and is more or less of the same width throughout, whereas in *Schasicheila* it is strongly bent inward at the center, and is noticeably thickest at the midline and thinnest at both terminations.

The radulae of *E. silacea*, *sagraiana*, and *ciliata* were described by H. B. Baker

(1922). In this discussion, we are using Baker's concepts and terms as defined on his page 30. He found that the radula of *Emoda* is typically that of the subfamily Helicininae. It possesses the central tooth complex of seven plates (one rhachidian and three paired), and a strong capituliform complex consisting of a strong, subrhomboid comb-lateral plate and a smaller, but heavy, accessory plate which is only weakly articulated with the comb-lateral. Baker found some variation among the three species he studied and felt that *ciliata* might belong in a special section. The paired central teeth and the comb-lateral are well cusped, with *ciliata* having a somewhat smaller number of cusps on the comb-lateral than the other two species. In addition, it has a few more inner bicuspid marginals than the other two: six or seven instead of four or five. Troschel (1857: 82, pl. 5, fig. 12) described and figured the radula of *E. submarginata* in much more general outline. His figure shows the accessory plate completely separated from the comb-lateral, whereas Baker demonstrates that the former articulates weakly with the latter.

Isenkrahe (1867) investigated the anatomy of *Helicina titanica* (= *Emoda pulcherrima titanica*). Bourne (1911), although he did not specifically study any *Emoda*, was able to make certain rectifications in Isenkrahe's work on the basis of his investigations of the closely allied genus *Alcadia*. Baker (1926) provided some notes on the anatomy of *E. sagraiana* and *E. submarginata*. Both Bourne (1911: 777) and Baker (1926: 35) commented on the general uniformity of the genitalia in the family and the uselessness of these characteristics for diagnostic purposes. For the present study, Dr. R. D. Turner of the Museum of Comparative Zoology dissected a specimen of *E. sagraiana* obtained from near Sumidero, Pinar del Río, which Dr. Hortensia Sarasúa of Marianao, Havana, Cuba, most graciously provided. A complete report of this investigation will be published by Dr. Turner later in this series of studies. For the moment, we are providing a few remarks and figures of the gross anatomy (Pl. 6).

In alcoholic specimens the color is variable, ranging from nearly uniformly ivory in immature specimens to dark gray or black in the adult. The base of the tentacles and the mantle are dark gray, the color gradually growing paler on the dorsal part of the foot and becoming almost ivory at the foot margin and the distal portion of the tentacles. The tentacles are long and slender, somewhat wider proximally. The eye is located on a low peduncle on the outer part of the base of the tentacle. The sole of the foot is creamy white, rounded anteriorly and bluntly pointed posteriorly. The columellar muscle at the insertion edge is long, curved, cream colored, and rounded at the interior end. The odontophore is long and curved and is provided with a short hook at the inner termination. Other details of the anatomy can be found in Baker (1926: 48).

KEY TO THE SPECIES OF *EMODA*

1. Shell large, adult generally 24–32 mm in diameter 2
   Shell smaller, adult generally 16–22 mm in diameter 10
2. Shell strongly sculptured 3
   Shell smooth or with weak growth lines only 6
3. Sculpture regular 4
   Sculpture irregular, of strong diagonal growth lines, shell yellow .... SILACEA
4. Sculpture of prominent spiral furrows, reddish color .... EMODA
   Sculpture of axial lines only 5
5. Shell green, generally *c.* 24 mm in diameter .... BAYAMENSIS
   Shell brownish red, generally *c.* 28–30 mm .... PULCHERRIMA TITANICA
6. Lip strongly expanded and strongly reflected .... SAGRAIANA
   Lip weakly expanded, not reflected 7
7. Shell wine colored, with white band at periphery and subsuturally .... BRIAREA
   Shell without band 8
8. Shell rufous, periostracum olivaceous .... CALEDONIENSIS
   Shell yellowish green 9

9. Shell with spiral lines on periostracum only .... CILIATA CILIATA
   Shell with spiral lines incised on surface .... CILIATA GUISANA
10. Distinct spiral as well as axial sculpture present 11
    Spiral sculpture very weak or absent 12
11. Shell with rounded carina, generally brownish .... SUBMARGINATA
    Shell with subacute keel, generally faintly greenish .... NAJAZAENSIS
12. Shell with distinct notch at parietal insertion of upper lip .... BERMUDEZI
    Shell without notch 13
13. Shell shape turbinate .... PULCHERRIMA PULCHERRIMA
    Shell shape subglobose 14
14. Sculpture of diagonal, straight, regular lines .... BLANESI
    Sculpture of vermiculate wrinkles 15
15. Shell small, adult reaching 16 mm .... MAYARINA MAYARINA
    Shell larger, adult reaching 22 mm 16
16. Sculpture strong, shell reddish green .... MAYARINA GUTIERREZI
    Sculpture narrower, color reddish .... MAYARINA MIRANDENSIS

Emoda silacea (Morelet)

Plate 1, figures 20, 21; Plate 5.

Helicina silacea Morelet 1849, Testacea Novissima Insulae Cubanae et Americae Centralis, 1: 20 (Cuba; type-locality, here restricted, El Yunque de Baracoa, Oriente; 3 syntypes, BM(NH) 1893.2.4.813–15).

Helicina ochracea Poey 1851, Memorias Historia Natural Isla de Cuba, 1: 112, pl. 11, figs. 1–4 (Baracoa; type, probably MP).

Helicina silacea Morelet, Pfeiffer 1862, Novit. Conch., 2: 197, pl. 52, figs. 11–15.

Alcadia (*Emoda*) *silacea* Morelet, Wagner 1908, *in* Martini & Chemnitz, Conch.-Cab., (2) 1: sect. 18, pt. 2, p. 100, pl. 18, figs. 10–12, 15.

Description. Shell reaching 28.5 mm in diameter, depressed turbinate, rather rough and solid. Whorls 4½, flattened, body whorl moderately inflated. Color pale greenish yellow, occasional specimens showing a faint brownish tinge, the color stronger at the interstices than on the axial cords. Some specimens with lighter peripheral band bordered by subperipheral brown band of varying width; spire and base generally lighter. Spire moderately raised, rounded. Aperture semilunate, outer lip unevenly curved, columella white, short, weakly convex above, concave below. Peristome strongly flaring but weakly reflected above, unevenly thickened, widest and thickest at or near the periphery, narrow above where it merges into the parietal callus, and below where there is a small protuberance of varying shape. Parietal callus thin, white in the columellar area, transparent near outer margin. Suture weakly impressed. Penultimate and body whorls prominently marked by more or less irregular, diagonal, somewhat wavy axial cords, separated by wider but quite shallow intervals. Sculpture weak on the early postnuclear whorls. Protoconch 1½ whorls, lighter in color than the rest of the shell, flattened, marked with faint, curved, diagonal, axial wrinkles. Periostracum thin and lusterless. Operculum as in genus, reddish in color, the internal corneous layer darker than the external, moderately lustrous calcareous lamina.

Height mm	Diameter mm	
17.0	28.5	El Yunque, Baracoa, Oriente
17.0	27.5	El Yunque, Baracoa, Oriente
15.5	23.5	Mayarí, Oriente
15.5	21.5	Finca "La Caridad," near Baracoa, Oriente

Remarks. This species is well characterised by its large size, prominent diagonal axial ornamentation, and striking uniformity of color, yellow predominating, with occasional specimens having a brownish tinge. At the type-locality, a large number of specimens have a lighter peripheral band bordered by a brown subperipheral band of varying width. The typical forms seem to be confined to El Yunque itself, the specimens from Mayarí being somewhat smaller and the ones from Finca "La Caridad" considerably so. This variation in size in different populations is quite common in the genus, and may be associated with the size of the area inhabited and/or variations in other features of the locality, such as the availability of food, shelter, etc. *E. silacea* differs from *pulcherrima titanica* of about the same size, in color, in being more depressed, in having a thicker lip and more irregular and lower axial costae.

Poey described *ochracea* because he failed to find the decussate base that Morelet had mentioned in his description of *silacea*. However, as Pfeiffer pointed out (1862: 198), Morelet was in error because he did not have a large enough sample when he wrote his description and considered an occasional variation to be a consistant feature.

Specimens examined. ORIENTE. El Yunque de Baracoa; Mayarí; Soledad, Guandoa, Baracoa; Finca "La Caridad" on road from Baracoa to Duaba.

Emoda sagraiana (Orbigny)

Plate 1, figures 16–19; Plate 4, figure 1.

Helicina sagraiana Orbigny 1842, Mollusques, *in* Sagra, Histoire Physique, Politique et Naturelle de l'Ile de Cuba, 1: 240, pl. 18, figs. 12, 13 (l'intérieur de l'Ile de Cuba; Cerro de Cuzco [not "aux environs de Trinidad"]; 4 syntypes, BM(NH) 1854.10.4.163).

Helicina sagra Sowerby 1847, Thes. Conch., 1: 3, pl. 1, fig. 10, pl. 3, fig. 126 (Cuba [error for *H. sagraiana* Orbigny]).

Trochatella (*Viana*) *sagra* "d'Orbigny" Chenu 1859, Manuel de Conchyliologie, Paris, 1: 496, fig. 3691 [error for *sagraiana*].

Helicina catalinensis Pfeiffer (July) 1856, Malak. Blät. 3: 56 (prope Catalina, provincia occidentalis insulae Cubae; type destroyed); Pfeiffer (Dec.) 1856, Novit. Conch., 1: 83, pl. 23, figs. 1–6.

Helicina cataliniana Sowerby 1866, Thes. Conch., 3: 278, pl. 1, fig. 8 [error for *catalinensis*].

Alcadia (*Emoda*) *sagraiana* d'Orbigny, Wagner 1908, *in* Martini & Chemnitz, Conch.-Cab., (2) 1: sect. 18, pt. 2, p. 94, pl. 17, figs. 1–4, pl. 18, fig. 13.

Emoda sagraiana percrassa Aguayo & Jaume 1954, Torreia, 21: 12, pl. 1, figs. 1–3 (Luis Lazo, Provincia de Pinar del Río; holotype, MP 17341).

Description. Shell 17 to 29 mm in diameter, depressed to moderately raised, generally smooth. Whorls about 5¼, very slightly rounded, body whorl depressed, rather narrowly rounded at the periphery. Color generally brownish, from pale yellowish buff to bright orange-brown; occasional specimens with an olivaceous tinge, others with a lighter peripheral band, spire and callus frequently reddish. Spire moderately raised, rounded, domelike, the same color as the rest of the shell, occasionally reddish, rarely darker, sometimes lighter. Aperture widely semilunate, somewhat extended laterally and more or less regularly rounded in peripheral region, white near lip, brownish in the interior. Lip thickened, occasionally very much so, slightly flaring, rarely reflected above. Basal callus slightly raised, white in columellar region, transparent near outer margin, as extensive as, but more rounded than, the aperture. Columella short, oblique, white, concave below; basal notch usually deep, acute or obtuse; basal tooth low, rounded. Suture moderately impressed. Axial sculpture of very fine, irregular, diagonal growth lines. Spiral sculpture wanting. Protoconch 1¼ whorls, sublustrous, slightly raised, faintly marked by curved, retractive, axial wrinkles. Periostracum thin but strong, light or dark brown or olivaceous, in some specimens brown tinged with green. Operculum as in genus, large, strong, calcareous lamina white, or tinged with faint reddish brown, generally on one plane but curved sharply and shortly inwardly below; internal corneous lamella thin, brownish, somewhat darker at the margins.

Height mm	Diameter mm	
21.5	29.0	La Claraboya, Luis Lazo
17.5	28.3	Ensenada de los Burros, Cabezas
17.5	26.0	Caiguanabo, Consolación del Norte
17.5	25.5	Bejarano, Canalete
16.0	25.5	Galalón, San Andrés
16.0	24.5	Catalina, San Diego de los Baños
15.5	23.5	Sierra Paso Real, Guane
15.5	23.3	Cafetal "La Villa," Candelaria
15.0	23.5	Galalón, San Andrés
14.5	24.0	Pan de Azúcar, Viñales
13.5	19.5	La Muralla, Guane

Remarks. A highly polymorphic species, *E. sagriana* varies from a small brownish form with an acute basal notch and relatively thin peristome to large greenish forms with a red spire and/or callus and an exceedingly heavy lip. In between are found all kinds of intergrades scattered throughout the range. The smallest forms come from around Guane near the western terminus of the Sierra de los Organos, but almost similar forms are found near Catalina, toward the eastern end. The heavy, thicklipped form, to which Aguayo & Jaume gave the subspecific name of *percrassa*, occurs generally in the region of Luis Lazo, Sumidero, and Cabezas, in the west central portion of the Sierra de los Organos; specimens which cannot be separated from those found here also occur, together with the smaller, more typical specimens toward the east at San Andrés, Consolación del Norte, and San Diego de los Baños. The populations at Ensenada de los Burros in Cabezas and at Finca "La Güira" near Luis Lazo can be readily divided into the small brownish form with the acute notch and thin lip, and the large, heavy lipped form with the obtuse notch and heavy peristome. The complete lack of intergrades in these localities argues strongly that here are two distinct sympatric groups that readily deserve specific distinction. These clear differences, however, fade away in the populations from the eastern end of the range around the Sierra San Andrés and San Diego de los Baños, where many arbitrary decisions are needed to place the majority of the specimens.

Aguayo & Jaume (1954: 4) well described the confusion that seems to exist: "We are confronted by the following dilemma: either we name all the variants which occupy more or less restricted areas ('microspecies' or incipient subspecies), thus increasing the confusion of the present nomenclature, or we put all the diverse forms under a single specific name, thereby creating the error of postulating a uniformity that is far from the truth" (translated). They go on to suggest that only the two extreme forms be given names (*sagraiana* and *percrassa*) and that the intermediary colonies be designated by the "conventional" formula: *Emoda sagraiana* Orbigny tr. *percrassa*. This is obviously no solution, since the determination of just where extreme forms end and the intermediary forms begin will have to be largely subjective. Moreover, we agree with Mayr (1969: 46) who wrote, "Now that it is being realized that every local population is different from every other one, even if they live only a few miles apart or less . . . . there is no longer any excuse for a formal recognition of innumerable local subdivisions of subspecies." On the basis of the data and the large amount of material available to us at present, we can only conclude that we are dealing with a highly complex and variable species whose component parts cannot be completely understood without intensive biometric and ecological study. For the present, we feel that least confusion will result if all the *Emoda*-like populations in the Sierra de los Organos mountain complex are considered *sagraiana*. This interpretation should prove as utilitarian as calling all the polymorphic populations of the littoral marine species *Thais lapillus* in the Western Atlantic or *T. lamellosus* in the Eastern Pacific.

Specimens examined. PINAR DEL RÍO. *Guane:* Sierra de Guane; "Sierra Mendoza"; Sierra Paso Real; La Muralla; Punta de la Sierra. *Luis Lazo:* Sierra San Carlos; La Caoba; Sierra Los Acostas; La Cetricina; La Claraboya; La Güira; El Potrerito; La Estrechura; El Junco; Ensenada del Barrio, Pica Rica, and Mogote La Güira, Sumidero. *Cabezas:* Valle Isabel María; Ensenada de los Burros; Sierra La Majequilla, Petiablanca; Ensenada Chica; Valle de Cabezas; Mogote Cementerio; Sierra del Quemado. *Viñales:* Potrero de Manuel Sánchez near Capón; Arroyo Melindre; Kilometer 14; Mogote de la Vega No. 3; Mogote Capón; Sierra Penitencia; Sitio del Infierno; Sierra Derrumbada; Sierra Celadas; Sierra Celadas on the road to La Mina Matahambre; Mina Matahambre; Hoyo de los Cimarrones, Sierra del Infierno; El Cuajaní; Los Peladores at summit of Sierra del Infierno; Sierra del Infierno; Sierra el Martillo; El Queque; Ensenada del Valle, El Queque; Sierra de Galeras; Mogote Pequeño; Mogote Rojas; Mogote Dos Hermanos; Puerta del Ancón; Lorenzo López, 1 km N of Viñales; Hoyo Jutía; El Cejanal; Hoyo de Fania, Palmarito; Ensenada de Martín Miranda, Palmarito; Hoyo de Lorenzo Martínez, Palmarito; Las Delicias; Cueva de los Santos, Palmarito; Sierra de Palmarito; Mogote Quillo; El Punto, Pan de Azúcar; Pan de Azúcar; Hoyo Largo, San Antonio; Hoyo de los Muertos; Mogote José María García. *San Vicente:* La Chorrera; Mogote la Mina Constancia; Mogote Jutía, 1 km E of Baños de San Vicente; Baños de San Vicente; Ensenada de los Baños; Mogote Pequeño, Costanera de San Vicente; Hoyo del Ruiseñor, Ancón; Cueva del Río, Baños de San Vicente; Costanera de San Vicente; Mogote de la Resbalosa; Mogote del Marmol and Laguna de Piedras; Sierra del Abra; Punta de la Costanera de San Vicente; Ensenada de San Vicente; Las Cuevitas, Ancón; Puerta del Ancón. *Consolación del Norte:* Monte Largo, Pico Chico; Mogote Caseajal near Pico Chico; Mogote Grande SW of Pico Chico; Puertecitos de Caiguanabo; Los Portales, Caiguanabo; Farallón de las Avispas; Pico Grande; Bejarano, Canalete; Abra de Bejarano; "Sierra Canalete"; Sierra San Andrés; La Sierra; Sitio de la Sierra; Mogote de la Cidra; Mogote de la Palma; Mogote el Indio; Ensenada de la Ayúa; Pasada de la Ayúa; La Jagua; La Jagua de Azquiz; Sierra Gloria, N of Colmillo de la Vieja; Colmillo de la Vieja; Los Caracoles; Abra de la Colmena; Colmena de Piedra, Galalón; Sierra Grande, Guacamaya. *San Diego de los Baños:* Mogote de la Finca; Mogote el Bosque; La Catalina, N of San Diego; Cayito, 3 mi. from La Catalina; Hoyada de la Catalina; Mogote Colorado; Pinalito; Mogote de los Indios; Los Cayitos, Catalina, N of San Diego de los Baños; Cueva del Indio. *Guajaibón:* San José de Sagua; SW of Pan de Guajaibón; San Juan de Sagua; Sierra Chica; Rancho Lucas, W of Guajaibón; Sierra de Juan de Guacamaya, Bahía Honda; Hato Sagua; Caimito; La Furnia; Sierra la Güira; El Toro, Sierra Limones. *Cabañas:* El Guabinacho; 2 mi. N of Santa Cruz; Las Animas, Rangel; El Retiro, Rangel; El Mamey, Callajabos (Cayajabos); Loma de Gloria; Rancho Mundito, Rangel; Subida al Rangel; El Taco. *Candelaria:* Escuela de Frias; Cafetal "La Villa."

Emoda pulcherrima pulcherrima (Lea)

Plate 1, figures 14, 15; Plate 2, figures 13, 14; Plate 3, figures 6, 7; Plate 5.

Helicina pulcherrima Lea 1834, Trans. American Phil. Soc. (NS), 5: 49, pl. 19, fig. 57 (Java?); 1834, Observations on the Genus *Unio*, Philadelphia, 1: 161, pl. 19, fig. 57 ("Java?"; lectotype, probably figured specimen, here selected, USNM 104613; paralectotypes, USNM 104613a, 104609, 104595, all from Lea collection; type-locality, here selected, Guantánamo).

Helicina crassa Orbigny 1842, Mollusques, *in* Sagra, Histoire Physique, Politique et Naturelle de l'Ile de Cuba, 1: 243, pl. 19, fig. 5 [not fig. 6] (intérieur de l'Ile de Cuba; type, BM(NH) 1854.10.4.167).

Helicina pulcherrima Lea, Pfeiffer 1850, *in* Martini & Chemnitz, Conch.-Cab., (2) 1: sect. 18, pt. 1, p. 17, pl. 1, figs. 5–7, pl. 6, figs. 5, 6 (die Insel Cuba).

Helicina rubrocincta Poey 1854, Memorias Historia Natural Isla de Cuba, 1: 417, pl. 33, figs. 16–19. ("Probablemente en el departmento oriental"; type, probably MP.)

Description. Shell about 18 mm in diameter, depressed globose, strong. Whorls 4½, flat, body whorl descending shortly near the aperture. Color varied, light green with darker green, irregular, faintly sigmoid, axial bands, or light to dark reddish brown; spire usually lighter. Occasional specimens have a narrow, light-colored peripheral band. Spire moderately raised, rounded. Aperture widely semilunate, white inside; peristome thickened, moderately reflected, widest at center, gradually narrowing at extremities, with a small, elongate, rounded, toothlike protuberance near the basal notch. Columella short, white, barely convex, more strongly so below the mid-point. Parietal callus strong, as wide as the aperture, white in the columellar region, darker near the outer, rounded edge; in occasional specimens the entire callus is white, a possible gerontic sign. Body whorl sculptured with strong, regular, rounded axial cords, wider than the intervals, weaker and less regular on the base and the spire. Protoconch 1½ whorls, moderately raised, with irregular, curved axial wrinkles. Periostracum strong, shining, usually wanting on early whorls. Operculum with white or light reddish calcareous lamina, and brown or reddish corneous one.

Height mm	Diameter mm	
15.1	20.6	Lectotype (USNM)
15.5	21.5	Mayarí, Oriente
13.5	19	Monte Turquino, Oriente
13.0	19	Los Arroyos, Miranda, Oriente
11	16.5	Loma del Gato, Guantánamo, Oriente

Remarks. This subspecies is confined to the entire southern portion of Oriente Province. It is characterized by its generally small size, green or brown color, and especially by the strong, regular axial sculpture on the body whorl. Even brown specimens, which superficially resemble *submarginata*, can be distinguished by their sculpture. Near the Loma del Gato in Guantánamo, there is a well-marked race of small specimens in which the color is grayish green or pale olivaceous with a light-colored spire and strong basal callus. They have the characteristic strong axial ridges.

We agree with Pfeiffer (1850: 17) that *crassa* Orbigny is synonymous with *pulcherrima*. Orbigny wrote, "fortement striée dans le sens de l'accroissement" (1842: 243), which is characteristic of *pulcherrima* (pl. 3, figs. 6, 7). We have no way of judging *crassa* from Cajo [sic] Seco, "westlich von Cuba" (Wagner, 1907: 98, pl. 19, figs. 5, 6). This is certainly an error in locality.

Poey gave the name *rubrocincta* to specimens of *pulcherrima* with a rather vivid red and white peripheral band. But in *pulcherrima*, as in other species of *Emoda*, banded and unbanded forms exist in the same populations. Lea (1834b: 162) noted that the species had an "indistinct white and brown band," and in his remarks, he mentioned the fact that the band sometimes consists of a white line only. We therefore follow Wagner (1907: 97) in recognizing *rubrocincta* Poey as a synomym of *pulcherrima.*

The lectotype, here selected, appears to be the specimen figured by Lea. Both have the same dimensions and the descriptions agree. The copied label in the USNM read "Cuba," though Lea's (erroneous) locality was "Java." No original Lea label was found.

Specimens examined. ORIENTE. Níquero; Road to Mora; La Vigía, E of Mora; Pico Turquino; Loma del Gato; Mountains N of Imias; Finca "Santa Teresa," Barrio Florida, Songo; Los Arroyos, Miranda; Banabacoa; Dos Bocas, N of Santiago de Cuba (USNM); Santa María de Loreta, near Tiarriba (USNM); Loma Gran Piedra, N of Santiago de Cuba (USNM); between Aguadores and Las Lagunas, E of Santiago de Cuba (USNM); loma (hill) E of Siboney (USNM); road from Loma de la Bandera near Pinar de Mayarí; woods at Arroyo Blanco, Mayarí (USNM); Canapa, Mayarí; El Purio, Mayarí.

Emoda pulcherrima titanica (Poey)
Plate 2, figures 8, 9; Plate 5.

Helicina titanica Poey 1851, Memorias Historia Natural Isla de Cuba, 1: 110, pl. 11, figs. 13–16 (las costas de Baracoa [Oriente]; type[1], probably MP).

Helicina titanica Poey, Pfeiffer 1862, Novit. Conch., 2: 196, pl. 52, figs. 6–10 (Mata [Baracoa]).

Alcadia (*Emoda*) *pulcherrima titanica* Poey, Wagner 1908, *in* Martini & Chemnitz, Conch.-Cab., (2) 1: sect. 18, pt. 2, p. 99, pl. 17, figs. 13–15, pl. 18, fig. 16.

Description. Shell like that of *pulcherrima* but differing from the nominate form in its generally considerably larger size,

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[1] The type-specimens can be identified by the crab hole (10 mm × 5 mm) in the columellar region (Poey, 1851: 111).

which reaches 29 mm in diameter. The color is more uniformly brownish; occasional specimens have an olivaceous tinge. The characteristic strong axial sculpture is easily apparent, even to the naked eye.

Height mm	Diameter mm	
23.0	29.0	Baracoa, Oriente
21.0	28.0	Mandinga, Baracoa, Oriente
20.5	26.0	Barigua, Oriente
18.0	25.0	Baracoa, Oriente
16.5	21.0	Veguitas, Baracoa, Oriente

Remarks. This subspecies is limited to the area around Baracoa, Oriente. This distribution and its considerably larger size would be enough to regard it as a full species, but the only difference in shell morphology from *pulcherrima pulcherrima* is its size. Consequently we concur with Wagner in considering it a subspecies. One lot of four specimens from Veguitas, Baracoa, can almost be regarded as intermediate in size between *p. pulcherrima* and *p. titanica.*

Poey described this form from a series of dead shells, each of which had a hole in the columellar region. Poey thought the shells had been perforated by the animal to provide more space for its oversized body (1851: 110). Pfeiffer (1862: 197) correctly identified the holes as having been made by hermit crabs, which inhabit empty shells. (See also Arango, 1878: 87).

Specimens examined. ORIENTE. *Baracoa:* Veguitas; Mandinga; Barigua; Boca de Yumurí; La Cantera de Miranda; Mata; Manglito, Barigua.

Emoda submarginata (Gray)

Plate 1, figures 1, 2; Plate 4, figure 2; Plate 5.

Helicina submarginata Gray 1825, Zool. Jour., 1: 68, pl. 6, fig. 11 (no locality given; type-locality, here restricted, Sierra El Grillo, near Cotorro, Havana Province, Cuba; type,[1] BM(NH) ?).

Helicina rubra Pfeiffer 1839, Wiegmann, Arch. Naturg., 5th year, 1: 355 (Cuba); type destroyed.

Helicina submarginata Gray, Orbigny 1842, Mollusques, *in* Sagra, Histoire Physique, Politique et Naturelle de l'Ile de Cuba, 1: 244, pl. 19, fig. 8 [not 7] (l'intérieur de l'Ile de Cuba).

Helicina submarginata Gray, Pfeiffer 1850, *in* Martini & Chemnitz, Conch.-Cab., (2) 1: sect. 18, pt. 1, p. 16, pl. 1, figs. 8–10 (Matanzas, Retiro).

Alcadia (*Emoda*) *pulcherrima planospira* Wagner 1908, *in* Martini & Chemnitz, Conch.-Cab., (2) 1: sect. 18, pt. 2, p. 98, pl. 19, figs. 8–10 (die Insel Cuba; type in Warsaw Zoological Museum 8338).

Emoda zayasi Aguayo & Jaume 1954, Torreia, No. 21, p. 12, pl. 2, fig. 7 (Sierra del Cristal, Sagua de Táñamo, Provincia de Oriente, Cuba; holotype, MP 17366).

Description. Shell 15 mm to 20.5 mm in diameter, depressed conic, strong, barely carinate. Whorls 5½, flattened, body whorl barely descending at aperture. Color varied, yellowish olivaceous with light green spire, or reddish with a pale orange base, or reddish brown with paler spire and base, usually with light colored, narrow peripheral band. Spire moderately raised, broadly depressed conic or low turbinate, generally same color as rest of shell. Aperture sublunate, palatal lip thickened, barely expanded, with a shallow notch just in front of a low basal tooth. Columella white, gently concave, barely rounded at insertion in basal portion of lip and extended into a triangular lamella that ends at the basal tooth. Parietal callus porcellanous, as wide as the aperture, ground color of shell showing through on outer margin. Sculpture of variously strong, diagonal growth lines and a few widely spaced, concentric spiral lines, seen as slightly raised cords in the periostracum. These periostracal cords are reflected as lines of minute pits in the shell surface. Protoconch 1½ whorls, usually lighter in color than the rest of the shell, faintly marked with gently curved, diagonal, irregular axial wrinkles. Periostracum thin, usually absent on upper whorls. Operculum as in genus, calcareous layer lustrous, thin, white, internal corneous lamina orange-brown.

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[1] Peake writes (in litt.) that the BM(NH) has several lots of specimens, but nothing to identify any as the type.

Height mm	Diameter mm	
13.0	20.0	Yaguajay, Las Villas
12.5	20.5	El Grillo, Havana
12.0	18.0	Piedras de Amolar, Escambray, Las Villas
11.5	15.0	El Retiro, Matanzas

Remarks. This species ranges from the eastern[1] part of Pinar del Río Province at Artemisa to Mayarí in Oriente and thus has the most extensive range of any *Emoda.* The distribution is not continuous. This discontinuity is probably due to incomplete collecting in the intervening areas. We have but a single record of this species from Camagüey. This province, however, is probably the least collected area in Cuba. In Camagüey, *submarginata* is replaced in two important localities, Sierra Najaza and Sierra Cubitas, by the closely related species *najazaensis* and *bermudezi,* respectively.

E. submarginata is quite uniform throughout its range. The color varies somewhat from dark brown to light brown, and some olivaceous specimens appear. Occasional specimens have a light colored peripheral band. The incised spiral cords vary in strength but some indications of them are usually present. There is likewise little significant variation in size. The smallest specimens are from El Retiro, Matanzas (15 mm in diameter), and the largest from Havana (20.5 mm), but the great majority vary between 18 and 20 mm.

The color, weak axial ribs, and the presence of spiral lines on *pulcherrima planospira* Wagner place this form in the synonymy of *submarginata* rather than in *pulcherrima.*

Specimens examined. PINAR DEL RÍO. Las Cañas; Las Mangas, Artemisa; foothills of Rangel. HAVANA. San Antonio de los Baños; Sierra El Grillo (type-locality); Sitio Perdido; Loma Camoa; Mantilla; Madruga; El Inglés; La Canabrava; Finca "La Belianza," Cotorro; Peña Blanca, Sierra Anafe; Jaruco. MATANZAS. Elena, El Palenque; Cotorra; Dos Cecilias, Coliseo; Jaguey Grande; Abra de Figueroa, Valle de Yumurí; Cueva el Negro, San Miguel; Canasí Rd., near El Pacito; Loma del Fine, Cárdenas; Bridge over R. Canímar, Matanzas-Limonar Rd.; 20 mi. SE of Matanzas; Ceiba Mocha; Vista Alegra (USNM). LAS VILLAS. *Soledad:* Mogote el Palmar; Botanical Garden; Guabairo; Loma de la Jutía, Vilche's Potrero; Sagua la Grande; Mina Carlota, about 12 mi. E of Soledad; Laza del Medio; El Mamey; San Lorenzo; Jumagua; Mogote W of La Jumagua. *Trinidad:* Northwest of La Vigía; Sierra de Santa Rosa. *Yaguajay:* Yaguajay-Remedios Rd.; Cerros de Yaguajay; Guainabo; El Tigre; Punta Judas; Sierra Judas de la Cunagua. *Remedios*: El Mamey; Los Hatillos; La Culebra; Loma Caraballo; Dos Sierras; Buenavista; La Puntilla (USNM); Cerro Guajabana. *Caibarién:* Finca "Cueta"; Loma de Petrera; Punta Caguanes, Buenavista Bay; Santa Rosa; Cayo Conuco; Cayo Lucas; San Joaquín, Esperanza; El Boquerón, Jatibonico; San Agustín, Zulueta; Piedras de Amolar, Escambray; Villa Ciba, Carretera de Camajuaní; Chicharrón, Sierra Vega Alta; La Vigía, Mayajigua; Sierra de Canoa, Los Llanados; Monte Cagüeiras, Sancti Spiritus; Sierra 3 km S of Dolores. CAMAGÜEY. Punta Alegre. ORIENTE. Camino de la Loma de la Bandera, Pinar de Mayarí; Mayarí; between Sagua de Táñamo and Cananova.

Emoda ciliata (Poey)

Plate 1, figures 7–9; Plate 4; figure 1.

Helicina ciliata Poey 1851, Memorias Historia Natural Isla de Cuba, 1: 109, pl. 11, figs. 5–8 (Trinidad [Las Villas]; type, probably MP).

Helicina fossulata Poey 1857, Memorias Historia Natural Isla de Cuba, 2: 25 (Trinidad, [Las Villas]; syntypes, probably MP; paratype, MCZ 263901 from the Anthony Collection collected by Dr. Gutierrez, San Juan de Letrán, Santa Clara [= Las Villas]).

Alcadia (*Emoda*) *ciliata* Poey, Wagner, 1908, *in*

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[1] Fořcart (1950: 71) identified *E. submarginata* from Pinar del Río between the city of Pinar del Río and Viñales. We have not seen the specimens but suspect that the identification is in error.

Martini & Chemnitz, Conch.-Cab., (2) 1: sect. 18, pt. 2, p. 102, pl. 8, figs. 5–6; pl. 19, figs. 14–17 (Trinidad und Banao auf Cuba).

Description. Shell reaching 27 mm in diameter, strong, widely turbinate, smooth but lusterless, rounded at periphery. Whorls 5½, moderately convex, body whorl rounded at base, barely descending near aperture. Color predominantly light yellow, occasional specimens faintly tinged with brown; white when decorticated, with an indistinct, whitish subsutural band continued subperipherally on the body whorl. Spire depressed, dome shaped. Aperture widely semilunate, yellowish within. Palatal lip white, strongly thickened, moderately flaring. Basal denticle small and obtuse. Parietal callus smooth, thick, white in the columellar region, transparent near the rounded outer margin, more rounded than the aperture. Columella short, oblique, very weakly sigmoid, angled above, slightly rounded at insertion with basal lip. Suture moderately impressed. Shell smooth, marked by very fine, curved, diagonal growth lines. Protoconch 1¼ whorls, barely raised, moderately lustrous, approximately same color as rest of shell, marked by fine, curved, axial wrinkles. Periostracum strong, closely marked by irregular spiral cords of raised periostracal material, not reflected in the shell surface beneath. Operculum as in genus, light to dark reddish brown near the outer margin.

Height mm	Diameter mm	
19.0	27.0	Banao, Las Villas
19.0	25.5	Ciegos de Ponciano, Las Villas
15.5	19.5	San Juan de Letrán, Las Villas; paratype of *fossulata*.

Remarks. This relatively large-shelled species is readily distinguishable from the others of more or less equal size by its uniformly yellow color and depressed shape. It differs from *silacea*, the other species in which yellow predominates, by its smooth, almost unsculptured surface. It apparently has a limited range in the mountains between Trinidad and Sancti Spiritus in the southeastern part of Las Villas Province.

Helicina fossulata Poey is only a color form with a peripheral band. Poey wrote of *ciliata*, "Color es ya de un amarillo bajo, ya de un moreno rojizo," and of *fossulata*, " . . . . sordide rubra . . . cingulis duobus flavidis ornata, quorum alter ad suturam, alter ad peripheriam." The type locality of both forms is "Trinidad" and the only difference seems to be the presence of a spiral peripheral band in *fossulata*. Elsewhere we show that banded and unbanded forms frequently occur in single populations.

Specimens examined. LAS VILLAS. Banao, Sancti Spiritus; Ciegos de Ponciano; Camino de Banao, Sancti Spiritus; San Juan de Letrán.

Emoda ciliata guisana (A. J. Wagner)
Plate 1, figures 10, 11.

Alcadia (Emoda) ciliata guisana A. J. Wagner 1908, *in* Martini & Chemnitz, Conch.-Cab., (2) 1: sect. 18, pt. 2, p. 102, pl. 18, figs. 7–9 (Guisa auf Cuba; types in Warsaw Zoological Museum 8353).

Description. Shell like that of *ciliata*, differing from the nominate form by the presence of shallowly incised, parallel, spiral lines on the shell, as in *submarginata*. These lines seem to correspond to periostracal structures found in *ciliata ciliata*, but in that subspecies they do not affect the shell, being found in the periostracum only. Color yellowish, as in *ciliata*, but in some specimens there is a faint reddish tinge.

Height mm	Diameter mm	
18.5	25.5	"Cuba"
18.0	25.0	[Guisa, Bayamo, Oriente] (?)

Remarks. Wagner stated that this subspecies came from "Guisa auf Cuba." Some students have taken this to mean Guisa, near Bayamo in Oriente Province. This is most unlikely, since *ciliata ciliata*, whose distribution is limited to central Las Villas, has not been found in Camagüey Province, which separates Las Villas from Oriente Province. Either there is a Guisa—a small finca or miniscule settlement—in Las Villas, or Wagner's locality is in error. The military map of Cuba cites no Guisa from Las Villas. We are keeping this name provisionally since the material at hand is not sufficient to indicate whether the incised spiral lines are characteristic of individuals or of an entire colony.

Specimens examined. "Cuba"; Guisa.

Emoda emoda (Pfeiffer)

Plate 2, figures 6, 7; Plate 5.

Helicina emoda Pfeiffer 1865, Novit. Conch., 2: 253, pl. 64, figs. 6–8 (parte orientali ins. Cubae; [Monte Toro, based upon Pfeiffer 1860: 77]; type destroyed).

Alcadia (*Emoda*) *sagraiana emoda* Pfeiffer, Wagner 1908, *in* Martini & Chemnitz, Conch.-Cab., (2) 1: sect. 18, pt. 2, p. 96, pl. 17, figs. 7–9.

Description. Shell reaching 31 mm in diameter, moderately strong and relatively smooth. Whorls 5½, moderately rounded, body whorl depressed, descending sharply at aperture. Color of body whorl bright green, reddish brown when decorticated; spire reddish, periphery banded by a whitish line margined above and below by dull, narrow, reddish bands. Spire relatively high and dome-shaped. Aperture widely semilunate, white inside; peristome thickened, moderately flaring, not reflected, basal tooth generally weak. Parietal callus smooth, rounded, larger than the aperture, white near the columella and transparent near the outer margin. Columella short, white, slightly sigmoid, the wider curve below, and briefly rounded near the basal tooth. Suture moderately impressed, roughened by the terminations of the growth lines. Sculpture of low, irregular, moderately strong growth lines crossed by impressed, closely spaced spiral furrows, most closely approximated at the base and weaker on upper whorls. Protoconch 1¼ whorls, reddish, smooth, faintly marked by irregular, curved, diagonal axial riblets. Periostracum strong, green on body whorl, weaker and reddish on spire. Operculum as in the genus.

Height mm	Diameter mm	
23.5	31.0	Manatial, Santa Fé, Oriente
22.0	30.5	Guaso, Guantánamo, Oriente
18.0	28.0	El Codrito, Monte Libano, Oriente

Remarks. This is a well-marked species from near Guantánamo in Oriente Province. Pfeiffer thought it might be related to *briarea* from Las Villas Province because of its large size, but *emoda* has a more elevated shape, the shell is not so solid, the color differs markedly and the spiral sculpture is completely wanting in *briarea*. Wagner (1907: 96) confused it with the larger *sagraiana* from Luis Lazo in Pinar del Río Province, but that shell is somewhat smaller, more depressed, heavier, has a far thicker, more reflected lip, and lacks the spiral sculpture. Pfeiffer's figures are of decorticated, weathered specimens but they show (especially his fig. 8) the spiral sculpture quite clearly. This species is remarkably constant in its color but, like many *Emoda*, it varies in size. The populations from Monte Libano consist of smaller shells which, however, clearly belong to *emoda* because of the elevated shape, the green and reddish color, and the presence of spiral lines. Although the type-specimens have been destroyed, there is no doubt regarding the identity of this species. Pfeiffer's figures are unusually good and we have examined several lots from near the type-locality.

Specimens examined. ORIENTE. La Subida de la Hembrita; Guantánamo; El Codrito; Monte Libano; Montaña de Guantánamo; Manatial de Santa Fé; 1 mi. NW of Guaso; N of Guantánamo City.

Emoda caledoniensis, new species

Plate 2, figures 11, 12; Plate 5.

Holotype, MCZ 261352, from Mina Caledonia, Mayarí, Oriente. L. R. Rivas, collector.

Paratypes, MCZ 261350; USNM 463790, both from the same locality as the holotype; MCZ 261348, from Brazo del Pino, Woodfred, Mayarí, Oriente; MCZ 261351 from Sierra del Cristal, Mayarí, Oriente.

Height mm	Diameter mm	
21.5	30.5	Brazo del Pino, Paratype
21.0	28.0	Brazo del Pino, Paratype
20.0	29.0	Sierra del Cristal, Paratype
19.5	28.0	Mina Caledonia, Holotype
17.0	24.0	Mayarí, 1 km from the pine forest, Paratype

Description. Shell reaching 30.5 mm in diameter, inflated, smooth and moderately solid. Whorls 5½, moderately rounded, body whorl inflated, weakly shouldered obliquely below the suture, rounded at the periphery, shortly descending near the aperture, where it blends into the basal callus. Color olivaceous, with irregular darker axial streaks, light brick red in decorticated specimens. Spire moderately raised, rounded, darker than rest of shell. Aperture semilunate, lip moderately thickened, flaring, barely reflected above, widest near the center, narrowing at each extremity; basal tooth small, rounded, basal notch barely perceptible. Columella short, white, slightly sigmoid and rounded below. Basal callus smooth, larger than the aperture, white in columellar region, transparent at outer margin. Axial sculpture of very fine, diagonal growth lines, spiral sculpture wanting. Suture moderately impressed, somewhat roughened by the terminations of the growth lines. Protoconch 1½ whorls, faintly marked by curved, axial wrinkles. Periostracum strong, olivaceous or green. Operculum as in genus, calcareous layer white, inner corneous layer reddish, darker at margins.

Remarks. The four lots in MCZ upon which this description is based all come from the region around Mayarí in Oriente Province. This new species belongs to the group of large, predominantly greenish or olivaceous shells with a reddish spire from the eastern part of the country. It differs from *pulcherrima titanica* from Baracoa by its higher spire and in the absence of the strong, regular, axial sculpture; it is generally smaller and more rounded than *E. emoda* from Guantánamo and lacks the spiral sculpture of closely set incised lines.

Emoda bayamensis (Poey)

Plate 2, figures 4, 5; Plate 5.

Helicina bayamensis Poey 1854, Memorias Historia Natural Isla de Cuba, 1: 416, pl. 33, figs. 7–10 [not 8–11] (Bayamo [Oriente]; lectotype, here selected, MCZ 73855, Buena Vista, Bayamo, Oriente, Anthony Collection, from Poey; paralectotype MCZ 256496, same locality. The shells in MCZ from which the type selections were made were identified as type material by Torre in June 1912).

Helicina bastidana Poey 1854, Memorias Historia Natural Isla de Cuba, 1: 415, pl. 33, figs. 11, 12 (Puerto Príncipe [= Camagüey]; type, probably MP).

Helicina bayamensis Poey, Pfeiffer 1862, Novit. Conch., 2: 199, pl. 53, figs. 1–5.

Helicina jeannereti Pfeiffer 1862, Malak. Blät., 9: 6 (Mayarí [Oriente]; type destroyed).

Helicina bayhamensis "Poey" Reeve 1873, Conch. Icon., Helicina, 19: pl. 2, fig. 11 (Cuba) [error for *bayamensis*].

Helicina bastidiana "Poey" Reeve 1873, Conch. Icon., Helicina, 19: pl. 8, fig. 61 (Cuba) [error for *bastidana*].

Description. Shell reaching 23 mm in diameter, depressed globose and solid. Whorls 4¼, weakly convex, body whorl moderately inflated, depressed but not carinate at the periphery. Color of body whorl olivaceous and sometimes tinged with brown, with narrow, irregular, dark green axial stripes; spire much lighter; occasional specimens with a yellowish peripheral band generally margined with red. Spire moderately raised, rounded, lighter in color than the rest of the shell. Aperture semilunate, irregularly rounded, inside margin of upper lip diagonal, almost straight. Lip white, well expanded, but not reflected, unevenly rounded, somewhat extended just above the periphery, widest centrally, narrowing rapidly at the extremities; basal tubercle small. Columella short, white and weakly sigmoid. Parietal callus smooth, thin, white in the columellar region, transparent near outer margin. Suture moderately impressed. Sculpture of irregular, curved, axial cords, weaker and less regular than in *pulcherrima*, weaker on the base, almost obsolete on earlier whorls. Operculum and periostracum as in the genus.

Height mm	Diameter mm	
15.0	23.0	Buena Vista, Bayamo, Oriente, Lectotype
14.0	21.5	Paralectotype

Remarks. Poey described *bastidana* and *bayamensis* at the same time, but in 1865 (p. 144) he selected *bayamensis* as "el tipo común" and wrote that *bastidana* "es una variedad, y muy rara." It seems to be nothing but a color variant.

This species differs from the larger *Emoda* by the irregular rather than rounded inner edge of the periostome. There is a distinct rounded angle above and below the periphery; in other *Emoda* this entire area is evenly rounded. In fully adult shells there is also an extension of the central portion of the outer lip, so that the shell has a somewhat lengthened rather than a rounded appearance. This feature is illustrated by Poey (1854, pl. 33, figs. 11, 12) and is present in the lectotype. Submature shells generally lack this characteristic. The species differs from *pulcherrima titanica* in its smaller size and weaker axial costae. It differs from *ciliata* in its lively colors and comparatively stronger axial sculpture, and from *sagraiana* from the other end of the island, in its far weaker basal notch and tooth. We could discover no feature to distinguish it from *jeannereti*. Pfeiffer, in his discussion of the latter, noted several differences between *jeannereti* and *sagraiana* but failed to compare his species with *bayamensis*. Wagner (1907: 99) cited this as a subspecies of *pulcherrima*, but it lacks the strong axial sculpture on the body whorl that is characteristic of *pulcherrima* and, at the present state of our knowledge, is probably best regarded as a species.

We have not succeeded in clearly identifying *jeannereti* Pfeiffer. The species has never been figured satisfactorily. Reeve (1874: pl. 1, fig. 3a) had a poor figure of a shell with a bright green color which he referred doubtfully to *jeannereti*. This figure seems to have been copied from Sowerby (1847: pl. 3, fig. 126), where it appears as *Helicina sagra* [sic]. Sowerby (1866, pl. 1 [266], fig. 5) figured a typical brown *sagraiana* and referred *jeannereti* doubtfully to it. The green form (fig. 6) he now called *bastidiana* (sic) [= *bayamensis*]. Arango (1879: 46) copied Pfeiffer's data but cited Wright as the collector instead of Jeanneret. Wagner (1907–1908) omitted the name from his monograph and Fulton (1915) failed to note this omission. The only specimens available for our inspection come from Palma Soriano (Bermúdez collection), about 60 km southwest of Mayarí, Pfeiffer's type-locality of the species. We do not know who made the determination. In his discussion, as we have noted, Pfeiffer did not compare his species with *bayamensis*. Hence our placing *jeannereti* in the synonymy of *bayamensis* is provisional.

Specimens examined. ORIENTE. La Cantera de Miranda; Buena Vista, Bayamo (type-locality); Guisa, Bayamo; Miranda, Palma Soriano.

Emoda bermudezi Aguayo & Jaume
Plate 1, figures 5, 6; Plate 4, figure 1.

Emoda bermudezi Aguayo & Jaume 1954, Torreia, No. 21, p. 10, pl. 1, figs. 4, 6 ("Paso de las Trincheras," Sierra de Cubitas, Provincia de Camagüey; holotype, MP 17346).

Description. Shell reaching 19.5 mm in diameter, rather solid, depressed conic, periphery moderately carinate. Whorls 4½, flat, body whorl descending rapidly near aperture, where it blends into the thickened, slightly raised basal callus. Color generally olivaceous at base, tinged with brownish orange above, occasional specimens with a narrow, yellowish peripheral band. Spire low, rounded, same color as rest of shell. Aperture widely semilunate; peristome white, thickened, very weakly expanded. There is a distinct notch above near the parietal margin from which a short, raised marginal lamella extends to the basal callus. The basal callus as wide as the aperture, porcellanous, rounded, slightly raised in mature specimens. Columella weakly sigmoid, the basal tooth quite weak. Suture very slightly impressed. Later whorls marked by irregular diagonal lines of growth; surface with concentric, spiral rows of impressed pits. Protoconch 1½ whorls, slightly raised, weakly marked by diagonal and regular axial sculpture. Periostracum thin; operculum as in genus, inner corneous layer light brownish, slightly darker at the margins.

Height mm	Diameter mm	
14.5	19.5	San Francisco, near La Tinaja, Camagüey
13.0	17.5	Santa Rita, Camagüey
12.5	19.5	Paso de las Trincheras, Sierra de Cubitas, Camagüey
12.5	16.5	El Cercado de Cubitas, Camagüey

Remarks. This species is very close in its relationships to the widely distributed *submarginata*, which it resembles in color and in the presence of concentric, though weak, spiral lines that consist of a series of pits. It is easily distinguished by the sharp, triangular notch near the posterior (upper) angle of the peristome, a characteristic which, as Aguayo & Jaume pointed out (1954: 10), is found in no other *Emoda*. The color as given above, as well as the description of the operculum, is from a lot of fresh shells from the Bermúdez collection labelled merely "Camagüey." The other and better localized shells that were available were dead shells, the color having been somewhat faded or stained by reddish earth. In all specimens the concentric spiral lines were quite weak. The species apparently is limited to the Sierra de Cubitas in the northeastern part of Camagüey Province. This species, as well as *najazaensis*, was misidentified as *bastidana* Poey and appeared in the Museo Poey and other museum collections under this name. Aguayo & Jaume (1954: 11) pointed out that *bastidana* is a mere color form of *bayamensis*, an observation made originally by Poey himself (1865: 144).

Specimens examined. CAMAGÜEY. Las Cuevas; Santa Rita y la Entrada del Camino de La Guanaja [Santa Rita and the entrance to La Guanaja Highway]; Banao; Paso de los Burros; Paso de los Trincheras y Cueva de los Indios; San Francisco. N of La Tinaja; East side of Vereda de Burro, Finca San Clemente (USNM); Paso del Este (USNM); El Círculo (USNM); Los Corrales de Cangilones (USNM); North entrance to Paso Escalera (USNM). All of the above localities are in the Sierra de Cubitas.

Emoda najazaensis Aguayo & Jaume
Plate 1, figures 3, 4; Plate 4, figure 1.

Emoda najazaensis Aguayo & Jaume 1954, Torreia, No. 21, p. 9, pl. 1, figs. 7, 9, 10 ("El Cacaotal," Sierra de Najaza, Provincia de Camagüey; holotype, MP 16222; paratypes, MCZ 257558, from "Vereda del Telégrafo," Sierra del Chorillo, ex MP).

Description. Shell reaching 22 mm in diameter, smooth, depressed conic, periphery roundly carinate. Whorls 5¼, very weakly rounded, body whorl descending sharply at the aperture, where it blends into the basal callus. Color varied, pale olivaceous, pale brown, buff, or faintly orange, a pale narrow band at the periphery. Spire low, mammiform and somewhat darker than rest of shell. Aperture widely semilunate, lip slightly thickened and barely reflected. Columella shallowly concave below, weakly convex above; basal callus weakly lustrous, white, as wide as the aperture, rounded at outer margin. Basal tooth quite small. Suture moderately impressed. Spiral sculpture of closely set, concentric cords, which are raised in the periostracum, and reflected below as a line of minute impressed pits in the shell, most prominent on the body whorl, weaker at the base. Protoconch 1½ whorls, raised nipplelike above the succeeding whorls, sculptured with faint, regular axial striae, almost the same color as the rest of the shell. Periostracum thin. Operculum closely resembles that of *E. bermudezi*, but the internal corneous layer is not darker at the margin.

Height mm	Diameter mm	
15.5	20.0	Vereda del Telégrafo, Sierra del Chorrillo, Camagüey
14.5	20.0	El Cacaotal de Sifonte, Sierra Najaza, Camagüey
13.0	19.0	El Palomar de San José, Camagüey

Remarks. This species is similar to *submarginata*, especially in color and in the presence of spiral concentric incised striae, though in *najazaensis* these are more closely spaced. However, it has a generally larger shell, which is more depressed and more strongly keeled. It appears to be confined to the area around the Sierra Najaza (Najasa) in the southeastern part of Camagüey Province. The specimens we were able to examine, including several lots from the type-locality, did not show the colors mentioned by Aguayo & Jaume (1954: 9).

Specimens examined. CAMAGÜEY. Najaza; El Palomar de San José; El Cacaotal, Najaza; Sierra Guaicanamar; Sitio Afuera; Vereda del Telégrafo, Sierra del Chorrillo; Sierra del Cochimbo; El Cacaotal de Sifonte, Sierra de Najaza.

Emoda briarea (Poey)

Plate 2, figures 1–3; Plate 4, figure 1.

Helicina briarea Poey 1851, Memorias Historia Natural Isla de Cuba, 1: 108, pl. 11, figs. 9–12 (San Diego de los Baños [sic]; lectotype, here selected, MCZ 73854, from the J. G. Anthony Collection, collected by Gundlach [Trinidad Mountains, Santa Clara (= Las Villas)]. The specimen appears originally in the MCZ collection as a syntype, identified as such by Torre in June 1912).

Helicina briarea Poey, Pfeiffer 1862, Novit. Conch., 2: 195, pl. 52, figs. 1–5 (Trinidad).

Helicina briaraea "Poey," Sowerby 1866, Thes. Conch., 3: 278, pl. 1, figs. 1–3, [error for *briarea*].

Description. Shell very large for the family, reaching 34.5 mm in diameter, depressed turbinate, solid, roundly carinate, sharply so in juvenile specimens and relatively smooth. Whorls about 5, flat, body whorl moderately inflated, flattened basally, descending shortly near the aperture. Color purplish brown on the body whorl and somewhat lighter on the spire. There is a variously wide, yellowish or whitish subsutural band that is extended as a suprapheripheral band on the last whorl, where it is separated from the light colored basal area by a moderately narrow, purplish red band. Subsutural band wanting on early postnuclear whorls. Spire depressed, weakly rounded except for the slightly raised protoconch. Aperture widely semilunate, evenly rounded, white, ground color and spiral band showing through inside. Peristome expanded, barely flaring above, widest just above the periphery and slightly thickened. Basal denticle quite small, obtuse, somewhat lengthened. Parietal callus smooth, or yellowish white, more rounded than the aperture. Columella oblique, white, short, concave below. Suture weakly impressed. Sculpture of very fine, irregular growth lines, without spiral lines. Protoconch 1¼ whorls, somewhat raised, light brown, with faint, curved axial wrinkles. Periostracum thin, yellowish, not carrying the shell color, with faint, well-spaced spiral ridges. Operculum reddish, darker at margins, relatively thin.

Height mm	Diameter mm	
22.5	34.5	Puriales, Las Villas
22.0	31.5	Puriales, Las Villas
18.0	25.5	Caracusey, Las Villas
16.0	22.0	San Blas, Las Villas

Remarks. Most specimens of this species can be readily recognized by their large size. In populations where the specimens are smaller (San Blas, Ciegos de Ponciano, etc.), they are determined without difficulty by their smooth surface, depressed shape, characteristic color, and by the subsutural band, which has the same color as the base. The species differs from the larger specimens of *sagraiana* from Luis Lazo in Pinar del Río Province in its color and in the far less strongly thickened and unreflected lip. It differs from *E. emoda* in its more depressed shape, stronger shell, and color. The species seems to be confined to the area around Trinidad in the south central part of Las Villas Province. As Pfeiffer noted (1862: 196), Poey's locality was in error. We here select Trinidad, Las Villas Province, Cuba, as the type-locality. Poey selected the trivial name referring to the mythological giant Briareus, because of the large size of the shells.

Specimens examined. LAS VILLAS. *Trinidad:* Fomento; Finca Pitajones, Caracusey; Santa Rosa, Cafetal Los Puriales; Río Caballero; Portillo, Río de Ay; Río Caburní; Ciegos de Ponciano; San Blas Dam above San Blas.

Emoda mayarina mayarina (Poey)

Plate 2, figure 17; Plate 5.

Helicina mayarina Poey 1854, Memorias Historia Natural Isla de Cuba, 1: 417, pl. 34, figs. 6–8. (Mayarí [Oriente]; holotype, MP 17034).

Helicina mayarina Poey, Pfeiffer 1856, Malak. Blät., 3: 144; Pfeiffer 1858, Monographia Pneumonopomorum Viventium, Suppl. I, p. 184; Pfeiffer 1862, Novit. Conch., 2: 200, pl. 53, figs. 6, 7.

Emoda mayarina (Poey), Aguayo & Jaume 1954, Torreia, No. 21, p. 7, pl. 2, figs. 1, 6.

Description. Shell reaching 16 mm in diameter, subglobose, solid, moderately strong, sublustrous. Whorls 4, convex, the last somewhat descending at the aperture below the periphery. Color brownish red with several faint reddish wrinkles, base somewhat yellowish, with a darker peripheral band margined above by a lighter band of approximately the same width. Spire moderately raised, submammiform. Aperture slightly oblique, subsemilunate, white at the lip, darker within. Lip simple and thin. Parietal callus very thin, white and glassy in center, transparent near outer margin. Protoconch with fine, curved axial striae that grow stronger on the later whorls and become vermiculate on the entire body whorl, being obsolete only on the base and near the aperture, where they turn into straight axial lines. Spiral sculpture wanting. Operculum not seen, but presumably like others in this subgenus.

Height mm	Diameter mm	
13.0	16.0	Mayarí, Oriente, (USNM)

Remarks. This species, according to Aguayo & Jaume (1954: 7), is exceedingly rare; the Museo Poey has only a single specimen. The shells of this species and of its two subspecies are easily identifiable by their globular shape and especially by the variously strong vermiculate or wrinkled sculpture. This latter feature alone will prevent confusion with any other species.

Aguayo & Jaume believed that the nominate species came from the mountains of Nipe or Mayarí rather than from the lowlands around the port of Mayarí as Poey stated.

This species was omitted by Wagner in his monograph (1907–1908), nor did it appear on the list that Fulton (1915) published, citing the species Wagner had overlooked.

Emoda mayarina gutierrezi Aguayo & Jaume

Plate 2, figures 15, 16; Plate 5.

Emoda mayarina gutierrezi Aguayo & Jaume 1954, Torreia, No. 21, p. 7, pl. 2, figs. 3, 5 ("Finca [Lorenzo Cobos] Estable," Mayarí Arriba, Provincia de Oriente; holotype, MP 17342; paratype, MCZ 187562).

Description. This subspecies resembles the nominate species in the globular shape of the shell, but differs in being larger and more strongly sculptured, by having stronger spiral ridges on the base, and in color, which is predominantly reddish with a greenish tinge.

Height mm	Diameter mm	
15.0	19.5	"Finca Estable," Mayarí Arriba

Remarks. As Aguayo & Jaume comment (1954: 8), the color in this form is not of specific importance. In this case it is the larger size and the more rugose, vermiculate sculpture which are definitive.

Specimens examined. ORIENTE. Finca "Lorenzo Cobos Estable," Mayarí [Arriba], Oriente (E. Pujals).

Emoda mayarina mirandensis Aguayo & Jaume

Plate 5.

Emoda mayarina mirandensis Aguayo & Jaume 1954, Torreia, No. 21, p. 8, pl. 2, figs. 2, 4 ("Loma de la Cantera" cerca del Central Miranda, Palmarito de Cauto, Provincia de Oriente; holotype, MP 12593).

Description. "The present variety is distinguished from the typical subspecies by its larger size, its somewhat more depressed form, reddish color and narrower and less irregular sculpture" (translated).

Height mm	Diameter mm
16.0	21.0

Remarks. We have not seen specimens of this subspecies.

Emoda blanesi Clench & Aguayo

Plate 1, figures 12, 13; Plate 5.

Emoda blanesi Clench & Aguayo 1953, *in* Aguayo, Mem. Soc. Cubana Hist. Nat., 21: 301, pl. 35, figs. 1, 2 ("Embarradas" al norte de Banes, Oriente; holotype, MP 17324, from Embarradas north of Banes, Oriente, Cuba; paratype, MCZ 257553).

Description. Shell about 18 mm in diameter, subglobose, sublustrous and moderately strong. Whorls 4¼, moderately rounded, body whorl subinflated and barely descending at the aperture. Color reddish, tinged with yellow on the penultimate and body whorls, the yellow color generally becoming stronger as it approaches the aperture; peripheral band light colored with a darker reddish band bordering it below. Spire depressed, rounded. Aperture semilunate, white near lip, darker inside. Lip thickened inside, rounded, not flaring, basal tooth barely perceptible. Parietal callus very thin, white in the columellar region, transparent near outer margins. Suture moderately impressed. Postnuclear whorls sculptured with fine, curved axial cords that grow stronger on the successive whorls, the intervals being twice as wide as the axial cords on the body whorl. These cords are irregular and in occasional specimens run together, extending to the base without growing narrower. Spiral sculpture consisting of a subsutural depression on the last whorl, and composed of one to three small incisions on the wider and more depressed axial costae. Protoconch 1¼ whorls, slightly raised and sculptured with fine, curved axial wrinkles. Operculum with a thin internal corneous layer, yellowish and darker at the outer margins.

Height mm	Diameter mm	
13.8	16.8	Río Seco, Banes, Oriente
13.8	16.2	La Campana, Río Banes, Oriente
12.4	17.2	Río Seco, Banes, Oriente

Remarks. This species has a limited distribution along the north central shore of Oriente Province between Banes and Gibara. The shell is easily recognized by its color, the simple, nonflaring lip, the subglobose shape, and the impressed subsutural line. It differs from *pulcherrima* in having stronger axial costae, a simple lip, and in the presence of the subsutural groove with the incisions on the summit of the axial cords.

Specimens examined. ORIENTE. La Campana, Río Banes; Río Seco, Banes; Antilla; Loma de Carbón, barrio de Río Seco; N of Banes (both USNM).

Genus *Glyptemoda* Clench & Aguayo

Glyptemoda Clench & Aguayo 1950, Rev. Soc. Malacol. 'Carlos de la Torre,' 7: 61 (as a subgenus; type-species, *Helicina torrei* Henderson 1909, original designation).

Description. Shell like that of *Emoda sensu stricto*, but more depressed, exceedingly rough, dirty white in color, occasionally tinged with lemon yellow or purple, and sculptured with strong, thin lirae, separated by flat, much wider intervals. The operculum has the outer surface covered with small, more or less equisized, rounded, glassy granules. In this character it is between the operculum of *Emoda* with its unmarked surface and the strongly roughened surface of the operculum of *Schasicheila*. Periostracum wanting.

Remarks. Keen (1960: 286) synonymized *Glyptemoda* with *Emoda s. s.* We cannot agree with this decision. Instead we feel that this taxon should be raised to full generic rank.

Baker (1922) showed that the lateral tooth complex in Helicininae consists of a hammer-shaped comb-lateral structure with the basal pillar located at one end. In the subfamily Proserpininae, the pillar is centrally located, giving an anvil or T-shape to the structure. In *Glyptemoda* the basal pillar, consisting of two united portions separated by a deep vertical furrow, is almost as large as the top of the tooth itself (Pl. 7, fig. 1). Apparently this type of pillar can be derived more easily from Proserpininae than Helicininae but may be distinct enough to stand in a subfamily itself. There are other radular peculiarities in *Glyptemoda*. Five of the seven central teeth are oblong in shape and are weakly cusped. In this respect they differ from the lanceolate or obliquely lanceolate corresponding teeth of the Helicininae and Proserpininae. The numerous uncinals are strongly curved and have one or two weak cusps on the inner marginals to three to five rather strong cusps on the outer ones.

These radular characteristics, together with the strong surface sculpture and depressed shape of the shell, as well as the granule-covered outer surface of the operculum, induce us to recognize *Glyptemoda* as a full genus.

Glyptemoda torrei torrei (Henderson)
Plate 3, figures 1, 2; Plate 5.

Helicina torrei Henderson 1909, Nautilus, 23: 50, pl. 4, figs. 1–3 (Los Negros, 25 miles [sic] southeast of Bayamo in the province of Oriente, Cuba, "in woods on low limestone hills"; holotype, USNM 463791, paratypes, MCZ 20863).

Description. Shell much depressed, reaching almost 30 mm in diameter, lustreless, rough and very solid. Whorls 4¼, rapidly widening, almost flat, the last whorl descending shortly at the aperture. Color grayish white or cream, occasional specimens showing yellow or reddish purple on the spire. Spire planiform or slightly raised. Aperture semilunate, evenly rounded, generally white inside, occasional specimens with a tinge of yellow deep within. Lip flaring, white, thickened within, reflected above, widest above, gradually narrowing at the base, where it terminates in a very small, rounded tubercle. Parietal callus white, lustrous, not raised at the outer edge. Columella white, short, convex above, almost straight below. Suture well impressed. Surface with 17 to 20 thin, sharply raised spiral cords, crossed by regular, rather strong, diagonal axial sculpture. This sculpture crenulates the upper edge of the spiral cords. Intervals much wider than the cords, crossed by the axial growth lines. Protoconch 2 large whorls, smooth but with closely spaced, curved axial wrinkles, rather more closely spaced than in most species of *Emoda sensu stricto*. No periostracum. Operculum as in subgenus.

Height mm	Diameter mm	
16.5	28.9	Los Negros, Jiguaní, Oriente, paratype
16.0	29.0	Los Negros, Jiguaní, Oriente, paratype
14.0	30.5	Los Negros, Jiguaní, Oriente, paratype
13.5	26.0	Los Negros, Jiguaní, Oriente, paratype

Remarks. The number of spiral ridges varies from 17 to 20 in a series of paratype specimens and from 15 to 20 in a series from the de la Torre collection merely labelled "Los Negros, Jiguaní." This variation in number may be due to the presence of thinner and lower subsidiary ridges in the intervals in some specimens. The colors as given by Henderson do appear in isolated specimens, but most, even those taken alive, are white or cream colored under an encrusting layer of dirt. The spire, which is completely flat in some specimens, is moderately to well raised in others. This might be a secondary sexual characteristic. Henderson's location of Los Negros at 25 miles southeast of Bayamo is in error. Los Negros in Oriente is only about nine miles from Bayamo.

Specimens examined. ORIENTE. Los Negros, 15 km SE of Bayamo.

Glyptemoda torrei freirei Clench & Aguayo

Plate 3, figures 3, 4; Plate 5.

Emoda (*Glyptemoda*) *torrei freirei* Clench & Aguayo 1950 Rev. Soc. Malacol. 'Carlos de la Torre,' 7: 61, pl. 12, figs. 1–3 (La Manuela, antes de llegar a la Furnia de la Mina Los Negros, Baire, Oriente; holotype, MP 12918; paratypes, MCZ 185798).

Emoda pujalsi Aguayo & Jaume 1954, Torreia, No. 21, p. 5, pl. 1, fig. 8 ("La Gloria," Union del Camino de Maffo a San Lorenzo y a Los Negros, Jiguaní, Provincia de Oriente; holotype, MP 17386).

Description. Shell as in *torrei* but differing in its smaller diameter (5 to 8 mm less than the nominate species), its proportionately more elevated shape, and by the spiral ridges, which are lower and flattened at the top rather than sharp. The specimens from the Cueva de Pepín are tinged with yellow or brick red.

Height mm	Diameter mm	
14.5	20.0	"La Gloria," Maffo (as *E. pujalsi*)
14.3	20.0	"La Gloria," Maffo (as *E. pujalsi*)
14.0	21.5	La Manuela (type-locality)

Remarks. According to Clench & Aguayo, José A. Freire, who collected the type specimens, reported that he found this subspecies in the lowlands, whereas *torrei torrei* lives in the higher elevations. We have not seen the operculum, but presumably it is similar to that of *torrei torrei.*

Emoda pujalsi Aguayo & Jaume is a neighboring population that differs from the present subspecies only in degree. The two forms are found close together in the vicinity of Los Negros, and there is little doubt that they are the same.

Specimens examined. ORIENTE. La Muela; Cueva de Pepín, Baire (USNM); "La Gloria," Maffo, Jiguaní (type locality of *E. pujalsi*).

Emoda (?) *clementis* Clench & Aguayo

Plate 3, figure 5.

Emoda clementis Clench & Aguayo 1950, Rev. Soc. Malacol. 'Carlos de la Torre,' 7: 62, pl. 12, figs. 1, 5; (Cayo del Rey, Mayarí, Oriente; holotype, MP 12923; paratype, MCZ 185799).

Description. Shell imperforate, thin, fragile, and translucid. Color uniformly bluish green. Whorls 2 in the juvenile specimens, suture well impressed, body whorl with rounded keel. Spire depressed, little raised above the plane of the body whorl. Aperture semilunate; umbilical callus microscopically granulose. Columella short, blending gradually into the basal lip. The spiral sculpture consists of irregular microscopic striae grouped in unequal series; axial sculpture of fine irregular, diagonal, growth lines. Protoconch 1½ whorls, axially striated, the striations crossed by spiral lines; with four curved, rounded furrows at the distal portion. Periostracum imperceptible; operculum thin, green, smooth, nucleus submarginal, with a sculpture of concentric lines.

Height mm	Diameter mm	
6.5	10	(juvenile)

Remarks. This species was described on the basis of four juvenile specimens, and was doubtfully assigned to *Emoda.* These doubts are justified. The protoconch, as described by the authors and as seen in the specimen in MCZ, lacks the regular, curved, axial striae or wrinkles that characterize the genus, and also shows faint spiral sculpture that is not found on the protoconch of *Emoda sensu stricto.* The shell is very fragile, almost transparent, weaker than the customarily strong shell of *Emoda,* even in juvenile specimens. The true placement of *clementis* Clench & Aguayo must await the discovery of additional and more mature specimens.

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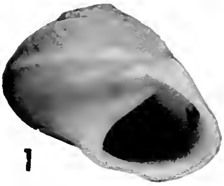
PLATE 1. Figs. 1 and 2. *Emoda submarginata* (Gray), El Grillo, Madruga, Havana, MCZ 60969, Topotype (1.5 ×). Figs. 3 and 4. *E. najazaensis* Aguayo & Jaume, El Cacaotal, Sierra de Najaza, Camagüey, MCZ 257422, Paratypes (1.5 ×). Figs. 5 and 6. *E. bermudezi* Aguayo & Jaume, Banao, Cubitas Mountains, Camagüey, MCZ 262719 (1.5 ×). Fig. 7. *E. ciliata* (Poey), San Juan de Letrán, Trinidad, Las Villas, Lectotype, MCZ 262717 (1.5 ×). Figs. 8 and 9. *E. ciliata* (Poey) same locality, MCZ 127230, Topotypes (1.5 ×). Figs. 10 and 11. *E. ciliata guisana* Wagner, "Cuba," MCZ 262718 (1.5 ×). Figs. 12 and 13. *E. blanesi* Clench & Aguayo, Río Seco, Banes, Oriente, MCZ 135961 (1.2 ×). Fig. 14. *E. pulcherrima* (Lea), USNM 104613, Lectotype (1.5 ×). Fig. 15. *E. pulcherrima* (Lea), Trans. American Philos. Soc. (NS), pl. 19, fig. 57, photographic copy. Figs. 16 and 17. *E. sagraiana* (Orbigny), Ensenada de los Burros, Cabezas, Pinar del Río, MCZ 127148 (1.5 ×). Figs. 18 and 19. *E. sagraiana* forma *percrassa* Aguayo & Jaume, La Güira, Luis Lazo, Pinar del Río, MCZ 127253 (1.5 ×). Figs. 20 and 21. *E. silacea* (Morelet), Yunque de Baracoa, Oriente, Topotype, MCZ 127229.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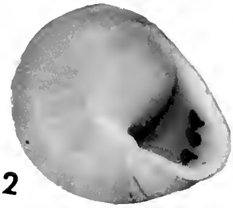
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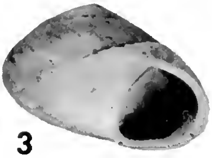
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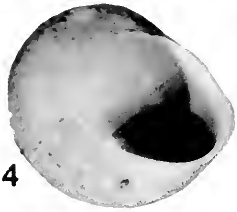
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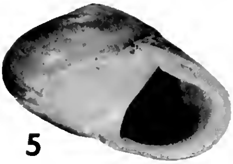
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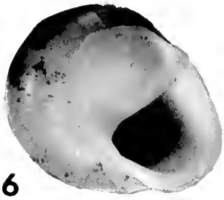
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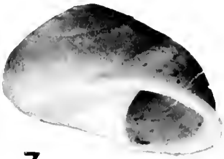
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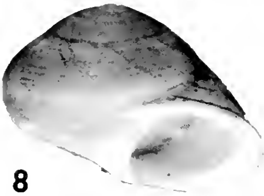
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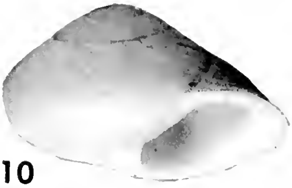
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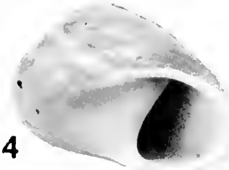
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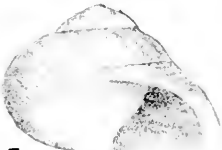
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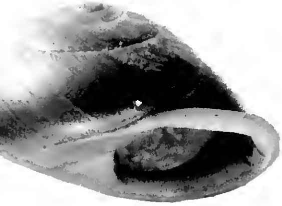
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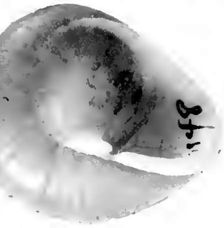

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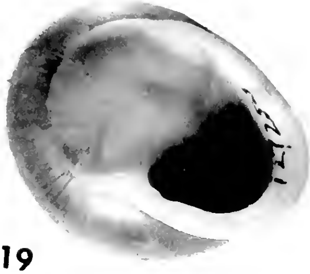

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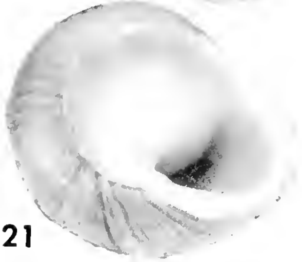
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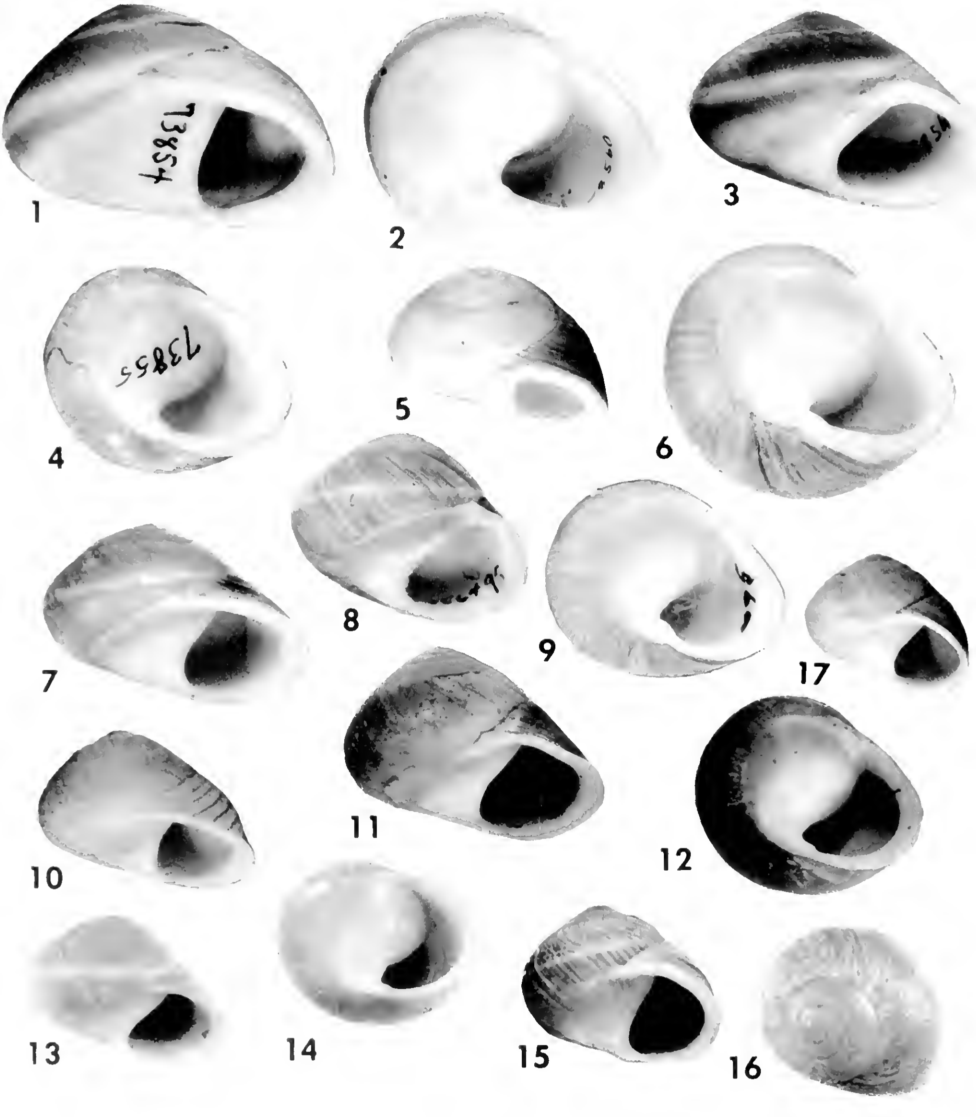
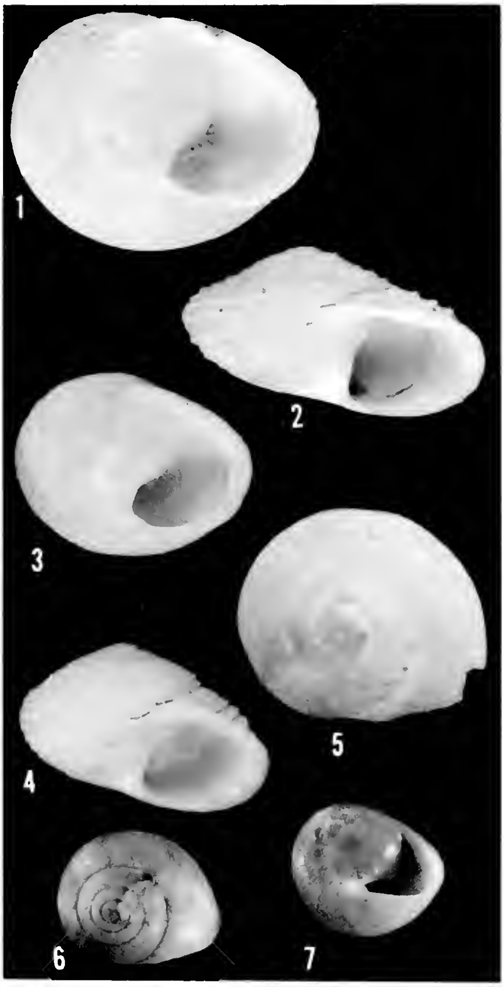


PLATE 2. Fig. 1. *Helicina briarea* Poey, Trinidad Mountains, Santa Clara [Las Villas], MCZ 73854, Lectotype (1.4 ×). Figs. 2 and 3. *E. briarea* (Poey), "Puriales," Trinidad Mountains, Las Villas, MCZ 58560 (1.4 ×). Fig. 4. *Helicina bayamensis* Poey Buena Vista, Bayamo, Oriente) MCZ 73855, Lectotype (c. 1.4 ×). Fig. 5. ditto, MCZ 256496, Paralectotype. Figs. 6 and 7. *Emoda emoda* Pfeiffer, Manatial de Santa Fé, Oriente, MCZ (1.2 ×). Figs. 8 and 9. *Helicina titanica* Poey, Baracoa (Oriente), MCZ 256495, Syntypes (1.2 ×). Fig. 10. *Emoda pujalsi* Aguayo & Jaume (= *torrei freirei* Clench & Aguayo), Loma La Gloria, Maffo, Jiguaní, Oriente, MCZ 263902, Topotype (2.1 ×). Fig. 11. *Emoda caledoniensis* n. sp., Mina Caledonia, Mayarí, Oriente, MCZ 261352, Paratype (1.2 ×). Fig. 12. ditto, 1 km from pine forest, Mayarí, MCZ 261349, Paratype (1.2 ×). Figs. 13 and 14. *E. pulcherrima* (Lea), Pico Turquino, bet. 2000 and 5000 ft., Oriente, MCZ 267577 (1.5 ×). Figs. 15 and 16. *E. mayarina gutierrezi* Aguayo & Jaume, Finca Estable, Mayarí Arriba, Oriente, Paratype, MCZ 187562 (1.2 ×). Fig. 17. *Helicina mayarina* Poey, Mayarí, Oriente, Syntype, USNM. (1.5 ×).



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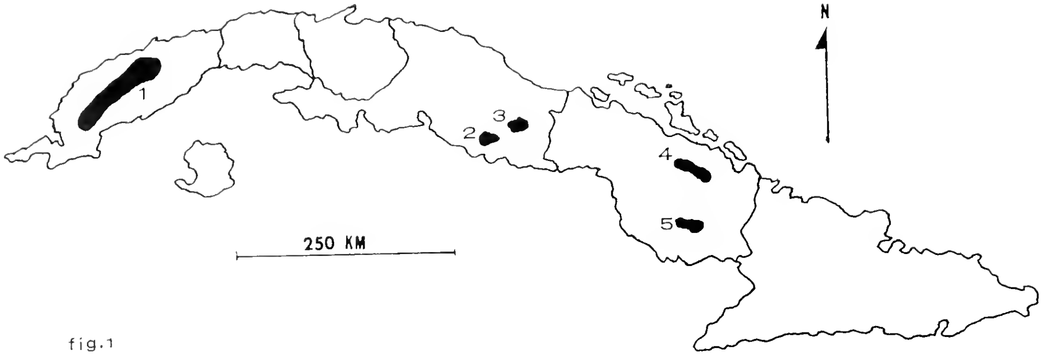

fig.1

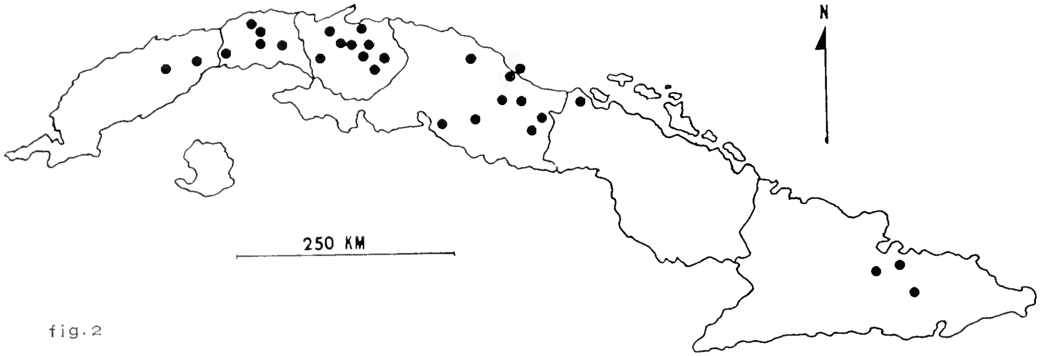

fig.2

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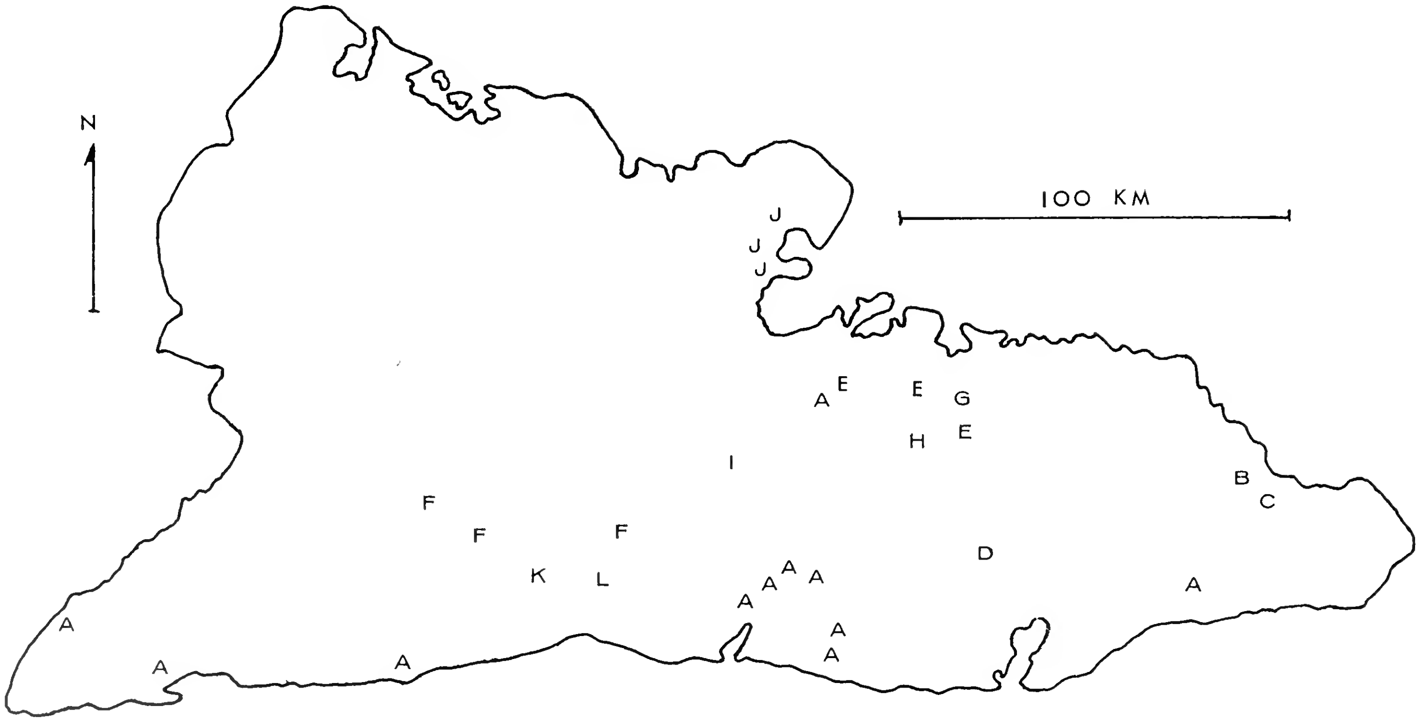

PLATE 5. Distribution of *Emoda* in Oriente Province. (A) *Emoda pulcherrima* (Lea); (B) *E. pulcherrima titanica* (Poey); (C) *E. silacea* (Morelet); (D) *E. emoda* (Pfeiffer); (E) *E. submarginata* (Gray); (F) *E. bayamensis* (Poey); (G) *E. caledoniensis* Clench & Jacobson, n. sp.; (H) *E. mayarina gutierrezi* Aguayo & Jaume; (I) *E. mayarina mirandensis* Aguayo & Jaume; (J) *E. blanesi* Clench & Aguayo; (K) *Glyptemoda torrei torrei* (Henderson); (L) *G. torrei freirei* Clench & Aguayo.

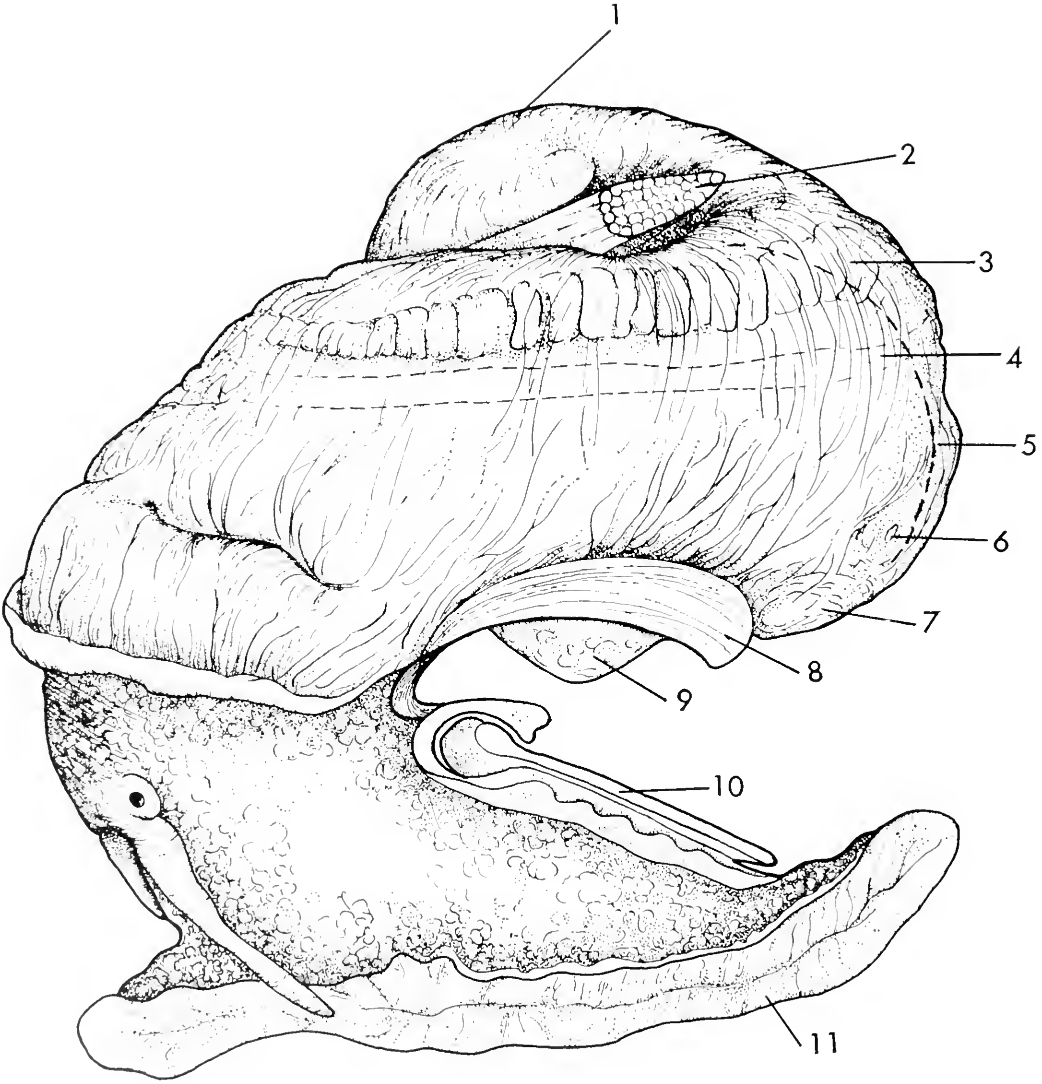

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Table 1. Distribution of the Species of *Emoda* and *Glyptemoda*

	Pinar del Río	Havana	Matanzas	Las Villas	Camagüey	Oriente
sagraiana	X					
silacea						X
pulcherrima						X
p. titanica						X
submarginata	X	X	X	X	X	X
ciliata				X		
c. guisana				?		
emoda						X
caledoniensis						X
bayamensis						X
bermudezi					X	
najazaensis					X	
briarea				X		
mayarina						X
m. gutierrezi						X
m. mirandensis						X
blanesi						X
torrei torrei						X
torrei freirei						X

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NOTE: Synonyms are italicized.

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THE *DIADEMATUS* GROUP OF THE ORB-WEAVER GENUS *ARANEUS* NORTH OF MEXICO (ARANEAE: ARANEIDAE)

HERBERT W. LEVI

ABSTRACT

Among our commonest spiders are the large *Araneus* orb-weavers. Eighteen species are found north of Mexico. They are redescribed, their diagnostic characters illustrated, their ranges mapped, and notes on their habits recorded. Three species turned out to be new: *A. washingtoni* from northeastern U. S. and eastern Canada; *A. yukon* from Yukon Territory; and *A. pima* from the Southwest.

INTRODUCTION

Among the species included in the present revision are some of the commonest spiders of North America, although several *Araneus* species are quite rare. Collections were examined not only to get an idea of the variation and distribution of common species, but also with the hope of finding members of the rarer species. The enormity of the collections available slowed down the work immensely.

Because of the urgent need for identification and information on the distribution of the common spiders, I am presenting separately the *diadematus* group of the genus *Araneus*, some members of which have never been illustrated before. It may take many years before I have examined types of all names of the numerous genera placed within the family and the many species described in the genus *Araneus* in the Americas. At present I do not know the limits of the genus and have not decided whether certain species are best included in the genus *Araneus*.

The recognition of reliable diagnostic morphological features of species was one of the critical questions to be resolved. My conclusions agree entirely with those of Grasshoff (1968), but differ from those published by Archer (1951a, b). Archer thought that the species can be diagnosed by the shape of one single sclerite of the male palpus, the median apophysis, and the ventral view of the scape and epigynum of the female. Perhaps these structures will prove of value in differentiating genera; they certainly are of quite limited value for species diagnosis. Also, I agree with Grasshoff that leg spines have doubtful value in separating males of *Araneus* species; they are extremely variable within populations (L. D. Carmichael, in manuscript).

As in my revisions of theridiid spiders, long established names of common species were kept; changing them does not make sense.[1]

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[1] I am following the purpose of the *International Code on Zoological Nomenclature* as expressed in its Preamble, although other authors have occasionally in my opinion interpreted individual provisions out of the context to obligate the changing of names. For many common North American species older names are available, but these often have doubtful application as the types have been lost, and interpretation of the usually inadequate description depends on the experience of the reader. Doubtful also are many of the names used by Chamberlin and Ivie (1944) in

In this study the work of the late Dr. H. Wiehle on European spiders has been of tremendous help, as has also the recent study on variation and morphological criteria of several European *Araneus* species by Grasshoff (1968).

I wish to thank the numerous biologists who have contributed specimens for study: Mr. J. D. Berman; Mr. D. Bixler; Dr. R. E. Crabill of the United States National Museum; Mr. Bruce Cutler; Dr. C. D. Dondale sent collections of the Canadian National Museum; Dr. M. G. Emsley of the Academy of Natural Sciences, Philadelphia; Dr. W. J. Gertsch of the American Museum of Natural History; Dr. O. Kraus of the Senckenbergische Naturforschende Gesellschaft; Mr. Robin Leech; Mr. G. H. Locket; Dr. D. C. Lowrie; Dr. M. Moritz of the Zoologisches Museum der Humboldt Universität, Berlin; Mr. P. I. Persson of the Natural History Museum, Stockholm; Mr. T. R. Renault of the Canada Department of Forestry, Fredricton, New Brunswick; Miss Susan Riechert; Mr. V. D. Roth of the Southwestern Research Station; Dr. J. G. Sheals and Mr. D. Clark of the British Museum (Natural History); Dr. R. Snetsinger; Mr. W. A. Shear; Dr. E. Sutter of the Naturhistorisches Museum, Basel; Dr. S. L. Tuxen and Mr. B. Petersen of the Universitetets Zoologiska Museum, Copenhagen; Mr. I. Valovirta, University of Helsinki Zoological Museum; Dr. H. V. Weems, Jr. and Mr. K. J. Stone of the Florida Collection of Arthropods; Dr. T. Yaginuma; and Dr. G. Edmundson and the staff of the University of Utah collections. My wife has helped with writing and editing.

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their attempt to resurrect names of Walckenaer for the manuscript illustrations of Abbot. Subjective judgment has to be used in interpreting these rather primitive illustrations of the dorsal aspect of spiders, the types of these names. While other biologists may feel sure of their judgment in these doubtful cases, I am not, and after having obtained copies of Abbot's drawings I find that I disagree with many of the Chamberlin and Ivie assignments; many are obviously in error (Levi and Levi, 1961). The Statute of Limitations (Art. 23b) permits us now to assign many of these uncertain ancient names to the status of obsolete names, should they threaten familiar names that have been in common use for more than 50 years. Like any other tool used by the taxonomist, the *Code* has to be used with common sense.

My request to the Commission to resolve by plenary power the problem of the two family names, Araneidae versus Argiopidae, has been withdrawn because only a few, often those in opposition and those with least experience in taxonomy and nomenclature, state their opinions in writing to the Secretary. However, the noncontroversial request to place the name *Argiope* on the *Official List of Generic Names in Zoology* has not been withdrawn. Although sent to the Secretary of the Commission in May 1967, it has not been printed yet. Once printed the name is protected by Art. 80 of the *Int. Code Zool. Nomencl.*

Instead of submitting the problem of the family name to the Commission, I have circulated a request for the opinion of colleagues. The poll included, of course, nontaxonomists working with orb-weavers. A majority of correspondents favored Araneidae (Araneidae, 43; Argiopidae, 29; Argyopidae, 1; outside of North America, Araneidae, 28; Argiopidae, 25; Argyopidae, 1). I will continue to use the name Araneidae.

The problem of the spelling of spider generic names is puzzling. The *Code* (Art. 32) now considers incorrect the emendations of spellings by Thorell, almost universally adopted for 100 years. Changing the names now would conflict with Art. 23b (since the incorrect emendations are junior objective synonyms, Art. 33a), and also with the purposes of the *Code* and would certainly be wrong. Thus it seems to me that we have to follow the long accepted spellings of generic names as also generally adopted by Bonnet in the *Bibliographia Araneorum*, and attempt to bring critical cases to the attention of the Commission. It is possible that the pertinent paragraphs of the *Code* might be clarified by a future International Congress to avoid unnecessary name changes.

Araneus Clerck[1]

Araneus Clerck, 1757, Svenska Spindlar, p. 15. Type species designated by Simon, 1893, Histoire Naturelle des Araignées, 1: 829, *A. angulatus* Clerck. But the type is said to be *A. diadematus* Clerck by Petrunkevitch, 1928, Trans. Connecticut Acad. Sci., 29: 136 and Bonnet, 1955, Bibliographia Araneorum, 2: 408, although the type species is correctly stated to be *A. angulatus* by Petrunkevitch, 1911, Bull. Amer. Mus. Natur. Hist., 29: 255 and by Bonnet, 1950, Bull. Soc. d'Hist. Natur. Toulouse, 85: 1–9.

Aranea Linnaeus, 1758, Systema Naturae, 10th ed. p. 619. The only genus of spiders; *A. diadema* is listed first. No valid type designation seems to have been made previously, thus I here designate *A. diadema* Linnaeus. The generic name *Aranea* has always assumed to be a synonym for *Araneus* Clerck.

Epeira Walckenaer, 1805, Tableau des Aranéides, p. 53. Type species designated by Latreille, 1810, Considérations Générales, p. 424, *Aranea diadema* Linnaeus; a second designation is by Thorell, 1869, On European Spiders, p. 53, *Epeira diademata* (Clerck). In 1928 Petrunkevitch (Trans. Connecticut Acad. Sci., p. 136) indicated that *E. cornuta* (Linnaeus) [sic] was the type. Presumably he meant *Araneus cornutus* Clerck.

Neopora Simon, 1864, Histoire Naturelle des Araignées, p. 261. A name for a subgenus. The type species is *N. diadema* (= *Araneus diadematus* Clerck) designated by Bonnet, 1958, Bibliographia Araneorum, 2: 3054.

Burgessia McCook, 1894, American Spiders, 3: 182. A subgenus for the group comprising *corticaria, miniata, bonsallae, mayo, bispinosa, pacificae* as well as *forata, lintcata,* and *juniperi.* The type species is *Epeira corticaria* (Emerton) (= *Araneus corticarius*) here designated. Bonnet, 1955, Bibliographia Araneorum, 2: 917, was in error when he said that McCook failed to include species in the subgenus.

Euaranea Archer 1951, Amer. Mus. Novitates, 1487: 34. Type species for new subgenus: *Aranea cavatica* (Keyserling) by original designation.

The structure of Araneus *genitalia.* The terms used for the sclerites of the palpus are those of Comstock (1910), which have become widely used. I used them in the revisions of Theridiidae and of *Argiope* (1968) and they were also used by Grasshoff (1968).

No terms are in general use to describe the female genitalia; I here follow Grasshoff. The epigynum has a prominent *scape* (Fig. 1). The scape is attached to the *base.* Below and behind the base are a pair of *basal lamellae* which are large and extend on each side of the epigynum of *Araneus marmoreus* (Figs. 1–3). The slit-like openings are on the venter and lead into a funnel which continues posteriorly but is partly open on one side as a *groove.* The groove, as can be seen in cleared or macerated preparations, runs into a funnel-shaped chamber toward the middle of the base and then bends toward the outside and continues under the lateral sclerites (crosshatched in Figs. 1–3). In *A. diadematus* a median posterior sclerite (Fig. 36) covers the grooves, while the funnels are more or less open posteriorly in *A. marmoreus* (Fig. 3).

The palpus of *Araneus* has a large *terminal apophysis* (term. apoph., Figs. 4–6, 8), a sclerite below the *subterminal apophysis* (subterm. apoph., Figs. 4–6, 8), and *distal hematodocha* (dist. hemat.) that are absent in *Argiope* and *Gea* (Levi, 1968).

Species differences. Archer (1951) described and pictured only the median apophysis of the palpus (med. apoph. in Figs. 4–6, 8) and the scape of the epigynum. He erected numerous araneid genera on the basis of the shape of the median apophysis. Unfortunately, the median apophysis turns out to be unreliable for separating species of *Araneus* and is pre-

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[1] Although the starting point of zoological nomenclature is Linnaeus' *Systema Naturae,* 10th edition, with the arbitrary date of 1 January 1758, the work of C. Clerck, 1757, *Svenska Spindlar,* published before, is an exception permitted by Article 26 of the old *International Code on Zoological Nomenclature* passed at the XIII International Congress of Zoology of 1948. After the XV International Congress of Zoology in London in 1958 adopted a new Code (1961), Clerck's *Aranei Succici* was placed on the *Official List of Accepted Works* by Direction 104 of the International Commission on Zoological Nomenclature [1959, Bull. Zool. Nomencl., 17(3–5): 89–91].

sumably a poor character for separating genera. Related species often have a similar median apophysis (see *A. gemma* group, Figs. 199, 211, or *A. saevus* and *A. diadematus*, Figs. 38, 55). There are also individual differences in this structure within species (e. g., *A. nordmanni*, Figs. 61, 63, 65, 67). This unreliability of the median apophysis as a species specific character is of interest in view of its definite function in copulation: its median spine takes hold of the tip of the scape of the epigynum (van Helsdingen, 1965; Grasshoff, 1968). The form of the scape also varies among individuals of a species.

The distance between the spine and the distal spine or ridge on the median apophysis varies in different species with the length of the epigynal scape. The spine is close to the distal end of the median apophysis in species having a short scape (*A. gemma*, *A. gemmoides*, *A. pima*). The distance is large in those having a long scape (*A. bicentenarius*, *A. andrewsi*, *A. diadematus*, and *A. saevus*). In the related genus *Eriophora*, in which the particularly long scape reaches to the spinnerets, the scape is matched by a shift in position and elongation of the median apophysis.

The shape of the conductor is of diagnostic value only in some species: it is an unusually large sclerite in *A. corticarius* (Fig. 120), and a very small, narrow one in *A. trifolium* (Fig. 179). The conductor in copulation embraces the scape of the epigynum, facing the median apophysis, forming a track on which the scape can glide in two directions.

Of far greater diagnostic value in separating species are the shapes of the embolus and terminal apophysis (term. apoph. in Figs. 4–6, 8), structures easily seen but often slighted in illustrations of araneid species. (Seen in all illustrations of the mesal view of the palpus in this paper.) Part of the embolus enters the female duct system (the left embolus, the left opening and ducts). But during copulation the terminal apophysis comes to lie below the base of the scape, against the abdomen, and supplies support.

The cap that is present on the embolus of virgin males (Levi, in press) differs in shape in different species. The caps of some species (e.g., *A. illaudatus*) are very large and noticeable.

The paracymbium differs greatly among species within the genera *Meta* and *Zygiella* (Gertsch, 1964), but is similar in almost all *Araneus* species. This only illustrates the difficulty of making generalizations or of attempting to use only one sclerite of the palpus, such as the median apophysis, for species diagnosis in all genera of the family. The paracymbium, during copulation, lies near the base of the median apophysis; it prevents the median apophysis from turning and by hooking into the tegulum border, acts as a stopping wedge between median apophysis and tegulum.

In the female the best diagnostic characters are those of the epigynum. However, the length and wrinkling of the prominent scape varies, perhaps due to different folding. In most species the scape is short; however, in some species it is always long (*bicentenarius*, *andrewsi*, *diadematus*, and *saevus*). The general shape varies among species. The scape may break off during mating in almost any species, and usually is torn off in *A. corticarius* and *A. groenlandicolus*.

The general structure of the base of the epigynum is much less variable and differs more between species than among individuals of a species. As it is undesirable to cut off the scape to view the base, it is best examined in posterior view by pulling the epigynum slightly away from the abdomen. Unfortunately, most authors have not illustrated this posterior view, exceptions being Wiehle (1963) and recently Gertsch (1964) in revising American species of the araneid genus *Zygiella*. The basal lamellae are unfortunately also quite variable among different individuals of a species, as is shown by Grasshoff (1968, p. 46, fig. 41).

However, genitalia are not the only characters. *Araneus corticarius* has highly distinctive abdominal shape and coloration (Fig. 118). It cannot be confused with any other North American species. The cross-shaped arrangement of markings on the dorsum of *A. diadematus* (Fig. 37) is diagnostic in North America, although not in Europe.

The second tibia in males of many species has strong spines and is often bent. Grasshoff (1968, p. 24, fig. 17) illustrated the considerable variation within the four species studied. While the spine pattern is not a good character for separating species of *Araneus* (L. D. Carmichael, in manuscript), the presence or absence of spines and modifications of tibia 2 may be used to separate some species.

The male of most species has a hook on the distal margin of the first coxa (Fig. 183), which fits into a proximal depression on the dorsal surface of his second femur, coupling the legs during mating. The coxal hooks are small and more posterior in some species (*A. gemma*) and absent in others (*A. cavaticus*). A cone or spur is present on the second coxa (Fig. 183) in some species. The hook on the first coxa and the corresponding depression are found in species of many araneid genera and do not seem to reflect close affinity.

Any diagnostic feature of any animal species is subject to variability within a certain range. This is true also of spiders. Curiously, this is denied by some spider specialists who consider any differences in structure (individual or geographic) to represent a "species difference." The variability of many characters of four *Araneus* species of Europe has been beautifully illustrated by Grasshoff (1968). My observations support Grasshoff's completely: while sclerites in the palpus (Figs. 96–99, 103, 104) and all parts of the epigynum show some variation among individuals (Figs. 76–92), nevertheless there are gaps in the variability between species.

Character displacement. "Character displacement" is a useful term proposed by Brown and Wilson (1956) for the phenomenon that morphological characters of related species having overlapping ranges show greater difference in the area of overlap than in their allopatric distribution. Examples have been found whenever taxonomic revisions are made and there is abundant material. In my theridiid revisions I found character displacement between *Theridion montanum* Emerton and *T. lawrencei* Gertsch and Archer (Levi, 1957a, p. 72). Specimens of *Steatoda hespera* Chamberlin and Ivie and *Steatoda borealis* (Hentz) are more distinct where the borders of their ranges meet, although I failed to point this out in my revision (Levi, 1957b). *Argiope trifasciata* (Forskål) males have a noticeably smaller palpus in the area of overlap with the very similar *A. florida* Chamberlin and Ivie, which has a larger palpus (Levi, 1968, p. 335, 337).

The possibility of drawing erroneous conclusions by ignoring geographic and individual variation and picking up individual specimens is best shown in *Araneus nordmanni*. *Araneus nordmanni* is found in the same habitat, on forest trees, as the dark-colored *A. saevus*. Where the ranges of the two species overlap, *A. nordmanni* is rarely dark, and shows little variation in size and shape. However, outside the range of *A. saevus*, in the southern part of the range of *A. nordmanni*, it is often black, it varies in size, and in no two males are the embolus (Figs. 69–75) and median apophysis exactly the same shape. *Araneus nordmanni* is largest in the southwestern part of its range. By looking only at the median apophysis of the palpus of a few specimens and noting differences in size and color, Archer described *A. pseudomelaena* from the southwest and *A. darlingtoni* from southeast. The differences Archer observed are there, but by examining larger samples one can easily see that the differences are within the variation of *A. nordmanni*. Perhaps the differences among populations in the southwest are emphasized by the isolation of the habitats in which this forest species can survive.

Introgression. Of considerable interest is the *Araneus gemma* group of species, including five species north of Mexico. The eastern *A. cavaticus* is very distinct, but is closest to *A. gemma* of the Pacific coast. There is the widespread *A. gemmoides* from the central states and provinces to the Pacific coast. All these species build large webs on barns, houses, and porches although their original habitat may have been cliffs and entrances to caves. In addition there are *A. pima* in Utah and Arizona, and *A. illaudatus* from Arizona to Texas. The habitats of the last two are uncertain, although they probably are also found on buildings.

Araneus gemma McCook was split by Chamberlin and Ivie into three species: *A. gemma*, *A. gemmoides*, and *A. pirus*. With few specimens on hand the judgment was sound. However, any series shows that *A. gemma* is quite variable, as is *A. pirus;* furthermore, at times *A. gemma* is collected with *A. gemmoides.* Some females are intermediate and cannot be assigned to either species (Figs. 215–217). Populations of *A. gemmoides* are relatively uniform except for coloration in the area of overlap with *A. gemma.* Apparently the two species hybridize and introgression is taking place with gene flow into the *A. gemma* population. It is known that males may try to mate with females of the wrong species. Broken-off embolus caps are at times found on the epigynum of a different species. It is especially common to find large *A. illaudatus* tips in the epigynum of *A. pima.* Apparently the cross of *A. gemmoides* × *A. gemma* is fertile. This would produce a potentially interesting study. It is not followed up here.

It is not uncommon to collect females with the wrong males. This happened to as careful a naturalist as Emerton. Grasshoff (1964) reports that males of *Araneus diadematus* will court females of *A. pallidus* (Olivier) and tiny *A. pallidus* males will court *A. diadematus.* In courtship the male plucks web threads in a rhythm characteristic for his species. Females do not respond to the plucking of a male of the wrong species. One male of *A. diadematus* gave up only after five hours of courting a female of *A. pallidus.*

Habits. All North American *Araneus* of the *diadematus* group have similar life histories. There is one generation, which matures in summer, mates in summer, and dies in fall after making a loose fluffy egg sac (Plate 1). Spiderlings leave the egg sac in spring (*A. diadematus*).

The virgin male has the embolus capped (Levi, in press). The function of the cap is not known, but it is not believed to transmit sperm although a duct is at times visible. Males are known to mate several times and to survive mating. It has been suggested that mating before sperm induction, as observed in some spiders, may remove the cap and permit the embolus to function (Kullmann, van Helsdingen, personal communication). The cap is diagnostically different in each species. About half the males in collections are virgin and still have the cap, half have mated and have lost it. Virgin males wandering in search of a mate may be more likely to be collected.

In all collections examined, only one male was marked as having been killed and eaten by a female *A. diadematus.* The male when examined turned out to be an *A. cavaticus*, not the partner of the female. However, Grasshoff (1964) reports that the female of *Araneus pallidus* has to bite into the male's abdomen to permit holding on during copulation. In one case the female, feeding on an insect, was prevented from biting; the male could not hold on to the female, slid off, and was wrapped in silk like prey.

All species make an almost vertical orb web with about 18–30 radii, with a retreat above to the side of the web in leaves, bark, or lichens and connected with the

Plate 1. Egg sac of captive *Araneus pima* sp. n. from Arizona

hub by a signal line (Plate 2). During the day the spider rests in the retreat, at night usually in the center. The center has an irregular mesh. *Araneus diadematus* is more likely than other species to be found in the center of the web at daytime. Although all species mature at the same time, their variation in size is reflected in the diameter of the orb and the size of the prey handled. Also each species seems to have its own habitat, some preferring forests (*A. saevus*, *A. nordmanni*, and the small *A. corticarius*), some meadows (*A. trifolium*, *A. marmoreus*), city gardens (*A. diadematus* in North America), buildings or cliffs (*A. cavaticus* group). *Araneus bicentenarius*, often brightly colored, makes its retreat among lichens (Plate 3), the color of which it matches.

Species living in the open in herbaceous vegetation tend to have an oval abdomen (*A. marmoreus*, *A. trifolium*), while those living on trees and cliffs have humps (*A. nordmanni*, *A. saevus*, *A. cavaticus*). The adaptation of this curious correlation is not known, but is also believed true of

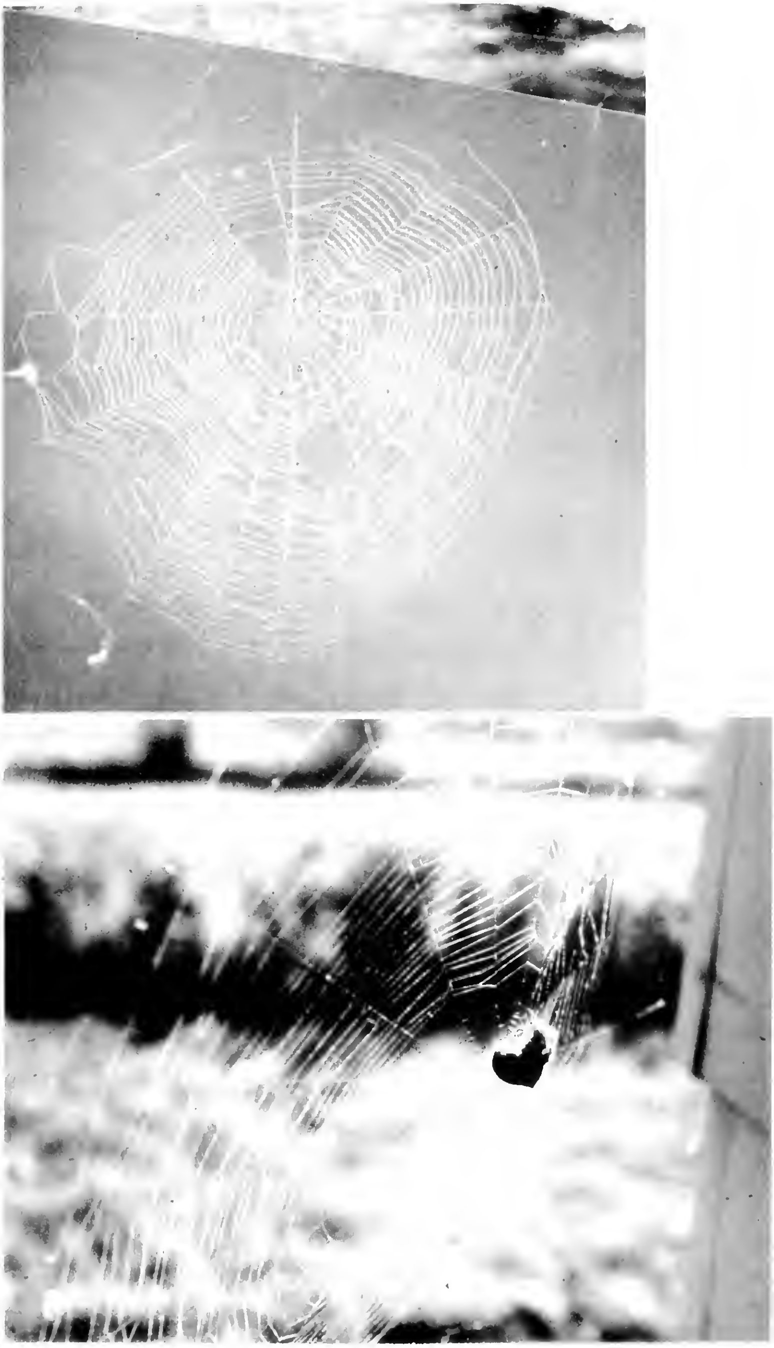


Plate 2. (Top) Web of *Araneus cavaticus* (Keyserling) powdered with corn starch, West Virginia. (Photo by W. A. Shear.) (Bottom) Web of *A. gemmoides* Chamberlin and Ivie with adult female, Wisconsin.

Plate 3. *Araneus bicentenarius* (McCook) in retreat among lichens, West Virginia. Both spider and the lichens are the same shade of green. (From Ektochrome photo by W. A. Shear.)

European species. It has been suggested (W. S. Shear, personal communication) that only those that have a retreat in curled up leaves lack humps.

Western *A. gemmoides* and some *A. gemma* have black bars on the venter, which are distinct "eyes" in *A. pima* (Plate 4). I assume that when disturbed the spider zooms down its signal thread to appear at the center of the orb web. In South America I watched an araneid make maximum use of its ventral spots, which in the particular individual observed were in the shape of a face.

The habitat observations reported here are gleaned from the labels on vials. Only mature individuals were used. Most checklists and literature on habits are unreliable because the species determinations are in doubt and often wrong. The specimens usually have not been turned over to a museum for safe keeping as voucher specimens. In mapping distributions, only specimens examined have been used.

KEY TO FEMALES

1a. Abdomen with humps or angular anteriorly (Figs. 21, 37, 118) 6
1b. Abdomen oval to spherical, without humps or anterior angles (Figs. 144, 177) 2
2a. Posterior lamellae of epigynum showing on each side in ventral view as large curved folds; scape overhanging a depression bordered on each side (Figs. 1, 107) .... *marmoreus*
2b. Posterior lamellae not visible in ventral view or, if visible, scape not overhanging a depression bordered on each side 3
3a. Scape of epigynum with more or less parallel sides, very rarely broken off (Figs. 138, 174) 4
3b. Scape of epigynum tapered toward tip, or often broken off (Figs. 159, 167) 5
4a. Legs banded; a bordered depression on each side of epigynal scape in ventral view (Fig. 174); no median keel in posterior view (Fig. 176) .... *trifolium*
4b. Legs not banded; base of epigynum a domed area truncate on the posterior side; openings posterior and separated by a keeled septum (Figs. 140, 142) .... *iviei*
5a. Scape of epigynum widest at base; on each side of scape a shallow depression with a narrow rim (Fig. 167) .... *yukon*
5b. Scape, if present, widest close to its middle; scape hiding ventral depression (Fig. 159) and if scape is broken, rims wide (Fig. 162) .... *groenlandicolus*
6a. Abdominal humps projecting toward sides; usually a transverse line between humps anterior of which abdomen is usually dark, posterior light (Fig. 118) .... *corticarius*
6b. Humps dorsal, transverse markings not as contrasting 7
7a. Scape long, at least twice as long as width of base 8
7b. Scape short 12
8a. Scape coiled (Fig. 52); southwest .... *santarita*
8b. Most of scape straight (Figs. 45, 48) 9
9a. In posterior view of epigynum there is a median light groove (Figs. 17, 20, 29) 10
9b. No such groove in posterior view 11
10a. Venter of groove (toward scape) dark and swollen, epigynal lamellae on each side large (Fig. 29); Pacific coast .... *andrewsi*
10b. Venter of groove not swollen toward scape, lamellae small (Figs. 17, 20);

Plate 4. *Araneus pima* sp. n. showing eye spots on venter of abdomen.

Canada, eastern United States to Southwest .... *bicentenarius*

11a. Spider dark, abdomen very dark, black, usually with a white lanceolate cardiac mark on abdomen (Fig. 51); forests; epigynum as in Figs. 42, 44, 45, 47, 48, 50 .... *saevus*

11b. Spider light, abdomen almost always with light dorsal marks in shape of a cross (Fig. 37); city gardens; epigynum as in Figs. 34, 36 .... *diadematus*

12a. Epigynal scape with transverse annuli separated by grooves (Figs. 123, 124, 187, 188) 13

12b. Epigynal scape lacking transverse annuli (Figs. 207, 224, 233) 14

13a. Scape twisted (Figs. 123, 124); base on each side of scape with a diagonal rim enclosing the median depression (Fig. 123); Newfoundland to New Hampshire .... *washingtoni*

13b. Scape straight (Figs. 187, 188); rims of depression hidden by scape (Fig. 187) 15

14a. Width of scape more than half width of epigynum (Fig. 187); epigynum in posterior view with median triangular sclerite (Fig. 189); Eastern United States and Canada, on overhanging cliffs, common on buildings .... *cavaticus*

14b. Width of scape less than half base of epigynum (Figs. 87, 90); epigynum in posterior view with heart-shaped depression (Figs. 89, 92); widespread in forests .... *nordmanni*

15a. Anterior end of epigynal scape constricted (Fig. 233); Texas and southwest .... *illaudatus*

15b. Anterior end of scape is wide, scape tapered toward tip 16

16a. Epigynum and scape very small, scape triangular (Fig. 195); widespread in central Canada and United States to Pacific coast .... *gemmoides*

16b. Epigynum and scape otherwise (Figs. 203, 205, 218); Pacific coast and Southwest 17

17a. Scape without lateral rims (Figs. 218, 221); a deep transverse groove in posterior view (Figs. 220, 223); California to Texas .... *pima*

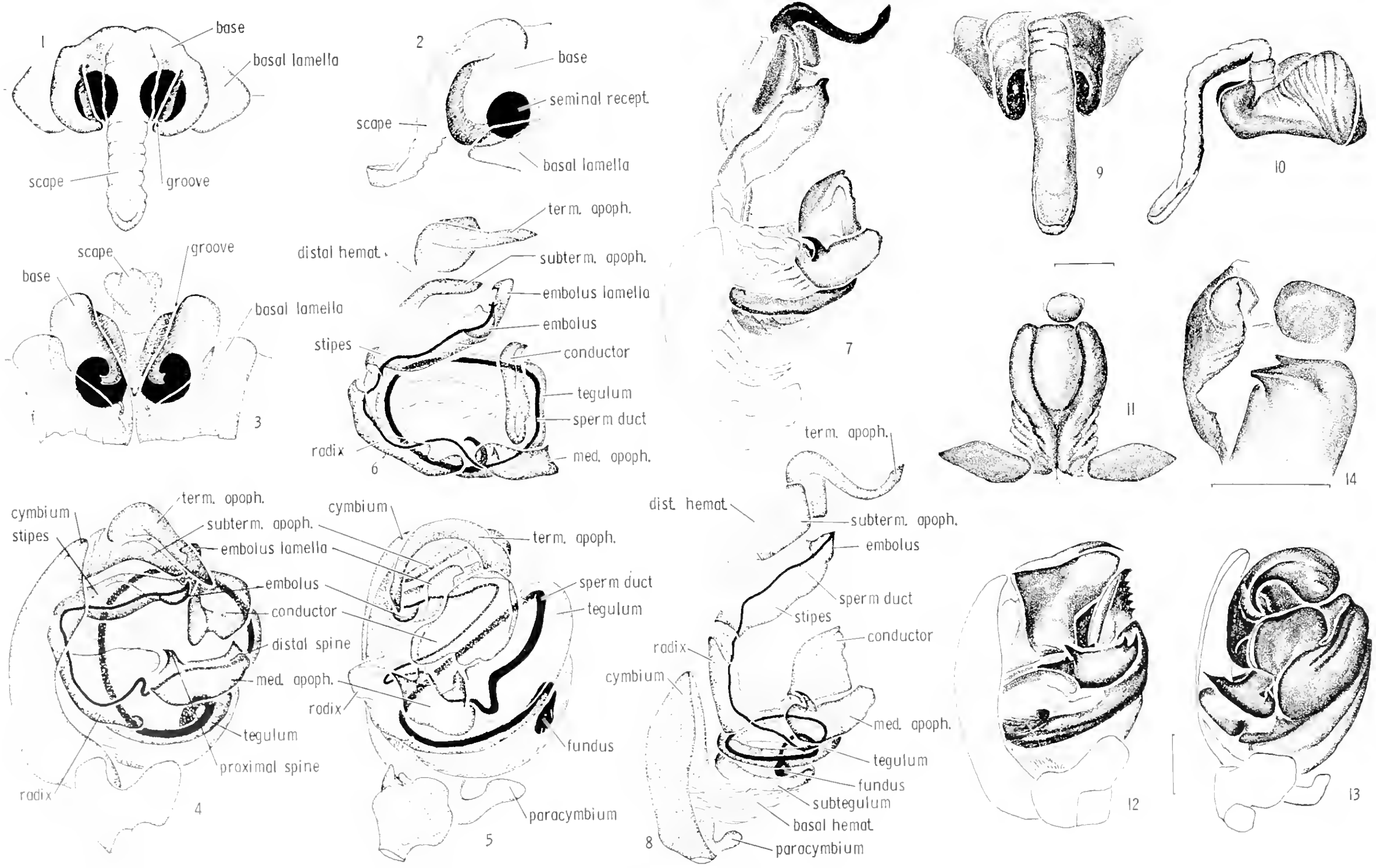
17b. Scape with lateral rims, very variable (Figs. 203, 205); transverse groove very narrow if present (Figs. 204, 206); Pacific coast .... *gemma*

KEY TO MALES

1a. First coxa with a hook on distal margin facing second coxa (Fig. 183) 2

1b. First coxa without hook on distal margin 9

2a. Conductor of palpus with teeth around margin (Figs. 23, 24, 31); median



Figures 1–3. Structure of epigynum of *Araneus marmoreus*, a transparent diagram. 1. Ventral. 2. Lateral. 3. Posterior.

Figures 4–6. Structure of left palpus of *A. marmoreus*, a transparent diagram. 4. Mesal. 5. Ventral. 6. Expanded.

Figures 7–8. Structure of left palpus of *A. saevus*. 7. Expanded. 8. Expanded, a transparent diagram.

Figures 9–14. *A. angulatus* Clerck (Europe). 9–11. Epigynum. 9. Ventral. 10. Lateral. 11. Posterior. 12–14. Palpus. 12. Mesal. 13. Ventral. 14. Embolus, pulled out, ventral view.

(All size indicators, 0.5 mm)

apophysis with at least 2 distal spines (Figs. 23, 32) 3

2b. Conductor of palpus smooth around margin; median apophysis with a keel on distal edge (Figs. 4, 110) 4

3a. Terminal apophysis with drawn-out tip (Figs. 31, 32); teeth around edge of conductor subequal (Fig. 31); Pacific coast .... *andrewsi*

3b. Tip of terminal apophysis an acute triangle (Figs. 23, 24); first tooth on embolus side of conductor noticeably larger than others (Figs. 23, 24); Canada, eastern U. S. to Southwest .... *bicentenarius*

4a. Second coxa with spur (Fig. 183) 6

4b. Second coxa without spur 5

5a. Palpal conductor unusually large (Fig. 120); in mesal view median apophysis about 3 times as long as wide (Fig. 119); Pennsylvania to Alaska .... *corticarius*

5b. Palpal conductor of normal size (Fig. 128); median apophysis about 2 times as long as wide (Fig. 127); Newfoundland to New Hampshire .... *washingtoni*

6a. Terminal apophysis paralleled by a long subterminal apophysis (Figs. 4, 96–99, 103, 104, 110) 7

6b. Subterminal apophysis a short stub 8

7a. Embolus sclerotized, subcircular at end (Figs. 4, 103, 104, 110); holarctic .... *marmoreus*

7b. Embolus longer than wide as in Figs. 69–75, 96; holarctic .... *nordmanni*

8a. Embolus a curved hook (Figs. 38, 40, 41); apical apophysis short, curved, sickle-shaped (Figs. 38, 39) .... *diadematus*

8b. Embolus otherwise (Figs. 55, 57, 58); apical apophysis a long, strongly curved prong (Figs. 55, 56) .... *saevus*

9a. Inner lamella of embolus a wide projecting plate of larger visible area than narrow conductor (Fig. 179); embolus with distal notch (Figs. 178, 180, 181) .... *trifolium*

9b. Inner lamella of embolus, if projecting, with visible part always much smaller in area than conductor (Fig. 172); embolus otherwise 10

10a. Second tibiae modified by being swollen or curved (Fig. 184) 11

10b. Second tibiae straight, not swollen 12

11a. Median apophysis with slender, graceful proximal spine and distal projections with strong, straight spines, the lower one with a dentate edge (Figs. 171, 172) .... *yukon*

11b. Median apophysis with proximal spine stout and distal projections both bent out at right angles to main axis of median apophysis (Figs. 164, 165) .... *groenlandicolus*

12a. Terminal apophysis a sclerotized prong, widened just before tip (Figs. 145–148); conductor with a pocket on lateral side (Figs. 146, 148); embolus as in Figs. 145, 149–151 .... *iviei*

12b. Terminal apophysis lightly sclerotized, fleshy, never widened near tip; conductor and embolus of different shape 13

13a. Males more than 10 mm total length; proximal spine of median apophysis placed in proximal half of sclerite; distal edge a keel (Figs. 191, 192); eastern United States, Canada .... *cavaticus*

13b. Males less than 9 mm in total length; proximal spine of median apophysis placed close to distal spine (Figs. 211, 212, 238, 239); central, western and southwestern region 14

14a. Palpal tibia almost equal in size to bulb (Figs. 199, 200); spines of median apophysis slender; terminal apophysis truncate (Figs. 199, 200); widespread in central and western North America .... *gemmoides*

14b. Palpal tibia less than half area of bulb; spines of median apophysis stout; terminal apophysis more pointed; Pacific states, southwest to Texas 15

15a. Embolus pointed (Figs. 211, 214); embolus cap short (Fig. 213) .... *gemma*

15b. Embolus truncate (Fig. 232); embolus cap elongate, pointed (Figs. 231, 240); Texas to California 16

16a. Total length 5–11 mm; spines of median apophysis stout (Figs. 228, 229) .... *pima*

16b. Total length less than 4 mm; spines of median apophysis slender, recurved (Figs. 238, 239) .... *illaudatus*

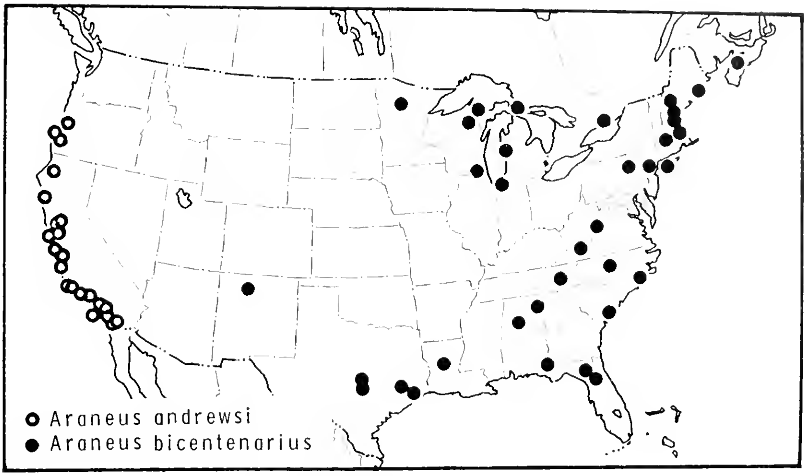
Araneus angulatus Clerck

Figures 9–14

Araneus angulatus Clerck, 1757, Svenska Spindlar, p. 22, pl. 1, figs. 1–3, ♀. Type specimens in the Natural History Museum, Stockholm, lost. Locket and Millidge, 1953, British Spiders, 2: 127, figs. 80, 83, ♀, ♂. Bonnet, 1955, Bibliographia Araneorum, 2: 433 (in part).

Aranea angulata, — Wiehle, 1931, *in* Dahl, Die Tierwelt Deutschlands, 23: 52, figs. 4, 5, ♀, ♂. Roewer, 1942, Katalog der Araneae, 1: 795 (in part).

Note. Although there are many literature records of this species in North America, all refer to large specimens of various other species (*A. andrewsi; A. bicentenarius; A. saevus; A. marmoreus; A. nordmanni*) that had been misidentified. No specimens of *Araneus angulatus* coming from North America have been found in collections.



Map 1. Distribution of *Araneus bicentenarius* (McCook) and *A. andrewsi* (Archer).

The differences between *A. angulatus* and North American species are discussed under *A. bicentenarius*.

The web, described by Wiehle (1931) has bridge threads up to 5 m long at 3 m height. The number of spokes averages 21 and the snare region is 40–63 cm across.

Araneus bicentenarius (McCook)

Plate 3; Figures 15–26; Map 1

Epeira gigas Leach, 1815, Zoological Miscellany, 2: 132, pl. 109. Female type probably from America in the British Museum, Natural History, examined. (Not *A. gigas*, — Comstock, 1912, 1940, The Spider Book and some other authors[1].)

Epeira bicentennaria McCook, 1888, Proc. Acad. Natur. Sci., Philadelphia, p. 195, figs. 3, 5, ♀. Syntypes from "northwestern Ohio and Allegheny mountains" lost.

Epeira angulata var. *bicentenaria*, — McCook, 1893, American Spiders, 3: 186, pl. 10, figs. 3–5, pl. 11, figs. 2–4, ♀, ♂.

Aranea bicentenaria, — Archer, 1951, Amer. Mus. Novitates, 1487: 31, figs. 68, 78, ♀, ♂.

Aranea kisatchia Archer, 1951, Amer. Mus. Novitates, 1487: 27, fig. 69, ♀. Female holotype from Grant Parish, Louisiana, in the American Museum of Natural History, examined. NEW SYNONYMY.

Note. Leach's description suggested that his *Epeira gigas* is *A. bicentenarius*. The type of *E. gigas* was found pinned and stuffed with cotton in the British Museum by Mr. D. J. Clark. After placing it in alcohol Mr. D. J. Clark examined the specimen and reported it to be an unusually large specimen of *A. angulatus;* upon comparing it to my drawings he found it to match Figures 18, 19 of a southern *A. bicentenarius*. I have since examined it myself. The name *A. gigas* has been used by some authors for *A. marmoreus*, never before for *A. bicentenarius*. A junior homonym, *Epeira gigas* C. L. Koch, 1830, has been renamed *A. grossus* (C. L. Koch) and belongs to a species also closely related to *A. angulatus*. The spider was collected by McCook in 1882 at the bicentennial of the city of Philadelphia. By misprint the name was spelled with two n's in the first publication.

Description. Female from New Jersey. Carapace dark brown. Sternum dark brown with a lighter, branched mid-longitudinal band. Legs mottled brown with darker

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[1] The International Commission on Zoological Nomenclature will be asked to place the name *Epeira gigas* Leach on the Official List of Rejected Names in Zoology and the name *Epeira bicentenaria* McCook on the Official List of Specific Names in Zoology.

bands. Abdomen very dark with folium. Venter dark brown to black, sometimes with a median light area. Abdomen with large humps. The dorsum has small sclerotized spots, the bases of setae, but all setae are short. Total length, 15 mm. Carapace, 5.9 mm long, 5.0 mm wide. First femur, 6.8 mm; patella and tibia, 9.2 mm; metatarsus, 5.4 mm; tarsus, 1.8 mm. Second patella and tibia, 8.4 mm; third, 5.0 mm; fourth, 7.6 mm.

Male from New Hampshire. Coloration as in female except for an anterior, diamond-shaped, longitudinal white mark on dorsum of abdomen. The first coxa has a hook on the distal margin, the second a spur. The second tibia is very strong with strong macrosetae. Total length, 7 mm. Carapace, 6.5 mm long, 4.6 mm wide. First femur, 6.9 mm; patella and tibia, 8.4 mm; metatarsus, 4.9 mm; tarsus, 1.7 mm. Second patella and tibia, 8.4 mm; third, 5.0 mm; fourth, 6.7 mm.

Variation. Individuals of this rare species differ in size and coloration. The largest specimens come from the southern United States. Females are up to 28 mm in total length; one measuring 21 mm in total length had the carapace 10.0 mm long, 8.6 mm wide. The smallest specimen comes from Canada; the smallest female measured 13 mm in total length, carapace 6.1 mm long, 5.6 mm wide. Many northern and southern specimens are strikingly colored on the abdomen (Plate 3, Fig. 22), others are just shades of brown in alcohol (Fig. 21). The scape of the epigynum is variable in length, and the median depressed area in posterior view is of variable width, narrowest in some southern specimens (Fig. 20) called *A. kisatchius* by Archer. However, intermediate epigyna are common.

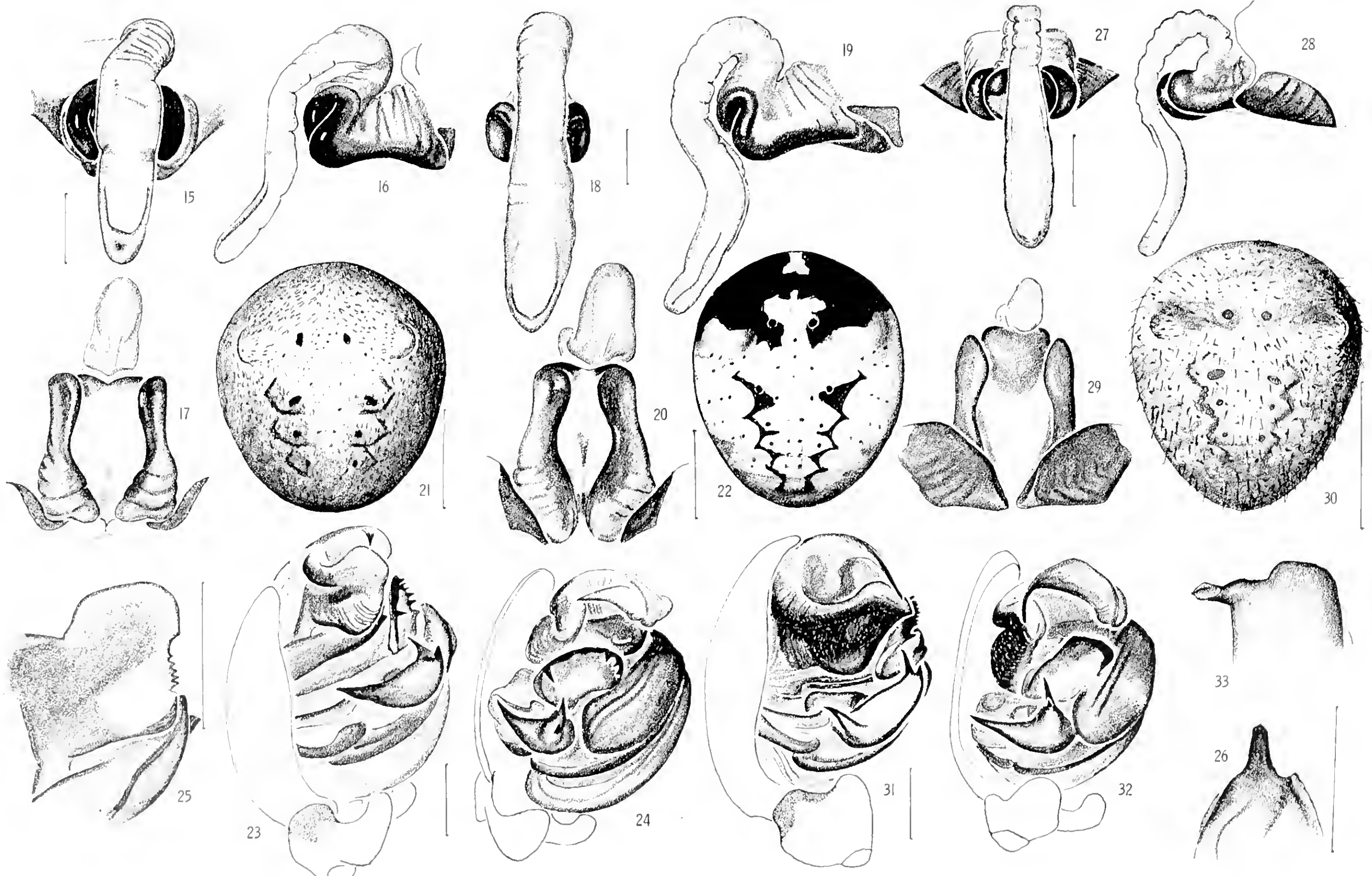
Diagnosis. Females of *A. bicentenarius* and *A. andrewsi* differ from *A. diadematus* and *A. saevus*, both of which also have a long epigynal scape, by having the median area of the epigynum in posterior view depressed and light (Figs. 17, 20, 29). Males of *A. bicentenarius* and *A. andrewsi* differ from males of other groups by having the margin of the conductor toothed (Figs. 23, 24, 31, and easily seen in apical view) and by the shape of the embolus, the tip of which can only be seen in ventral view (Figs. 26, 33) after removal of the conductor.

The related Eurasian *A. angulatus* has the median, posterior area of the epigynum swollen and sclerotized, rather than depressed (Fig. 11), and the embolus and terminal apophysis of the palpus (Figs. 12–14) differ in shape from those of the two North American species.

In females of the related Pacific coast *A. andrewsi*, the median posterior depressed area of the epigynum is distally (ventrally) black and swollen (Fig. 29); that of *A. bicentenarius* is not swollen and is light in color (Figs. 17, 20). Males of *A. andrewsi* have the tip of the terminal apophysis sclerotized and pointed (Figs. 31, 32), while that of *A. bicentenarius* is an acute fleshy lobe (Figs. 23, 24). The embolus can be seen under the terminal apophysis inside the palpus. The embolus differs slightly in shape in different specimens; its opening is ventral and is partly hidden by the conductor.

Note. In collections and literature *A. bicentenarius* has often been called *A. angulatus*, as have large specimens of various North American *Araneus* species.

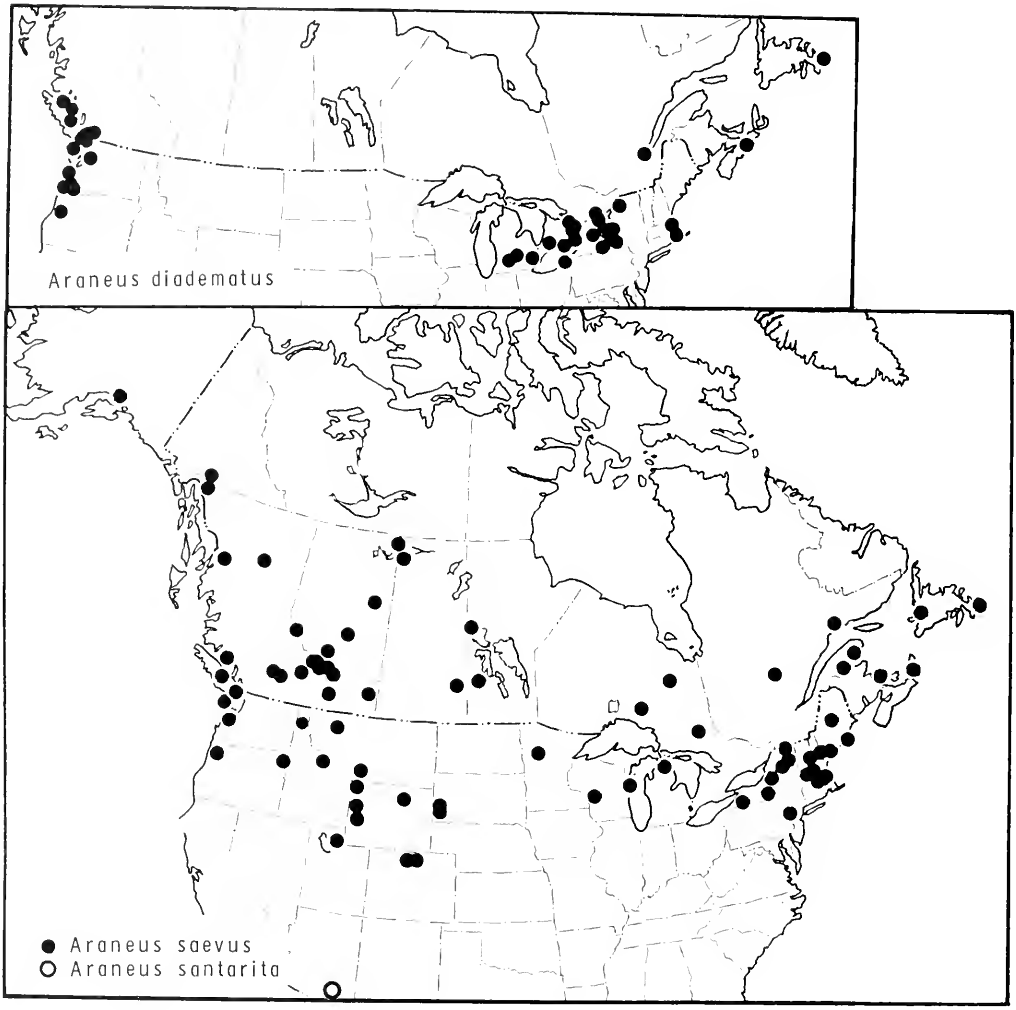
Habits. Araneus bicentenarius is found on trees in woods. One brightly marked specimen was collected by a botanist among lichens on jack pine (*Pinus banksiana*). The dorsal pattern makes the spider disappear among *Evernia mesomorpha, Parmelia aurulenta*, and *P. caperata*. (L. L. Darrow, personal communication.) Another was green when collected, and "blended perfectly with lichens, etc." on a maple tree in West Virginia. (Plate 3) (W. A. Shear, personal communication). This last specimen was brown in alcohol and did not have contrasting markings. Most collections of this rare species consist



Figures 15–26. *Araneus bicentenarius* (McCook). 15–20. Epigynum. 15–17. (New Jersey). 18–19. (Alabama). 15, 18. Ventral. 16, 19. Lateral. 17, 20. Posterior. 21, 22. Darsum of female abdomen. 23–26. Left palpus. 23. Mesal. 24. Ventral. 25. Embolus and conductor. 26. Embolus, ventral.

Figures 27–33. *A. andrewsi* (Archer). 27–29. Epigynum. 27. Ventral. 28. Lateral. 29. Posterior. 30. Female abdomen. 31–36. Palpus. 31. Mesal. 32. Ventral. 33. Embolus, ventral.

(Size indicators 0.5 mm, except abdomens: 5 mm)



Map. 2. Distribution of *Araneus diadematus* Clerck, *Araneus saevus* (L. Koch) and *Araneus santarita* (Archer).

of single specimens, very few of which are males.

Distribution. Eastern North America from Nova Scotia, Minnesota to northern Florida and Texas (Map 1); one male came from Coyote, New Mexico.

Araneus andrewsi (Archer)
Figures 27–33; Map 1

Aranea andrewsi Archer, 1951, Amer. Mus. Novitates, 1487: 31, figs. 63, 64, 82, ♀, ♂. Male holotype from Claremont, California, in the American Museum of Natural History.

Description. Female. Carapace brown, darker on sides. Sternum mottled brown. Legs mottled dark brown, indistinctly banded. Dorsum of abdomen brownish black, mottled, with a folium. Ventrally, area between epigynum and spinnerets dark gray. Carapace hairy. Abdomen with two large humps, very hairy, and with many very small sclerotized plates, the bases of setae. Total length, 14 mm. Carapace, 6.7 mm long, 5.9 mm wide. First femur, 6.3 mm; patella and tibia, 9.2

mm; metatarsus, 5.1 mm; tarsus, 1.8 mm. Second patella and tibia, 8.4 mm; third, 5.1 mm; fourth, 7.6 mm.

Male. Coloration like that of female; very dark and hairy. Abdomen with distinct humps. First coxa with a hook on distal margin, second with a large cone. Second tibia strong and bent, armed with macrosetae. Total length, 11 mm. Carapace, 5.2 mm long, 4.4 mm wide. First femur, 5.9 mm; patella and tibia, 8.4 mm; metatarsus, 4.6 mm; tarsus, 1.7 mm. Second patella and tibia, 7.6 mm; third, 4.2 mm; fourth, 5.9 mm.

Variation. Many individuals are almost black with the folium outline barely visible. Females measured 11–22 mm in total length, with carapace 5.0–7.8 mm long, 4.8–6.1 mm wide. Males measured 8–11 mm in total length; the smallest had the carapace 4.7 mm long, 3.6 mm wide.

Diagnosis. This Pacific coast species cannot be confused with any others in California. It differs from the related eastern North American *A. bicentenarius* in details of the genitalia (see under *A. bicentenarius*).

Habits. Specimens have been collected in a house basement. Another was in curled-up bark of a eucalyptus tree, with the web at chest height, strung toward a fence below the spider. Other specimens were collected on tree bark, and on the trunk of a walnut tree (*Juglans californica*).

Distribution. Araneus andrewsi is found from Oregon to southern California along the coast (Map 1).

Araneus diadematus Clerck, Cross Spider[1]
Figures 34–41, 95, 184–186; Map 2

Araneus diadematus Clerck, 1757, Svenska Spindlar, p. 25, pl. 1, fig. 4. The type specimens in the Natural History Museum, Stockholm, lost. Locket and Millidge, 1953, British Spiders, 2: 127, figs. 84a, 85a, 86a, 87a, ♀, ♂. Bonnet, 1955, Bibliographia Araneorum, 2: 486. Grasshoff, 1968, Abhandl. Senckenbergischen Naturforsch. Ges., 516: 1–100.

Epeira diademata, — Wiehle, 1927, Z. Morphol. Ökol. Tiere, 8: 492; Nielsen, 1932, Biology of Spiders, Copenhagen, Vol. 2: 421.

Aranea diadema, — Wiehle, 1931, *in* Dahl, Die Tierwelt Deutschlands, 23: 70, figs. 103–108, ♀, ♂. Roewer, 1942, Katalog der Araneae, 1: 797. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 249, figs. 779–782, ♀, ♂.

Description. Female. Carapace yellow-brown, sternum dark brown, coxae light brown. Legs yellow-brown banded with darker brown. Dorsum of abdomen with white marks anteriorly in form of a cross (Fig. 37), a folium posteriorly. Venter with a median black band and a pair of white spots closer to spinnerets than to epigastric groove. Dorsum of abdomen often with two humps. Female from Massachusetts measured total length, 13 mm. Carapace, 4.6 mm long, 3.9 mm wide. First femur, 5.0 mm; patella and tibia, 6.7 mm; metatarsus, 4.5 mm; tarsus, 1.7 mm. Second patella and tibia, 5.9 mm; third, 3.5 mm; fourth, 5.5 mm.

Male. Banding of legs less distinct than in female and color generally darker. Abdomen with a distinct white cross, and folium more distinct than in female. The abdomen lacks humps. Second tibia modified by being stronger and having very strong short spines. A specimen from Massachusetts measured 8 mm in total length. Carapace, 3.8 mm long, 3.4 mm wide. First femur, 5.2 mm; patella and tibia, 7.1 mm; metatarsus, 4.7 mm; tarsus, 1.5 mm. Second patella and tibia, 5.7 mm; third, 3.4 mm; fourth, 5.2 mm.

Variation. Females vary 6.5–20 mm in total length, carapace 3.5–7.2 mm long, 3.2–6.1 mm wide. Total length of males, 5.7–13 mm.

The shape of the abdomen and size of humps varies. The epigynal scape may vary slightly in length and the posterior triangular sclerite (Fig. 36) varies in shape and is often much less pointed behind. There are also small differences in the embolus curvature. This species and its variation were recently studied by Grasshoff (1968).

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[1] Garden Spider in Great Britain.

Diagnosis. Almost all females and many males can readily be recognized by the white marks arranged in the form of a cross on the dorsum of the abdomen (Fig. 37). No other species in North America has the cross mark. In addition, females are distinguished by the posterior face of the epigynum, which has a median triangular sclerite with the straight edge out, pointed end in (dorsally) (Fig. 36). The homologous sclerite in *A. saevus* has the outer flat edge with a median notch (Figs. 44, 47, 50) and the sclerite heart-shaped; the notch leads to a depression under the scape (Fig. 45) not present in *A. diadematus* (Fig. 34). *Araneus diadematus* has the openings usually distinctly visible in ventral view anterior of the triangular plate (Fig. 34).

Males are separated from all other *Araneus* species by the recurved embolus, triangular and pointed at its tip (Figs. 38, 40, 41), from *A. saevus* by the short, slightly curved terminal apophysis, and by the shape of the conductor (Figs. 38, 39).

Habits. In Europe the species is widespread and common in woods, gardens, and fields. In eastern North America, *A. diadematus* seems to do well only in cities in shrubs between houses, a habitat not to the liking of any native species of *Araneus*. In the west records are "from floor of food store," "web in woodpile," and many in cities. It may take two years for the animal to mature in Europe (Locket and Millidge, 1953). The female is more likely to remain in the center of the web at daytime than other American species. The species has been used for experimental research. The web has about 30 spokes and is made at up to 1.5 m height. The web has been illustrated by Wiehle, 1927, and Nielsen, 1932; the egg sac by Nielsen.

Distribution. This Eurasian species appears introduced, judging by its limited distribution in North America and its preferred habitat of shrubs surrounding city houses. It survives only in a narrow belt from Newfoundland south to Rhode Island, west to Vancouver and Oregon, more abundant on the milder coasts than in the Great Plains and mountain states (Map 2). Samples of records are St. Johns, Newfoundland; Quebec; Toronto; Vancouver; Victoria; Boston; Newport, Rhode Island; Syracuse; Ithaca; Rochester; Detroit; East Lansing; Seattle; Portland, and some smaller towns. The oldest American collections are about 100 years old and come from the northeast. The species does occur in Siberia and Japan. Specimens from the USSR, 64 km SSW of Irkutsk on Lake Baikal, were examined; they differed more from European ones than do North American specimens, presumably due to geographic variation.

Araneus saevus (L. Koch)

Figures 7–8, 42–51, 55–60; Map 2

Epeira saeva L. Koch, 1872, Z. Ferdinandeum Tirol Vorarlberg, (3) 17: 323. Male holotype specimens from Bad Ratzes, Austria [above Siusi, Trentino Alto Adige, Italy], in the British Museum, Natural History, examined.

Epeira solitaria Emerton, 1884, Trans. Connecticut Acad. Sci., 9(6): 299, pl. 33, fig. 11, pl. 35, fig. 3, ♂. Male holotype from Peabody, Massachusetts, in the Museum of Comparative Zoology, examined.

Epeira silvatica, — Emerton, 1884, Trans. Connecticut Acad. Sci., 9(6): 300 (in part), pl. 35, figs. 1–6, ♀. Female paralectotype here designated, not lectotype.

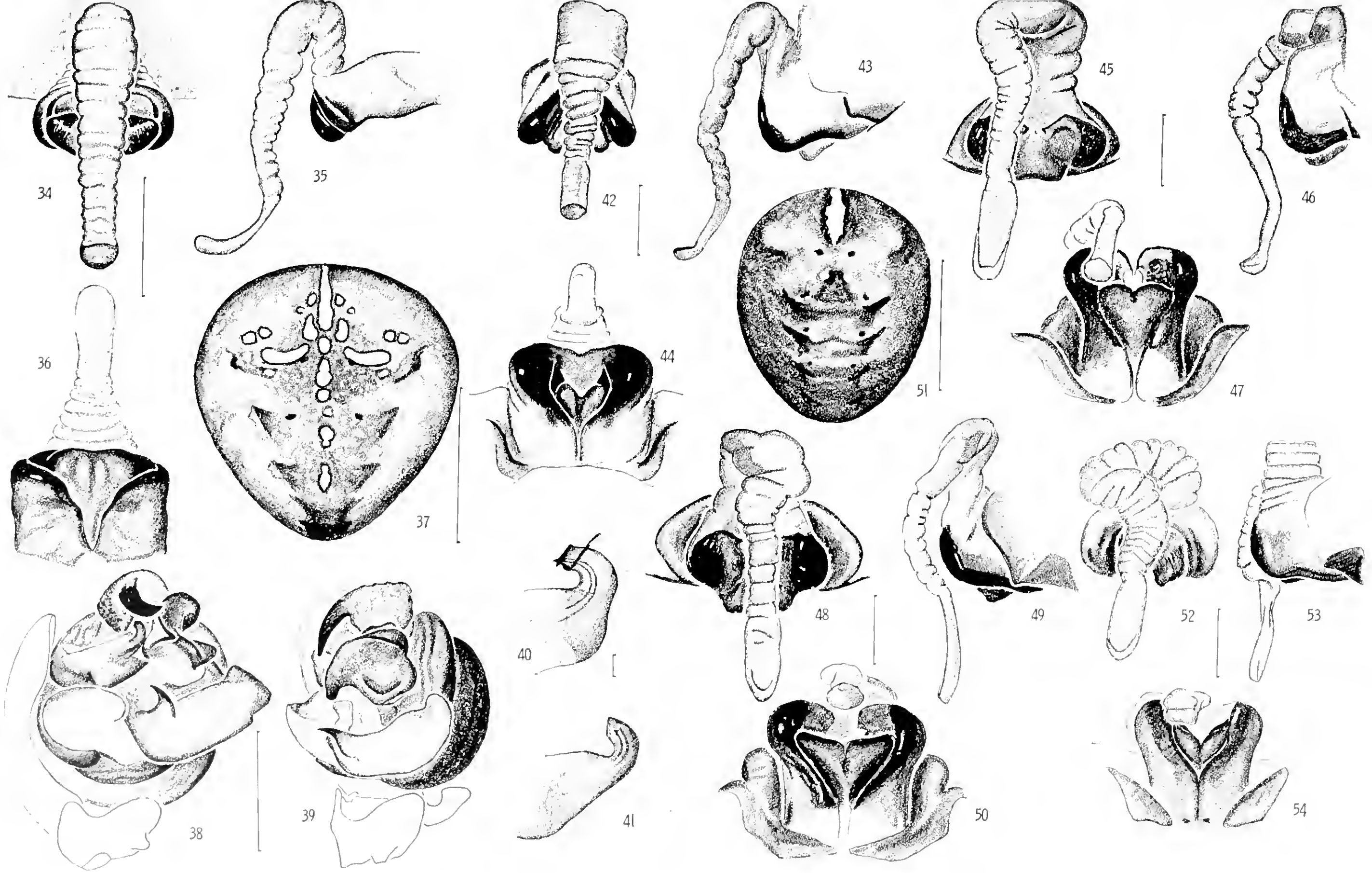
Epeira nigra Emerton, 1894, Trans. Connecticut Acad. Sci., 14(3): 402, pl. 1, fig. 1, ♀, ♂. Male and female syntypes from Laggan, Canada ["5000–8500′ in Rocky Mountains near Canadian Pacific Railway" a station near present-day Lake Louise], in the Museum of Comparative Zoology, examined.

Aranea saeva, — Roewer, 1942, Katalog der Araneae, 1: 791.

Aranea solitaria, — Roewer, 1942, Katalog der Araneae, 1: 863. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 250, figs. 785–786, 796–797, ♀, ♂.

Araneus saevus, — Tullgren, 1952, Entomol. Tidskr., 73: 164, figs. 10, 12, ♀, ♂. Bonnet, 1955, Bibliographia Araneorum, 2: 588. Wiehle, 1963, Zool. Jahrb. Abt. System., 90: 276, figs. 84–92, ♀, ♂.

Description. Female from near Lake Louise, Alberta. Carapace, sternum and



Figures 34–41. *Araneus diadematus* Clerck. 34–36. Epigynum. 34. Ventral. 35. Lateral. 36. Posterior. 37. Female abdomen. 38–41. Left palpus. 38. Mesal. 39. Ventral. 40, 41. Embolus. 40. With cap. 41. Without cap.

Figures 42–51. *A. saevus* (L. Koch). 42–50. Epigyna. 42–44. (Colorado). 45–50. (New York). 42, 45, 48. Ventral. 43, 46, 49. Lateral. 44, 47, 50. Posterior. 51. Female abdomen.

Figures 52–54. *A. sontorita* (Archer) epigynum. 52. Ventral. 53. Lateral. 54. Posterior.

(Size indicotors 0.5 mm, embolus tips 0.05 mm, and abdomens 5 mm) legs dark brown to black with some silvery hair. Abdomen dark brown with a darker folium, usually with a white anterior longitudinal cardiac mark and two ventral white spots side by side. Abdomen covered with long and short hair. Total length, 13 mm. Carapace, 5.4 mm long, 4.6 mm wide. First femur, 5.3 mm; patella and tibia, 7.1 mm; metatarsus, 4.2 mm; tarsus, 1.7 mm. Second patella and tibia, 6.4 mm; third, 4.2 mm; fourth, 6.5 mm.

Male from same locality. Male a little darker than female. First coxa with a hook on distal margin, the second with a spur. Second tibia swollen and with macrosetae. Total length, 9 mm. Carapace, 5.0 mm long, 4.0 mm wide. First femur, 5.0 mm; patella and tibia, 6.3 mm; metatarsus, 3.5 mm; tarsus, 1.4 mm. Second patella and tibia, 6.1 mm; third, 3.8 mm; fourth, 5.4 mm.

Variation. Although the abdomen is usually black with an anterior white cardiac mark (Fig. 51), at times the color is brown, but the white mark may persist. Females varied in total length 11–17 mm, carapace, 4.0–6.0 mm long, 3.2–5.2 mm wide; males were 9–11 mm in total length, carapace, 5.0–5.2 mm long, 4.0–4.5 mm wide.

Diagnosis. Although many specimens in collections were misidentified, females can be confused only with *A. diadematus.* The abdomen of *A. saevus* does not have the spots arranged in the cross typical of *A. diadematus* and the epigynum differs in details (see *A. diadematus*).

The male may be confused with *A. nordmanni,* but unlike *nordmanni* the terminal apophysis, a black prong, is very strongly curved (Figs. 7, 8, 55, 56).

Habits. Araneus saevus is found in forests on trees; it has been found on lodgepole pine (*Pinus contorta*) in the Canadian Rockies, and on a poplar tree (*Populus* sp.) in Maine.

Distribution. Comparison of specimens confirmed Wiehle's recent observation (Wiehle, 1963) that *A. solitarius* of North America is the same as the Eurasian *A. saevus.* The species is found in America probably from southern Alaska south to New York state and Oregon (Map 2).

Araneus santarita (Archer)
Figures 52–54; Map 2

Aranea santarita Archer, 1951, Amer. Mus. Novitates, 1587: 24, fig. 65, ♀. Female holotype from Santa Rita Mtns., Arizona, in the American Museum of Natural History, examined.

Description. Female holotype. Head area dark brown; posterior and sides of carapace lighter. Sternum brown with white median longitudinal band. Legs brown with bands barely showing. The damaged abdomen is slightly reddish in color, and has small humps. Total length, 17 mm. Carapace, 6.0 mm long, 5.9 mm wide. First femur, 8.6 mm; patella and tibia, 10.0 mm; metatarsus, 6.7 mm; tarsus, 2.4 mm. Second patella and tibia, 9.6 mm; third, 6.0 mm; fourth, 8.8 mm.

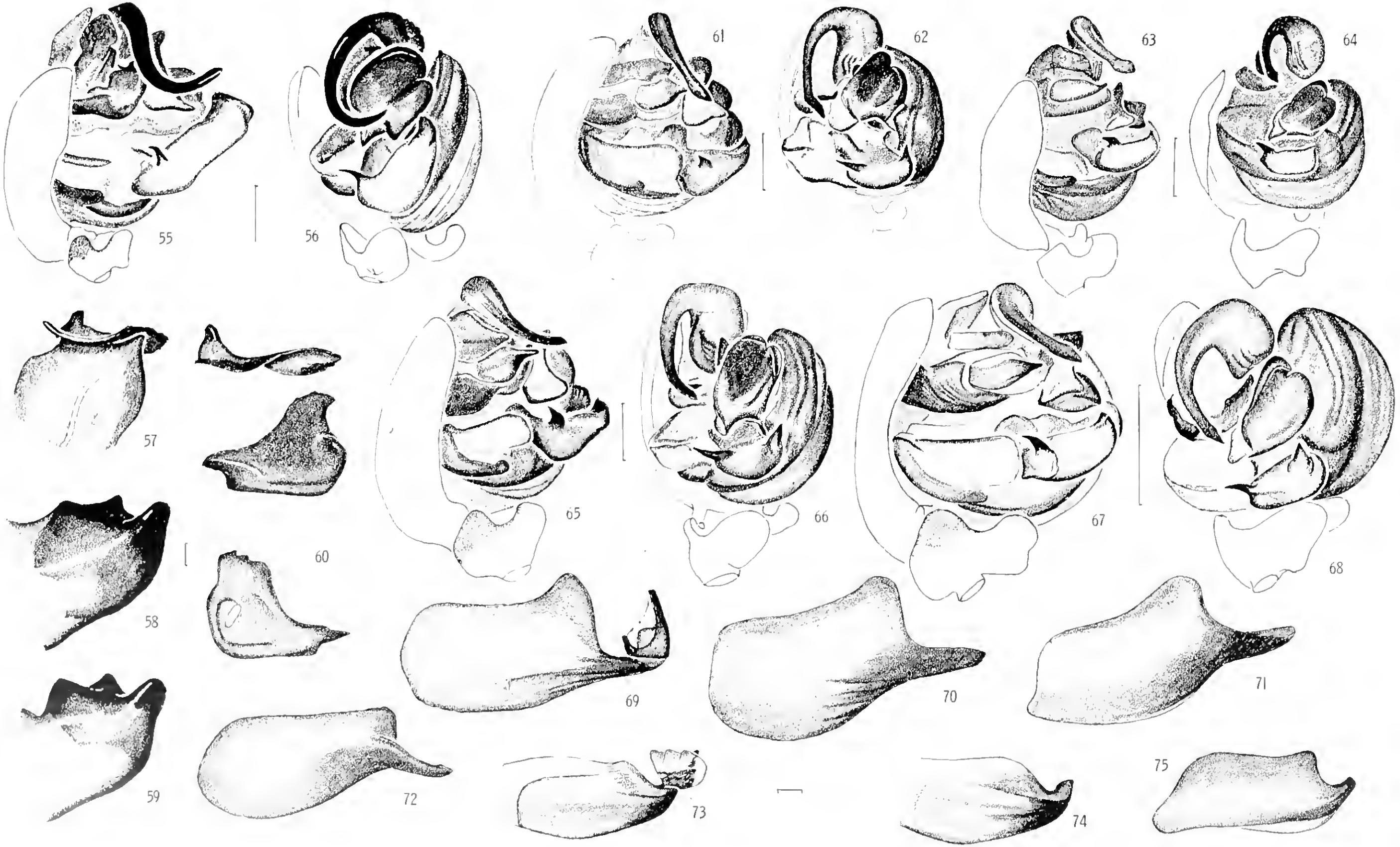
Diagnosis. This may be an atypical specimen of *A. saevus.* It differs by its more twisted epigynal scape (Fig. 52) and details in posterior aspect of the epigynum (Fig. 54).

Distribution. This species is known only from the type specimen from Arizona (Map 2).

Araneus nordmanni (Thorell)
Figures 61–94, 96–99; Map 3

Epeira nordmanni Thorell, 1870, Remarks on Synonyms of European Spiders, p. 4. Holotype from Uppland, Sweden [area north of Stockholm including Uppsala]. The type was destroyed when the Swedish freighter "Oklahoma" carrying it in the mail sank off Great Britain in December 1953. Thorell, 1873, Remarks on Synonyms of European Spiders, p. 514. Emerton, 1885, Trans. Connecticut Acad. Sci., 6: 301, pl. 33, fig. 6, ♀; Emerton, 1894, Trans. Connecticut Acad. Sci., 9: 403, pl. 1, fig. 2, ♀, ♂. Nielsen, 1932, The Biology of Spiders, Copenhagen, Vol. 1, fig. 38.

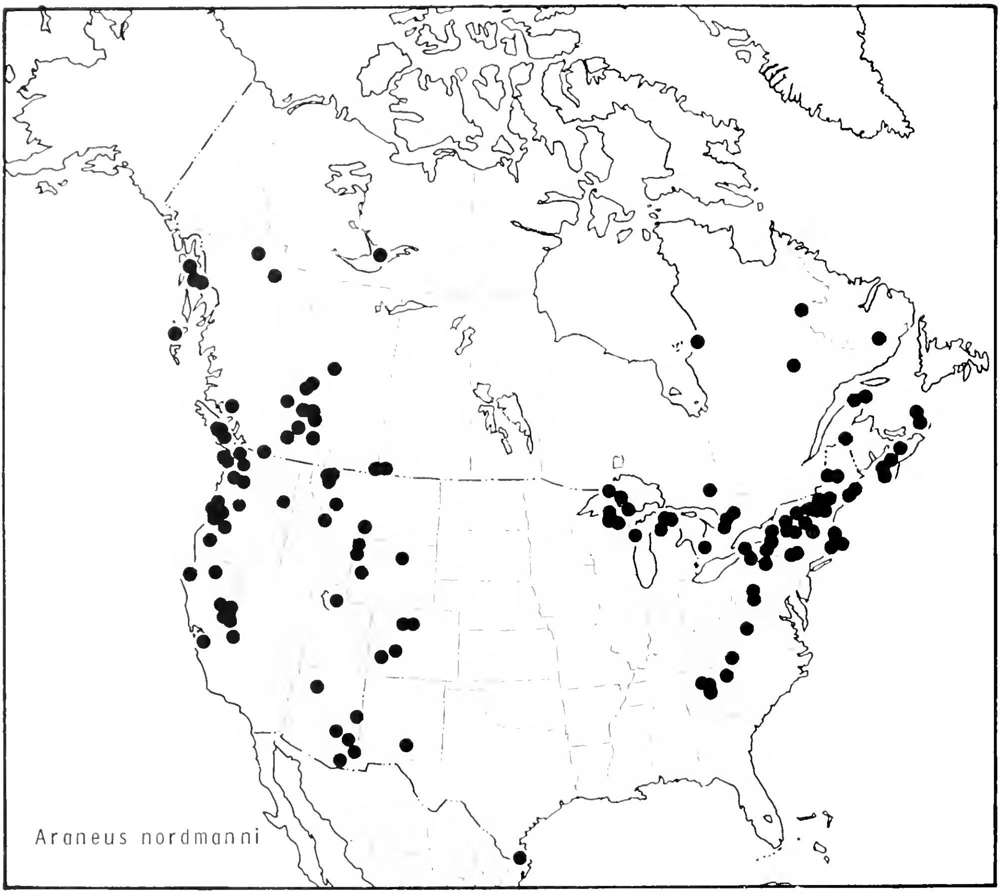
Epeira silvatica Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 300, pl. 33, fig. 13, pl. 35, figs. 1, 4, ♂. Male lectotype from Beverly, Massachusetts, in the Museum of Comparative Zoology, here designated, examined.



Figures 55–60. *Araneus saevus* (L. Koch), left palpus. 55. Mesal. 56. Ventral. 57–60. Embolus. 57. With cap. 58, 59. Without cap. 60. Different aspects of a cap.

Figures 61–75. *A. nordmanni* (Thorell), palpus. 61, 62. (Colorado). 63, 64. (Massachusetts). 65, 66. (Arizona). 67, 68. (Montana). 61, 63, 65, 67. Mesal. 62, 64, 66, 68. Ventral. 69–75. Embolus. 69, 70. (Colorado). 71. (Arizona). 72. (New Mexico). 73, 74. (Montana). 75. (Massachusetts). 69, 73. With cap.

(Size indicators 0.5 mm, embolus tips 0.05 mm)



Map 3. Distribution of *Araneus nordmanni* (Thorell).

Aranea nordmanni, — Wiehle, 1931, *in* Dahl, Tierwelt Deutschlands, 23: 58, figs. 84, 85, ♀. Roewer, 1942, Katalog der Araneae, 1: 801. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 250, figs. 783–784, 793–795, ♀, ♂.

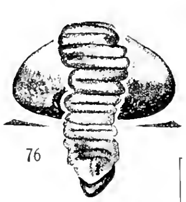
Aranea darlingtoni Archer, 1951, Amer. Mus. Novitates, 1487: 25, figs. 71, 75, ♀, ♂. Female holotype from Durbin, West Virginia, in the American Museum of Natural History; paratypes examined. NEW SYNONYMY.

Aranea pseudomelaena Archer, 1951, Amer. Mus. Novitates, 1487: 26, figs. 70, 79, ♀, ♂. Male holotype from Long's Peak, Colorado, in the American Museum of Natural History, examined. NEW SYNONYMY.

Araneus nordmanni, — Bonnet, 1955, Bibliographia Araneorum, 2: 553. Wiehle, 1963, Zool. Jahrb. Abt. System., 90: 271, figs. 74–83, ♀, ♂.

Note. Archer named American specimens *A. darlingtoni* because he thought that European ones lack the basal spur on coxa II. Wiehle (1963) illustrated the spur, and all European males examined had it. Also Archer indicates that "on the endal side [of the median apophysis] below the spur is a rounded angle, a feature entirely missing in *A. nordmanni*." As discussed in the introduction, the median apophysis by itself is not a good character to separate species.

Araneus pseudomelaena Archer was thought to be a valid entity, but extremely variable. As more collections were examined it was found that those specimens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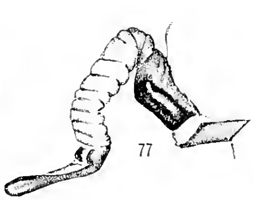
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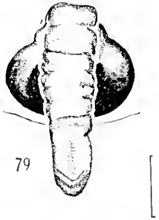
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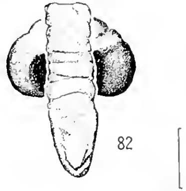
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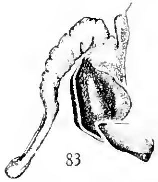
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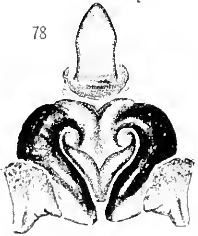
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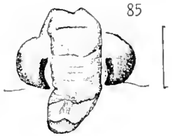
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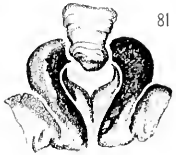
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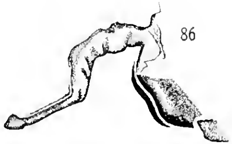
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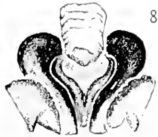
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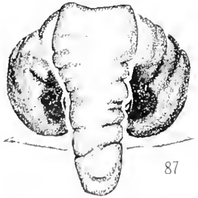
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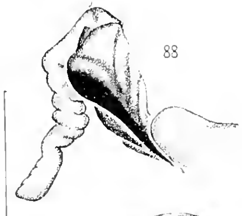
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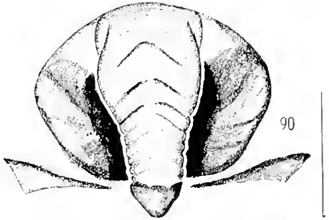
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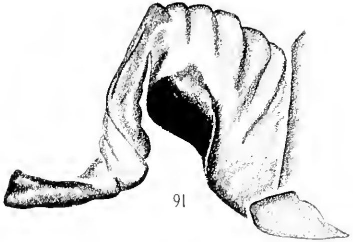
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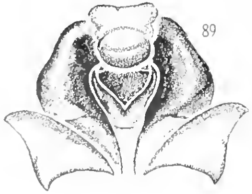
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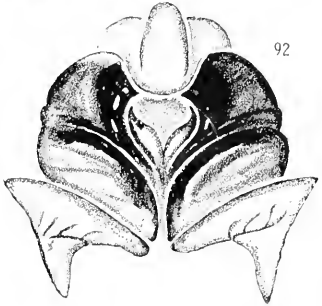
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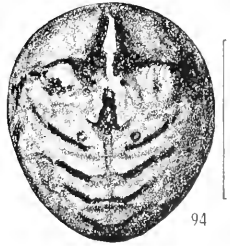
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Figures 76–94. *Araneus nordmanni* (Thorell). 76–92. Epigynum. 76–78. (Arizona). 79–81. (Texas). 82–84. (Oregon). 85–86. (Brit. Columbia). 87–89. (Montana). 90–92. (North Carolina). 76, 79, 82, 87, 90. Ventral. 77, 80, 83, 86, 88, 91. Lateral. 78, 81, 84, 89, 92. Posterior. 93, 94. Female abdomen. 93. (Montana). 94. (Texas).

Figure 95. *A. diadematus* Clerck, female, venter of cephalothorax.

(Size indicators 0.5 mm, abdomens 5 mm)

ascribed to *pseudomelaena* were all allopatric with *A. nordmanni*, and also that many specimens had to be arbitrarily placed in one or the other. The problem of *A. pseudomelaena* is discussed in greater detail in the introduction and in the paragraph on variation below.

Description. A female specimen from Montana had carapace light brown, sternum dark brown, coxae and femora light brown, distal segments of legs banded, dorsum of abdomen with a distinct folium (Fig. 93), venter with a dark brown band between epigynum and spinnerets, on each side of which is a white bracket. Dorsum of abdomen with two humps. Total length, 8.5 mm. Carapace, 3.2 mm long, 2.5 mm wide. First femur, 3.4 mm; patella and tibia, 4.3 mm; metatarsus, 2.8 mm; tarsus, 1.2 mm. Second patella and tibia, 3.8 mm; third, 2.4 mm; fourth, 3.5 mm.

A female from Arizona had the carapace rich dark brown, sternum dark brown, and legs dark brown. Only edges of labium and of endites light. Abdomen brown to black. Venter with two white spots side by side. Sometimes a white longitudinal mark between two humps (Fig. 94) on abdomen. Total length, 15 mm. Carapace, 6.5 mm long, 5.6 mm wide. First femur, 6.8 mm; patella and tibia, 8.5 mm; metatarsus, 5.5 mm; tarsus, 1.7 mm. Second patella and tibia, 8.4 mm; third, 5.4 mm; fourth, 8.0 mm.

Male. A specimen from Montana had coloration as in female. Venter with a black band and two white brackets, or brackets often reduced to four white spots. The abdomen is longer than wide and much wider in front than behind. The humps are small. The first coxa has a distal hook, the second a spur. The second tibia is bent and bears strong macrosetae. Total length, 7.5 mm. Carapace, 4.2 mm long, 3.2 wide. First femur, 4.6 mm; patella and tibia, 5.8 mm; metatarsus, 3.4 mm; tarsus, 1.2 mm. Second patella and tibia, 4.7 mm; third, 3.0 mm; fourth, 4.6 mm.

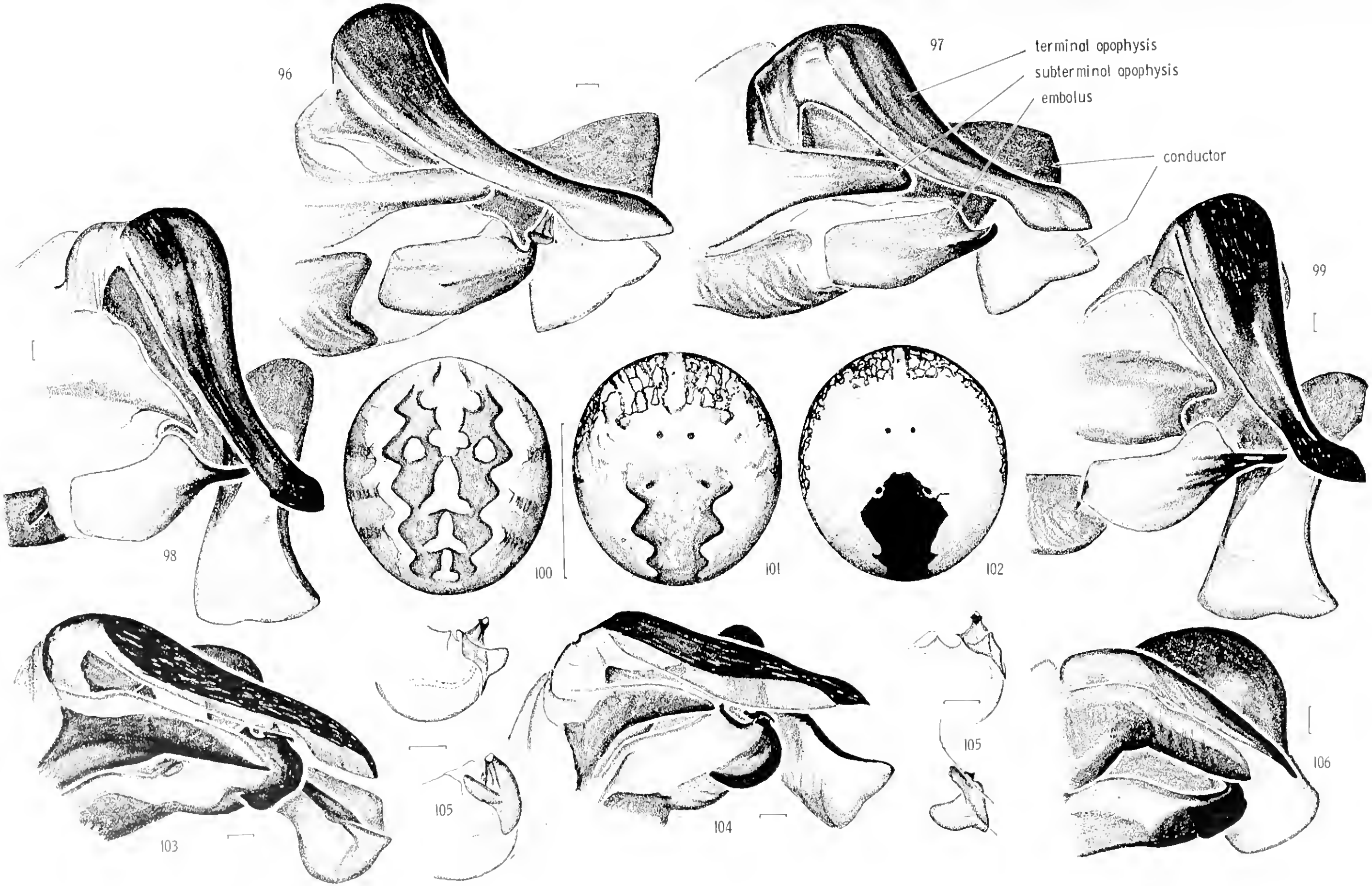
A male from Graham Mountains, Arizona, had coloration like that of female from Arizona. Distal segments of legs lighter and banded. Abdomen almost black with two humps. First coxa with a hook on distal margin, second with a spur. Second tibia modified with spines and swollen. Total length, 10 mm. Carapace, 6.4 mm long, 5.5 mm wide. First femur, 7.5 mm; patella and tibia, 9.2 mm; metatarsus, 5.7 mm; tarsus, 1.7 mm. Second patella and tibia, 8.0 mm; third, 5.0 mm; fourth, 7.6 mm.

Variation. The size and coloration of this species are variable. The largest and darkest specimens are found in the southwestern part of the range; the size given above is for the largest. The total length of females is 7–19 mm, the smallest having the carapace 3.0 mm long, 2.8 mm wide. Males range 6–10 mm, the smallest having the carapace 3.1 mm long, 2.8 mm wide.

Often specimens in alcohol are strikingly colored black and white, the legs contrastingly banded.

The genitalia of *A. nordmanni* become increasingly variable as one moves south, especially the structures of the male palpus, including the median apophysis so carefully studied by Archer (Figs. 61–68). But no two males in the southern part of the range have the median apophysis or the embolus identical (Figs. 69–75, 96–99), and as these variable southern populations are allopatric with the less variable northern *A. nordmanni*, and many males would have to be arbitrarily placed, they are considered one species. Except for epigynum size and scape length and shape, the epigyna are all alike.

Diagnosis. In the part of the range in which *A. nordmanni* overlaps with *A. saevus*, the former is smaller than the latter species; outside the range of *A. saevus* it is larger. Females of *A. nordmanni* have a much shorter scape (Figs. 87, 90) than those of *A. saevus*. The species can be confused with the sympatric *A. cavaticus*



Figures 96–99. *Araneus nordmanni* (Thorell), terminal apophysis and embolus of left male palpus, mesal. 96. (Tennessee). 97. (Montana). 98, 99. (California).

Figures 100–105. *A. marmoreus* Clerck. 100–102. Female abdomen. 103, 104. Terminal apophysis and embolus of palpus, mesal. 103. (Saskatchewan). 104. (Nova Scotia). 105. Embolus cap of a male which has just molted.

Figure 106. *A. washingtoni* sp. n., terminal apophysis and embolus of palpus, mesal.
(Size indicators 0.05 mm for palpal parts, about 5 mm for abdomens)

in the eastern part of Canada and United States; however, in posterior view of *A. nordmanni* the rims of the epigynum enclose a semicircular, heart-shaped depression (Figs. 89, 92) that is absent in *A. cavaticus* (Fig. 189). *A. nordmanni* females have humps on the abdomen, distinguishing them from females of *A. manitobae*, which have a somewhat similar epigynum.

The prong of the terminal apophysis of the male palp (Figs. 96–99) is less sclerotized and less strongly curved in *A. nordmanni* than in *A. saevus*. The shape of the embolus, which opens on a tip pointing away from the cymbium, is quite characteristic (Figs. 69–75) and distinguishes all male specimens of *A. nordmanni* from all other North American *Araneus* species.

Habits. Araneus nordmanni is found on trees or, sometimes, boulders, often in dark coniferous forests, and often at high elevations in mountains (for instance, Mt. Grizzly, Brit. Col., at 1600–2200 m elevation and Long's Peak in Colorado). Collection comments read: On lodgepole pine (*Pinus contorta*) in Alberta; on bush in Montana; on birch (*Betula* sp.) on Mt. Katahdin, Maine; on building in Porcupine Mts., Michigan; mixed ponderosa pine (*Pinus ponderosa*) and juniper (*Juniperus* sp.) in Springerville, Arizona. Nielsen (1932) shows a retreat among lichens on branches.

Distribution. Araneus nordmanni was first described from Scandinavia. It has since only rarely been found in Europe. I have examined specimens from Adelboden, Switzerland; Giant Mountains, now eastern Poland; Uppland, Sweden; and Järve, Finland. All are much alike and much like specimens from the northern parts of North America. A new record from 64 km SSW of Irkutsk, on Lake Baikal, Siberia, USSR, 13. VIII. 1968 (B. and J. Hocking), indicates that this species does have a wide distribution in Eurasia. In North America it seems to occur in forested regions north of Mexico (Map 3).

Araneus marmoreus Clerck, Marbled Spider Figures 1–6, 100–105, 107–113, 183; Map 4

Araneus marmoreus Clerck, 1757, Svenska Spindlar, p. 29, pl. 1, fig. 2, ♀. Female type from Sweden in the Natural History Museum, Stockholm, lost. Locket and Millidge, 1953, British Spiders, 2: 130, figs. 79d, 84e, 85c, 86c, 87b, ♀, ♂. Bonnet, 1955, Bibliographia Araneorum, 2: 534. Grasshoff, M., 1968, Abhandl. Senckenbergischen Naturforsch. Ges., 516: 1–100.

Aranea raji Scopoli, 1763, Entomologia Carniolica, p. 394. The Scopoli collection was destroyed in the 18th century (Horn and Kahle, 1936, Entomol. Beihefte, 3: 252). Wiehle, 1931, *in* Dahl, Die Tierwelt Deutschlands, 23, p. 75, figs. 109–114, ♀, ♂. Roewer, 1942, Katalog der Araneae, 1: 802.

Epeira insularis Hentz, 1847, Boston J. Natur. Hist. Soc., 5: 470, pl. 30, fig. 10, ♀. Female holotype from an island in the Tennessee River, destroyed. Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 309, pl. 33, fig. 1, pl. 35, fig. 18, ♀, ♂. Keyserling, 1892, Die Spinnen Amerikas, 4: 170, pl. 8, fig. 126, ♀.

Epeira obesa Hentz, 1847, Boston J. Natur. Hist. Soc., 5: 471, pl. 30, fig. 11, ♀. Female holotype from Maine, destroyed.

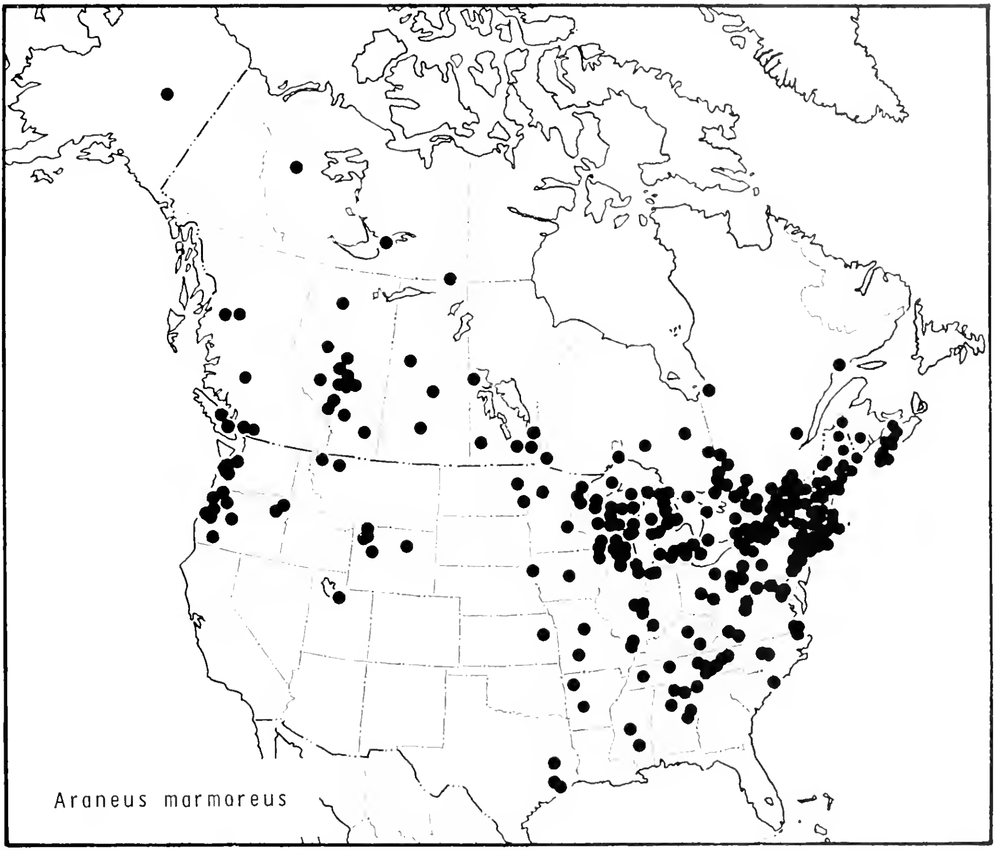
Epeira marmorea,—Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 307, pl. 33, fig. 2, pl. 35, fig. 17, ♀, ♂.

Aranea gigas,—Comstock, 1912, The Spider Book, p. 475, figs. 493–498, ♀, ♂; 1940, The Spider Book, rev. ed., p. 489, figs. 493–498, ♀, ♂. Not *A. gigas* Leach; not *A. gigas* C. L. Koch.

Aranea tusigia Chamberlin, 1919, Ann. Entomol. Soc. Amer., 12: 254, pl. 19, fig. 3, ♂. Male holotype from Chalk Creek, Utah, in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Epeira raji,—Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 257, figs. 816–822, 2048–2049.

Description. Female from Michigan. Carapace light brown, sternum dark brown, legs light brown, indistinctly banded. Abdomen with dorsum white to yellow or orange, having a dark pattern of grays and blacks, with black lines around light spots. Venter with a black band enclosed by white brackets. Total length, 14 mm. Carapace, 5.2 mm long, 4.5 mm wide. First femur, 5.4 mm; patella and tibia, 6.7 mm; metatarsus, 4.0 mm; tarsus, 1.6 mm. Second



Map 4. Distribution of *Araneus marmoreus* Clerck.

patella and tibia, 6.4 mm; third, 4.0 mm; fourth, 6.0 mm.

Male from Michigan. Coloration like that of female with legs more distinctly banded. The first coxa has a hook on the distal ventral rim, the second coxa a spur. The second tibia is swollen and bears macrosetae. Total length of a specimen from Michigan, 8.4 mm. Carapace, 5.0 mm long, 3.7 mm wide. First femur, 5.0 mm; patella and tibia, 6.7 mm; metatarsus, 3.6 mm; tarsus, 1.2 mm. Second patella and tibia, 5.9 mm; third, 3.5 mm; fourth, 5.0 mm.

Variation. Total length of females, 9–18 mm; carapace 2.7–5.2 mm long, 2.3–4.5 mm wide. Total length of males, 5.9 mm; Carapace 2.9–4.3 mm long, 2.3–3.6 mm wide.

There is considerable variation in color and pattern. One female from Texas had black bands on its legs. The abdomen has a black folium in many females collected in Alberta, Montana, Wyoming, Europe, and isolated other places (Figs. 101, 102); in females from other areas the folium encloses symmetrical light patches (Fig. 100), or sometimes it has a reticulated pattern. The shape of the terminal apophysis and the length of the subterminal apophysis vary from specimen to specimen (Figs. 103, 104). Although the median apophysis of *A. marmoreus* is just as variable as that of other *Araneus* species (Grasshoff, 1968, figs. 36e–h). *A. marmoreus* has escaped being split into several species.

Diagnosis. The common *A. marmoreus* differs from related *A. corticarius* and most other North American *Araneus* species by having an oval, subspherical abdomen. The female can be recognized by the large basal lamellae of the epigynum which almost always extend on each side beyond the base and are visible in ventral view (Figs. 1–3, 107–109). They also extend at times in *A. iviei.*

Males, despite the distinct palpus, are often misidentified. The terminal apophysis is sclerotized and along its proximal side is a translucent edge. The terminal apophysis is paralleled by a subterminal apophysis (Figs. 4, 6, 103, 104, 110). In *A. nordmanni* and *A. saevus* the subterminal apophysis is shorter. The embolus resembles that of *A. corticarius,* being semicircular below the tip. The embolus lamella, if it shows at all, is in the shape of a flat hook (Figs. 4–6, 111), not a piece with parallel sides as in *A. trifolium* (Fig. 179). The conductor (Figs. 5, 111) is much wider than that of *A. trifolium* (Fig. 179) and has a clearly set off, narrower tongue facing the median apophysis.

Habits. Araneus marmoreus prefers tall meadows, and places its webs in grasses or low shrubs, sometimes on trees. In the West it has been collected in light lodgepole pine (*Pinus contorta*) forest, its retreat under bark, in a relatively humid place. Kaston (1948) reports the egg sac to be "13 mm in diameter, a flattened sphere of loose white silk. There were 653 orange, agglutinated eggs, each about 1.15 mm in diameter." The web has been illustrated by Comstock (1912, 1940) and Kaston (1948), the egg sac by Comstock. The web has 24–29 spokes and is made 50–90 cm high in grass.

Distribution. Araneus marmoreus is holarctic in distribution. The borders of its Eurasian distribution have not been critically mapped. The many literature citations of misidentified specimens will give a mistaken idea of the distribution. In North America *A. marmoreus* is found from Alaska to the southern United States (Map 4).

Araneus corticarius (Emerton)
Figures 114–122; Map 5

Epeira corticaria Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 300, pl. 33, fig. 14, pl. 35, fig. 9, ♀. Two female syntypes from Beverly, Mass., in the Museum of Comparative Zoology, examined. McCook, 1893, American Spiders, p. 176, pl. 8, fig. 7, ♀. Emerton, 1909, Trans. Connecticut Acad. Sci., 14: 199, pl. 5, fig. 3, ♂.

Epeira incestifica Keyserling, 1892, Die Spinnen Amerikas, 4: 132, pl. 7, fig. 98. Female holotype from Sitka, Alaska [?] (G. Marx), in the U. S. National Museum, examined.

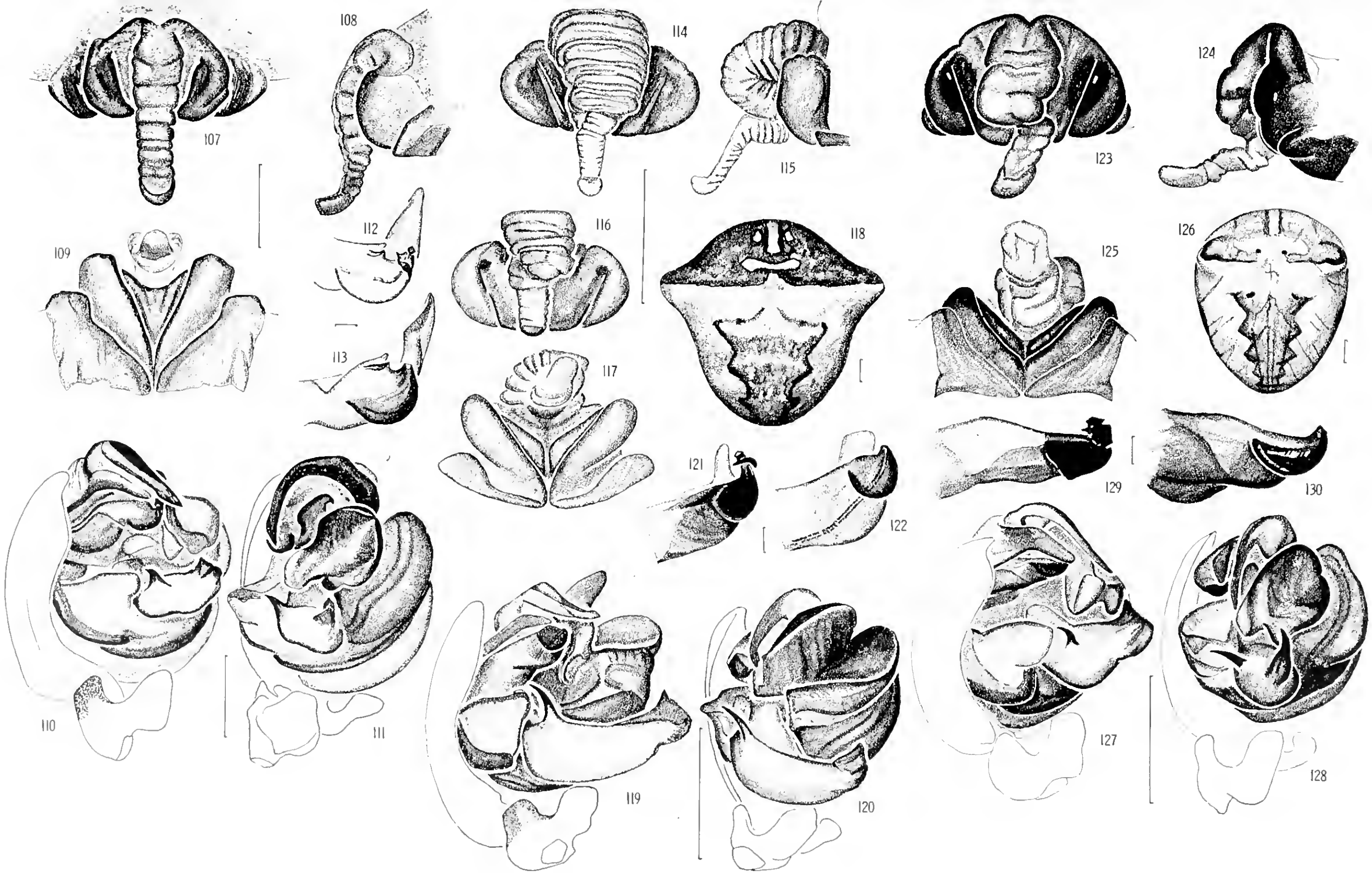
Aranea corticaria, — Roewer, 1942, Katalog der Araneae, 1: 860. Kaston, 1948, Bull. Connecticut State Geol. Natur. Hist. Surv., 70: 252, figs. 800–802, ♀, ♂.

Aranea denningi Archer, 1951, Amer. Mus. Novitates, 1487: 30, fig. 81, ♂. Male holotype from The Pas, Manitoba, in the American Museum of Natural History, examined. NEW SYNONYMY.

Araneus corticarius, — Bonnet, 1955, Bibliographia Araneorum, 2: 470.

Description. Female from Maine. Carapace brown with some hairs and some irregular marks. Sternum dark brown. Coxae light. Legs light, contrastingly banded. Anterior of dorsum of abdomen black with a white cross (Fig. 118). Venter black with a white bracket on each side. Abdomen with large humps. Eyes large and close together. Epigynum with a folded scape (Figs. 114, 116). Total length, 6 mm. Carapace, 2.1 mm long, 1.9 mm wide. First femur, 2.5 mm; patella and tibia, 3.0 mm; metatarsus, 1.6 mm; tarsus, 0.8 mm. Second patella and tibia, 2.7 mm; third, 1.6 mm; fourth, 2.4 mm.

Male from Maine. Less contrastingly colored than female. Abdomen marked like that of female but with less contrast. Abdomen has humps laterally. First coxa with hook, second without spur. The second tibia is swollen. Total length, 4.7 mm. Carapace 2.5 mm long, 1.8 mm wide. First femur, 3.0 mm; patella and tibia, 3.5 mm;

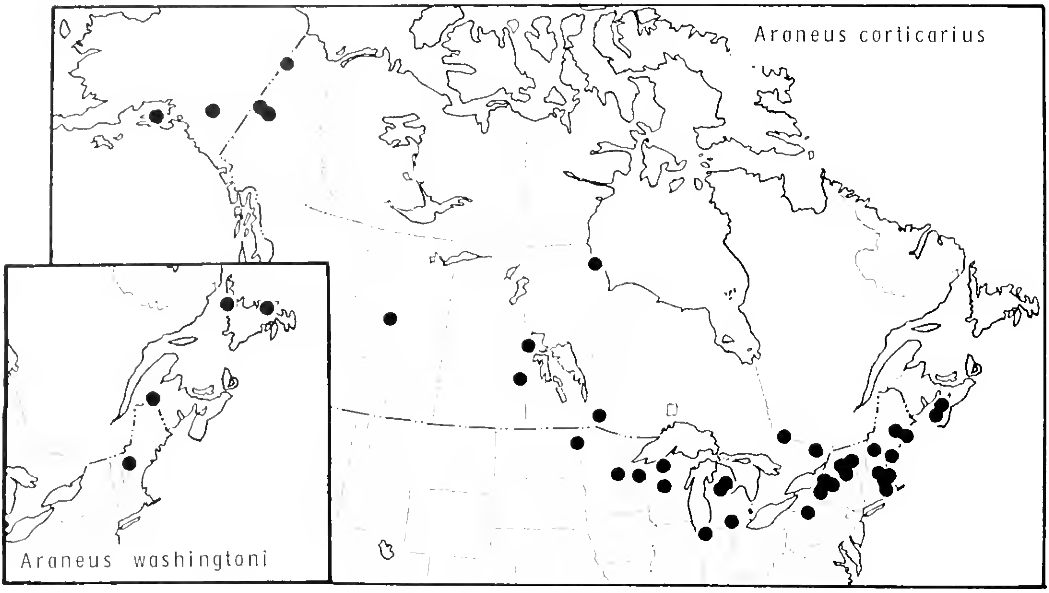


Figures 107–113. *Araneus marmoreus* Clerck. 107–109. Epigynum. 107. Ventral. 108. Lateral. 109. Posterior. 110–113. Left male palpus. 110. Mesal. 111. Ventral. 112, 113. Embolus. 112. With cap. 113. Without cap.

Figures 114–122. *A. corticarius* (Emerton). 114–117. Epigynum. 114, 116. Ventral. 115. Lateral. 117. Posterior. 118. Female abdomen. 119–122. Male palpus. 119. Mesal. 120. Ventral. 121, 122. Embolus. 121. With cap. 122. Without cap.

Figures 123–130. *A. washingtoni* sp. n. 123–125. Epigynum. 123. Ventral. 124. Lateral. 125. Posterior. 126. Female abdomen. 127–130. Male palpus. 127. Mesal. 128. Ventral. 129, 130. Embolus. 129. With cap. 130. Without cap.

(Size indicators 0.5 mm, for palpal parts 0.05 mm)



Map 5. Distribution of *Araneus corticarius* (Emerton) and *Araneus washingtoni* sp. n.

metatarsus, 1.8 mm; tarsus, 0.8 mm. Second patella and tibia, 3.0 mm; third, 1.8 mm; fourth, 2.5 mm.

Variation. Total length of females varied between 5.2–8.0 mm, the carapace 2.1–2.9 mm long and 1.9–2.3 mm wide. Total length of males, 4.2–5.2 mm. The shape of the abdomen is variable.

Diagnosis. The shape of the abdomen, with the humps projecting toward the sides, is not seen in any other large North American *Araneus* including *A. washingtoni.* The epigynum of the female (Figs. 114–117) resembles that of *A. marmoreus*, but the epigynal lamellae are smaller, only rarely visible in ventral view, and the median field behind the scape between the rims is wider than in *A. marmoreus.* The scape usually breaks off during mating.

The embolus shape (Figs. 119, 121, 122) resembles that of *A. marmoreus*, but the enormous conductor, its length half that of the bulb in ventral view (Fig. 120), and the longer median apophysis (Figs. 119, 120) separate the species from *A. marmoreus* and *A. washingtoni.*

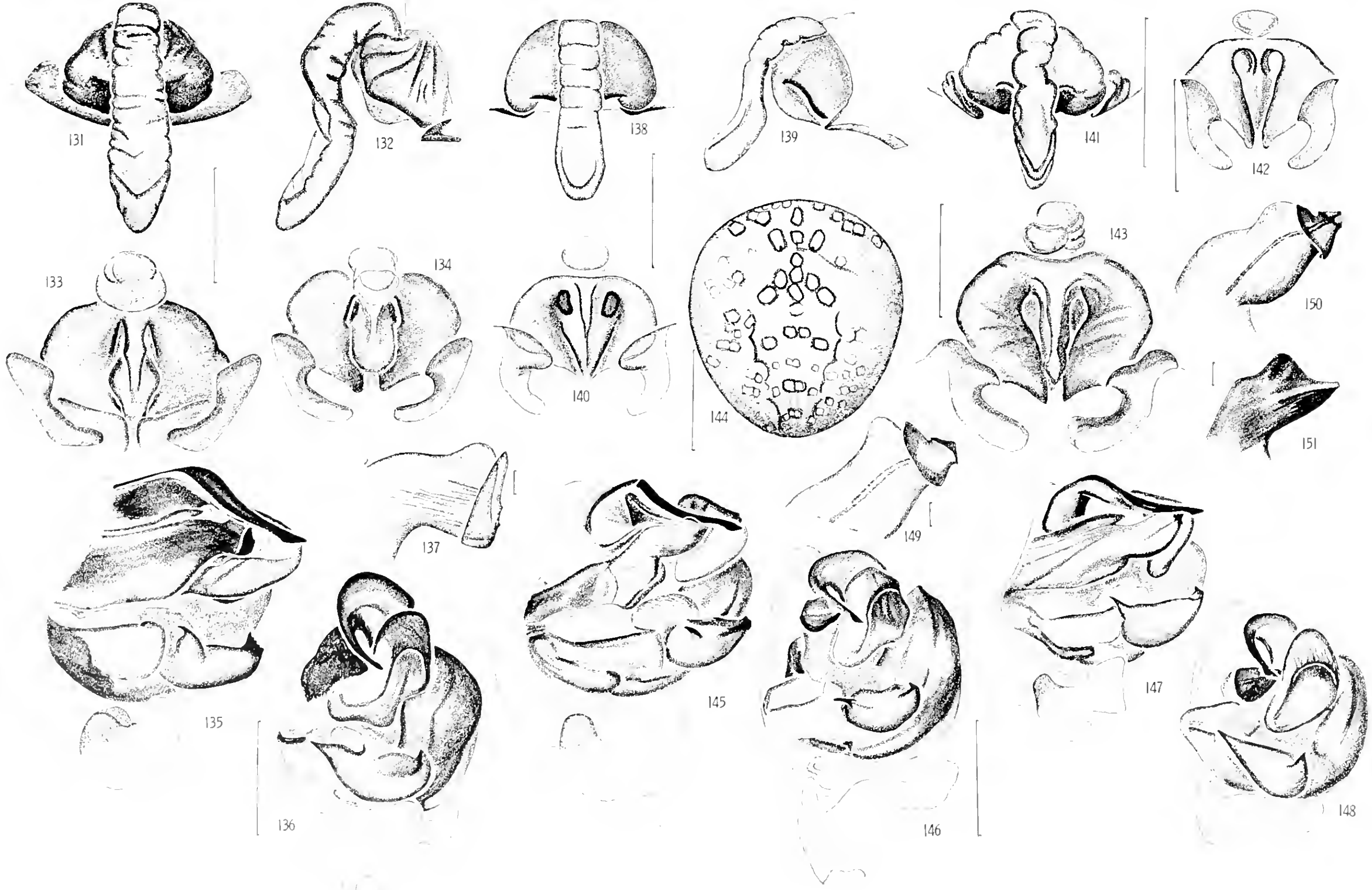
Habits. Kaston (1948) reports having collected *A. corticarius* in moist meadows and woods. It has been collected from a cranberry bog in Massachusetts, from a swamp in Wisconsin, swept from a hemlock seedling (*Tsuga canadensis*) in a swamp in Pennsylvania.

Distribution. Araneus corticarius is found from Alaska to New England. Its known range matches the range of black spruce (*Picea mariana*) and tamarack (*Larix laricina*), both bog inhabitants. The southernmost records are Ice Mine, Potter Co., Pennsylvania, and Beverly Shores, Porter Co., Indiana; the northernmost, Rampart House, Yukon Terr. (Map 5).

Araneus washingtoni sp. n.
Figures 123–130; Map 5

Holotype. Male from 3 miles up road, Mt. Washington [no date] (J. H. Emerton), in the Museum of Comparative Zoology. The species is named after George Washington, as is the mountain.

Description. Female. Carapace brown, sternum dark brown. Coxae light brown,



Figures 131–137. *Araneus alsine* (Walckenaer). 131–134. Epigynum. 131–133. (Germany). 134. (Great Britain). 131. Ventral. 132. Lateral. 133, 134. Posterior. 135–137. Left male palpus. 135. Mesal. 136. Ventral. 137. Embolus.

Figures 138–151. *A. iviei* (Archer). 138–143. Epigynum. 138–140. (New Jersey). 141. (Alberta). 142. (Massachusetts). 143. (Saskatchewan). 144. Female abdomen. 145–151. Male palpus. 145–146. (Pennsylvania). 147, 148. (Michigan). 145, 147. Mesal. 146, 148. Ventral. 149–151. Embolus. 149. (Vermont). 150. (Michigan). 151. (Pennsylvania). 149, 150. With cap. 151. Without cap, slightly ventrolateral.

(Size indicators 0.5 mm, embolus tips 0.05 mm, abdomen 5 mm) legs brown, indistinctly banded. Dorsum of abdomen with a folium and a black line between humps, darker anterior of line with a white cardiac mark and a transverse white line (Fig. 126). Venter of abdomen black with a white bracket on each side. Each side of abdomen has a black patch which fades toward the venter. The shape of the abdomen resembles that of most other species having humps; the humps are on the dorsum rather than the sides. Total length, 6.5 mm. Carapace, 3.5 mm long, 2.5 mm wide. First femur, 3.0 mm; patella and tibia, 4.0 mm; metatarsus, 2.3 mm; tarsus, 1.0 mm. Second patella and tibia, 3.5 mm; third, 2.2 mm; fourth, 1.0 mm.

Male. The coloration is like that of the female except that the legs are banded. The first coxa has a hook, the second lacks a spur. The second tibia is swollen and has strong setae. Total length, 5.0 mm. Carapace, 2.5 mm long, 2.0 mm wide. First femur, 2.9 mm; patella and tibia, 3.5 mm; metatarsus, 2.0 mm; tarsus, 0.7 mm. Second patella and tibia, 3.0 mm; third, 1.5 mm; fourth, 2.2 mm.

Diagnosis. The female differs from *A. corticarius* in having the humps of the abdomen dorsal rather than lateral (Fig. 126). The anterior section of the scape of the epigynum is posteriorly directed in *A. washingtoni* (Figs. 123, 124); in *A. corticarius* it is directed anteriorly and then folds back (Figs. 114–116). The male differs from *A. corticarius* by the dorsal position of the abdominal humps, by the much smaller conductor (Fig. 128), and the shorter median apophysis (Figs. 127, 128).

Habits. Emerton collected the specimens on low bushes. The label was written in India ink and at some later time Emerton pencilled "*corticaria*" behind the inked *Epeira.* The female from New Brunswick was collected on balsam fir (*Abies balsamea*).

Distribution. Newfoundland to New Hampshire (Map 5).

Records. Newfoundland: Gambo, 25. IV. 1949, ♀ (E. Palmén); Eddies Cove, west St. John Bay, 30. VII. 1949, ♀ (E. Palmén). *New Brunswick:* Green River Forestry Station, 22 July 1965, ♀; 18 July 1967, 2♂ (T. R. Renault). *New Hampshire:* 2♀, 2♂ paratypes collected with the holotype.

Araneus alsine (Walckenaer)

Figures 131–137

Aranea alsine Walckenaer, 1802, Faune Parisienne, 2: 193. Type for the Paris, France, vicinity, lost. Wiehle, 1931, *in* Dahl, Die Tierwelt Deutschlands, 23: 83, figs. 119–123, ♀, ♂. Roewer, 1942, Katalog der Araneae, 1: 781.

Epeira alsine, — Wiehle, 1927, Z. Morphol. Ökol. Tiere, 8: 493.

Araneus alsine, — Locket and Millidge, 1953, British Spiders, 2: 133, figs. 85d, 86d, ♀, ♂. Bonnet, 1955, Bibliographia Araneorum, 2: 429.

This Eurasian species, distributed from Europe to Kamchatka, has not been found in North America. It is very similar to *A. iviei* of North America. *Araneus alsine* is found on grasses of moist woods or clearings, and the hub of the web is about 15–20 cm above the ground. The rolled-up leaf or leaves which are used as a retreat are pulled up from the ground (Wiehle, 1927). A web with 20 spokes was illustrated by Wiehle (1931).

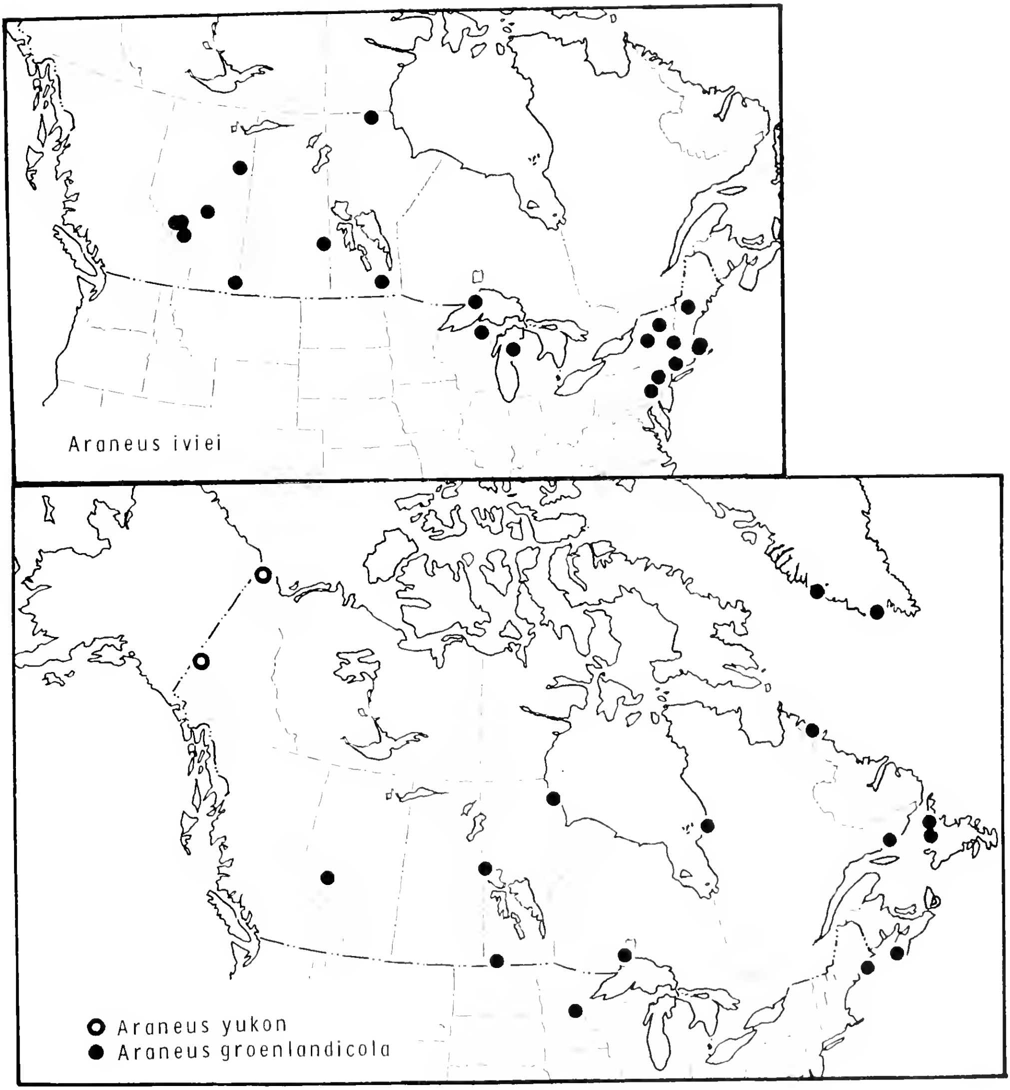
Araneus iviei (Archer)

Figures 138–151; Map 6

Aranea iviei Archer, 1951, Amer. Mus. Novitates, 1487: 33, fig. 53, ♀. Female holotype from Keene Valley, Essex Co., New York, in the American Museum of Natural History, examined.

Aranea sachiman Archer, 1951, Amer. Mus. Novitates, 1487: 33, fig. 55, ♀. Female holotype from Norwell, Plymouth Co., Massachusetts, in the American Museum of Natural History, examined. NEW SYNONYMY.

Description. Female paratype of *A. iviei* from New Jersey. Carapace, sternum, legs orange-brown without any marking. Abdomen whitish with an orange cast, and with a few whitish spots framed by darker orange. Venter between epigynum and



Map 6. Distribution of *Araneus iviei* (Archer), *Araneus yukon* sp. n., and *Araneus groenlandicolus* (Strand).

spinnerets has a white square with orange center. Abdomen lacks humps. Total length, 12 mm. Carapace, 5.0 mm long, 4.2 mm wide. First femur, 4.4 mm; patella and tibia, 5.4 mm; metatarsus, 3.2 mm; tarsus, 1.5 mm. Second patella and tibia, 4.9 mm; third, 2.9 mm; fourth, 4.6 mm.

Male from Michigan. Carapace and sternum brown, darker on each side. Legs brown, very indistinctly marked. Dorsum of abdomen whitish with outline of a folium. Brownish venter has a light mark followed by a dark mark between epigastric furrow and spinnerets. Coxa without hooks or spurs. Second leg not modified. Total length, 6.7 mm. Carapace, 4.2 mm long, 3.2 mm wide. First femur, 4.9 mm; patella and tibia, 5.2 mm; metatarsus, 3.6 mm; tarsus, 1.4 mm. Second patella and tibia, 4.2 mm; third, 2.9 mm; fourth, 4.1 mm.

Variation. Females vary from 8.5–12 mm in total length, carapace 4.1–5.0 mm long, 3.2–4.2 mm wide. Males varied from 5–7 mm in total length, carapace 3.6–4.2 mm long, 2.9–3.2 mm wide. In posterior view no two epigyna are exactly alike (Figs. 140, 142). Figure 142 illustrates a specimen designated as paratype of *A. sachimau* by Archer.

Diagnosis. *Araneus iviei* superficially resembles *A. trifolium*; the genitalia are unlike those of any other North American species but very similar to those of the Eurasian *A. alsine*. The epigynum, unlike that of any other North American species, has a strongly domed base anteriorly and is truncate posteriorly (Figs. 138, 141). In *A. iviei* the shape of the median septum in posterior view narrows dorsally toward the abdomen (Figs. 140, 142), while in *A. alsine* it widens into a flat plate more or less truncate toward the abdomen (Figs. 133, 134).

The male's palpal conductor has a distal "pocket" (Figs. 146, 148) unlike other Northern American *Araneus* species. It differs from *A. alsine* in the shape of the conductor, and in the shape of the embolus (Figs. 145–150).

Habits. The species has been collected from a cedar (*Thuja occidentalis*) swamp in Michigan, sweeping old fields in open forest vegetation on Isle Royale, on base of lodgepole pine (*Pinus contorta*) and in lodgepole woods in Alberta, and in conifer-aspen (*Populus tremuloides*) with pockets of black spruce (*Picea mariana*) with dense undercover of rosebushes, grasses, and sedges in the damp area, at Lake George, Alberta (R. E. Leech, personal correspondence).

Distribution. From Alberta southeast to Pennsylvania. The northernmost record is Riverton, Manitoba, the southernmost Lenhartsville, Berks Co., Pennsylvania (Map 6).

Araneus quadratus Clerck
Figures 152–158

Araneus quadratus Clerck, 1757, Svenska Spindlar, p. 27, pl. 1, fig. 3, ♀. Female holotype from Sweden in the Natural History Museum, Stockholm, lost. Locket and Millidge, 1953, British Spiders, 2: 130, figs. 84b, 85b, 86b, ♀, ♂. Bonnet, 1955, Bibliographia Araneorum, 2: 575.

Aranea reaumurii Scopoli, 1763, Entomologia Carniolica, p. 393. Types from Austria. Scopoli's collection was destroyed about 1776. (Horn and Kahle, 1936, Entomol. Beihefte, 3: 252.) Wiehle, 1931, *in* Dahl, Tierwelt Deutschlands, 23: 79, figs. 115–118, ♀, ♂. Roewer, 1942, Katalog der Araneae, 1: 804.

Epeira quadrata,—Wiehle, 1927, Z. Morphol. Ökol. Tiere, 8: 496. Nielsen, 1932, Biology of Spiders, 2: 292.

Note. This European species closely related to *A. yukon* has not been found in America. Japanese specimens alleged to be *A. quadratus* were examined, but large differences in the shape of the conductor and median apophysis make me think neither specimen is correctly identified. *Araneus quadratus* reported from Greenland are *A. groenlandicolus* (Strand). The web is made in high grasses of moist areas, the center about 50 cm above the ground, and has about 20 spokes (Wiehle, 1931; Nielsen, 1932).

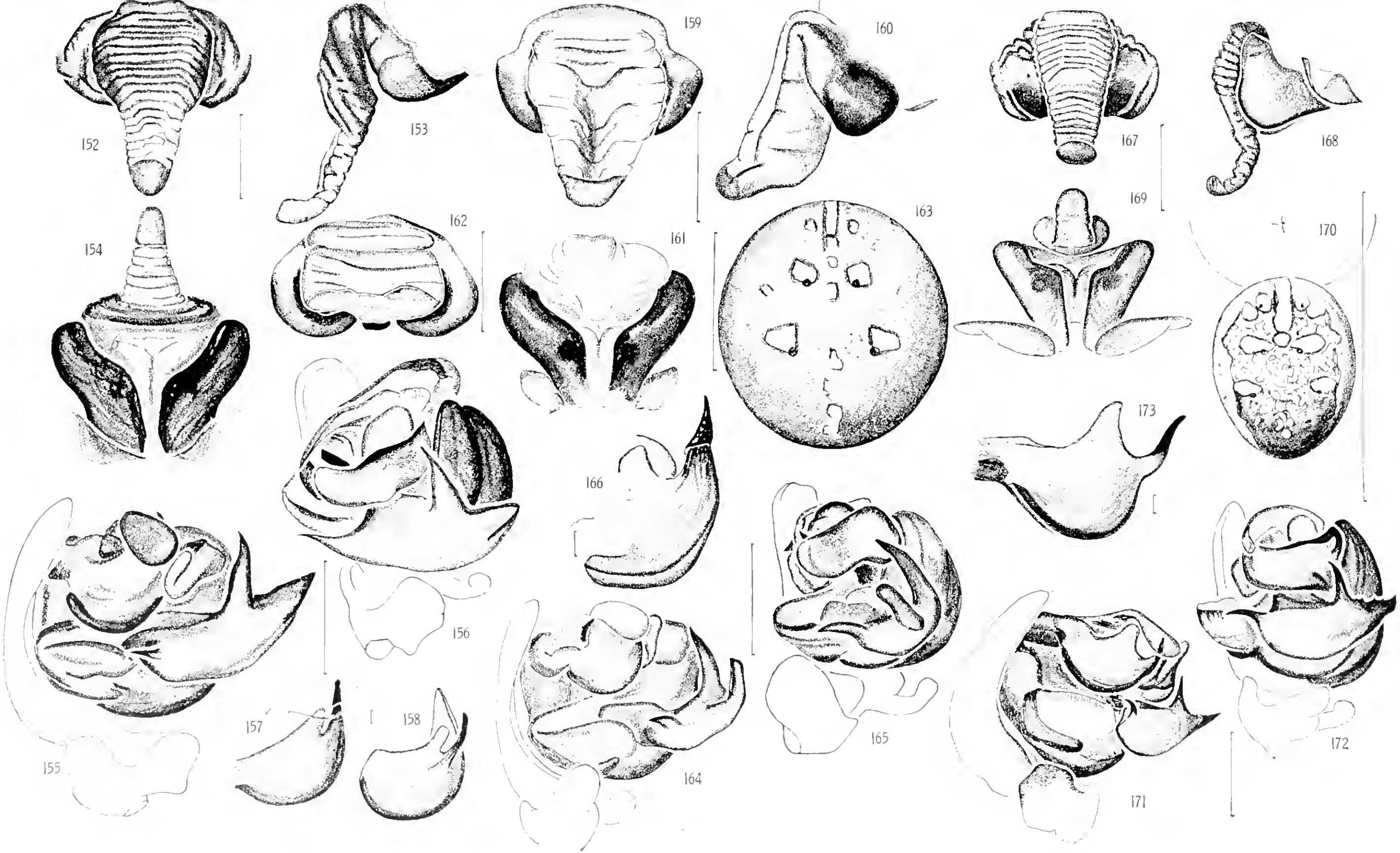
Araneus groenlandicolus (Strand)
Figures 159–166; Map 6

Epeira quadrata,—Sørensen, 1898, Vidensk. Meddel. Naturhist. Foren. Kobenhavn, 1898. Not *A. quadratus* Clerck.

Aranea reaumuri var. *groenlandicola* Strand, 1906, Fauna Arctica, 4: 458. New name for specimens of *Epeira quadrata* described by Sørensen from Greenland. Female lectotype here designated from Ivigtut, Greenland, 15. VIII. 1889 (Lundbeck) in the Universitetets Zoologiske Museum, Copenhagen, examined.

Aranea manitobae Archer, 1951, Amer. Mus. Novitates, 1487: 37, figs. 51, 59, 62, ♂. Male holotype from The Pas, Manitoba, in the American Museum of Natural History, examined. NEW SYNONYMY.

Description. Female. Carapace light brown with median longitudinal darker band and a dark band near each margin. Distal tips of chelicerae brown. Labial



Figures 152–158. *Araneus quadratus* Clerck (Europe). 152–154. Epigynum. 152. Ventral. 153. Lateral. 154. Posterior. 155–158. Left male palpus. 155. Mesal. 156. Ventral. 157, 158. Embolus. 157. With cap. 158. Without cap.

Figures 159–166. *A. groenlandicolus* (Strand). 159–162. Epigynum. 159–161. (Minnesota). 162. (Greenland). 159, 162. Ventral. 160. Lateral. 161. Posterior. 163. Female abdomen. 164–166. Male palpus. 164. Mesal. 165. Ventral. 166. Embolus with cap.

Figures 167–173. *A. yukon* sp. n. 167–169. Epigynum. 167. Ventral. 168. Lateral. 169. Posterior. 170. Male abdomen. 171–173. Male palpus. 171. Mesal. 172. Ventral. 173. Embolus without cap.

(Size indicators 0.5 mm, embolus tips 0.05 mm, for abdomens 5 mm) endites almost black except anterior border. Sternum black with a small, anterior median light mark. Legs very strongly banded. Abdomen white or red with white dorsal spots (Fig. 163). Venter is dark in front of spinnerets, light behind epigynum, and has two longitudinal bands. Abdomen without humps. Total length, 9 mm. Carapace, 4.0 mm long, 3.3 mm wide. First femur, 3.5 mm; patella and tibia, 4.3 mm; metatarsus, 2.7 mm; tarsus, 1.1 mm. Second patella and tibia, 4.5 mm; third, 2.3 mm; fourth, 3.5 mm.

Male holotype. Carapace, legs light brown. Sternum light brown with median longitudinal white line. Abdomen all white with white pigment spots around spinnerets. Coxae without hooks or spurs. Tibia of second leg swollen and with strong spines. Total length, 6.1 mm. Carapace, 3.2 mm long, 2.6 mm wide. First femur, 3.2 mm; patella and tibia, 4.0 mm; metatarsus, 2.7 mm. Second patella and tibia, 3.0 mm; third, 1.9 mm; fourth, 2.9 mm.

Variation. The scape of the epigynum of most females is broken off (Fig. 162), apparently it tears when mating. Females varied from 9–12 mm in total length, males from 5.5–7.5 mm.

Diagnosis. Araneus groenlandicolus lacks humps on the abdomen. Females have been confused with *A. trifolium* because of the reddish coloration of the abdomen and the median dark carapace stripe; however, the epigynum of *A. groenlandicolus* is very different (Fig. 159–162). The epigynum has wider rims than that of *A. quadratus;* the inside edges of the rims are covered by the scape (Fig. 159) (often broken off). The male of *A. groenlandicolus* has strongly bent distal hooks on its median apophysis (Figs. 164, 165) differing from those of *A. quadratus* and *A. yukon* and other *Araneus* species.

Habits. Almost nothing is known about the habits of *A. groenlandicolus*, but it is assumed to prefer open ground to forest as do other species of *Araneus* with a round abdomen. In Alberta it has been found in sedge.

Distribution. Alberta to Greenland and south to Minnesota and Maine (Map 6). Specimens examined from Greenland came from Ivigtut and Godthaabsfjord.

Araneus yukon sp. n.
Figures 167–173; Map 6

Holotype. Male from Snag, lat 62° 24′, long 140° 22′, Yukon Territory, 24 July 1948, in the American Museum of Natural History. The specific name is a noun in apposition.

Description. Female paratype. Carapace brown with darker median and lateral bands. Sternum very dark brownish black with median longitudinal line of white pigment. Legs brown with very distinct dark banding. Abdomen with a folium posteriorly, a median light longitudinal mark anteriorly. Venter light with two dark spots side by side and a dark ring around spinnerets. Spinnerets blackish brown. Abdomen oval to subspherical without humps. Total length, 10 mm. Carapace, 4.2 mm long, 3.5 mm wide. First femur, 4.0 mm; patella and tibia, 4.9 mm; metatarsus, 3.0 mm; tarsus, 1.4 mm. Second patella and tibia, 4.4 mm; third, 2.8 mm; fourth, 4.0 mm.

Male holotype. Carapace with indistinct markings. Sternum dark with a median white line. Leg banding indistinct. Dorsum of abdomen has two pairs of white spots anterior to a dark folium and an anterior longitudinal white mark (Fig. 170). Ventral dark spots are fused to each other and the posterior one to the dark ring around the spinnerets. There are no hooks or spurs on coxa. The second tibia is slightly swollen. Total length, 6.5 mm. Carapace, 3.4 mm long, 2.8 mm wide. First femur, 3.5 mm; patella and tibia, 4.4 mm; metatarsus, 3.0 mm; tarsus, 1.3 mm. Second patella and tibia, 3.4 mm; third, 2.0 mm; fourth, 3.2 mm.

Diagnosis. Araneus yukon palpus differs from that of related *A. quadratus* in having teeth on the lower distal lobe of the median apophysis (Fig. 172) instead of a straight carina; the conductor of *A. yukon* is wider and the "upper" lobe of the embolus (left in Figs. 171, 173) is wider than in *A. quadratus* (Fig. 158). European specimens showed little variation in these characters.

Habits. Firth River, a locality in which the species is found, is on the north slope of the British Mountains, 25 miles from the Arctic Ocean. Although north of the tree line, pockets of spruce (*Pica* sp.) to 3–4 m high occur in sheltered spots along the creeks; probably the specimen was found in these (R. E. Leech, in letter).

Records. Yukon Territory. Female paratype collected with holotype; Firth River, British Mountains, ♀ paratype, 24. VII. 1956 (R. E. Leech) in the Canadian National Museum.

Araneus trifolium (Hentz), Shamrock Spider
Figures 174–182; Map 7

?*Epeira vulpecula* Walckenaer, 1841, Histoire Naturelle des Insects Aptères, 2: 69. Syntypes are Abbot, Georgian Spider Illustrations, figs. 131, 356 from Georgia in the British Museum of Natural History, examined. A *nomen dubium* and a *nomen oblitum*.

?*Epeira approximata* Blackwall, 1846, Ann. Mag. Natur. Hist., 17(1): 80. Specimen from vicinity of Toronto, lost. A *nomen dubium* and *nomen oblitum*.

Epeira trifolium Hentz, 1847, J. Boston Soc. Natur. Hist., 5: 471, pl. 31, fig. 1, ♀. Types from Maine, destroyed. Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 306, pl. 33, fig. 8, pl. 35, figs. 13, 14, 21, 22, ♀, ♂. McCook, 1893, American Spiders, 3: 145, pl. 1, figs. 3–6, pl. 2, fig. 3, ♀, ♂. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 258, figs. 823–825, 2047.

Epeira aureola Hentz, 1847, J. Boston Soc. Natur. Hist., 5: 471, pl. 31, fig. 2, ♀. Type from Maine, destroyed.

Epeira trifolium var. *candidans* McCook, 1893, American Spiders, 3: 146, pl. 1, fig. 4, ♀. Female holotype from California, lost, the color of the abdomen was yellowish-white.

Aranea trifolium,—Comstock, 1912, The Spider Book, p. 479, figs. 501–508, ♀; 1940, rev. ed., The Spider Book, p. 493, figs. 501–508, ♀. Roewer, 1942, Katalog der Araneae, 1: 863.

Aranea gosogana Chamberlin, 1920, J. Entomol. Zool., 12: 8, pl. 4, fig. 6, ♀. Female holotype from desert region in California, in the Museum of Comparative Zoology, examined.

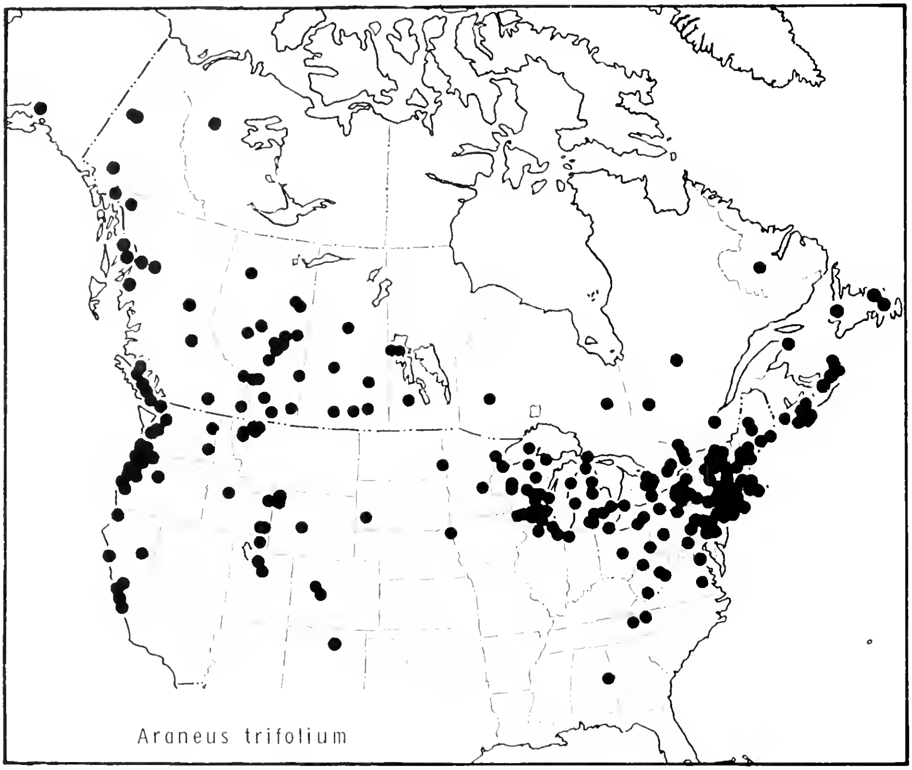
Araneus trifolium,—Bonnet, 1955, Bibliographia Araneorum, 2: 614.

Note. Epeira jaspidata Walckenaer, 1837, has been placed as a synonym, first by McCook: the type, Abbot, fig. 111, however, seems to have humps. Abbot's figure is either *A. nordmanni* or *A. bicentenarius.* However, Walckenaer indicated in the description of the figure that the abdomen was round.

Description. Female. Carapace brown with a lighter band on each side of a dark median longitudinal band; sides dark with a lighter brown border. Sternum dark brown. Legs brown with strongly marked darker bands. Dorsum of abdomen reddish with white spots (Fig. 177), venter usually reddish brown without markings in adult. A specimen from Ithaca, New York, measured 15 mm in total length. Carapace, 6.5 mm long, 5.5 mm wide. First femur, 6.3 mm; patella and tibia, 8.0 mm; metatarsus, 5.5 mm; tarsus, 1.7 mm. Second patella and tibia, 6.9 mm; third, 4.2 mm; fourth, 6.7 mm.

Male. Carapace, sternum and legs brown, abdomen whitish, sometimes all white, sometimes with ventral marks. None of the coxae have hooks or spurs. The tibia of the second leg is only slightly thicker than that of other legs. A specimen from Montana measured 7.5 mm in total length. Carapace, 4.2 mm long, 3.4 mm wide. First femur, 4.6 mm; patella and tibia, 5.1 mm; metatarsus, 3.5 mm; tarsus, 1.5 mm. Second patella and tibia, 4.5 mm; third, 2.7 mm; fourth, 3.9 mm.

Variation. Many specimens have the dorsum of the abdomen white. Total length of females varied between 9–20 mm, with carapace 4.0–6.8 mm long, 3.6–5.4 mm wide. Total length of males, 5–8 mm, with carapace 3.0–3.6 mm long, 2.5–3.0 mm wide.

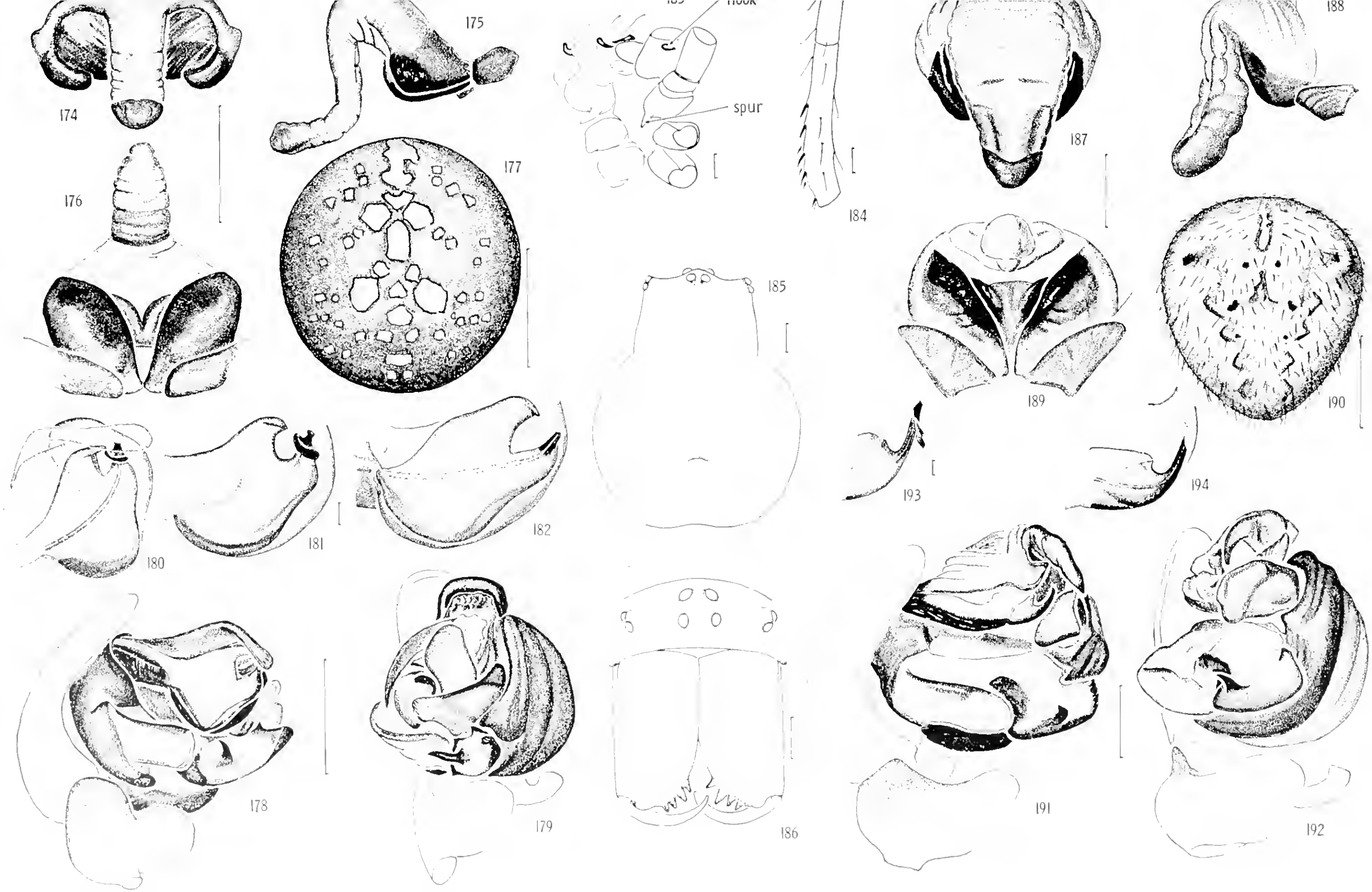


Map 7. Distribution of *Araneus trifolium* (Hentz).

Diagnosis. Araneus trifolium is not close to any other species, although females have been confused with *A. groenlandicolus* and *A. iviei* on account of the spherical abdomen, red coloration, and dark leg bands. But the epigynum of *A. trifolium* is very distinct: a scape (only rarely broken off) flanked on each side by a depression in the base; the margin of the depression and the depression itself are sclerotized and black posteriorly (Fig. 174).

The male palpus of *A. trifolium* has the embolus of an unusual shape (Figs. 178, 180–182); the embolus lamella is a huge flat scale with parallel sides of about the same visible area or larger than the small, narrow conductor (Fig. 179). The lamella, always easily seen, readily separates males from all other North American species. As no illustrations of the male palpus have been readily available, many males of this common species are misidentified in collections.

Habits. Araneus trifolium is found in meadows and edges of fields making its web between herbaceous plants, often goldenrod (*Solidago* sp.), or shrubs, with the hub about 0.5–2 m off the ground. The web has about 20 spokes. The web and egg sac have been illustrated by Comstock (1912, 1940). During the recent years of drought the spiders disappeared completely from the fields around our house in Massachusetts but reappeared with the first wet season in summer of 1967, to reach unusual abundance in 1968 and 1969. Kaston (1947) describes the egg sacs after Scheffer as "white, about an inch in diameter and delicate enough for the mass of several hundred yellow eggs to show



Figures 174–182. *Araneus trifolium* (Hentz). 174–176. Epigynum. 174. Ventral. 175. Lateral. 176. Posterior. 177. Female abdomen. 178–182. Left male palpus. 178. Mesal. 179. Ventral. 180–182. Embolus. 180, 181. With cap. 182. Without cap.

Figure 183. *A. marmoreus* Clerck, male, cephalothorax subventral.

Figures 184–186. *A. diadematus* Clerck. 184. Male left patella-tibia, lateral. 185, 186. Female cephalothorax.

Figures 187–194. *A. cavaticus* (Keyserling). 187–189. Epigynum. 187. Ventral. 188. Lateral. 189. Posterior. 190. Female abdomen. 191–194. Male palpus. 191. Mesal. 192. Ventral. 193, 194. Embolus. 193. With cap. 194. Without cap.

(Size indicators, genitalia 0.5 mm, for embolus tips 0.05 mm, for other body parts 5 mm) through. The young leave the egg sac in fall or spring." The egg sac is illustrated in Comstock, 1912 and 1940.

Distribution. *Araneus trifolium* is found from Alaska to southern California and northern Florida (Map 7).

Araneus cavaticus (Keyserling)
Plate 2; Figures 187–194; Map 8

Epeira cavatica Keyserling, 1882, Verh. Zool. Bot. Ges. Wien, 31: 269, pl. 11, fig. 1, ♀. Female holotype from a Kentucky cave, Carter Co., Kentucky (Sanborn, 1874) in the Museum of Comparative Zoology, examined.

Epeira cinerea Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 302, pl. 33, fig. 10, pl. 35, figs. 7, 8, ♀. Female syntypes from Sable Chasm, New York, in the Museum of Comparative Zoology, examined.

Aranea cavatica, — Comstock, 1912, The Spider Book, p. 470, figs. 487–489, ♀. Roewer, 1942, Katalog der Araneae, 1: 859. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 251, figs. 798–799, ♀, ♂.

Araneus cavaticus, — Bonnet, 1955, Bibliographia Araneorum, 2: 453.

Note. *Aranea sinistra* F. P.-Cambridge, 1904, Biologia Centralia-Americana, 2: 510, pl. 48, fig. 21, ♀, from Omilteme, Mexico, may also be this species. The genitalia are similar but not identical. No specimens from intermediate areas were available. This species has been renamed *A. sinistrella* by Roewer, 1942, Katalog der Araneae.

Description. Female. Carapace yellow-brown, darker anterior of thoracic depression. Sternum dark brown. Coxae light yellow. Legs yellowish brown with darker brown bands. Abdomen gray to brown dorsally with an indistinct folium and anterior white mark (Fig. 190). Venter black between epigynum and spinnerets, with a white bracket on each side. Abdomen with two humps and covered by short hairs on dorsum, longer hairs on sides, and fine hair between humps. Total length of a specimen from Kentucky, 18 mm. Carapace, 7.3 mm long, 5.9 mm wide. First femur, 10.0 mm; patella and tibia, 11.8 mm; metatarsus, 8.4 mm; tarsus, 2.7 mm. Second patella and tibia, 11.1 mm; third, 6.0 mm; fourth, 9.6 mm.

Male. Coloration like that of female, usually light. The tibia is not modified and the coxae lack hooks or spurs. A specimen from Kentucky measured 15 mm in total length. Carapace, 7.6 mm long, 6.7 mm wide. First femur, 13.5 mm; patella and tibia, 17.2 mm; metatarsus, 13.8 mm; tarsus, 3.4 mm. Second patella and tibia, 15.0 mm; third, 8.4 mm; fourth, 12.5 mm.

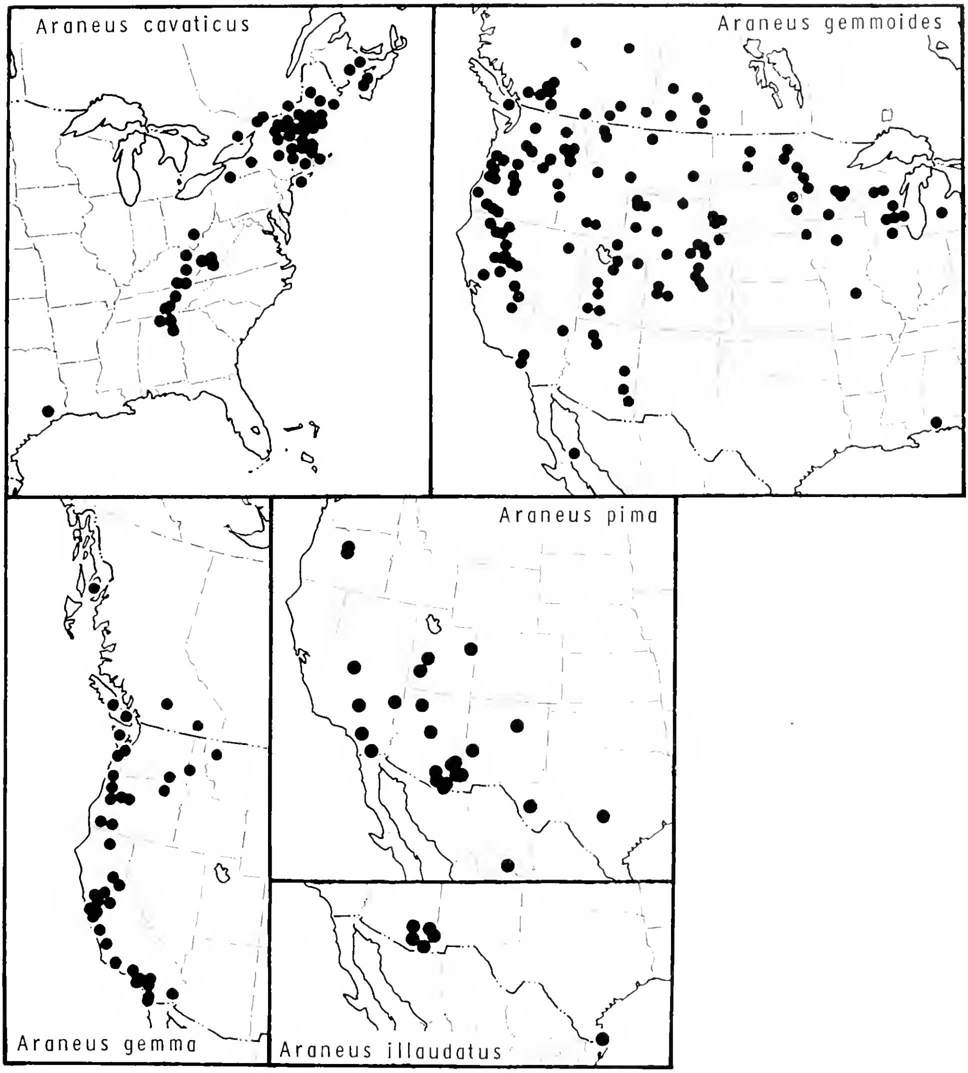
Variation. Females vary from 13–22 mm in total length, with the carapace 6.1–7.5 mm long, 5.4–6.1 mm wide. Males vary from 10–19 mm in total length, with the carapace 6.9–8.7 mm long, 5.2–7.8 mm wide.

There is little color or morphological variation in this light-colored species.

Diagnosis. The epigynum of the female of this large humpbacked species can be confused with that of *A. nordmanni.* In posterior view the epigynum has a median sclerotized triangular piece (Fig. 189), that of *A. nordmanni* encloses a heart-shaped depression (Figs. 89, 92). The males can be recognized by their giant size and long legs. The large size separates males from those of the closely related Pacific coast *A. gemma* which has a somewhat similar embolus and terminal apophysis.

Habits. *A. cavaticus* makes its large webs with about 20 spokes (Plate 2) on barns, on porches, and bridges. One old collection from 1874 indicated that the spider was collected from under a natural bridge in Kentucky. It also has been reported from under overhanging cliffs, probably its original habitat. One male was collected while being fed on by a female *A. diadematus* in Ontario. Archer (1940, J. Alabama Acad. Sci., 12: 28) reports the species from caves in Alabama.

Distribution. *Araneus cavaticus* is found from New Brunswick, eastern Ontario and Nova Scotia to Texas. The southernmost record is of a pair collected at Houston, Texas (Map 8).



Map 8. Distribution of *Araneus cavaticus* (Keyserling), *Araneus gemmoides* Chamberlin and Ivie, *Araneus gemma* (McCook), *Araneus pima* sp. n., and *Araneus illaudatus* (Gertsch and Mulaik).

Araneus gemmoides Chamberlin and Ivie
Plate 2; Figures 195–202; Map 8

Epeira gemma, — Keyserling, 1892, Die Spinnen Amerikas, 4: 115, pl. 6, fig. 85, ♀. Not *A. gemma* McCook.

Araneus gemmoides Chamberlin and Ivie, 1935, Bull. Univ. Utah, Biol. Ser., 2(8): 22, pl. 10, fig. 80, ♀. Female holotype from Salt Lake City belonging to the Utah collection, kept at the American Museum of Natural History, examined. Bonnet, 1955, Bibliographia Araneorum, 2: 507.

Aranea gemmoides, — Roewer, 1942, Katalog der Araneae, 1: 860.

Araneus cannonus Schenkel, 1950, Verh. Naturf. Ges. Basel, 61: 65, ♀. Female lectotype, here designated, from Canmore, Banff National Park, Canada, in the Naturhistorisches Museum Basel, examined. NEW SYNONYMY.

Description. Female from Wisconsin. Carapace light brown, sternum brown with a median light longitudinal streak. Coxae yellowish. Legs yellow-brown, with indistinct darker bands. Dorsum of abdomen light grayish brown with almost no pattern at all. Venter with two longitudinal dark marks behind epigynum and two light marks in front of spinnerets. Total length, 15 mm. Carapace, 4.6 mm long, 4.2 mm wide. First femur, 4.9 mm; patella and tibia, 5.9 mm; metatarsus, 3.7 mm; tarsus, 1.5 mm. Second patella and tibia, 5.5 mm; third, 3.0 mm; fourth, 4.9 mm.

Male from Idaho. Coloration almost like that of female. Abdomen with remains of outline of a folium and an anterior median dorsal light streak and humps large. Coxae, legs not modified. Total length, 8 mm. Carapace, 4.5 mm long, 3.5 mm wide. First femur, 5.7 mm; patella and tibia, 6.7 mm; metatarsus, 4.5 mm; tarsus, 1.5 mm. Second patella and tibia, 5.7 mm; third, 3.5 mm; fourth, 4.9 mm.

Variation. Total length of females varied from 13–25 mm; carapace 6.3–8.5 mm long, 5.0–7.5 mm wide. Total length of males 5.4–7.9 mm; carapace 3.2–4.3 mm long, 2.6–3.5 mm wide.

This species, unlike *A. gemma*, shows little variation except in color. Sometimes there is a distinct folium, sometimes not, and there may be a white cardiac mark. Only on the Pacific coast where it is in contact with the very similar *A. gemma* are some specimens dark. A single British Columbia specimen was black like *A. saevus*.

Diagnosis. The very tiny epigynum with a triangular scape (Fig. 195) readily separates *A. gemmoides* from other species, except for some *A. gemma* which may be hybrids. Males have a small bulb barely larger than the tibia (Figs. 199, 200); these proportions separate males from *A. gemma*. The male of *A. gemmoides* is much smaller in size than that of *A. cavaticus*.

Habits. The habitat of this species is similar to that of the eastern *A. cavaticus*. I have collected it from under eaves of houses and on barns in Wisconsin that accommodated its huge web with about 20 spokes (Plate 2). But in the west it seems to have been collected in lodgepole (*Pinus contorta*) woods, and on the Pacific coast on houses. It has been found in natural situations in cave entrances, rocky ledges, and one record is from Manzanita chaparral, 1100 m, San Gabriel C., Los Angeles Co., California (L. Pinter).

The egg sac of *A. gemmoides* made in the laboratory is a fluffy, loosely woven sphere of orangish silk, 2 cm in diameter. A color illustration can be found in Gertsch (1949, American Spiders, Van Nostrand).

Distribution. *Araneus gemmoides* is found from British Columbia to Wisconsin, south to Missouri and Arizona (Map 8). It appears rare along the Pacific coast. Isolated records are: Michigan, Rose Lake, Clinton Co. (D. E. Bixler); Silver Hill, Alabama, Sept. 1945 (S. Nelson); and San Lorenzo Island [Baja California].

Araneus gemma (McCook)
Figures 203–215; Map 8

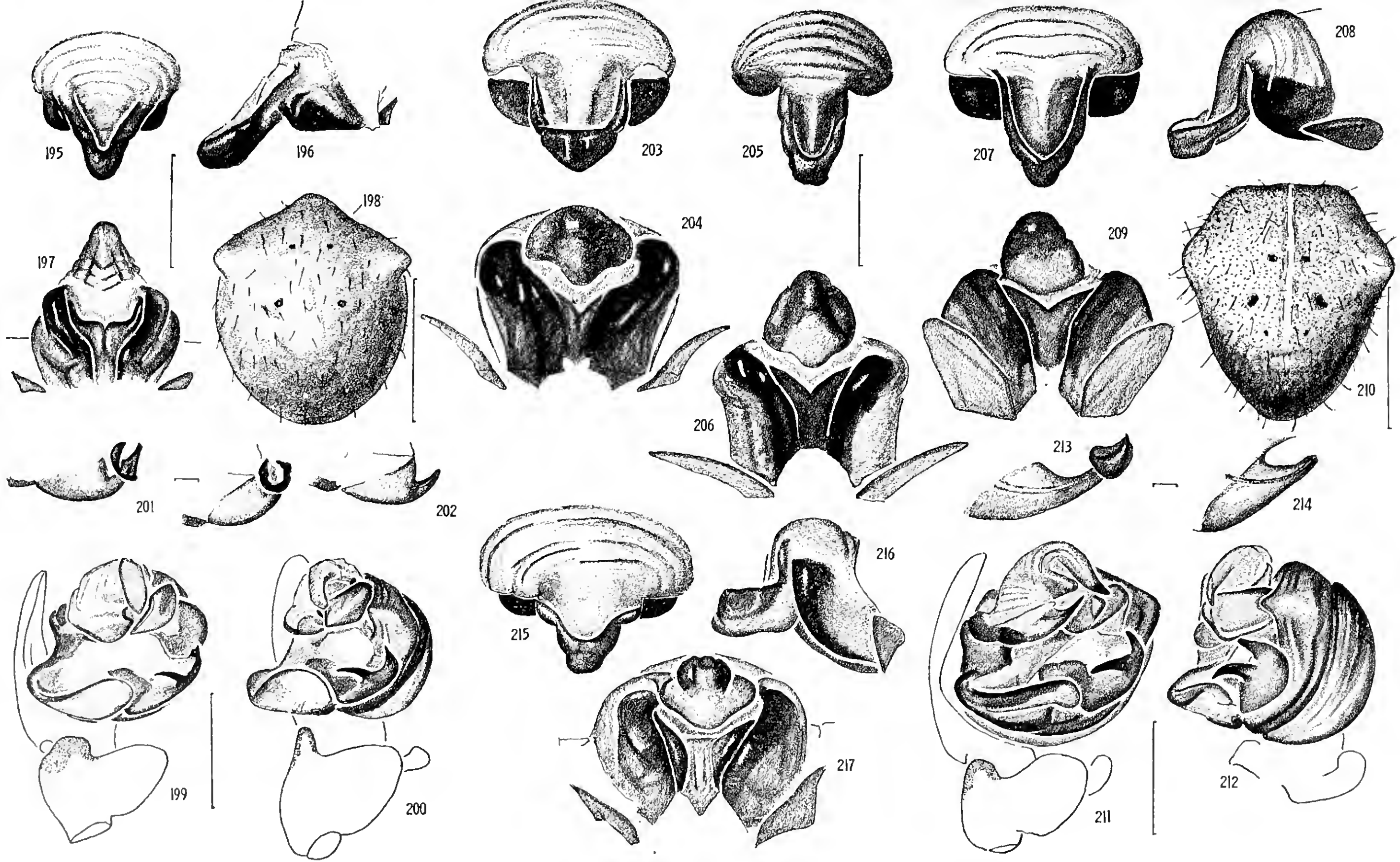
Epeira gemma McCook, 1888, Proc. Acad. Natur. Sci. Philadelphia, p. 193, figs. 1, 2, ♀. Female lectotype here designated from California in the Philadelphia Academy Natural Sciences, examined. 1894, American Spiders, 3: 182, pl. 9, figs. 1, 2, pl. 10, fig. 6, ♀, ♂.

Araneus gemmus,—Chamberlin and Ivie, 1935, Bull. Univ. Utah, Biol. Ser., 2(8): 21, pl. 10, fig. 79, ♀.

Araneus pirus Chamberlin and Ivie, 1935, Bull. Univ. Utah, Biol. Ser., 2(8): 22, pl. 10, fig. 81, ♀. Female holotype from Fillmore, California, in the University of Utah collection kept at the American Museum of Natural History, examined. NEW SYNONYMY.

Araneus gemma,—Bonnet, 1955, Bibliographia Araneorum, 2: 506.

Note. As pointed out first by Chamberlin and Ivie, McCook's description is a composite. The two syntypes are different species. One is clearly the common species in the San Diego, California, area, the type locality. The other is probably the



Figures 195–202. *Araneus gemmoides* Chamberlin and Ivie. 195–197. Epigynum. 195. Ventral. 196. Lateral. 197. Posterior. 198. Female abdomen. 199–202. Left male palpus. 199. Mesal. 200. Ventral. 201, 202. Embolus. 201. With cap. 202. Without cap.

Figures 203–214. *A. gemma* (McCook). 203–209. Epigynum (California). 203, 205, 207. Ventral. 208. Lateral. 204, 206, 209. Posterior. 210. Female abdomen. 211–212. Male palpus. 211. Mesal. 212. Ventral. 213, 214. Embolus. 213. With cap. 214. Without cap.

Figures 215–217. Epigynum of suspected cross *A. gemmoides* × *A. gemma.*

(Size indicators 0.5 mm, for embolus tips 0.05 mm, for abdomens 5 mm) same as what is called *A. pima* here. Other specimens in the McCook collection were *A. gemmoides.* The specimen which may be *A. pima* was not chosen lectotype because it either has the wrong collecting locality or comes from the very border of its range. Also the specimen appeared to be an atypical *A. pima.*

To favor stability of names, the other specimen was chosen lectotype even though as a result *A. pirus* will have to be synonymized. The range of the species whose name is now *A. gemma* is essentially that given by McCook and also McCook's description matches this species. *Araneus gemma* of Chamberlin and Ivie is certainly this species although the specimens could not be located. The name *A. gemma* has at times been used for *A. pima* on collecting vials only. The name *gemma* is a noun in apposition; its ending does not change with the gender of the genus (Bonnet, 1955).

Description. Female from California. Carapace maculated brown with some gray pattern. Legs yellowish, indistinctly banded brown. Abdomen brownish with a median longitudinal white line, or line absent. Venter with a black band enclosed by white brackets. Abdomen with large humps (Fig. 210). Total length, 12 mm. Carapace, 5.3 mm long, 4.6 mm wide. First femur, 5.9 mm; patella and tibia, 8.2 mm; metatarsus, 5.0 mm; tarsus, 1.9 mm. Second patella and tibia, 8.0 mm; third, 4.6 mm; fourth, 6.8 mm.

Male. Carapace, sternum, legs yellow-brown. Abdomen with a folium and anterior median white mark. Venter gray with a white bracket on each side. First coxa with a small tubercle on distal margin. Second tibia not modified. Total length, 8 mm. Carapace, 4.2 mm long, 3.3 mm wide. First femur, 5.9 mm; patella and tibia, 7.0 mm; metatarsus, 4.6 mm; tarsus, 1.7 mm. Second patella and tibia, 6.0 mm; third, 3.3 mm; fourth, 4.9 mm.

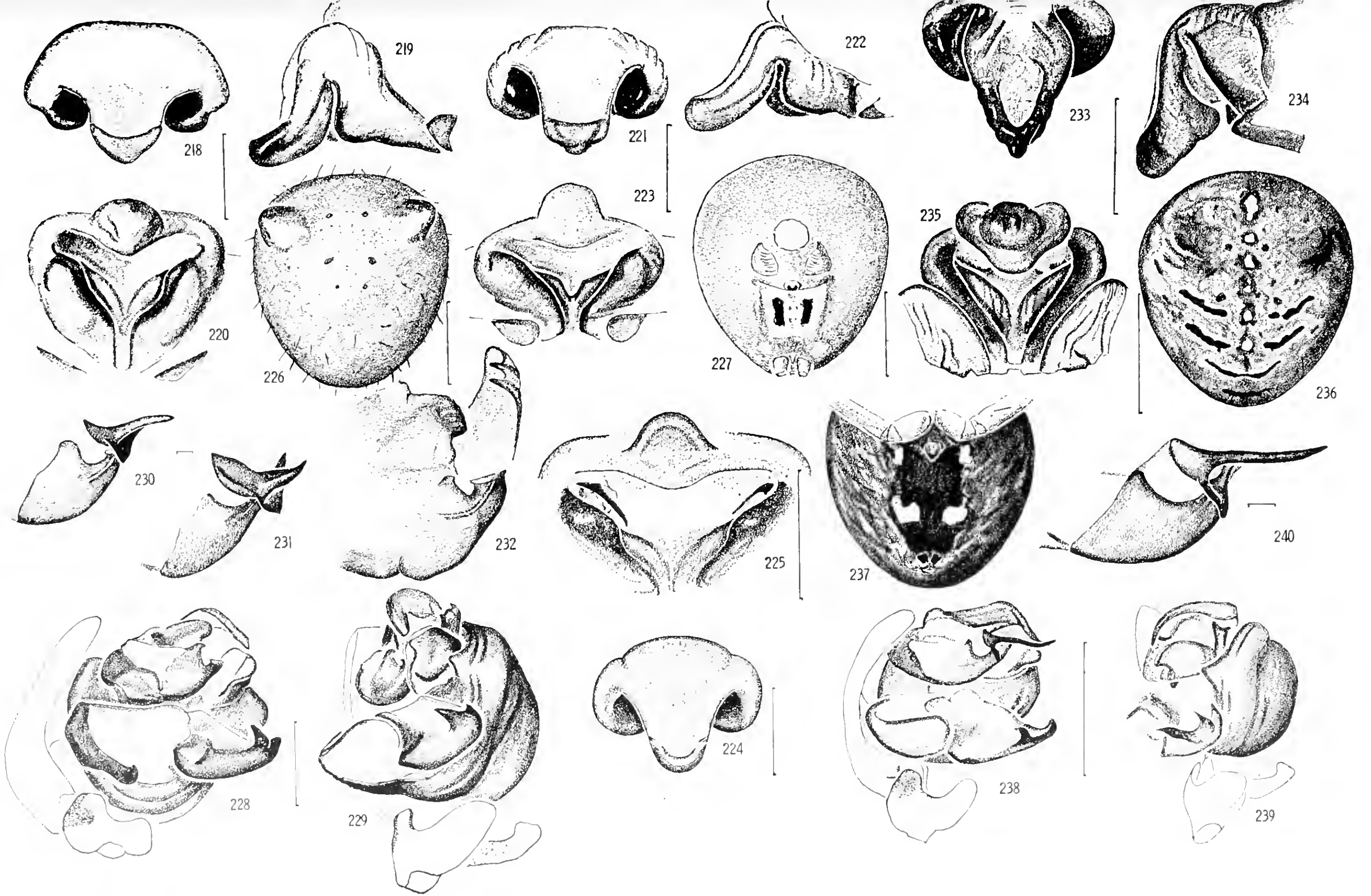
Variation. Females vary 9–19 mm in total length; carapace 4.4–6.4 mm long, 3.8–6.1 mm wide. Males vary 5.8–8.5 mm in total length; carapace 3.1–4.5 mm long, 2.5–3.6 mm wide.

The color varies in alcoholic specimens from light gray to almost black, some have two bars on the venter. Hardly two specimens have similar epigyna. It is believed that the species hybridizes with *Araneus gemmoides* and introgression is taking place. The male palpi, similar to those of *A. gemmoides* except for proportions, were not carefully studied for variation. (See introduction under species problems.)

Diagnosis. The short scape of the epigynum differs from that of related species in having a median ridge (Figs. 203, 205, 207, 208). But some females cannot be separated from *A. gemmoides.* (See Variation above and introduction under species problems.) The males are much smaller in size than those of the eastern *A. cavaticus.* The palpus has a larger bulb and smaller tibia (Figs. 211, 212) than the palpus of *A. gemmoides.* The upper surface of the embolus differs (Figs. 211, 213, 214) from that of *A. gemmoides* and the terminal apophysis is more pointed.

Note. McCook when describing *A. gemma* must have noted the problems of variation and applied one name to *A. gemmoides* and *A. gemma.* Presumably he could not readily separate the specimens which he had from California. Chamberlin and Ivie having smaller collections at hand used *gemma* for some specimens (Chamberlin and Ivie, 1935, fig. 79) and called others *A. pirus* (Chamberlin and Ivie, 1935, fig. 81), a reasonable judgment if only very few specimens are examined.

Habits. Little is known of the habits of *A. gemma,* although they are probably the same as those of *A. cavaticus* and *A. gemmoides.* One specimen was collected on a redwood (*Sequoia sempervirens*) trunk, San Jose, California. One from a porch at Walla Walla, Washington, others from Moscow, Idaho, came in the same collection with *A. gemmoides.* One *A. gemma* was collected from a hole in an olive tree



Figures 218–232. *Araneus pima* sp. n. 218–225. Epigynum. 218–220. (Santa Rita Mts., Arizona). 221–223. (San Bernardino Co., California). 224. (Jefferson Co., Oregon). 218, 221, 224. Ventral. 219, 222. Lateral. 220, 223, 225. Posterior. 225. Containing suspected *A. illaudatus* embolus caps. 226, 227. Female abdomen. 226. Dorsal. 227. Ventral. 228–232. Left male palpus. 228. Mesal. 229. Ventral. 230–232. Embolus. 230, 231. With cap. 232. Without cap.

Figures 233–240. *A. illaudatus* (Gertsch and Mulaik). 233–235. Epigynum. 233. Ventral. 234. Lateral. 235. Posterior. 236, 237. Female abdomen. 236. Dorsal. 237. Ventral. 238–240. Male palpus. 238. Mesal. 239. Ventral. 240. Embolus with cap.

(Size indicators 0.5 mm, for embolus tips 0.05 mm, for abdomens 5 mm)

(*Olea europea*) feeding on a ruby-crowned kinglet (*Regulus calendula*) which was caught in its web (Pasadena, California, 5 November, 1942, Mrs. H. Michener).

Distribution. Araneus gemma is found from southern Alaska to southern California; the northernmost collections are from Ketchikan, Alaska, the easternmost from Bigfork, Montana (Map 8).

Araneus pima sp. n.
Plate 1, 4; Figures 218–232; Map 8

Holotype. Female holotype from Madera Canyon, Santa Rita Mountains, Pima Co., Arizona, 29 July 1958 (A. Ross) in the American Museum of Natural History. The specific name is a noun in apposition after the type locality.

Description. Female from Arizona. Carapace brown. Sternum brown with median area lighter. Legs brown. Abdomen gray-brown, without folium, the venter with a pair of parallel longitudinal black bars surrounded by white (Plate 4, Fig. 227). Humps very large. Abdomen covered by sparse long setae. Total length, 20 mm. Carapace, 8.0 mm long, 6.4 mm wide. First femur, 7.8 mm; patella and tibia, 9.8 mm; metatarsus, 6.5 mm; tarsus, 2.2 mm. Second patella and tibia, 9.6 mm; third, 5.5 mm; fourth, 8.9 mm.

Male from Arizona. Coloration like that of female except that legs show some banding and abdomen has a folium and anterior median longitudinal white line. Coxae and second tibia are not modified. Total length, 9 mm. Carapace, 5.5 mm long, 4.3 mm wide. First femur, 7.0 mm; patella and tibia, 10.0 mm; metatarsus, 5.9 mm; tarsus, 1.9 mm. Second patella and tibia, 7.6 mm; third, 4.2 mm; fourth, 6.4 mm.

Variation. The largest female measured 27 mm in total length; the carapace was not measured. Another male measured 5.2 mm in total length, carapace, 2.5 mm long, 2.0 mm wide. Although what are believed to be tips of *A. illaudatus* emboli are found at times in the groove of the epigynum, the species do not seem to hybridize. There is not much variation except in length of scape.

Diagnosis. The flat rounded scape of the epigynum (Figs. 218, 221, 224) with a deep wide groove under it (Figs. 220, 223) distinguishes females of *A. pima* from *A. gemmoides* and *A. gemma.* The males are distinguished from *A. gemma* by the shape of the median apophysis, by having the median spine joined with the distal one, and by the truncate embolus (Figs. 228, 232). The more blunt terminal apophysis (Figs. 228, 229) and the shape of the median apophysis with the spines joined distinguishes *A. pima* from *A. illaudatus.*

Habits. Araneus pima has been collected under eaves of buildings of the Southwestern Research Station, near Portal, Arizona, under a bridge in New Mexico, along a trail in the Grand Canyon, and in cave entrance of O.T.L. cave north of Alpine, Texas.

The eggs are in an oval mass 2 cm long, 1.8 cm wide, 1 cm thick. About 700 eggs were estimated on the surface of the clump of eggs, which must have contained more than a thousand. A loose pink woolly web 4–5 cm^2 surrounded the eggs, quite similar to the egg sac of *A. gemmoides* (Plate 1).

Note. In some collections specimens of this species had been incorrectly determined as *A. gemma.* It is not *A. gemma* of McCook nor of Chamberlin and Ivie (1935, fig. 79).

Distribution. Araneus pima is found from eastern California to Utah and Arizona. Localities at the border of the range are: Gateway, Oregon, Kerrville, Texas (Map 8). Female and male paratypes from the type locality have been collected.

Araneus illaudatus (Gertsch and Mulaik)
Figures 233–240; Map 8

Aranea illaudata Gertsch and Mulaik, 1936, Amer. Mus. Novitates, 863: 19, figs. 36, 37, ♂. Male holotype from Edinburg, Texas, in the American Museum of Natural History, examined. Archer, 1951, Amer. Mus. Novitates, 1487: 36, fig. 74, ♂ (not fig. 67 ♀).

Note. Archer (1951) matched the wrong female to the male described previously as *A. illaudatus.* Archer's female is an *A. nordmanni* and as Archer correctly points out is quite different from females of *A. cavaticus* group.

Description. Female from Arizona. Carapace yellowish with dark brown mottling. Sternum black, coxae yellowish, legs banded yellowish and dark brown. Dorsum of abdomen with two rows of transverse black marks pointing posteriorly towards the middle on a mottled background (Fig. 236). A median dorsal longitudinal line of white spots not always present. Venter with a black band between pedicel and spinnerets containing a pair of prominent white spots side by side and sometimes a smaller pair of white spots. Abdomen with two humps. Total length, 11 mm. Carapace, 3.8 mm long, 3.4 mm wide. First femur, 4.2 mm; patella and tibia, 5.5 mm; metatarsus, 3.7 mm; tarsus, 1.4 mm. Second patella and tibia, 5.0 mm; third, 3.0 mm; fourth, 4.9 mm.

Male holotype. Carapace brown. Sternum brown. Legs yellow-brown. Abdomen yellow-brown. Dorsum with distinct folium, anterior border has a white cross. Venter with a pair of white spots side by side. Coxae and second tibia not modified. The abdomen has two distinct humps. Total length, 3.6 mm. Carapace, 2.0 mm long, 1.4 mm wide. First femur, 2.5 mm; patella and tibia, 2.8 mm; metatarsus, 1.8 mm; tarsus, 0.9 mm. Second patella and tibia, 2.3 mm; third, 1.3 mm; fourth, 2.0 mm.

Diagnosis. The female scape is constricted at its base and almost diamond shaped (Fig. 233), quite different from that of the related *A. pima* (Figs. 218, 221, 224). The male palpus has the spines of the median apophysis farther apart and the terminal apophysis more pointed and twisted (Figs. 238, 239) than that of *Araneus pima.* The cap of the embolus is the longest of any *Araneus* species, longer than the embolus (Fig. 240).

Habits. One female collected in the Chiricahua Mts., Arizona, at 7500–9000 feet [2300–2900 m] had its web on brush under pines in August.

Distribution. Araneus illaudatus is found from western Texas to Arizona (Map 8).

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Evolutionary Relationships of Some South American Ground Tyrants

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EVOLUTIONARY RELATIONSHIPS OF SOME SOUTH AMERICAN GROUND TYRANTS[1]

W. JOHN SMITH[2] AND FRANÇOIS VUILLEUMIER[3]

PREFACE

The Tyrannidae comprise about one out of ten of the approximately 2900 species of birds listed from the South American continent by de Schauensee (1966). Paralleling this large representation is ecological versatility; tyrant flycatchers occur in every major avian habitat from lowland rain forest to high Andean páramos. As a corollary to this radiation, many Tyrannidae have ecological characteristics which are typical of totally unrelated Old World avian groups. There are, among others, thrushlike tyrants, chatlike, shrikelike, warblerlike, and titmouselike tyrants, in addition to flycatchers.

The existence of the tyrannid radiation has been known to ornithologists for a long time. Yet a detailed evaluation of even a part of it and of the evolutionary processes involved has not been attempted. Failure to do so is due in a large measure to the provincialism (taxonomic as well as geographic) of many published accounts dealing with Tyrannidae. It is now evident that significant progress in our understanding of the radiation within the Tyrannidae depends on broad comparative surveys of geographic patterns and nonmorphological characters, especially ethological ones.

Until recently, few detailed studies of behavior in tyrant flycatchers have been made. Among the significant exceptions, one might mention analyses of genera such as *Myiarchus* (Lanyon, 1960, 1961, 1963, 1965, 1967), *Empidonax* (Stein, 1958; Johnson, 1963; Mumford, 1964), *Tyrannus* (Smith, 1966), and *Sayornis* (Smith, 1969 and in press, 1 and 2). In spite of these analyses, we still know virtually nothing about a large proportion of the genera and species. Museum skins and occasional field observations by collectors are literally all the information available today on whole genera or groups of genera of Tyrannidae.

During the past several years both of us have studied various tyrannids. We have approached our subject independently and with different outlooks. Smith has long been interested in the Tyrannidae from the viewpoint of behavior and evolutionary studies. Vuilleumier, on the other hand, has studied only some tyrannid genera in detail as part of an analysis of speciation phenomena in Andean birds. Despite our different approaches, we have found that we agree on all the more important points of relationships and evolution within a group of genera, most of which are called ground tyrants and live on or near the ground in open habitats of South America, especially in the Andes and Patagonia. These include *Muscisaxicola*, *Agriornis*, and *Xolmis* and appear closely related to *Ochthoeca*, *Sayornis*, and other genera which are, to varying degrees, less terrestrial.

Our results suggest a certain number of changes in the currently accepted taxonomic arrangement of these birds. More significantly, the results also suggest some ways in which flycatchers have radiated

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into some of the more open types of habitats of South America.

Because we employed different methods, we shall present our information separately. Nevertheless, the results converge, and the two papers constitute what we consider to be a unit: together they represent an attempt toward a better understanding of the relationships and evolution of several genera of ground tyrants and allied genera. We do not pretend to have reached the final word about the systematics of these genera, and are aware of the gaps in our knowledge. Some of our conclusions are provisional. We hope, however, that the uncertainties will be an incentive for further research by other workers.

W. John Smith

François Vuilleumier

Chapter I. Generic Relationships and Speciation Patterns in *Ochthoeca, Myiotheretes, Xolmis, Neoxolmis, Agriornis,* and *Muscisaxicola*

FRANÇOIS VUILLEUMIER

ABSTRACT. The open habitats of the high Andes, Patagonia, south-central Brazil and adjacent countries are inhabited by several more or less closely interrelated genera of Tyrannidae. The adaptive radiation of these flycatchers into nonforest vegetation resulted in a variety of forms that are the ecological counterparts of species from other families (Turdidae, Laniidae) elsewhere. At one extreme of this radiation are birds of a rather generalized "flycatcher type" (e.g., *Ochthoeca*), while at the other are birds that have diverged considerably, and are now entirely terrestrial in habits and wheatearlike in morphology (e.g., *Muscisaxicola*).

In Part I, morphological and ecological attributes of the genera *Agriornis, Neoxolmis, Xolmis, Pyrope, Muscisaxicola, Muscigralla, Myiotheretes,* and *Ochthoeca* (as listed by de Schauensee, 1966) are reviewed. As a result of this analysis, it is suggested that (a) the genus *Xolmis* be enlarged to include also species previously placed in the genera *Myiotheretes* and *Pyrope,* (b) *Neoxolmis* be retained as a monotypic genus, (c) *Xolmis murina* be transferred to the genus *Agriornis,* and (d) the genus *Muscigralla* be made a subgenus of *Muscisaxicola.* Diagnoses of the genera *Ochthoeca, Xolmis, Neoxolmis, Agriornis,* and *Muscisaxicola* are given, together with descriptions of the recognized species-groups.

In Part II, geographical variation, species limits, and interspecific relationships are analyzed in *Xolmis, Neoxolmis, Agriornis,* and *Muscisaxicola.* Active speciation can be detected in the genera *Xolmis, Agriornis,* and *Muscisaxicola.* One can find: (a) species with discontinuous geographical variation across ecological barriers (e.g., *Xolmis fumigata, Muscisaxicola maculirostris*), (b) geographically isolated taxa at the borderline between species and subspecies (superspecies) (e.g., *Xolmis pernix, X. fumigata,* and *X. fuscorufa*; *Muscisaxicola juninensis* and *M. albilora*), (c) instances of secondary contact involving marginal overlap (in the *Muscisaxicola alpina* superspecies), or possible hybridization (in *Xolmis striaticollis* and *Agriornis montana*).

The available data suggest that in this group of genera, speciation is now taking place chiefly in the high Andes, where geographical isolation occurs across several well-marked ecological barriers. Zones of secondary contact in other regions, now devoid of such barriers (in northern Bolivia), indicate that geographical isolation was once possible there.

Nevertheless, there is so much extensive sympatry between congeneric species, in the Andes (e.g., in *Muscisaxicola*) as well as in the lowlands (e.g., in *Xolmis*) that the early stages of their radiation cannot now be detected.

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INTRODUCTION

As was explained in the preface, this paper, together with the one by Smith, must be considered as an attempt to describe the adaptive radiation of some groups of tyrant flycatchers into open, nonforested habitats of South America, especially the grasslands and scrub of the high Andes.

My study of several genera of Tyrannidae was part of an analysis of speciation phenomena among Andean and Patagonian birds. Geographical variation and interspecies relationships were investigated in each genus selected for this work. I analyzed especially, first, patterns of range discontinuities within the distribution of species, and second, areas of secondary contact between taxa at, or slightly below, the level of species. Knowledge of these phenomena gives us insight about the course of speciation in these birds (Vuilleumier, 1969b). This original scope has been enlarged here to include a discussion of the probable relationships of these birds at the genus level.

This paper, then, is divided into two parts. In the first, the taxonomic and evolutionary relationships of several genera of bush and ground tyrants are examined, and a classification of these birds slightly at variance with that in current use (e.g., de Schauensee, 1966) is suggested. In the second part, evolutionary phenomena at the species level are discussed in the genera *Xolmis* (which here has been enlarged to include *Myiotheretes* and *Pyrope*), *Neoxolmis*, *Agriornis* (includes *murina*, a species formerly put in *Xolmis*), and *Muscisaxicola* (includes *Muscigralla*).

This paper is the third in a series of speciation studies on Andean birds (see Vuilleumier, 1968; 1969a).

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ground tyrants during trips to South America in 1964, 1965, and 1967–1968.

The illustrations of this paper were prepared by Margaret Estey, to whom I express my thanks. Finally, I wish to thank Penelope Lasnik for her editorial assistance.

PART I: THE GENERA AND THEIR RELATIONSHIPS

The taxa analyzed below include eight genera recognized by de Schauensee (1966), who followed the unpublished work of Zimmer. They are *Agriornis* (4 species), *Neoxolmis* (monotypic), *Xolmis* (8), *Pyrope* (1), *Muscisaxicola* (11), *Muscigralla* (1), *Myiotheretes* (6), and *Ochthoeca* (9). These eight genera are all more or less closely related to one another and probably represent a group of Tyrannidae that could conceivably be given suprageneric rank (e.g., tribe). I refrain from suggesting such a taxonomic procedure at the present time, however, because I have not made a sufficiently detailed analysis of other genera (*Tumbezia, Colorampluus, Ochthornis, Sayornis, Pyrocephalus*) that I believe to be more closely related to the above eight genera than their location in check-lists (Hellmayr, 1927; de Schauensee, 1966) would imply. In this part, I will discuss the relationships of groups of species currently classified in the above eight genera, and will show that an alternative classification to the one advocated by de Schauensee (1966) might better express the phenetic groupings of these species.

The birds belonging to the above eight genera are distributed in the high Andes, from the timber line up to the upper limits of vegetation near the snow line, and from Colombia and Venezuela in the north to Patagonia in the south. In the lowlands and uplands of the continent, they occur in nonforest vegetation along the Pacific coastal plain and especially east of the Andes in Bolivia, Brazil, Paraguay, Argentina, and Uruguay. They are even found on the Falkland Islands off southern Patagonia. In view of this broad distribution in South America, it is interesting to point out that this group of genera does not occur in two other regions where the vegetation is predominantly nonforest, and where they might be expected to be found. One is the llanos of Venezuela and Colombia, and the other the high altitude grasslands of the mountains of southeastern Brazil.

A first group of these genera (*Xolmis, Pyrope, Myiotheretes*, and *Ochthoeca*) can be called bush tyrants. A second group (*Agriornis, Neoxolmis, Muscisaxicola,* and *Muscigralla*) are ground tyrants: they usually live away from trees, in very open habitats such as scrub and grass associations.

Ecological preferences vary at two levels in these eight genera. (A) Interspecific differences can clearly be seen in *Xolmis*, where *X. rubetra* is largely terrestrial, in contrast to the other species, which are more arboreal, and in *Ochthoeca*, where species such as *O. cinnamomeiventris* inhabit forested slopes, whereas the others live in open scrub (e.g., *O. leucophrys*). (B) Intraspecific variability is evident in *Myiotheretes striaticollis*, which lives in wet woodlands in some parts of its range (e.g., in Ecuador), but in dry, xeric quebradas in others (e.g., in Argentina).

This ecological variability is, I believe, of evolutionary, and hence taxonomic, significance, and is interpreted here in terms of adaptive trends. In other words, these birds may have become adapted to increasingly open habitats during their evolutionary history. Such trends may have culminated in the adaptive radiation of *Muscisaxicola,* which has about ten species that live, often sympatrically, along the Andes in the páramo and puna grassland and scrub. Geologically speaking, these habitats are probably the most recent of any South American type of vegetation. The species of *Muscisaxicola* differ from most arboreal flycatchers in a series of characters that are probably all part of the adaptations (and concomitant evolutionary changes) to such extreme habitats: long legs, inconspicuous colors and patterns, and simplification of vocal manifestations.

Unfortunately, ornithologists have so far done relatively little work that might enlighten us about the modalities of this adaptive radiation. Part of the reason for this failure lies in the taxonomic treatment of these birds. It has been customary to keep the generic limits of taxa such as *Agriornis*, *Xolmis*, *Muscisaxicola*, and *Ochthoeca* relatively constant, because these genera contain species that resemble each other closely. But the more distinct or more intermediate taxa (usually single species) have either been placed in a monotypic genus or shifted back and forth from one genus to another. Such shifts can be made one way or the other, depending on which character a given author feels has more taxonomic weight as a "generic" character. Thus the species *rufiventris* is in some characters intermediate between *Xolmis* and *Myiotheretes*, but is distinct from either in other traits, and so was given generic rank (*Neoxolmis*) by Hellmayr (1927). The species *pyrope* differs in several ways from species ordinarily placed in *Xolmis*, and was consequently isolated in a monotypic genus *Pyrope* by Zimmer (MS; see de Schauensee, 1966). The species *rufipennis* was removed from *Cnemarchus* and placed in *Xolmis* by Zimmer (MS). Finally, the species *brevicauda* has been isolated in a monotypic genus for so long that no one has asked whether this taxon was possibly related to others, and which ones they might have been.

Part of the taxonomic problem just outlined can be resolved by taking into consideration ecological and behavioral factors, together with the more traditional ones of morphology. The classification presented in this paper is one attempt to do so. I suggest that the major ecological shift that has occurred in the evolutionary history of the bush and ground tyrants has been a change both from arboreal to terrestrial habits and from a relatively closed habitat (woodland) to a much more open one (steppe). The present geographical range of bush flycatchers in the nonforested Brazilian uplands, and various other nonforest vegetation formations of central and southern South America coincides in part with regions of great geological age that have not undergone major changes in their position or structure. Indirect evidence (e.g., from fossil mammals) suggests that the vegetation of such regions has been nonforest for a long time (i.e., since at least the mid-Tertiary). One may therefore suppose that the ecological shift has been chiefly in the direction of woodland to steppe, because the South American steppes (high Andean and Patagonian) appear to be much more recent than the central South American woodland formations. Whatever the actual direction of the shift, however, I have placed taxonomic weight on characters that appear to be correlated with it.

Since a classification that includes only the categories genus and species is, in my opinion, not able to express satisfactorily the multiple hierarchical relationships of taxa, I have, as in previous systematic papers (Vuilleumier, 1965, 1968, 1969a), made full use of the species-group and superspecies categories, which do not burden the formal nomenclature by additional names. I have also used subgenera in one case.

The classification of the bush and ground tyrants constructed on the basis of an analysis of variation in characters is outlined below prior to the character analysis, in order to maintain throughout the paper as much uniformity as possible in the nomenclature of these birds.

I am fully aware that a linear sequence of taxa cannot express all the possible relationships of these taxa. The sequence adopted here is therefore a compromise. The following conventions have been adopted. Genera having entirely or mostly arboreal and woodland-inhabiting species are placed before genera having terrestrial and steppe-inhabiting species. Thus *Ochthoeca* and *Xolmis* are placed before *Neoxolmis*, *Agriornis*, and *Muscisaxicola*. *Ochthoeca* precedes *Xolmis* because it may be more closely related to the two Andean species-groups of *Xolmis* (numbers 1 and 2 in the list below) than to other genera. *Agriornis* is listed between *Xolmis* and *Neoxolmis* on the one hand, and *Muscisaxicola* on the other, because in some ways, it is intermediate between them. Within genera, the species-groups are listed with the Andean group(s) first, and the lowland one(s) next, except in *Muscisaxicola*, where this procedure would have relegated the *maculirostris* species-group toward the end of the list, far away from the subgenus *Muscigralla*, with which it is more related than with other species-groups. Within species-groups, the species are listed either randomly if sympatric, or geographically from north to south if allopatric.

Species-groups and superspecies have been named after the oldest name of any taxon within each. Species or semispecies considered to be component members of a superspecies are included in braces.

Classification

Genus *Ochthoeca* Cabanis, 1847

1. *cinnamomeiventris* species-group
   - *O. cinnamomeiventris* (Lafresnaye, 1843)
2. *diadema* species-group
   - *O. diadema* (Hartlaub, 1843)
   - *frontalis* superspecies
     - *O. frontalis* (Lafresnaye, 1847)
     - *O. pulchella* Sclater and Salvin, 1876
3. *rufipectoralis* species-group
   - *O. rufipectoralis* (Lafresnaye and d'Orbigny, 1837)
4. *oenanthoides* species-group
   - *O. fumicolor* Sclater, 1856
   - *O. oenanthoides* (Lafresnaye and d'Orbigny, 1837)
   - *leucophrys* superspecies
     - *O. leucophrys* (Lafresnaye and d'Orbigny, 1837)
     - *O. piurae* Chapman, 1924

Genus *Xolmis* Boie, 1826

1. *fumigata* species-group
   - *X. striaticollis* (Sclater, 1853)
   - *fumigata* superspecies
     - *X. pernix* (Bangs, 1899)
     - *X. fumigata* (Boissonneau, 1840)
     - *X. fuscorufa* (Slater and Salvin, 1876)
   - (*X. signata* (Taczanowski, 1874) is maintained in this genus and species-group provisionally, pending critical examination of the one or two extant specimens.)
2. *erythropygia* species-group
   - *X. erythropygia* (Sclater, 1853)
   - *X. rufipennis* (Taczanowski, 1874)
3. *pyrope* species-group
   - *X. pyrope* (Kittlitz, 1830)
4. *cinerea* species-group
   - *X. cinerea* (Vieillot, 1816)
   - *X. velata* (Lichtenstein, 1823)
   - *X. coronata* (Vieillot, 1823)
   - *X. dominicana* (Vieillot, 1823)
   - *X. irupero* (Vieillot, 1823)
5. *rubetra* species-group
   - *X. rubetra* (Burmeister, 1860)

Genus *Neoxolmis* Hellmayr, 1927
- *N. rufiventris* (Vieillot, 1823)

Genus *Agriornis* Gould, 1839

1. *montana* species-group
   - *A. montana* (Lafresnaye and d'Orbigny, 1837)
   - *A. albicauda* (Philippi and Landbeck, 1863)
2. *livida* species-group
   - *A. livida* (Kittlitz, 1835)
   - *A. microptera* Gould, 1839
3. *murina* species-group
   - *A. murina* (Lafresnaye and d'Orbigny, 1837)

Genus *Muscisaxicola* Lafresnaye and d'Orbigny, 1837
- subgenus *Muscigralla* Lafresnaye and d'Orbigny, 1837
  - *M. brevicauda* Lafresnaye and d'Orbigny, 1837
- subgenus *Muscisaxicola* Lafresnaye and d'Orbigny, 1837

1. *maculirostris* species-group
   - *M. maculirostris* Lafresnaye and d'Orbigny, 1837
   - *M. fluviatilis* Sclater and Salvin, 1866
2. *macloviana* species-group
   - *M. macloviana* (Garnot, 1829)
   - *M. capistrata* (Burmeister, 1860)
3. *rufivertex* species-group
   - *M. rufivertex* Lafresnaye and d'Orbigny, 1837
   - *albilora* superspecies
     - *M. juninensis* Taczanowski, 1884
     - *M. albilora* Lafresnaye, 1855

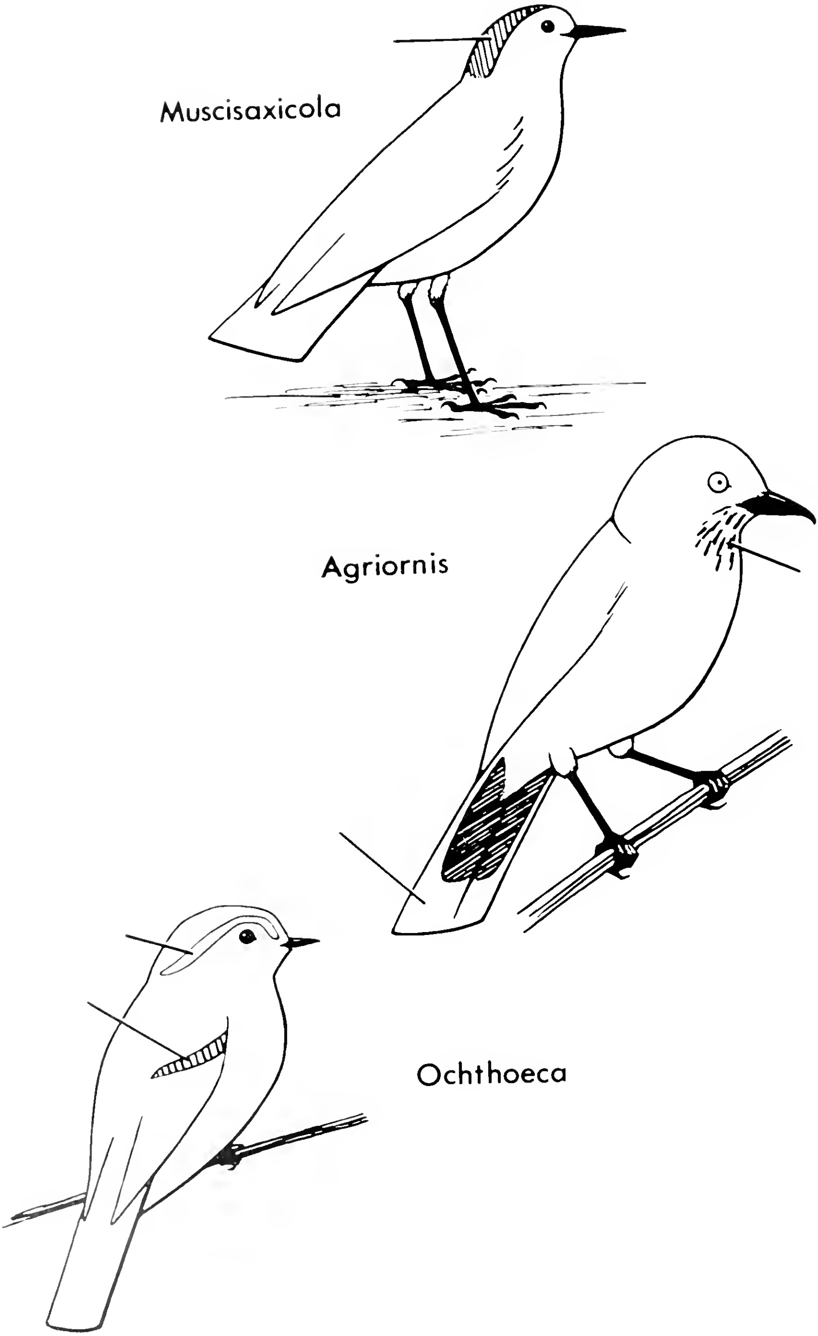

Fig. 1. Three of the four groups based on differences in color pattern. Top: *Muscisaxicola rufivertex*, an example of group 1 (unpatterned species with a contrasting crown patch). Center: *Agriornis montana*, an example of group 2 (species with streaked throat and patterned tail). Bottom: *Ochthoeca rufipectoralis*, an example of group 3 (species wih superciliary stripe and wing bars).

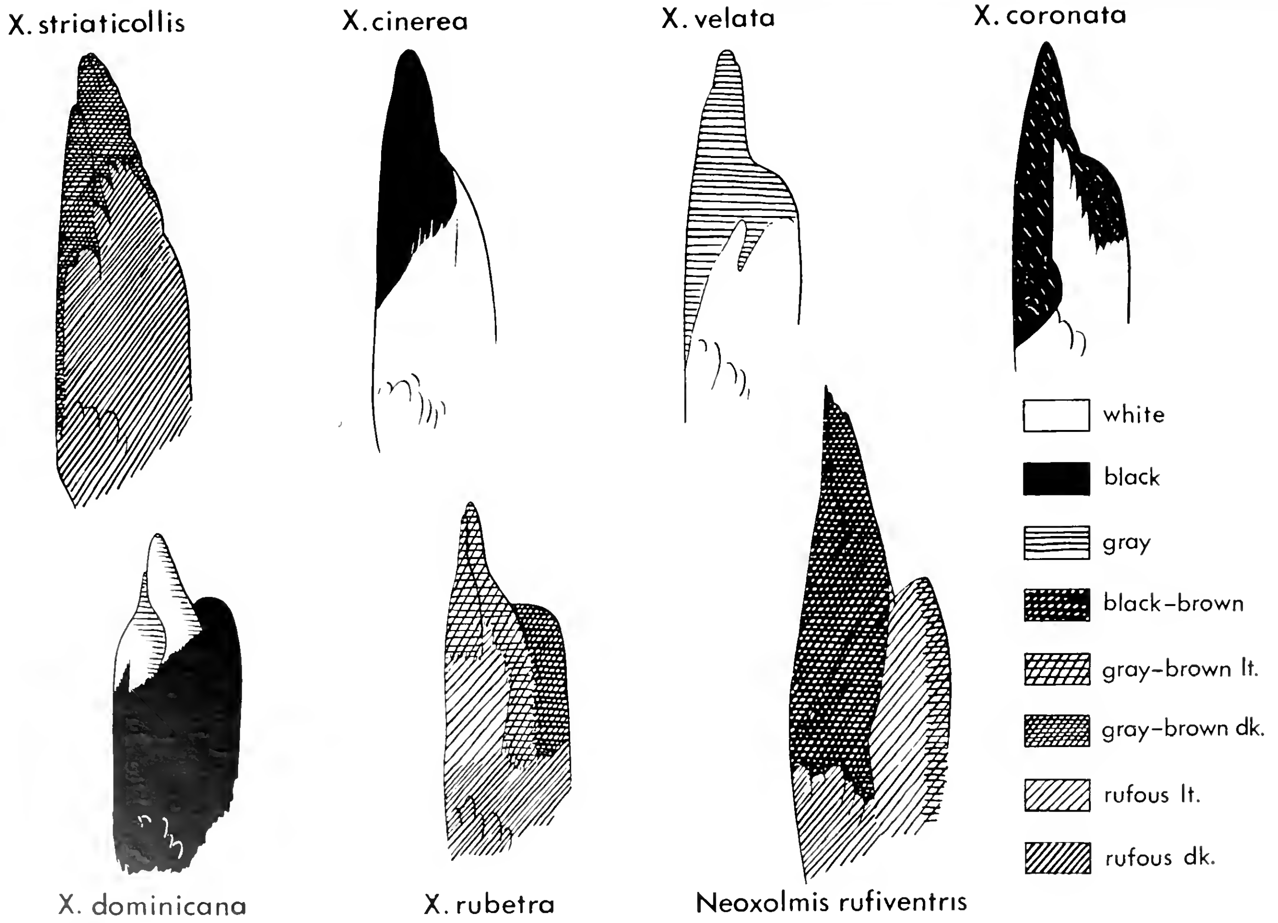

Fig. 2. Underwing patterns in selected species of group 4 (patterned wings, and either patterned or unpatterned body and tail). The colors composing the pattern vary from species to species, but the wing tip is usually dark, and the wing base pale, except in *Xolmis dominicana* and *X. rubetra*. Different shades of the same color are indicated by the symbols lt. (light) and dk. (dark). Drawn to scale.

4. *alpina* species-group
   alpina superspecies
   - *M. alpina* (Jardine, 1849)
   - *M. cinerea* Philippi and Landbeck, 1864
5. *albifrons* species-group
   albifrons superspecies
   - *M. albifrons* (Tschudi, 1844)
   - *M. flavinucha* Lafresnaye, 1855
   - *M. frontalis* (Burmeister, 1860)

Analysis of Some Characters

Color and Pattern

The color of the bush and ground tyrants varies from black and white (*Xolmis irupero*) to almost entirely dark smoky brown (*Xolmis fumigata*) or black (*Ochthoeca cinnamomeiventris*) and to different shades of gray and brown, and, in some species, even greenish and yellowish. Some species are unpatterned, while others have striking patterns.

This variability permits one to make four groups. (1) Largely unpatterned species having uniformly colored body, wing, and tail plumage. The outer rectrices usually have a pale margin. Some species have a conspicuous, others, a faint, crown patch of a yellowish, brownish, or reddish color; some species lack a crown patch altogether. This group includes all the species of *Muscisaxicola* plus *Xolmis pyrope* (Fig. 1). A partial exception is *Muscisaxicola brevicauda*, which has a somewhat patterned rump and tail, although otherwise it has dull, unpatterned body plumage and a (concealed) crown patch.

(2) Species having essentially unpatterned body and wings (save for pale outer edges of secondaries and coverts), and a white throat with dark streaks. The tail is patterned with white in some species, but is essentially unpatterned in others. No species has a crown spot. This group comprises the five species here included in *Agriornis* (Fig. 1).

(3) Species having either patterned or uniformly colored body plumage, and a conspicuous white, buffy, or yellow superciliary stripe. Many species also have conspicuous wing bars. The tail is essentially unpatterned, although a few species have a whitish or pale buffy edge to the outer rectrices. This group includes the species of *Ochthoeca* (Fig. 1).

(4) Species having patterned wings (often the pattern is concealed), and either patterned or unpatterned body plumage and tail. The underwing pattern is very uniform. The distal one-third to one-half of the primaries is black or dark brown, the basal part rufous, white, or buff (Fig. 2). The exceptions are a white wing tip and black basal part (*Xolmis dominicana*), and a pale rufous distal part of the primaries (*Xolmis rubetra*) (Fig. 2). All other species of *Xolmis* (but not *X. pyrope,* mentioned above under 1) and *Neoxolmis* can be included in the patterned group.

Attenuation of the Outer Primaries

The two outer wing feathers vary from unmodified to highly attenuated at the tip. In most, and probably all, of the species having attenuated outer remiges, this attribute appears restricted to adult males. The possible functions of this modification during displays, for example, is still largely unknown. Wetmore (1926a: 302) indicated that *Xolmis rubetra* made some sort of rattlelike noise in flight, which is most likely related to the attenuation of its outer primaries. Smith describes wing displays in several bush and ground tyrants.

Two groups of birds can be made on the basis of variation in the degree of emargination of the remiges. In the first (no attenuation) are all species of *Ochthoeca*, all species of *Muscisaxicola*, and several species of *Xolmis* (Fig. 3). In the second group are species having moderate to marked attenuation. They include all species of *Agriornis* (adult males only), several species of *Xolmis*, and *Neoxolmis.* Within *Xolmis,* variation in emargination appears to be species-specific as depicted in Figure 3.

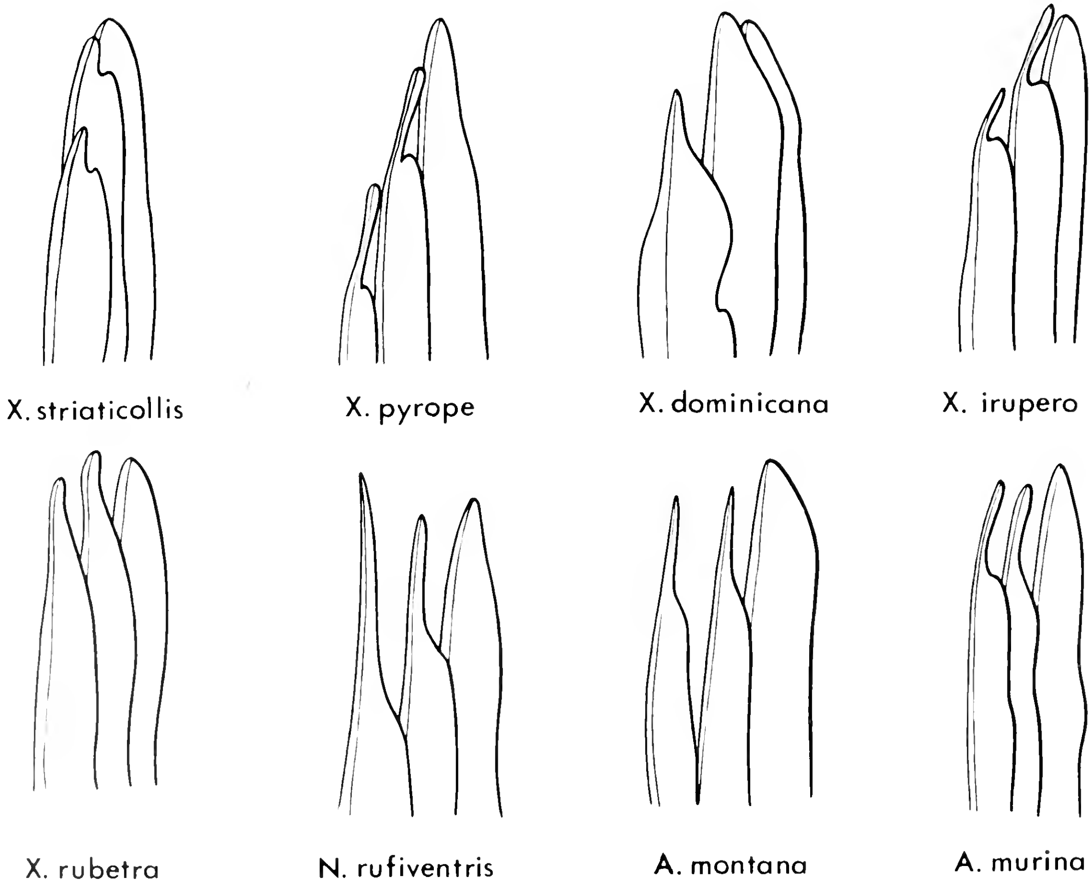

Fig. 3. Attenuation of primaries in *Xolmis*, *Neoxolmis*, and *Agriornis*. Attenuation is restricted to the two outermost feathers, and seems limited to adult males. The differences in attenuation are species-specific. Drawn to scale.

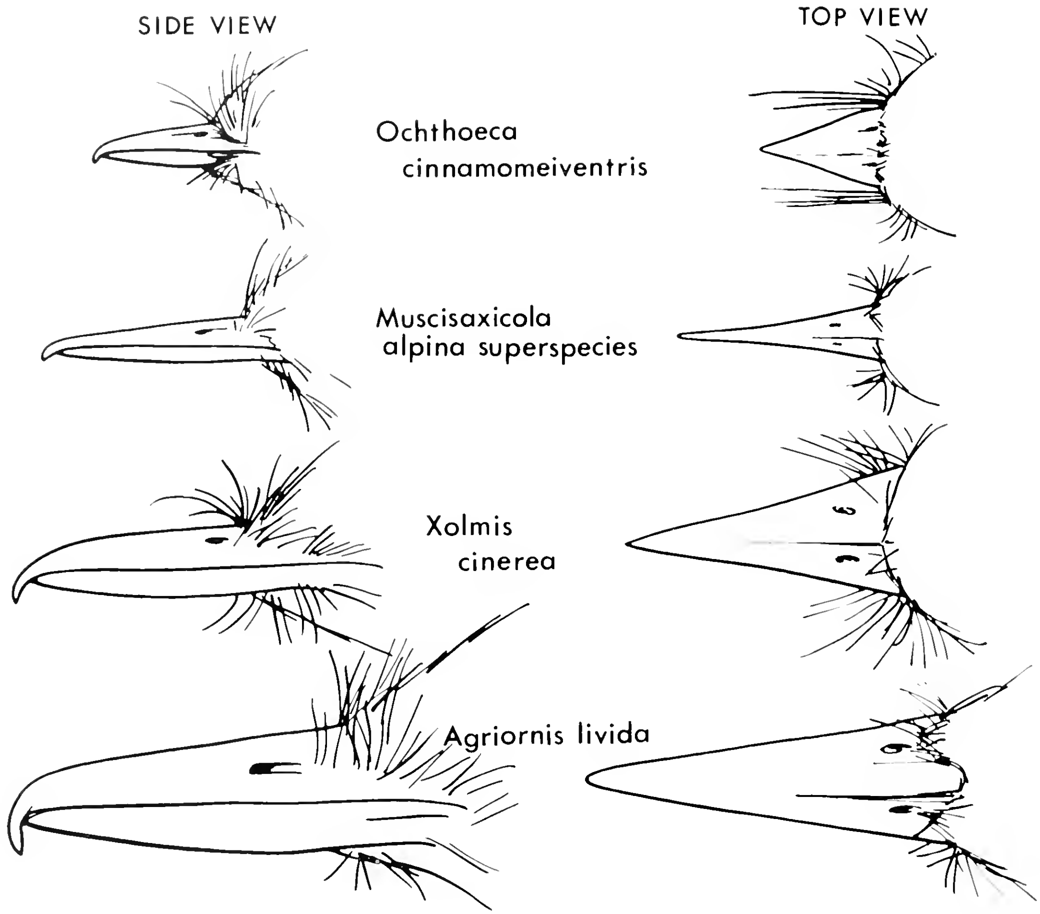

Fig. 4. Bill structure of *Ochthaeca*, *Muscisaxicola*, *Xolmis*, and *Agriornis*. O. *cinnamomeiventris*: short, broad bill, with long rictal bristles, correlated with insectivorous diet and wet, forested habitat. *M. alpina*: thin, narrow bill, with short rictal bristles, correlated with insectivorous diet and dry, nonforested habitat. *X. cinerea*: relatively long, broad bill, with long rictal bristles, correlated with partially insectivorous diet and moderately dense habitat. *A. livida*: long, narrow, and sharply-hooked bill, with short rictal bristles, correlated with varied diet and nonforest habitat. Drawn to scale.

Bill Structure

The bill of the bush and ground tyrants is a very variable organ. Although the precise diets and feeding methods of most species are still very poorly known, it is possible to correlate positively certain characters of bill size and shape with food. Thus, small and insectivorous species (*Ochthoeca* and *Muscisaxicola* species) have relatively small bills, whereas larger species, of the genera *Xolmis* and *Agriornis*, having more diversified diets and occasionally or regularly capturing small vertebrates, have relatively powerful bills, often with a sharp hook at the tip (Fig. 4).

Bill width varies considerably in the bush and ground tyrants. Species living in wetter and structurally denser habitats seem to have proportionately broader bills than do species living in dry and open habitats (Fig. 4). This correlation is more or less independent of size. Among open-country species, small-sized *Muscisaxicola* and large-sized *Agriornis* all have relatively narrow bills.

Shape of Tail

Most species have a square or slightly forked tail. In some species, however, the tail is markedly forked (*Neoxolmis rufiventris*) or markedly rounded (*Xolmis coronata*). These differences appear to be only species-specific, and of little use for supraspecific groupings.

Proportions

There is a tremendous amount of variation in the proportions of wing, tail, tarsus, and culmen lengths within the bush and ground tyrants. In most instances, it is difficult to establish correlations between proportions and other characters, or between proportions and habits. The most terrestrial species, such as all species of *Muscisaxicola,* have proportionately long, thin legs. Arboreal species usually have proportionately shorter legs than do terrestrial ones. More detailed discussions of the possible taxonomic significance of variation in proportions will be found in the generic accounts below.

Size

The flycatchers under consideration vary from very small (*Muscisaxicola brevicauda*) to very large (*Agriornis livida*). Most of this variation appears to be interspecific. In *Muscisaxicola,* some of the interspecific variability in size occurs between pairs or among triplets of sympatric species living either in the same or in adjacent biotopes. These differences might represent character divergence permitting resource partitioning, whereas other differences, such as species-specific head or crown patterns, may permit recognition of conspecific individuals.

In *Agriornis,* the two high Andean species (*montana* and *albicauda*) are sympatric over much of their respective ranges. They are very similar in pattern but differ in absolute size. The lowland species *livida* and *microptera,* although entirely allopatric, differ conspicuously in size rather than in pattern.

These two examples, in *Muscisaxicola* and *Agriornis,* show that ecological correlates of size differences may or may not exist. It seems difficult to assign any taxonomic significance to size variation among the bush and ground tyrants.

Eye Color

The iris of most species of bush and ground tyrants is dark brown or blackish, but that of *Xolmis pyrope* and of *Xolmis cinerea* is red. This color is conspicuous in the field. Such variation does not seem to be of great taxonomic significance, except to suggest that *X. pyrope* is relatively closely related to birds of the *X. cinerea* species-group.

Nest Site

When considered together with other characters, such as color pattern, proportions, habitat, and perhaps behavioral traits, nest site may be of help in assessing the interrelationships of some taxa. I have made use of such correlations especially in the case of *Neoxolmis rufiventris* and *Muscisaxicola brevicauda* (see below). In the genus *Agriornis,* however, the variation in nest site may be of less taxonomic significance. One of the three species living in high Andean steppes (*montana*) builds its nest on the ground in protected sites, whereas another (*microptera*) does not. Finally, *A. livida,* found in open woodlands and scrubby vegetation in lower zones along the Andes, builds its nest in trees. Data about nests and nest sites are given by Smith.

Habitat Preferences and Distribution

As I pointed out earlier, there is both intra- and interspecific variation in ecological preferences among the bush and ground tyrants. Further information is given by Smith. Three species occur in rather specialized habitats, and the possible taxonomic significance of this fact needs to be examined. *Xolmis pyrope* appears restricted to open woodlands and the edges of Patagonian forests dominated by trees of the genus *Nothofagus*. In other characters this species resembles *Muscisaxicola* (absence of patterning) or *Xolmis* (proportions, eye color, arboreal habits, behavior). Since I have placed some weight on the transition from arboreal to terrestrial adaptations, I have maintained this species in *Xolmis* (in a distinct species-group) because it exhibits few of the more typical adaptations to terrestrial life found in other ground tyrants.

Another ecological specialist is *Neoxolmis rufiventris*. This species occurs at the southern tip of South America, in open boglike grasslands or steppes with low *Berberis* shrubs. It apparently shares this habitat with no other species of the groups discussed in this paper. In its nest site, proportions, and general behavior, this species can only be considered a true ground tyrant. But in color pattern it resembles some of the arboreal species of *Xolmis*, especially of the Andean species-groups. Assuming that *N. rufiventris* has fully evolved to the terrestrial adaptive zone, I have maintained it in the monotypic genus erected by Hellmayr (1927).

The third species is *Muscisaxicola brevicauda*. It lives in the lowlands of southwestern Ecuador and northwestern Peru, in open habitats ranging from steppelike man-made biotopes (cotton plantations) to natural savannas and open woodlands. In habits it is partly terrestrial, like other *Muscisaxicola*, and partly arboreal, like other birds such as *Xolmis*. In pattern and behavior it is closest to *Muscisaxicola*, but its habitat is clearly denser. I have considered it here the most aberrant member of the genus *Muscisaxicola*, and have placed it in a subgenus of its own.

The Genus *Ochthoeca*

Diagnosis

A genus of about seven to nine species of small to medium-sized flycatchers living along the Andes in high altitude steppes, open woodlands, and, occasionally, wet montane forests. All forms of this genus have a relatively short but rather broad bill, and long and conspicuous rictal bristles (see Fig. 4). The outer primaries are not emarginated. Colors are usually browns and grays, but one species is largely greenish and another black and chestnut. All species have a head pattern with the loral spot and a superciliary stripe of a different color than the crown and cheeks (see Fig. 1). Most species have one or two wing bars (see Fig. 1), but this character is geographically variable in at least one species (*O. rufipectoralis*). The underwing color patterns, so striking in the genus *Xolmis*, are absent in *Ochthoeca*. Species of *Ochthoeca* have a characteristic field silhouette, with large head and convex forehead (see Fig. 1).

Species Included

I accept here the treatment of de Schauensee (1966: 338-340), who recognized nine species. These species can be arranged into four species-groups, described below. (I believe that the following taxa, now placed rather far from *Ochthoeca* in the lists of Hellmayr [1927] and de Schauensee [1966], are closely related to, or even possibly congeneric with, *Ochthoeca*: *Tumbezia salvini* [Taczanowski, 1877], *Coloramphus parvirostris* [Darwin, 1839], and *Ochthornis littoralis* [Pelzeln, 1868].)

1. *The cinnamomeiventris species-group.* The only species included, *Ochthoeca cinnamomeiventris*, is black with a white loral spot and supercilium. The underparts vary geographically from black to black and chestnut. Some populations of this species have conspicuously white axillary feather tufts. *O. cinnamomeiventris* has the broad-

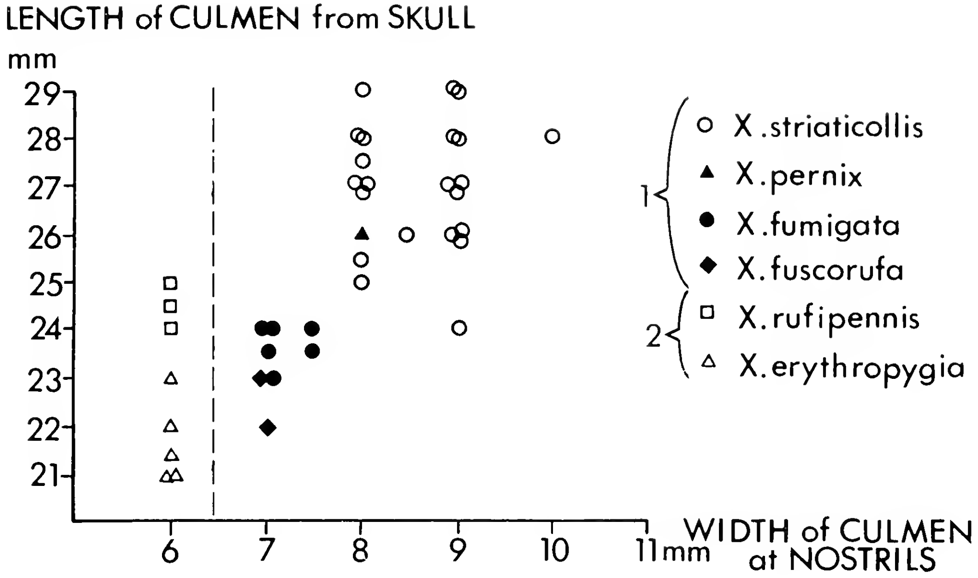

Fig. 5. Length of culmen plotted against width of culmen in the *Xolmis fumigata* species-group (1) and the *X. erythropygia* species-group (2). Note the absence of overlap in width of culmen between the two groups.

est and flattest bill of any species of *Ochthoeca* (see Fig. 4). This species may be the most strictly forest-inhabiting species of *Ochthoeca* or, indeed, of the entire group of genera considered in this paper.

2. *The diadema species-group.* This group contains *Ochthoeca diadema*, and a superspecies that includes *O. frontalis* and *O. pulchella.* All three species have a yellow loral spot, and a yellow or white supercilium. The upper parts vary from dark brown (in *pulchella*) to greenish (in *diadema*). The species of this group are forest birds, but they occupy relatively open biotopes, such as clearings, rather than the forest interior.

3. *The rufipectoralis species-group. Ochthoeca rufipectoralis,* the only species of this group, has a buffy supercilium and patterned underparts, with contrasting rufous chest and pale gray lower abdomen. A similar pattern is not found in any other species of the genus. *O. rufipectoralis* lives in more open habitats than birds of the first two species-groups.

4. The *oenanthoides species-group.* The four species I include in this group (*O. fumicolor, O. oenanthoides,* and the two species of the *leucophrys* superspecies: *O. leucophrys* and *O. piurae*) are characterized by their being somewhat larger sized than the species of the other groups, by their relatively long and thin bill, and their brown or gray coloration. *O. fumicolor* is almost entirely dark rufous, *O. oenanthoides* is gray above and pale rufous below, whereas birds of the *leucophrys* superspecies are gray both above and below. The birds of this species-group live higher, as a group, than any other in the genus. They are found in wet páramos (*O. fumicolor*) or in dry scrub associations of the puna (*O. oenanthoides* and *O. leucophrys*).

The Genus *Xolmis*

Diagnosis

A genus of 13 to 14 species of medium to large sized flycatchers distributed along the high Andes, in the uplands and lowlands of central South America, and in

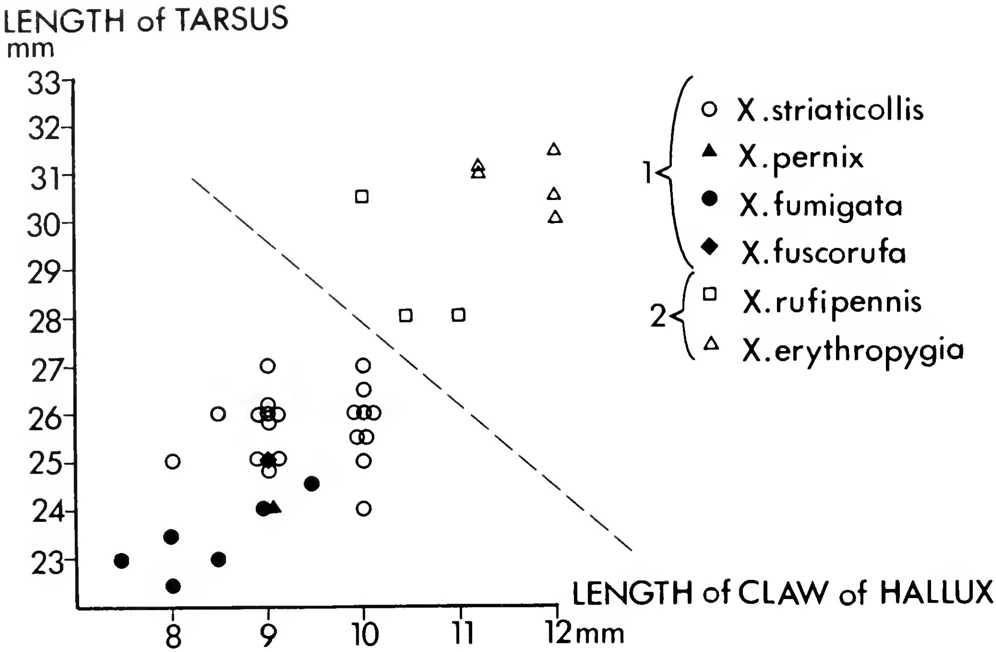

Fig. 6. Length of tarsus plotted against length of claw of hallux in the *Xolmis fumigata* species-group (1) and the *X. erythropygia* species-group (2). Note that tarsus and claw of hallux are proportionately longer in the two species of the *erythropygia* group, and are separated from the measurements of the *fumigata* group.

Patagonia, where they inhabit forest edges, woodlands, dense scrub, and, more rarely, open steppes.

All species of *Xolmis*, except *X. pyrope*, are patterned, but the details of color and color combinations vary widely from species to species. The colors making up the patterns are white, gray, and black in some species (in the *cinerea* species-group), gray and brown in others (the *fumigata*, *erythropygia*, and *rubetra* species-groups). The underwing patterns are relatively uniform throughout the genus (Fig. 2), although the colors can be either rufous and dark brown, or black and white, as was mentioned earlier.

Species of the genus *Xolmis* have a long and relatively narrow bill with a terminal hook (see Fig. 4). There is interspecific variation in bill width within the *fumigata* species-group. All species of *Xolmis*, except the rather terrestrial species, *X. rubetra*, have moderately long and conspicuous rictal bristles. The following species have emarginated outer wing feathers: *X. striaticollis*, *X. pyrope*, *X. dominicana*, *X. irupero*, and *X. rubetra* (see Fig. 3). Only in the latter species is there any evidence of a sound being produced in flight, which may be attributed to this emargination (Wetmore, 1926a; see Smith).

Species Included

The genus *Xolmis* as understood here includes species formerly placed in the genera *Myiotheretes* Reichenbach, 1850; *Cnemarchus* Ridgway, 1905; *Ochthodiaeta* Cabanis and Heine, 1859; and *Pyrope* Cabanis and Heine, 1859. (One species, *Xolmis murina*, has been removed from *Xolmis* and transferred to *Agriornis*, and will be discussed below under that genus.) The five above genera have been merged into one because neither morphological nor ecological characters permitted unequivocal delimitation of more than one genus. Thus, *X. pyrope* cannot satisfactorily be separated from *Xolmis sensu* Hellmayr (1927), and *X. rufipennis* can just as easily be included in de Schauensee's (1966) enlarged genus *Myiotheretes* as in *Xolmis*. It is as arbitrary to shift either or both of these two species back and forth from one genus to another as it is to isolate them in monotypic genera, since neither species really departs from the species composing the genera *Myiotheretes* and *Xolmis* in de Schauensee's list. Another solution (merging) is preferred here, but only if subdivisions within the enlarged *Xolmis* can be expressed. This is done here by means of species-groups.

1. *The fumigata species-group.* This species-group includes *Xolmis striaticollis*, *X. pernix*, *X. fumigata*, *X. fuscorufa*, and perhaps also *X. signata*.[1]

These species have relatively broader bills than other species of *Xolmis*, a whitish or grayish-colored throat with dusky streaks, unpatterned smoke-brown or rusty breast and belly, conspicuously patterned wings and tail (a given species can have either the tail or the wings patterned, or both), and relatively short tarsi and claws of hallux.

The species of the *fumigata* species-group resemble most those of the *erythropygia* species-group in color and pattern, but they differ from them in having proportionately broader bills (Fig. 5), shorter tarsi, and shorter claws of hallux (Fig. 6). These and other differences in proportions are illustrated in Figure 7 by means of a ratio-diagram.

The habitats favored by the species of the *fumigata* species-group include cool, moist, forested or wooded slopes of the tropical Andes in the ecotone between the montane forests (cloud forests) and the grasslands above. They do not occur in high altitude treeless steppes, where *Agriornis* and *Muscisaxicola* live. They also seem to avoid the dark montane forest interior, where *Ochthoeca cinnamomeiventris* is found.

The birds of the *fumigata* species-group converge both morphologically and in some of their behavioral traits toward thrushes of the genus *Turdus*. Note in particular the resemblance between *X. striaticollis* and *Turdus* spp. in color pattern and in stance when on the ground.

2. *The erythropygia species-group.* This species-group comprises two sympatric, probably not very closely related species, *Xolmis erythropygia* and *X. rufipennis*. They differ, as a group, from the species of the *fumigata* species-group, which also have streaks on the throat, by the combination of: relatively narrower bill, relatively longer tarsus, and longer claw of hallux (see Figs. 5–7). They differ from the other species-groups of *Xolmis* in having conspicuously patterned underwings with rufous instead of white (see Fig. 2).

X. erythropygia occurs in wet habitats at the upper altitudinal limit of montane Andean forests. *X. rufipennis* occurs in slightly drier and more open habitats, often within the puna grassland and scrub in *Polylepis* woodlands (Vuilleumier, 1969c). Both species, but *X. erythropygia* especially, have some superficial resemblance to chats, rather than to thrushes.

3. *The pyrope species-group.* The only species included, *Xolmis pyrope*, is gray above, with a whitish throat and belly and pale gray breast, without wing or tail markings, thus contrasting, in this lack of pattern, with all other species of the genus. Its red iris makes it resemble *X. cinerea* in this character, whereas its juvenal plumage resembles that of *Muscisaxicola* species in

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[1] *X. signata* (Taczanowski, 1874) is known from two specimens (*fide* Hellmayr, 1927). One of these is now deposited at the Polish Academy of Sciences in Warsaw (Pinowski, *in litt.*). I have not been able to examine this specimen and cannot, therefore, make any decision about its taxonomic allocation. I retain *X. signata* in the *fumigata* species-group and, indeed, in *Xolmis*, until the specimen(s) can be critically studied.

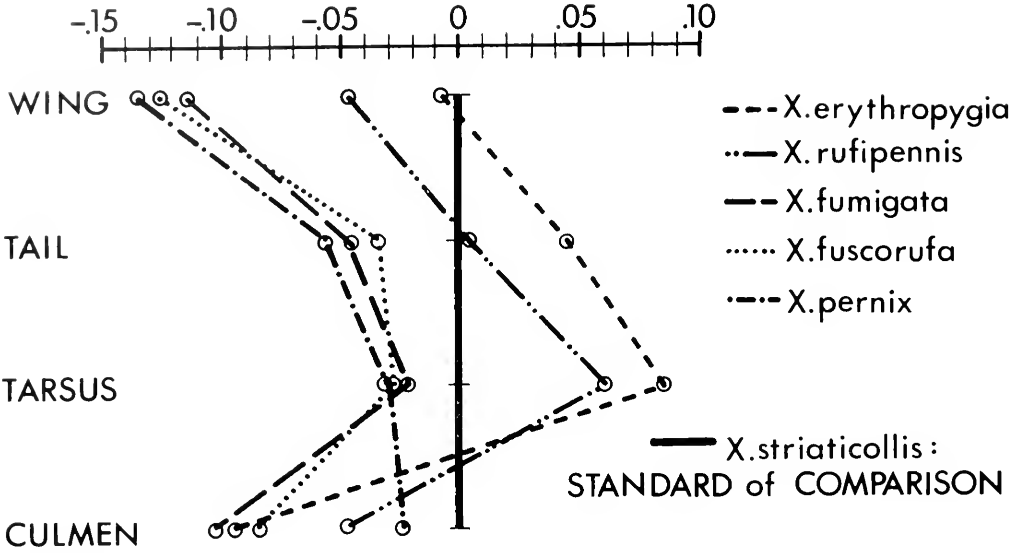

Fig. 7. Ratio-diagram illustrating differences in proportions between members of the *Xolmis fumigata* and *X. erythropygia* species-groups. Note that *X. erythropygia* and *X. rufipennis* (of the *erythropygia* group) have proportionately longer tarsi and shorter culmens than the species of the *fumigata* group. The scale is in units of difference from log of standard of comparison. For further information on the construction of ratio-diagrams, see Simpson (1941).

having faint streaks on the breast and buffy coloration along the edges of wing coverts. *X. pyrope* has markedly shorter tarsi than species of the *cinerea* and *rubetra* species-groups, and is thus closer in this character to *X. fumigata* of the *fumigata* species-group (see Fig. 8).

X. pyrope lives in Patagonia along the edge of, and in open situations within, *Nothofagus* (beech) forests.

4. *The cinerea species-group.* This group contains *Xolmis cinerea, X. velata, X. coronata, X. dominicana,* and *X. irupero.* These species are patterned in various combinations of white, gray, and black. *X. cinerea* has white throat and crissum and gray breast; the other four species have wholly white underparts. The details of patterns of wings and upperparts vary from one species to another. The possible reasons for the variation in color patterns have not been investigated. Friedmann (1927: 197) believed *X. irupero's* habit of nesting in holes in trees to be related to its black and white pattern, but he did not suggest how. In a general way, the species of this group have color patterns reminiscent of those of the genus *Oenanthe.* Cott (1947) showed that certain species of *Oenanthe* are unpalatable, and that their highly conspicuous patterns may be interpreted as warning coloration. It would be interesting to carry out experiments to check whether the same might be true in *Xolmis* also. In proportions, the five species of the *cinerea* species-group are rather similar to one another, except that *X. dominicana* has a longer tail (see Fig. 9).

Birds of the *cinerea* species-group are arboreal and live in woodlands, savannas, and other nonforest vegetation types of central South America, from central Brazil southward to eastern Bolivia, Paraguay, Uruguay, and central Argentina.

5. *The rubetra species-group. Xolmis rubetra,* the only species of this group, differs from the species of the *cinerea* species-group in having brown upperparts,

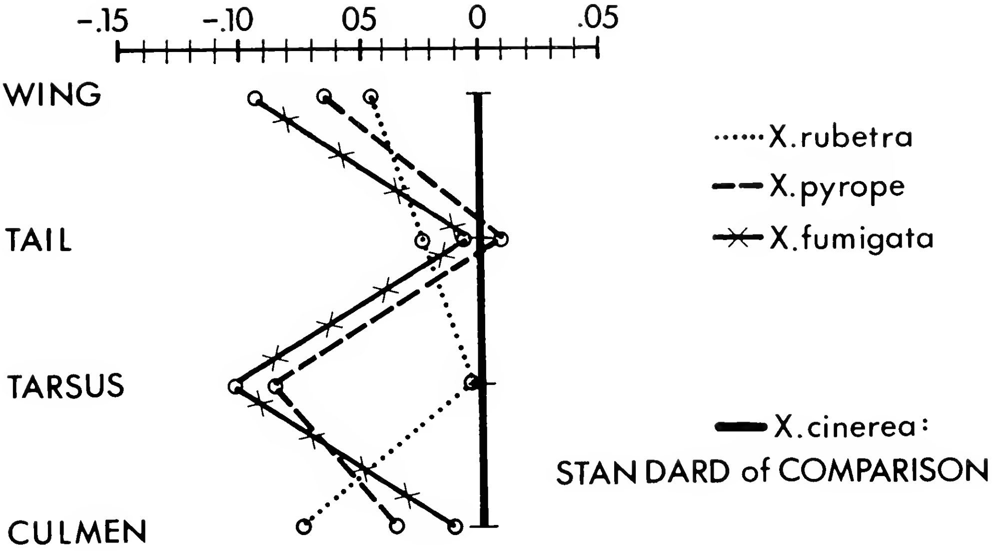

Fig. 8. Ratio-diagram illustrating differences in proportions between selected species of the genus *Xolmis*. Note that *Xolmis pyrope* (sole member of the *pyrope* species-group) resembles more closely *X. fumigata* (representative of the *fumigata* group) than *X. cinerea* (representative of the *cinerea* group), while the more terrestrial species *X. rubetra* (sole member of the *rubetra* group) differs from all of them in proportions of wing, tail, tarsus, and culmen.

a collar of blackish streaks on the breast, rufous flanks, and proportionately long tarsi (compare *X. cinerea* and other species in Figs. 8 and 9). *X. rubetra* lives in open scrub habitats of central and southern Argentina, and appears more terrestrial than the other species of the genus. In color, pattern, and habits, *X. rubetra* is intermediate between the other species of *Xolmis* and *Neoxolmis rufiventris*, and may represent an evolutionary transitional "stage" between arboreal and terrestrial tyrants.

The Genus *Neoxolmis*

Diagnosis

A monotypic genus of large terrestrial flycatchers living in open steppes of southern Patagonia. This genus is characterized by: gray throat and breast, chocolate brown belly and crissum (recalling the pattern of *Xolmis erythropygia*), brown and rufous underwing pattern (Fig. 2), and conspicuous pale edges to secondaries and wing coverts (recalling the patterns of *Xolmis velata* and *X. rubetra*). The proportions of *Neoxolmis* differ from those of species of *Xolmis; N. rufiventris* has proportionately long wings and tarsi but short tail and bill (Fig. 9). The lores and adjacent parts of the face are dark sooty gray, giving the head an aspect reminiscent of that of *Muscisaxicola macloviana,* which, incidentally, also lives in southern Patagonia. *Neoxolmis* has very short and inconspicuous rictal bristles.

Some of the above characters may be correlated with the terrestrial behavior and nesting habits of this species (Crawshay, 1907; Maclean, 1969): long legs, long wings, short rictal bristles.

Hellmayr (1927: 39) erected the genus *Neoxolmis* for the species *rufiventris*, which had usually been placed in *Myiotheretes*. Zimmer (MS) placed it in *Xolmis*, but de Schauensee (1966) maintained *Neoxolmis*.

From this history of taxonomic shifts, and from the intermediacy in characters

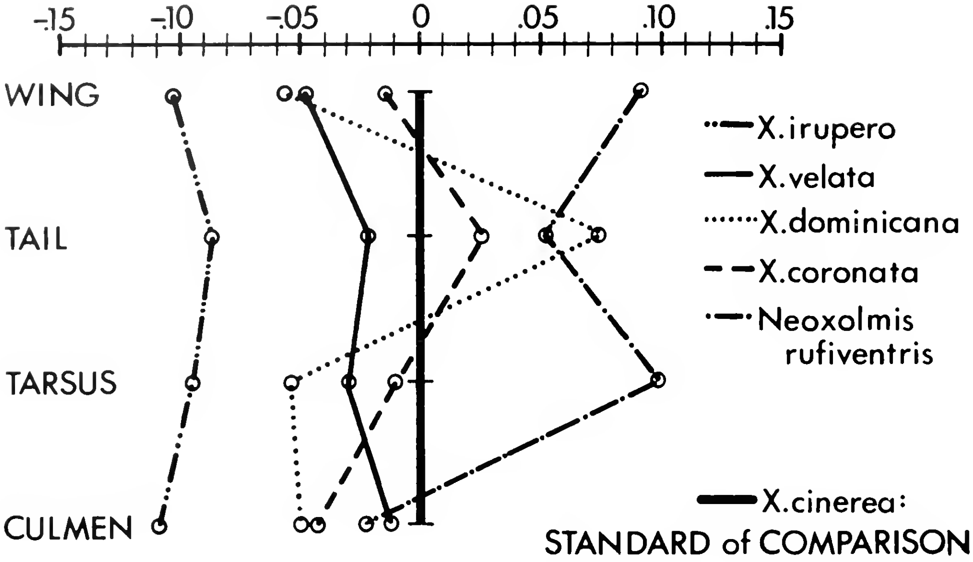

Fig. 9. Ratio-diagram illustrating the relative proportions of the five species of the *Xolmis cinerea* species group and of *Neoxolmis rufiventris*. *X. dominicana* differs markedly from all species of the *cinerea* group in tail-length, and *Neoxolmis* differs from all species of the *cinerea* group in its proportionately much longer wings and tarsi, but shorter culmen.

listed above, it is evident that *Neoxolmis rufiventris* is a problem species. In such cases, two alternatives occur for the taxonomist: either to place the aberrant species in a monotypic genus, or to lump it with another genus. Neither of these decisions is devoid of subjectiveness. My reason for maintaining *Neoxolmis rufiventris* in a monotypic genus distinct from an enlarged genus *Xolmis* (to which it is most closely related) is that *N. rufiventris* has gone farther toward the terrestrial adaptive zone (zone *sensu* Simpson, 1953) than any other *Xolmis*, including *X. rubetra*.

The Genus *Agriornis*

Diagnosis

A genus of five species of medium- to large-sized flycatchers distributed along the Andes and in Patagonia in open, nonforest vegetation. The plumage of all species is dull grayish or brownish above, with or without obsolescent streaks, and grayish brown below with a buffy wash on the flanks and undertail coverts. The throat and chin are whitish and streaked with dark brown or blackish, conspicuously so in some forms (see Fig. 1). The two outermost primaries are emarginated in adult males (see Fig. 3), but not in adult females or immatures of either sex. (Hellmayr's comments [1927] and footnotes about the emargination of outermost primaries in *livida* and *microptera* are not accurate.) The function of this emargination is not known; its presence in adult males suggests that it might have something to do with some sort of display, but I have not found any support for this in the available literature. I have seen *A. albicauda* perform a flight display, but unfortunately the displaying bird could not be collected, and its sex is unknown.

The remiges are not patterned, although the secondaries have buffy edges; the rectrices have either the outer web of the outermost rectrix whitish, or the outermost rectrices entirely or almost entirely white. The latter tail pattern is found only in *albicauda* and *montana*, and is geographically variable in *montana*.

The bill is strongest and most markedly hooked in the two largest species, *albicauda* and *livida*, which feed, perhaps regularly, on small vertebrates (see Fig. 4). Two other species (*montana* and *microptera*) also feed, at least occasionally, on small vertebrates, but *murina* does not, and to my knowledge, is strictly insectivorous. Because of their aspect (bill especially) and habits (hunting), the largest species of *Agriornis* have frequently been compared to shrikes (Laniidae), a group absent from South America. In other ways, however, *Agriornis* flycatchers look and act more like thrushes than shrikes.

Species Included

Until now (Hellmayr, 1927; de Schauensee, 1966), the genus *Agriornis* was considered to consist of four species: *A. montana*, *A. albicauda*, *A. livida*, and *A. microptera*. In this paper, I suggest removing *murina* from *Xolmis* and placing it into *Agriornis*. (De Schauensee, 1966: 334, remarked that "in plumage pattern this species [*murina*] suggests a small *Agriornis*.")

On the basis of absolute size, *murina* is smaller than any *Agriornis*, indeed it is smaller than any species of *Xolmis* except *X. irupero*. However, certain other characters exhibited by *murina* are, I believe, more conservative than size and are taxonomically more important above the species level.

There is much variation in proportions from species to species in *Xolmis* and less in *Agriornis;* it is obvious that *murina* resembles *Agriornis* more than *Xolmis*. In particular, the proportions of the small *murina* and the large *A. albicauda* are rather similar (see Fig. 10).

The general coloration and pattern of *murina* are not found in *Xolmis*, but are characteristic of *Agriornis* (see also remark in de Schauensee, 1966). No *Xolmis* is pale grayish brown and has a whitish throat with dark streaks, but these characters are observed in all *Agriornis*. The juvenal plumage of *murina* (not seen by me but described by Wetmore, 1926b: 447) appears to be like that of *Agriornis*, especially *A. microptera*.

Other characters, such as emargination of the two outermost primaries, general habits and behavior, and habitat, cannot be used because they are shared by *Xolmis* and *Agriornis* and are not good group characters. Nevertheless, it would seem that *murina* is more of a ground bird than are most *Xolmis*, thus resembling *Agriornis*, but *X. rubetra*, at least, is just as much a ground tyrant and an undoubted *Xolmis*.

In conclusion, *murina* seems unlike any *Xolmis* but is more like *Agriornis* in color, pattern, and proportions and should be transferred from *Xolmis* to *Agriornis*.

1. *The montana species-group.* The two species of this group, *A. montana* and *A. albicauda*, are very similar in color pattern of the tail, but differ in absolute size and in the color of the bill, especially the lower mandible (black in *montana*, horn-colored in *albicauda*). They are widely sympatric in the high Andes; I have found the two species together in the same habitats in Bolivia (rocky slopes with boulders and screes, vegetation of grasses, and sparse, low shrubs), but *montana* was more common than *albicauda*.

2. *The livida species-group. A. livida* and *A. microptera* are the two species of this group. They resemble each other in pattern but differ in size. *A. livida* is more rusty on the underparts than *A. microptera*. They are entirely allopatric, but both live in denser habitats than birds of the previous group (see Johnson, 1967), at least in southern South America. The high Andean populations of *microptera* occur in very arid steppes (personal observation). Both *livida* and *microptera* build their nests in shrubs or trees.

3. *The murina species-group.* The only species included is *Agriornis murina*, previously included in the genus *Xolmis*. *A. murina* is much smaller than the other spe-

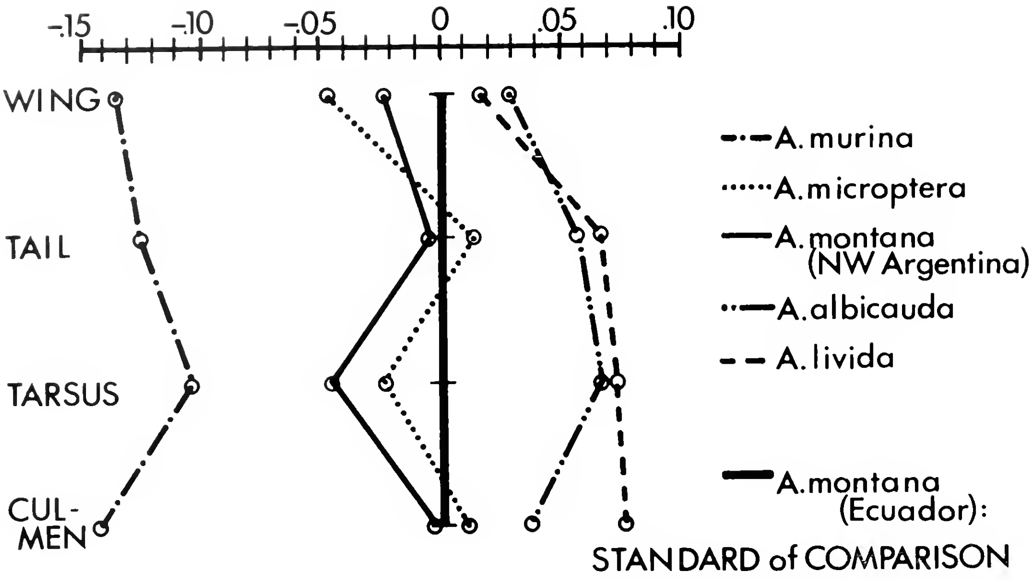

Fig. 10. Ratio-diagram illustrating the relative proportions of the five species of the genus *Agriornis*. *Agriornis murina*, although smallest in absolute measurements, is similar in proportions to the four other species. Two geographically distant populations of *A. montana* (from NW Argentina and Ecuador) are included to show geographical variation in proportions.

cies of *Agriornis*, and is not closely related to any of the four other species in the genus. *A. murina* lives in the open steppes of Patagonia.

The Genus *Muscisaxicola*

Diagnosis

A genus of twelve to thirteen species of small- to medium-sized flycatchers characterized by pale gray or sandy brown plumage, unpatterned except for a species-specific crown spot (Fig. 1) that either varies from yellow to ochre and chestnut or is absent, and a whitish or buffy outer edge to the outermost pair of rectrices. In fresh plumage, the tip of the tail is edged with pale gray, whitish, or pale buff, but in worn plumage, this edge may be altogether lacking.

Muscisaxicola (including *Muscigralla*) is a rather well-defined genus, with no close affinities with other tyrannid genera. *Xolmis pyrope*, although arboreal, actually resembles *Muscisaxicola* in having a similar juvenal plumage, in lacking a color pattern (it is uniformly gray), and possibly also in vocalizations (Smith). The monotypic *Lessonia rufa* (placed by Hellmayr, 1927, immediately after *Muscisaxicola*), although strikingly dimorphic, has some resemblance to *Muscisaxicola* in mannerisms, bill shape, and female plumage, but this could be convergence, since *Lessonia*, like *Muscisaxicola*, lives in open habitats. (*Ochthornis*, a monotypic genus found along rivers over a large area of tropical South America, looks much like *Muscisaxicola fluviatilis* in some ways, but I suspect its relationships to be rather with the *Ochthoeca* group.)

Species Included

Hellmayr (1927) included the following species in the genus *Muscisaxicola* (the sequence is his): *rufivertex, albilora, juninensis, flavinucha, capistrata, frontalis, albifrons, alpina, cinerea, macloviana, maculirostris,* and *fluviatilis*. Later, in his work on the avifauna of Chile (1932),

TABLE 1. COMPARISON OF CHARACTERS OF *MUSCIGRALLA* AND *MUSCISAXICOLA*

Character	*Muscigralla*	*Muscisaxicola*
Relative tail-length	In males, tail 62.6% of wing-length	In males, tail varies from 63.6% to 76.5% of wing-length
Relative tarsus-length	Tarsus 24 to 28 mm	Tarsus varies from 19 mm to 40.5 mm
General coloration	Pale sandy-brown	Pale gray to buff-brown, including sandy-brown
Crown spot	Yellow, more or less concealed	Ochraceous to yellowish and chestnut, not concealed
Rump	Buffy-brown, in contrast with back	Concolor with back
Uppertail coverts	Chestnut-brown	Black
Tip of tail	Pale buff, especially in fresh plumage	Pale whitish buff, especially in fresh plumage
Egg number and color	3–5, usually 4; white	Usually 3; white with reddish spots
Nest site	On ground, protected by vegetation	On ground, or in cavity, protected by rocks, pebbles
Nest shape	Open cup in protected sites; ⅔ domed in more open sites	Open cup (always in protected sites)
Stance	Upright	Upright
Tail and wing motions	Present	Present
Display flight and song	Display flight tyrannid-like; vocalizations *Muscisaxicola*-like, but more complex	Display flight more complex; vocalizations less complex than *Muscigralla*

however, he considered *cinerea* to be a subspecies of *alpina*. With this modification, his classification and sequence have been used by ornithologists working on Andean birds ever since, for example, by Bond and de Schauensee (1942), Bond (1947), Olrog (1963) and others. In this paper, *alpina* and *cinerea* are once more considered separate species taxonomically, but their very close relationship is indicated by placing them in a superspecies. Furthermore, as I will explain later, I think that the species should be grouped in a slightly different way. Finally, I believe that the monotypic *Muscigralla brevicauda* of the xeric savannas from southwestern Ecuador to northern Chile is closely related to *Muscisaxicola*.

Subgenus Muscigralla

Hellmayr's (1927) classification followed largely Berlepsch's earlier scheme (1907). These authors listed *Muscigralla brevicauda* as a member of the subfamily Fluvicolinae (which includes such genera as *Agriornis*, *Xolmis*, *Myiotheretes*, *Muscisaxicola*, *Ochthoeca*, *Sayornis*, *Knipolegus*, and *Pyrocephalus*) and placed it at the end of this subfamily, between the monotypic genera *Ochthornis* Sclater and *Tumbezia* Chapman. Hellmayr (1927) went as far as saying that *Muscigralla* was "a genus of doubtful affinity, possibly not belonging to this family" (Tyrannidae). Koepcke (1964), however, in her guide to the birds of Lima, gave *Muscigralla brevicauda* the same vernacular name (Dormilona) as *Muscisaxicola*, and indicated that this species has tail motions similar to those of *Muscisaxicola*.

Table 1 lists the main characters of *Muscigralla* and *Muscisaxicola*. *Muscigralla* appears to differ from *Muscisaxicola* by its small size (see Fig. 11), proportionately long legs, partially concealed crown spot, buffy-brown rump, and chestnut brown

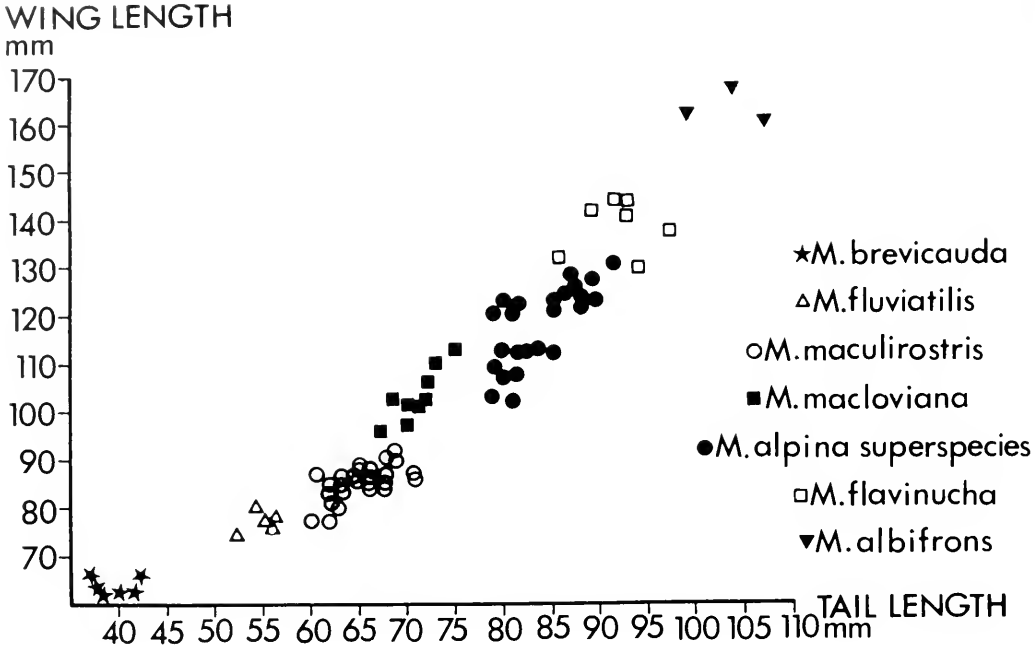

Fig. 11. Wing-length plotted against tail-length in selected species of the genus *Muscisaxicola*. *Muscisaxicola albifrons*, the largest species of the genus, appears as isolated from the other species, as is *M. brevicauda*, the smallest species.

uppertail coverts. *Muscigralla* resembles *Muscisaxicola*, however, in its general coloration, nest site, nest shape, stance, tail and wing motions, and display flight and vocalizations (see Smith).

There is no doubt that *Muscigralla brevicauda* is more different from all species of *Muscisaxicola* than any of the species of *Muscisaxicola* are from each other. Yet, *Muscigralla* appears more closely related to *Muscisaxicola* than to any other taxon, and I suggest formalizing this affinity by placing *Muscigralla brevicauda* in the genus *Muscisaxicola*, but in a subgenus of its own.

Subgenus Muscisaxicola

1. *The maculirostris species-group.* The two species (*maculirostris*, *fluviatilis*) that I include in this group differ from all other species of *Muscisaxicola*, except *brevicauda*, by their small size. *Muscisaxicola maculirostris* and *M. fluviatilis* are basically brown in color, thus differing from most other species of the genus, which are gray or grayish brown. (Here again *brevicauda* is more like *maculirostris* and *fluviatilis* than like the other species of the genus. See Table 1). *M. maculirostris* and *fluviatilis both* have the base of the lower mandible flesh or yellowish in life, and *both* have the edges of the wing coverts and secondaries varying from pale brownish buff to rich cinnamon (but many indications in the literature mention or imply species-specific differences in lower mandible and wing color: I wish to emphasize that they do not exist).

The differences between the two species are as follows:

(a) *M. fluviatilis* has a proportionately shorter tail and a shorter tarsus than *maculirostris*;

(b) In *M. maculirostris* belly and undertail coverts are concolor with the buffy breast, whereas in *fluviatilis,* belly and undertail coverts are whitish and in contrast with the buffy breast;

(c) *M. maculirostris* is a species inhabiting xeric regions in foothills and plateaus of the high Andes and Patagonia, whereas *fluviatilis* occurs along the banks or near the banks of tropical streams east of the Andes.

2. *The macloviana species-group. Muscisaxicola macloviana* and *M. capistrata,* two southern South American species, are very close to each other in size and proportions and also in head pattern. Both have dark foreheads and sooty brown loral regions, which give them a distinctive "dark-headed" aspect. *M. capistrata* has a dark chestnut brown crown patch, whereas in *M. macloviana* this region is sooty brown.

3. *The rufivertex species-group.* The three species I include in this group occur in the high Andes and are very similar to one another in size, proportions, and color. They are medium-sized, proportionately long-winged, and pale gray or grayish brown with a black tail and a reddish brown to pale buffy-brown crown patch.

The *albilora* superspecies consists of two allopatric species or semispecies, *juninensis* (Peru, Bolivia, northern Chile) and *albilora* (Chile), whereas the third species of this group, *M. rufivertex* (Peru south to central Chile), is sympatric with them.

4. *The alpina species-group.* This species-group includes a single superspecies, ranging widely in the high Andes from Colombia to Chile and Argentina. The birds are of medium size, are brownish gray to pale gray in color, have the outer web of the outermost tail feathers narrowly edged with whitish or buffy-white, and lack a contrastingly colored crown patch.

5. *The albifrons species-group.* The three species of this group are the largest of the genus. One, *M. frontalis,* has a distinctive head pattern with sooty brown forehead and a sooty brown line in the center of the crown, contrasting with a white loral spot. This species also has a proportionately long bill. *M. albifrons* and *M. flavinucha* are very similar to one another in general coloration, but differ in size (especially in wing length) and in crown color. Both *albifrons* and *flavinucha* have a whitish loral spot extending into a supercilium (visible in the field).

PART II: VARIATION AND SPECIATION IN THE GENERA *XOLMIS, NEOXOLMIS, AGRIORNIS,* AND *MUSCISAXICOLA*

In the first part of this paper, the flycatchers placed in the genera *Agriornis, Neoxolmis, Xolmis, Pyrope, Myiotheretes, Muscisaxicola, Muscigralla,* and *Ochthoeca* by de Schauensee (1966) were arranged into genera with limits slightly at variance with those of earlier classifications (including de Schauensee's). Furthermore, the taxa included in these modified genera were grouped into subgenera (in one instance), species-groups, and superspecies, in order to express the hierarchy between the categories genus and species in a manner not conveyed by earlier authors having worked with these flycatchers.

In Part II, I will analyze geographical variation and species formation in these birds. The genus *Ochthoeca* was not included, however, because my study of variation at the species level in that genus was not as thorough as in the other genera. Each species of the genera *Xolmis, Neoxolmis, Agriornis,* and *Muscisaxicola* (which are all diagnosed in Part I) was investigated to detect what sort of population structure (*sensu* Mayr, 1959) it exhibits: presence or absence of geographic variation, presence or absence of geographic isolates, degree of morphological differentiation of isolates when present, and instances of secondary contact involving, or not involving, range overlap and hybridization.

The characters selected to assess such population structure were: wing-length (chord), tail-length (from insertion of central pair of rectrices to tip of longest rectrix), culmen-length (from insertion of ramphotheca into skull to tip), tarsus-length (from the distal edge of the distalmost entire tarsal scute preceding the first scute of the digits, diagonally to the articulation of tarsometatarsus and tibiotarsus), color intensity, and color pattern. Intra- and interpopulation variation in these characters was studied by comparing series of specimens of comparable age, sex, and wear from different localities representative of the entire geographical range of each species being analyzed. Each locality consisted either of a single collecting spot (rarely, since series from such a spot were generally very small), or of a group of collecting spots located within relatively close distances of one another. Further details about the methods used need not be given here, because they are explained in the first paper of this series on Andean birds (Vuilleumier, 1968).

I must stress here that I have not tried to delineate infraspecific categories (subspecies) within the species of flycatchers treated in this paper. My chief reason for not doing so is my acceptance of the criticisms of Wilson and Brown (1953). Consequently, I have often ignored subspecies in my discussions of geographic variation within species. However, whenever I felt that it would be helpful to the reader, I have referred to subspecies if they were available. Thus, it might be convenient to refer to a small, geographically disjunct and morphologically differentiated population by its subspecific name, rather than by a geographical, and perhaps more cumbersome, term. On the other hand, I have deliberately avoided using subspecies when describing geographic variation of a continuous, especially clinal, nature; it is precisely in such instances that the criticisms of Wilson and Brown (1953) take full force.

The emphasis throughout my work on speciation, whether the birds studied were Tyrannidae, as in this paper, or other taxa, as Furnariidae (Vuilleumier, 1968) or Coerebidae (Vuilleumier, 1969a), has been to determine how continuous, or on the contrary, how discontinuous, the distribution of given species was. I paid particular attention to the presence of disjunct geographical variation, trying to answer the question whether such variation reflected the presence of an actual gap in the distribution of that species, and whether that gap had any significance in preventing gene flow between the isolated populations. I consequently made no special effort to examine large series of specimens for species having a small range and which would be likely to be geographically invariable, or for species having a broad range but which appear to be morphologically and distributionally very uniform over that range. Decisions about such differences in population structure were made on the basis of all available evidence: museum specimens, literature records, and field work. I make no apologies if I have overlooked geographical variation where it may indeed exist but may only be detectable to a worker using more refined techniques or many more specimens than I did. The following accounts are based on the examination of about 695 specimens (*Xolmis*, about 150; *Neoxolmis*, 10; *Agriornis*, 185; and *Muscisaxicola*, 350) and on personal field work with 4 species of *Xolmis*, 4 of *Agriornis*, and every species of *Muscisaxicola*.

The following abbreviations are used:
AMNH = American Museum of Natural History, New York; MCZ = Museum of Comparative Zoology.

The Genus *Xolmis*

1. The *fumigata* Species-Group

Xolmis striaticollis

Found mostly solitary or by twos (Koepcke, 1958: 168; personal observation), *X. striaticollis* occurs along the Andes from Venezuela and Colombia in the north to northwestern Argentina in the south. It hunts in the open, frequently on the ground, but requires some sort of shrubbery or trees for shelter. It is thus encountered along the edge of montane forests or in bushes, between 1500 and 3500 meters. In most regions, *X. striaticollis* seems to avoid either very wet or very xeric habitats, but in Bolivia and northwestern Argentina, I found it also in dry quebradas or in open valleys with a sparse growth of low xeric shrubs.

Geographical variation in *X. striaticollis* can be detected in size and color. Birds from southern Peru, Bolivia, and northwestern Argentina are smaller in winglength and paler in general coloration than those from Venezuela to central Peru. The change from relatively large and dark birds to small and pale ones (with fewer and narrower throat streaks) seems to occur rather abruptly in southern Peru, and might be considered either as a step in a cline of north to south geographical variation, or as an instance of secondary hybridization. I have not undertaken a special study of this problem, which is left open to further investigation. Furthermore, *X. striaticollis* has an isolated population in the Santa Marta Range of northern Colombia. but these birds do not appear to be morphologically differentiated from birds from other Colombian localities.

The fumigata Superspecies

Xolmis fumigata, *pernix*, and *fuscorufa* are three closely related, allopatric species (Fig. 12). *X. pernix* is isolated in the Santa Marta Range of northern Colombia, *X. fumigata* is widespread in the Andes from Venezuela to Peru but does not occur in the Santa Marta Mountains, and *X. fuscorufa* replaces *fumigata* from southern Peru to Bolivia. It appears that *pernix* and *fuscorufa* both have relatively narrow ranges, peripheral to the wide range of *fumigata*, and the question arises whether they have evolved as peripheral isolates from a proto-*fumigata*-like ancestral stock.

The evaluation of the relationships of these three forms is rendered somewhat difficult by two facts. The first is that the two peripheral populations (*pernix* and *fuscorufa*), although farthest apart geographically, look more similar to each other than either does to the central populations (*fumigata*). Such a phenomenon (polytopic taxa) is actually not so rare, and has been discussed by Mayr (1942), but it is not always easy to suggest an explanation for it. The second fact, discussed in the chapter by Smith, is that of his having observed in Ecuador (in other words, within the range of *fumigata*) a bird looking somewhat intermediate between *pernix* and *fuscorufa*. With much needed further data still pending, especially the collection of specimens from this population, I conservatively base my treatment of the three forms on present specimen information.

Xolmis pernix. This localized species is known from seven specimens collected around the turn of the century (Todd and Carriker, 1922) and nine others collected more recently (Wetmore, Zusi, *in litt.*) in the Santa Marta Range of northern Colombia. From this paucity of specimens, it would appear that *pernix* is rare, although, to be sure, ornithologists have not visited the Santa Marta Mountains very frequently. Like *X. fumigata*, *X. pernix* seems to be a forest-edge species (Todd and Carriker, 1922). *X. pernix* is identical in size and proportions to *X. fuscorufa* and *X. fumigata*, except that it has a longer bill (see Fig. 7). In color pattern, *pernix* is much closer to the geographically distant *fuscorufa* than to *fumigata*.

Xolmis fumigata. Xolmis fumigata is the only widespread species or semispecies of the *fumigata* superspecies. It occurs along the Andes from Venezuela through Colombia and Ecuador, and as far south as central Peru (Fig. 12). The seanty data on habitat preferences suggests that *fumigata* inhabits edge situations at elevations from about 2200 to at least 3600 meters. Lévêque (1964: 59) saw the species "on

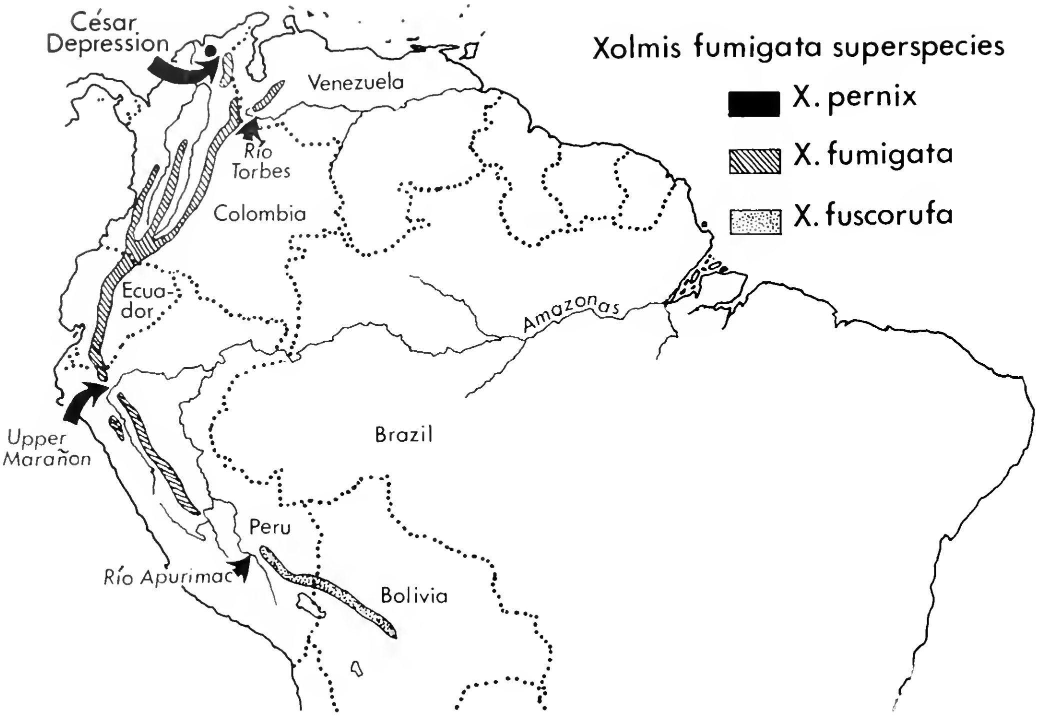

Fig. 12. Geographical distribution of the *Xolmis fumigata* superspecies. *Xolmis pernix* is isolated from the nearest population of *X. fumigata* by the César Depression. The Venezuelan isolate of *X. fumigata*, isolated from Colombian populations by the Río Torbes Valley, is clearly differentiated morphologically, whereas the Peruvian isolates, separated from one another by the Upper Marañon, are not, or are less well marked. *X. fuscorufa* does not seem to occur northwest of the Río Apurimac.

several occasions" around Quito, Ecuador, but in spite of numerous hours of field work in apparently suitable habitats around Quito and elsewhere along the Andes, I was never able to even glimpse it.

Examination of series of specimens from the entire range of the species revealed that there is practically no geographical variation in size (as measured by winglength), and only minor variation in color. The only discontinuous variation occurs from Venezuela to northeastern Colombia. Birds from the Andes of Táchira (west of the Río Torbes Valley), of Mérida, and of Trujillo can be considered as an isolate (see Fig. 12) (subspecifically separated as *lugubris*) distinguishable from other populations of Venezuela and northern Colombia by having the crissum ochraceous instead of sooty and concolor with the rest of the underparts. I suppose that the transition from ochraceous to dark sooty brown takes place across the dry valley of the Río Torbes (see Fig. 12), an important barrier for Andean species, as I pointed out elsewhere (Vuilleumier, 1969a, 1969b).

The birds from southern Ecuador and northern and central Peru appear to be geographically isolated from one another by the valley of the upper Río Marañon (see Fig. 12), and other rivers in the northern Peruvian Andes. From my study of a small series of specimens from the populations living on either side of the upper Río Marañon, I would conclude that morphological differentiation is not correlated with the apparent barriers. Yet, Chapman (1927: 4) assigned subspecific rank (*cajamarcae*) to the population living along the Pacific slope of the Andes west of the upper Río Marañon. The problem of whether or not the Peruvian isolates of *X. fumigata* are truly differentiated from each other, and from Ecuadorean populations, remains to be solved by examining more skins.

Xolmis fuscorufa. Xolmis fuscorufa is relatively rare, as I judge from the small number of specimens (about ten in major U. S. and European museums), but its range is more extensive than that of *pernix.* It has been collected at several localities in southern Peru (Paucartambo, Oconeque) and in Bolivia (Chulumani, Pucuyuni, Tilotilo, Incachaca, San Cristobal) (see Hellmayr, 1927; Bond, 1947; Bond and de Schauensee, 1942; and Niethammer, 1956). To my knowledge, no data on ecology are available in the literature. *X. fuscorufa* differs from *pernix* (and for that matter, from the other species in the species-group) in lacking the throat streaks. In color pattern, *fuscorufa* resembles *striaticollis* in having rufous on the tail feathers, although the exact pattern is not identical (by contrast, *pernix* and *fumigata* have only the outer web of the outermost rectrix rufous).

Xolmis signata

This species is apparently known only from the two specimens from central Peru mentioned in Taczanowski's description (1874: 532–533), one of which, at least, is at the Polish Academy of Sciences in Warsaw (Jan Pinowski, *in litt.*). Not having seen it, I cannot decide whether the allocation of *signata* to this species-group (or indeed to *Xolmis*) is correct. As I judge from the description, *signata* would seem distinctly smaller than any other species of the *fumigata* species-group and somewhat intermediate in color between *fumigata* and *erythropygia* (the latter species belonging to the next species-group).

2. *The erythropygia Species-Group*

Xolmis erythropygia

Xolmis erythropygia occurs from about 3000 to 3800 meters in wet montane forests or shrubbery at, or close to, the timber line. Lévêque (1964: 59) saw one pair in Ecuador "in a zone of low bushes and wet meadows." It is relatively rare, but might be fairly common locally (see, e.g., Peters and Griswold, 1943: 313–314); fifteen specimens from the Santa Marta Mountains are cited by Wetmore (1946), but the species was overlooked there during the early explorations of this range.

X. erythropygia occurs in the Santa Marta Mountains of northern Colombia (subspecies *orinoma*), and ranges from southern Colombia to central Peru (*erythropygia*), and from southern Peru to Bolivia (*boliviana*). Geographical variation in this species seems very slight. Even the isolated Santa Marta population does not seem well differentiated (as I judge from Wetmore's description, 1946: 5). Nevertheless, the pattern of geographic variation of *erythropygia* is interesting because it parallels the differentiation showed by the *X. fumigata* superspecies of the *fumigata* species-group. In other words, in *erythropygia*, as well as in the *fumigata* superspecies, the peripheral populations (Santa Marta isolate, and populations from southern Peru and Bolivia) show morphological divergence from the central populations (Colombia except Santa Marta, Ecuador, northern and central Peru). In the *fumigata* superspecies, morphological differentiation is extensive, and species status has surely been reached by the three taxa, whereas in *erythropygia*, the peripheral populations are only weakly differentiated, and can only be considered to be subspecifically distinct.

Xolmis rufipennis

Xolmis rufipennis ranges from northern Peru to north-central Bolivia (Cochabamba), and seems relatively uncommon (about 30 skins in major U. S. and European museums). There does not seem to be any geographical variation in this species. Notes about the habitat have been published elsewhere (Vuilleumier, 1969c).

3. The *pyrope* Species-Group

Xolmis pyrope, the only species of this group, is a common species inhabiting both slopes of the Andes up to about 1500 meters, where it is found in open woodlands and forest edges from central Chile southward to Patagonia and Tierra del Fuego. Migrants reach northward to Atacama during the southern hemisphere winter (Goodall et al., 1957: 151; Johnson, 1967: 265).

X. pyrope varies geographically on the continent, but this variation is very minor and probably entirely clinal. However, the birds from the Island of Chiloé, off southern Chile, are larger than those from the neighboring mainland ones, and were assigned subspecific rank (*fortis*) by Philippi and Johnson (in Goodall et al., 1957: 152–154).

4. The *cinerea* Species-Group

Xolmis velata, *X. coronata*, and *X. dominicana* do not exhibit any geographical variation. *X. cinerea* varies geographically in a minor way only; Hellmayr (1927: 12) did not recognize the two subspecies which had been previously described. Similarly, *X. irupero* shows only slight geographical variation: the two subspecies described were not deemed taxonomically distinguishable by Hellmayr (1927) and Pinto (1944).

There does not appear to exist any potential for further speciation in the *cinerea* species-group. On the one hand, the five species of this group do not seem to have isolated and morphologically differentiated populations that could be considered as incipient species. On the other hand, there is extensive sympatry of several species over a large part of central South America (Brazil south of the Amazon, eastern Bolivia, Paraguay, Uruguay, northern and central Argentina). Sympatry, combined with the morphological distinctness of the five species, makes it impossible to even attempt to reconstruct the past history of speciation in this species-group. Of the five species, *X. velata*, *X. cinerea*, and *X. irupero* appear to be common or relatively common, but *X. dominicana* and possibly *X. coronata* may be scarce or even rare. Hudson (1920: 142) said of *X. coronata:* "Old gauchos have told me that fifty years ago they were abundant all over the pampas, but have disappeared wherever the giant grasses have been eaten down and have given place to a different vegetation." Detailed study of the ecological preferences of the species of this group should be undertaken to determine to what extent the morphological differences they show can be correlated with habitat selection, predators, feeding habits, and nest sites.

5. The *rubetra* Species-Group

The only species of this group, *Xolmis rubetra*, does not exhibit any geographical variation. Its range includes the lowlands east of the Andes in northern Patagonia (during the breeding season) and the Argentine chaco and western pampas (in the southern hemisphere winter) (Olrog, 1963; Hudson, 1920: 148, however, thought *rubetra* not to be migratory).

The Genus *Neoxolmis*

Neoxolmis rufiventris, the only species of this genus, breeds in southern Patagonia, where its nest has recently been found by Maclean (1969); it winters in the Argentine pampas (Olrog, 1963), as far north as Uruguay (Cuello and Gerzenstein, 1962: 126). There is apparently no geographical variation in this species.

The Genus *Agriornis*

1. The *montana* Species-Group

Agriornis montana

This wide-ranging species occurs in the páramos of Colombia and Ecuador, in the

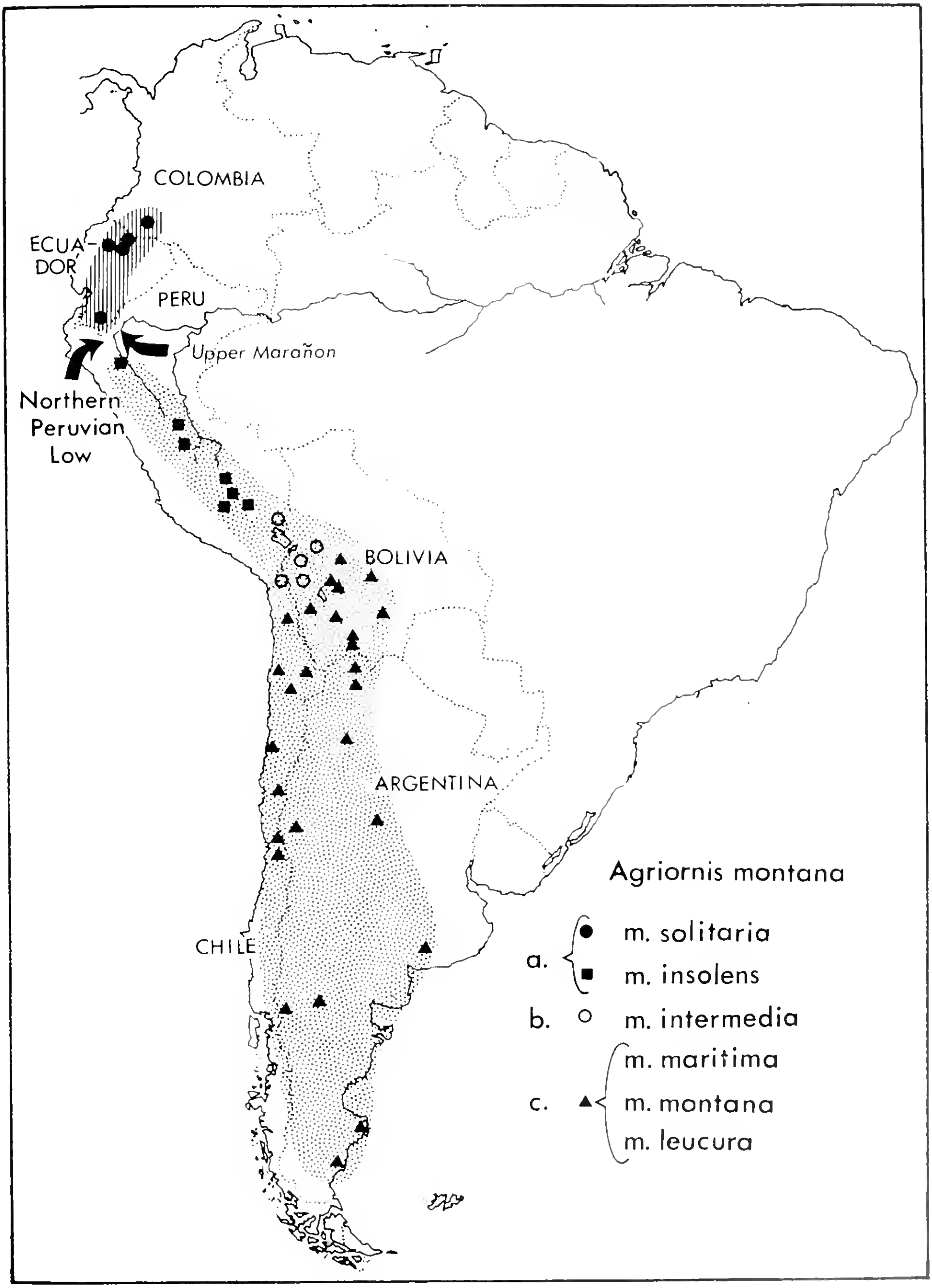

Fig. 13. Geographical distribution of *Agriornis montana*. Colombian and Ecuadorean populations (*solitaria*) are isolated from Peruvian ones (*insolens*) by the Northern Peruvian Low and Upper Marañon barriers (see text). The populations of southern Peru, northwestern Bolivia and extreme northern Chile (b) are intermediate in tail pattern between those to the north (a) and south (c). See text for further details.

puna of the high Andes of Peru, Bolivia, and Argentina, and in open habitats along the Andes (in some localities at relatively low elevations) all the way to southern Patagonia, except Tierra del Fuego (Fig. 13). *A. montana* shows some geographical variation in size, but an assessment of this variation was not possible because many specimens in my samples had molting or heavily worn tails or wings. There is geographical variation in body color, tail pattern, and perhaps in vocalizations.

Variation in body color appears to be extensive and gradual, but I cannot say whether it is truly clinal or not. The samples at my disposal consisted of specimens that had been collected in widely different years, and I found that individuals taken prior to about 1940 were generally darker than those taken since that time. More uniform samples would be necessary for meaningful intersample comparisons.

Geographical variation in tail pattern can be summarized as follows. Samples from southern Colombia to south-central Peru (Cuzco area) (labelled "a" on Fig. 13) have the four outermost tail feathers white, each rectrix having a white shaft. The fifth outermost feather has some gray but is still extensively white. In samples from southern Peru (Puno) the extent of white on outer tail feathers is diminished, so that the third outermost rectrix has gray on the inner web. In the La Paz Department of Bolivia the samples examined show much variation, and specimens collected at localities only a few kilometers apart may differ in their tail pattern. This situation was noticed by Hellmayr (1927: 5–6), who described the variable populations as a new subspecies, *intermedia*, labelled "b" on Figure 13 (see also the comments of Niethammer, 1956: 103).

In 1967–1968 I attempted to collect large series of these birds in northwestern Bolivia, but the low population density of *A. montana* made it impossible. Nevertheless, among the birds I collected, two taken within 4 kilometers of each other in the Ballivian area of the altiplano southwest of La Paz city exemplify this individual variation very clearly. One specimen (AMNH 793198, collected 21 October 1967) has the two outermost rectrices wholly white, the third has some gray at the base of the outer vane and along the edge of the inner vane, and the fourth has white only in the distal half. The second bird (AMNH 793199, collected 22 October 1967) has some gray at the base of the inner vane of the outermost rectrix, whereas the second and third tail feathers from the outermost have much gray at the base. In both specimens, the shaft of the outermost rectrix has at least some gray: at the base in AMNH 793198, and the entire proximal half in AMNH 793199.

However, other specimens I collected in the La Paz Department (such as AMNH 793202, taken along the eastern front of the Andes between Viloco and Caxata) and in the Potosí and Chuquisaca Departments have the same tail pattern as birds from farther south along the Andes in northwestern Argentina and in the Andes from northern Chile to Patagonia (labelled "c" on Fig. 13). In all specimens I have examined from these regions, the three outermost rectrices have a white outer vane and a white tip. The fourth and fifth tail feathers are only white-tipped.

In short, geographical variation in tail pattern does not seem pronounced either north of central Peru or south of north-central Bolivia. The populations living in a relatively narrow zone in southern Peru and northwestern Bolivia, around the basin of Lake Titicaca (Fig. 13), are intermediate between two types of tail pattern. Several genera other than *Agriornis* have species that exhibit geographical variation in the same area, or else have allopatric taxa at or immediately below the level of species coming in contact in this zone (see Vuilleumier, 1969b).

Detailed analysis of larger samples than I have seen will be necessary before it is possible to interpret the significance

TABLE 2. GEOGRAPHICAL VARIATION IN WING-, TAIL-, TARSUS-, AND CULMEN-LENGTH IN *AGRIORNIS ALBICAUDA*

Populations (Males only)	Wing-length (mm) Range (mean) (N)	Tail-length (mm) Range (mean) (N)	Tarsus-length (mm) Range (mean) (N)	Culmen-length (mm) Range (mean) (N)
Ecuador	137.0–156.0 (143.2) (5)	115.0–132.0 (120.0) (5)	41.0–44.0 (42.8) (5)	31.0–33.5 (32.2) (5)
Peru	136.0–145.0 (140.3) (7)	116.0–124.0 (119.2) (7)	39.0–42.0 (40.9) (7)	31.5–33.0 (32.2) (7)
Bolivia	133.0–138.0 (135.5) (2)	111.0 (1)	39.5–40.5 (40.0) (2)	33.0–33.5 (33.2) (2)
NW Argentina	130.0* (1)	101.0* (1)	40.0 (1)	36.0 (1)

Note: The single specimen from NW Argentina has worn tips to both tail and wing feathers, so that these two measurements (* in the table) are probably lower than those of birds in fresh plumage.

of the geographical variation in *A. montana*. Provisionally, I would consider this variation to be a case of secondary hybridization taking place before reproductive isolation was achieved by the ex-isolates. That hybridization, rather than primary intergradation, is taking place is suggested by the individual variation observed in northwestern Bolivian populations, which thus resemble hybrid swarms in other species.

Geographical variation in voice may take place in *A. montana*. Birds from Ecuador (see Smith) and from Bolivia (Department Potosí, personal observation) appear to have very similar vocalizations. On the other hand, birds from northern Argentina (Tucumán, see Smith) have slightly lower pitched and shorter calls. It would be most interesting to check, by means of additional recordings, whether such variation is indeed geographical, and, if so, whether it parallels the variation in tail pattern just described, or, on the contrary, is independent of it.

Agriornis albicauda

This species is similar to *montana* in both color and pattern, including the tail pattern. *A. albicauda* differs from *A. montana* in having broader streaks on the throat, in being much heavier (the average of three *albicauda* being 82.3 grams, and of six *montana* being 60.7 grams), and in having a thicker, more powerfully hooked bill with pale horn-colored lower mandible (the bill of *montana* is entirely black). *A. albicauda* is the only species of the genus *Agriornis* living strictly in the high Andes, where it occurs from Ecuador in the north to northern Chile and northwestern Argentina in the south.

There is some geographical variation, as pointed out by Zimmer (1937: 2–3). He stated that Ecuadorean birds are larger and darker than Peruvian ones. In order to check whether the variation in size might be discontinuous, I have measured specimens from Ecuador, Peru, and Bolivia. As can be seen from Table 2, there is very little variation in culmen-length, and only a slight cline of decreasing size from north to south in wing-, tail-, and tarsus-length.

Agriornis albicauda and *A. montana* are too extensively sympatric for any inference to be made about their past history, assuming, as I do here, that they originated from the same ancestral stock. The Andes could have been invaded at two different times by an early stock, or else speciation could have taken place *in situ* in the Andes. The two species share the same habitats: open

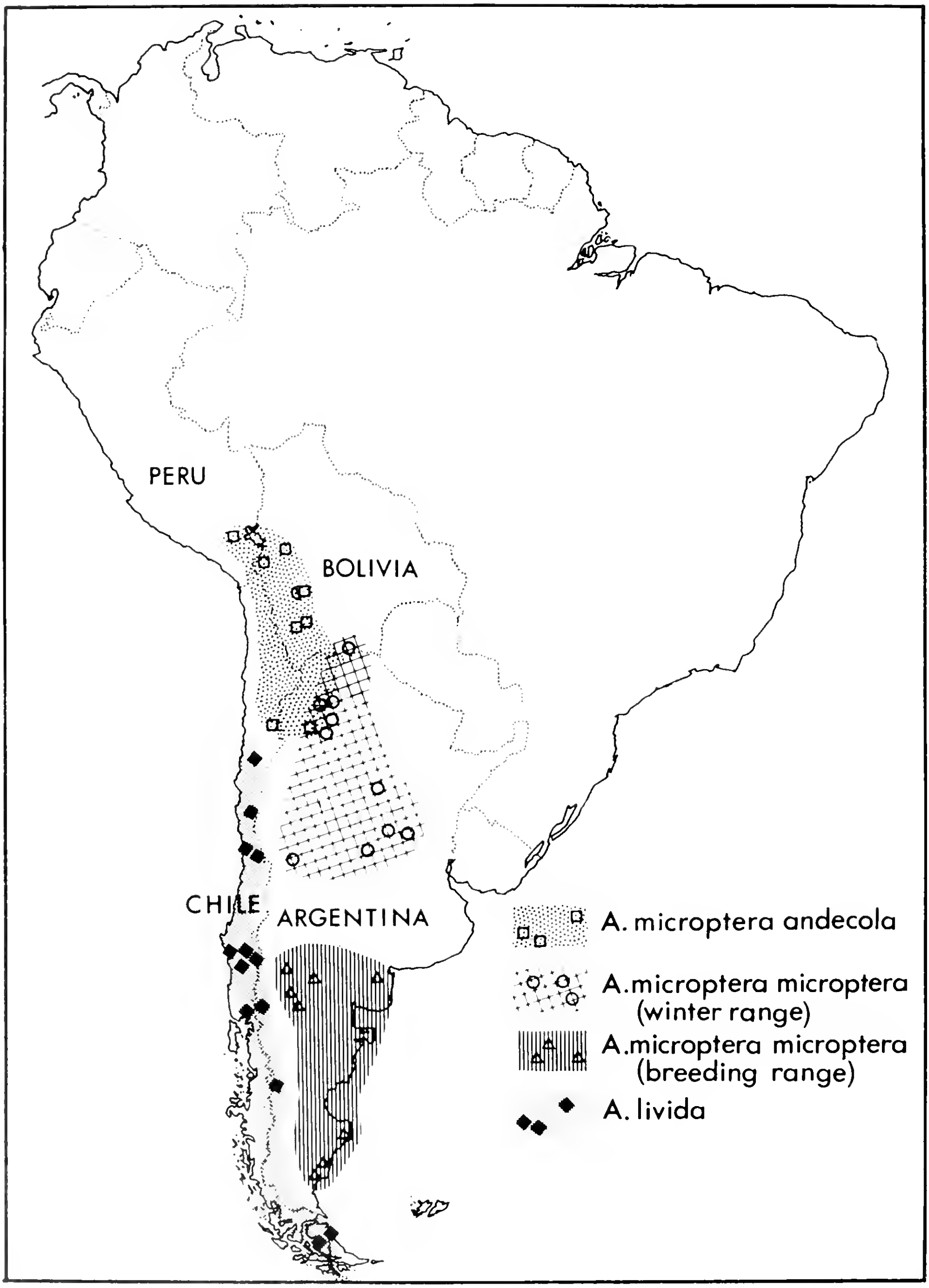

Fig. 14. Geographical distribution of *Agriornis livida* and *A. microptera*. *A. livida* and *A. microptera* are fully allopatric. Wintering populations of *A. microptera microptera* overlap slightly with resident ones of *A. microptera andecola* in northwestern Argentina.

slopes and valley floors of high Andean valleys, and areas having sparse and xeric vegetation of low shrubs, with scattered rocks and boulders used as observation posts. In Bolivia, I found that *montana* outnumbered *albicauda* about ten to one in such habitats. In northern Chile, however, *A. albicauda* was "more plentiful" than *A. montana* (Johnson, 1967: 233).

2. *The lívida Species-Group*

Agriornis livida

The distribution of this species includes the dry lowlands west of the Andes in Chile from Atacama (up to about 2000 meters altitude, Goodall et al., 1957: 141) southward to about 40°–41° S. In this region of south-central Chile, the Andes are much lower and are less of a barrier than they are farther north, and consequently, *A. livida* is found in the mountains, especially in dry valleys lying in rain shadows (the Lonquimay Valley, for example). South of about 41° S, *A. livida* does not occur west of the Andes because this zone is clothed by *Nothofagus* forests, which constitute unsuitable habitats; it occurs only along the dry eastern foothills of the Andes, mostly on Argentine territory (see Fig. 14). *A. livida* thus appears to avoid both very xeric and very wet habitats: its center of abundance, according to Hellmayr (1932) and Goodall et al. (1957), is in central Chile, from Aconcagua to Bío-Bío, and again in south-central Patagonia in Chubut and Aysén.

Geographical variation in *A. livida* is minor, and apparently involves only wing-length and tail-length (as pointed out by Hellmayr, 1932, and as confirmed by my examination of series of specimens). The samples seen, however, are not sufficiently large for one to conclude whether this variation is clinal or not. The populations living on Tierra del Fuego, although isolated geographically from other Patagonian birds, seem not to be morphologically differentiated.

Agriornis microptera

Agriornis microptera has two series of populations, in Patagonia and in the high Andes respectively, separated from one another by a hiatus of over 1000 kilometers (Fig. 14). The Patagonian birds (subspecies *microptera*) breed in open brushy steppes from Neuquén and Río Negro in the north to Santa Cruz in the south; they do not occur on Chilean territory or on the island of Tierra del Fuego. This fact is interesting, because it seems to suggest that *A. livida* (which does occur on Tierra del Fuego) and *A. microptera* are replacing each other ecologically. This supposition seems confirmed when the distribution of the two species is examined in Patagonia farther north: *A. livida* is restricted to the eastern Andean foothills, whereas *microptera* is found in the lowland steppes farther east toward the Atlantic Ocean.

The Patagonian populations of *A. microptera* leave their breeding grounds around February and migrate northward to their nonbreeding quarters in northern Argentina and southern Bolivia (see Fig. 14). Nonbreeding Patagonian *A. microptera* have been collected in the following Argentine provinces: Mendoza (March), Salta (March, April, May), Tucumán (May, June, July), Jujuy (May), Santiago del Estero (July), San Juan (August) (specimens examined personally), Córdoba, Buenos Aires, and Santa Fe (according to Hellmayr, 1927).

The high Andean populations of *A. microptera* (subspecies *andecola*) are supposed to be resident. Their geographical range includes northern Chile (Goodall et al., 1957: 143), northwestern Argentina, Bolivia, and probably southern Peru. In northern Chile, Johnson (1967: 232) found *A. microptera* in tola (*Baccharis*) steppes, where it was "fairly plentiful." On the Bolivian altiplano in 1967–1968, I saw *microptera* in similar habitats, but only twice during several months of field work, and can only conclude that the population density of the species is low.

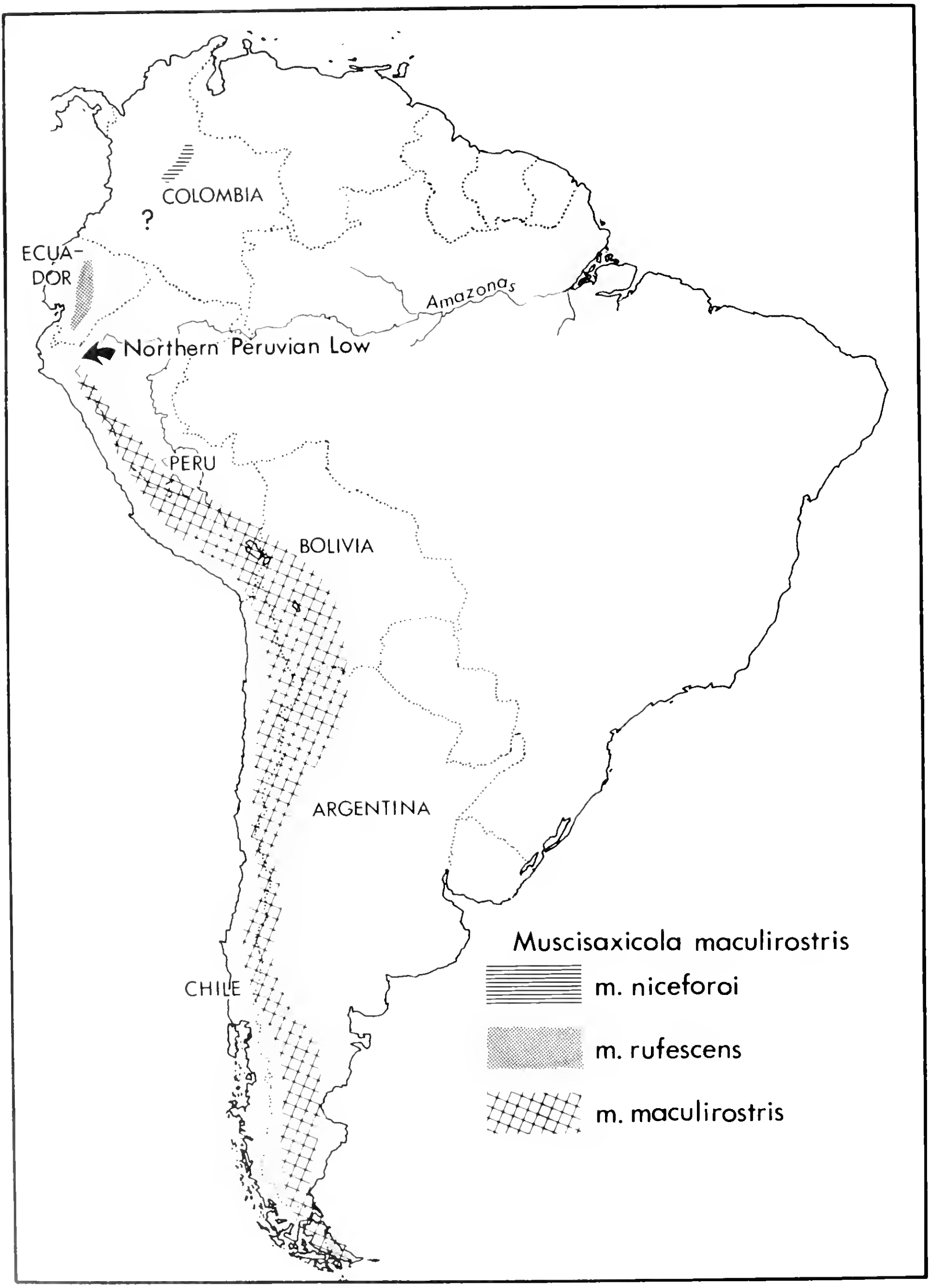

Fig. 15. Geographical distribution of *Muscisaxicola maculirostris*. The two peripheral isolates (*niceforoi* in Colombia and *rufescens* in Ecuador) are separated from each other by an ill-defined barrier (marked ?), whereas Ecuadorean and Peruvian populations are isolated by the Northern Peruvian Low.

The populations of *A. microptera* found in northwestern Argentina seem to be composed of migratory birds from Patagonia during part of the year, and of resident ones during the breeding season. The mixture of populations between March and July appears confusing. The only definitely breeding specimen I have seen so far is MCZ 99388, an adult male in worn plumage collected 12 December 1918 at Peñon, 4000 meters, in Catamarca. Other specimens collected at lower elevations seem to be migrants: for example, those collected by Steinbach at Cachi, 2500 meters (Salta), in March and April 1905. Olrog (1949b: 153), however, collected a specimen in the Aconquija mountains (Tucumán) at an altitude of 2900 meters in May, and allocated this bird to the local, breeding subspecies *andecola.* This identification suggests that the Andean populations breed at very high altitudes during the rainy season between November and March, then move to lower elevations, where they encounter nonbreeding individuals that have migrated from Patagonia. More data are needed to fully elucidate the breeding and nonbreeding ranges of Andean "residents" in northern Argentina.

In spite of the wide geographical gap between breeding Patagonian and Andean populations of *A. microptera*, morphological differentiation between the two is minor, and involves the color of streaks on the throat and thickness of the bill (Hellmayr, 1927: 4).

3. *The murina Species-Group*

Agriornis murina, the only species of this group, breeds in xeric scrub in Argentine Patagonia (Río Negro, Neuquén, and Chubut). It migrates northward to the lowlands of northern Argentina, southern Bolivia, and western Paraguay during the nonbreeding season. There does not seem to be any geographical variation in *A. murina.*

The Genus *Muscisaxicola*

The Subgenus Muscigralla

The similarities and differences between *Muscisaxicola brevicauda* and the species of the subgenus *Muscisaxicola* and my reasons for considering them all congeneric were given in detail in Part 1.

M. brevicauda occurs from southwestern Ecuador along the foothills of the Andes and the Pacific coastal plain of Peru to extreme southern Peru. The highest altitude at which the species has been collected is 1100 meters at Yamana (Loja), Ecuador (R. A. Paynter, Jr.). Marchant (1960: 372–373) found it "commonest in open country with or without scattered bushes," and often in "surprisingly thickly wooded places." My own observations in southern Ecuador and northern Peru agree with Marchant's.

M. brevicauda shows no detectable geographic variation in color, but birds from southern and central Peru (Lima, Pisco, Nazca) are a little larger in wing-length and tarsus-length than those from the Guayas Province, southwestern Ecuador, and Piura, northern Peru.

The Subgenus Muscisaxicola

1. *The maculirostris Species-Group*

Muscisaxicola maculirostris

This species is the most widespread of the genus, ranging from the Bogotá region of the Eastern Andes of Colombia southward along the Andes all the way to Tierra del Fuego (Fig. 15). It is found in a variety of habitats, which all have one thing in common: they are quite xeric, or even semi-desertic. Altitudinally *maculirostris* has a wide range, from about 1000 to about 4000 meters (and occasionally above).

As might be expected from this geographical range, there is geographical variation in this species. Color variation is not clinal, but sharply discontinuous. Ecuadorean birds (subspecies *rufescens*)

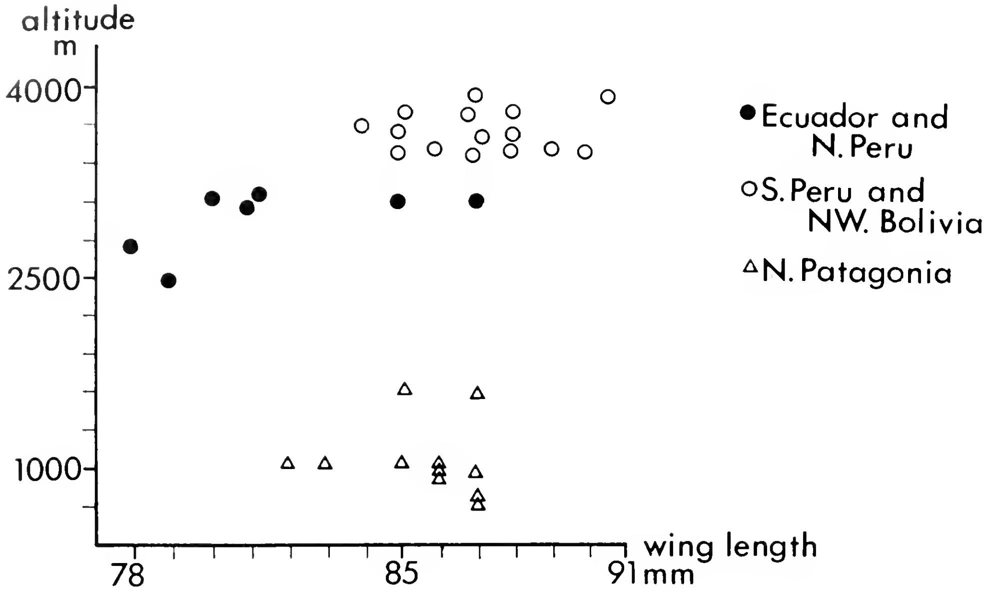

Fig. 16. Altitudinal variation in wing-length in *Muscisaxicola maculirostris*. Andean populations from Ecuador southward to Bolivia show an increase positively correlated with altitude, but Patagonian birds do not.

are very buffy, even pale rufous, on their underparts. In contrast, birds from northern Peru to Argentina and Chile are all very uniform (*maculirostris*), and of a much paler and more isabelline tone than Ecuadorean birds. This variation is shown in Figure 15. Interestingly, and perhaps unexpectedly, the birds from Colombia (*niceforoi*) do not resemble the geographically close Ecuadorean birds, but are more like those from Peru to Argentina and Chile, much farther south.

Geographical variation in size as measured by wing-length is somewhat obscured by altitudinal variation (see Fig. 16). Birds from southern Peru and northwestern Bolivia live very high (3000 to 4000 meters) and have long wings. Birds from northern Peru and Ecuador live at lower elevations (2000 to 3500 meters) and have shorter wings. There is, however, no correlation between altitude and wing-length in birds from northern Patagonia. They live at low elevations (below 1500 meters) but have long wings.

Geographical variation in wing-length does not seem to parallel geographical variation in color: there is apparently no more abrupt change in wing-length between southern Ecuador and northern Peru (see Fig. 16) than between other apparently not disjunct populations (e.g., Bolivia and northwestern Argentina).

Muscisaxicola fluviatilis

This is the only species of the genus to live in wet tropical lowlands and Andean foothills east of the Andes in Peru and Bolivia, and along streams and rivers in extreme western Brazil. However, there are in the literature a few reports of *M. fluviatilis* at high altitudes in the Andes, which are worth examining in detail.

Bond (1947: 130) synonymized *M. titicacae* (Carriker, 1932: 459) with *M. fluviatilis*. The type and only specimen of *titicacae* is an adult from Desaguadero along the shore of Lake Titicaca, at about 3900 meters. I have seen this specimen and can confirm its identification as *fluviatilis*.

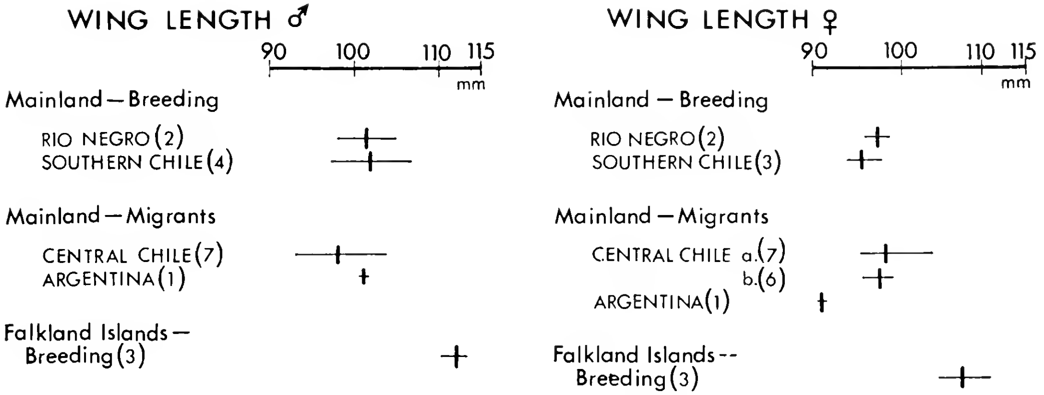

Fig. 17. Geographical variation in wing-length in mainland and Falkland Islands populations of *Muscisaxicola macloviana*. In both males and females, Falkland Islands birds have longer wings than do mainland birds, whether the latter are breeding or migrants. Number of specimens in parentheses. Females from Central Chile: a, with MCZ 94525, labeled "♀," but probably wrongly sexed; b, without this specimen.

Olrog (1963) mentioned that *fluviatilis* occurs in the highlands of northwestern Argentina. Through Olrog's courtesy, I examined four of the five specimens upon which this statement was based. Two of these five birds had been identified as *M. fluviatilis* by Hellmayr (Olrog, *in litt.*). The four specimens I studied are undoubtedly *M. maculirostris,* and I presume that the fifth belongs to this species also, since it is identical to them (Olrog, *in litt.*).

These specimens show not only that great caution must be exercised when identifying *fluviatilis,* but also that the species does occasionally occur high up in the Andes.

There is apparently no geographical variation in *M. fluviatilis.*

2. *The macloviana Species-Group*

Muscisaxicola macloviana

Muscisaxicola macloviana breeds in continental southern South America, from about 41°S, along the Andes southward to Tierra del Fuego, and in the Falkland Islands. Olrog (1948) noticed this species in flat country, along forests, and on seashores, as well as above the timber line in Tierra del Fuego. In the Falklands, Pettingill (personal communication) remarked that it was a "common resident in upland areas, usually in valleys near cliffs or rocky outcrops." He noticed further that "its particular habitat seemed to be governed by the availability of crevices in loose rock or ledges for nesting and grassy places, sheltered from the wind, for feeding and resting."

The mainland and Tierra del Fuego birds (subspecies *mentalis*) are very uniform in color and size, but have noticeably shorter wings than birds from the Falkland Islands (*macloviana*) (Fig. 17). I did not detect any parallel color variation.

M. macloviana is migratory. The mainland populations move northward along the Andes in both foothills and uplands, and spend the southern hemisphere winter in Peru, where, according to Koepcke (1964), the species is regularly found in loose flocks in the coastal lomas. The Falkland Islands populations, in contrast to the mainland ones, seem to be resident, although neither Bennett (1926) nor Cawkell and Hamilton (1961) say so explicitly. The resident status of Falkland Islands birds seems confirmed by an examination of wing-lengths among continental migrants, none of which were large enough to belong to the Falkland Islands populations (Fig. 17).

Muscisaxicola capistrata

The breeding range of this species includes extreme southern Chile and Tierra del Fuego, but very little is known about its breeding habits and ecological preferences. Neither Goodall et al. (1957) nor Olrog (1948) give any data about its habitat.

Muscisaxicola capistrata migrates northward along the Andes at high elevation, and spends the southern hemisphere winter in northern Chile, Bolivia, and southern Peru. There is no geographic variation in this species.

3. The rufivertex Species-Group

Muscisaxicola rufivertex

Muscisaxicola rufivertex breeds from northern Peru to central Chile and adjacent Argentina. In Chile (Goodall et al., 1957), this species undertakes altitudinal migrations and spends the nonbreeding season in the coastal regions of Coquimbo, Atacama, and Antofagasta. In Argentina, Bolivia, and Peru, I found *M. rufivertex* to inhabit xeric slopes with a rocky or gravelly soil and sparse shrubby vegetation, and rocky quebradas or small valleys with cliffs and rocky ledges. Dorst (1962) found *rufivertex* where small valleys open up into pampas, so that the ecological characteristics of grassy plains and rocky slopes of small valleys are combined. *M. rufivertex* has a rather extensive altitudinal distribution from about 3000 meters (Koepcke, 1964) up to about 4500 meters (personal observation).

Muscisaxicola rufivertex has some geographical variation in color and size. The detection of geographic variation is probably complicated by migratory movements of several populations. Zimmer (1937: 3) stated that "one specimen from Cuchacancha, Bolivia, belongs to *pallidiceps* although eleven other specimens from the same locality are *occipitalis*. The specimens were all taken in June, and there is little doubt that the individual belonging to *pallidiceps* was a migrant from the south."

Variation seems to be as follows: northern Peruvian birds are the largest, whereas birds from Chile (Santiago region) are smaller. The birds from northern Chile, northern Argentina, and southern Bolivia are distinctly paler than those from central Chile and adjacent Argentina, or than birds from Peru and northern Bolivia. The palest birds live in northern Chile and northern Argentina.

The albilora Superspecies

Muscisaxicola juninensis. This species is found apparently only at very high altitudes from central Peru to Bolivia, northern Chile, and northwestern Argentina, where it seems to be resident. It inhabits grassy steppes interrupted by rocky outcrops and small cliffs, above 4000 meters, and usually between 4200 and 4800 meters (personal observation).

Muscisaxicola albilora. Muscisaxicola albilora breeds in the Andes of Chile and Argentina from about 30°S to southern Patagonia, but not in Tierra del Fuego. It occurs at altitudes from about 1500 to 2500 meters (Goodall et al., 1957). It seems to prefer rocky, barren slopes with almost no vegetation, at least in Río Negro, Argentina (personal observation).

There is no detectable geographical variation in this species. Migrations are extensive, since *M. albilora* vacates its breeding grounds (Johnson, 1967) and spends the southern hemisphere winter in the high tropical Andes, as far north as Ecuador.

4. The alpina Species-Group

The alpina Superspecies

Hellmayr (1927) separated the various populations of *Muscisaxicola* having gray plumage and lacking a colored crown-patch into two species: *Muscisaxicola alpina,*

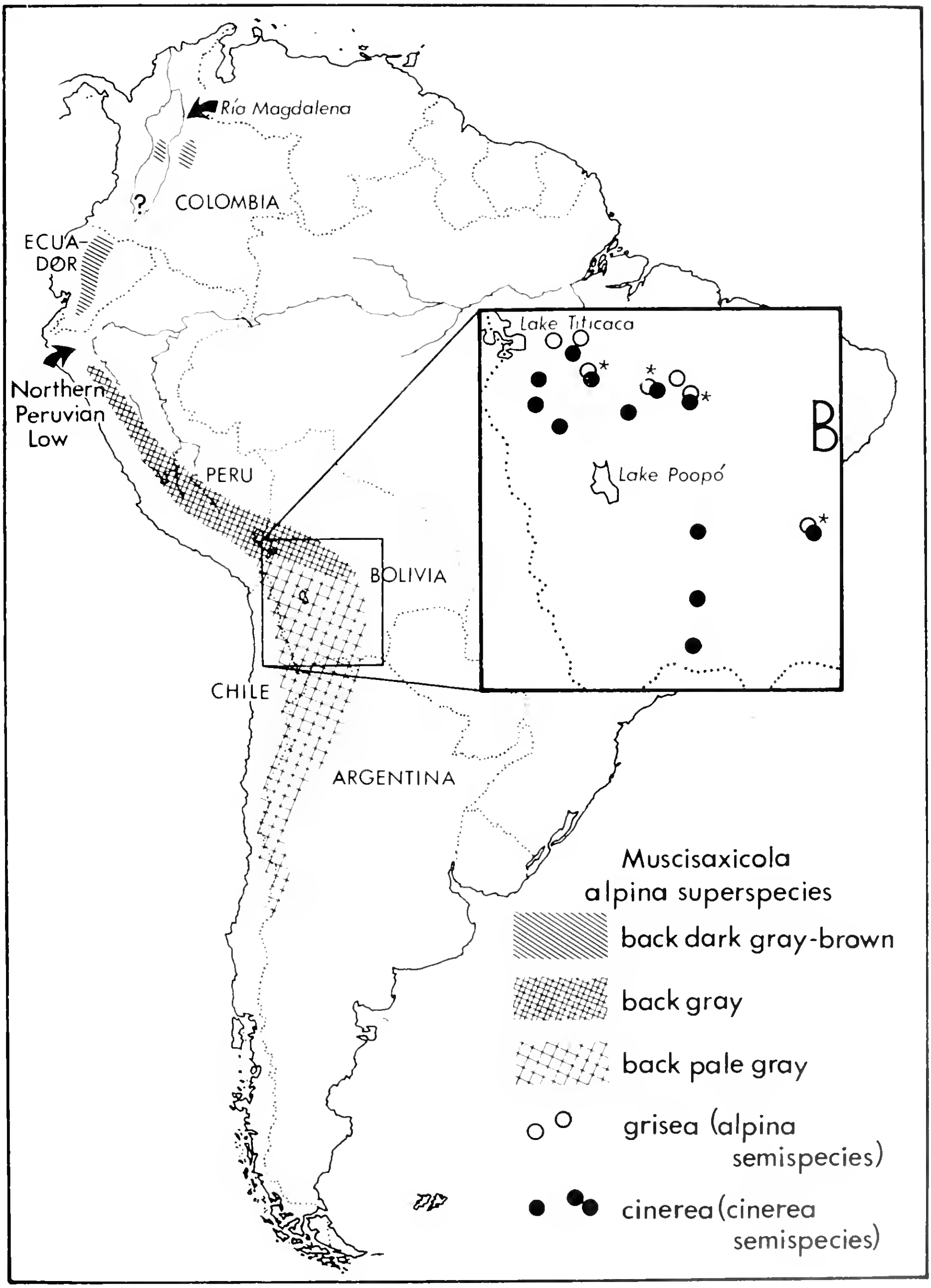

Fig. 18. Geographical distribution of the *Muscisaxicola alpina* superspecies. Dark-backed populations (*alpina* semispecies) have isolates in Colombia and Ecuador. In western Bolivia (and perhaps also in Peru: see text) the *alpina* semispecies comes in contact with pale-backed populations (*cinerea* semispecies). Insert: collecting localities, largely from personal field work, showing the contact area. Birds of the *grisea* phenotype (*alpina* superspecies) occur along the eastern front of the Andes. The *cinerea* phenotype (*cinerea* superspecies) occurs along the altiplano as well as along the eastern Andean front. Localities marked with an asterisk (*) represent possible overlap.

ranging from Colombia southward to Ecuador, Peru, and Bolivia in the department of La Paz, and *M. cinerea,* ranging from northwestern Argentina to central Chile. In a footnote (1927: 28) he indicated that *M. alpina* is larger and darker, has whiter edges to secondaries and wing coverts, and has a broader supraloral streak than *M. cinerea.* In a later publication, Hellmayr (1932: 125–126) merged the two species into one, *M. alpina.* His main justification for this taxonomic decision was that the populations from northwestern Argentina (Tucumán) were intermediate between *M. alpina* and *M. cinerea*: in size, these Argentine birds were similar to *M. cinerea,* but in color they resembled *M. alpina.*

Subsequent authors have followed Hellmayr's 1932 treatment of *alpina* and *cinerea* as conspecific (see Olrog, 1963: 246; Philippi, 1964: 141; Goodall et al., 1957: 164; Johnson, 1967: 244–245; de Schauensee, 1966: 336).

Geographical variation in the *alpina-cinerea* complex is detectable in both color and size, and can be described as follows. There is a decrease in color saturation (of both upper and underparts) from Colombia southward to Argentina and Chile. Samples from Colombia and Ecuador are uniformly dark, especially on the upperparts, whereas samples from Peru and Bolivia are distinctly paler, and finally, samples from northwestern Argentina and central Chile are palest. Although this variation is gradual, there is a clear-cut break between Ecuadorean and Peruvian samples. This break corresponds to an area between the two countries where the Andes are too low for birds of this group to occur, and where the dry to arid valleys, including the Marañon valley, cut across the Andean ranges and are a barrier to gene exchange between birds living on either side (Fig. 18). The geographical variation just described appears to be positively correlated with rainfall. As a whole, the Colombian and Ecuadorean Andes receive more rain, and have longer rainy seasons, than the Andes of Peru-Bolivia, and especially those of northern Argentina and central Chile (Lauer, 1952; Franze, 1927; Knoch, 1930). One might therefore conclude that geographical variation in color follows Gloger's rule.

Geographical variation in size, especially as measured by wing-length, is extensive, but does not follow exactly the same trend as variation in color. There is an increase in size between Colombian and Ecuadorean birds, the latter being the largest of any populations of this group. From Ecuador southward to Peru and Bolivia, there is a decrease in mean wing-length among the samples I have examined. This decrease continues into northern Argentina and central Chile, so that Chilean birds are the smallest of any in the group. On the whole, however, the north to south decrease in wing-length cannot be said to be clinal, because of some irregularities, which are worthy of careful examination. Indeed, within samples from central and south-central Peru and Bolivia, variation in wing-length is sharply bimodal, with part of the birds in a sample having relatively small wings and part having larger wings. Furthermore, the smaller birds also appear to be paler than the larger ones, thus suggesting sympatry of differentiated populations.

The published evidence bearing on this problem is as follows. In Huancavelica, south-central Peru, Morrison (1939) collected both large-dark and small-pale birds. His six large-dark specimens (four males and two females) were collected between 12 and 25 October. As I judge from the data on labels, the six males have relatively large testes, but the females have small ovaries. All six specimens have slightly worn plumage. Taxonomically, the six large-dark birds were assigned to the subspecies *grisea* (locally breeding), and the two small-pale birds to the subspecies *cinerea* (migrants from Chile). It is noteworthy that both taxa were collected in October, at a time when local Andean populations normally start breeding. Thus, either the two specimens of *cinerea* were late in beginning their southward migration to their breeding quarters in Chile, or else they were actually breeding in Peru.

Bond (1947: 130), reporting on birds collected in Peru by Carriker, noted that four small-pale specimens, which he assigned to the subspecies *cinerea*, "are adult, and were taken from April 10 to May 16." Since these dates correspond to the nonbreeding season of many high Andean birds (Dorst, 1955, 1962; personal observation), Bond concluded, I think correctly, that these individuals are "winter residents." These remarks, however, would not apply to the birds collected by Morrison (1939), cited previously.

In Bolivia, Bond and de Schauensee (1942: 340–341) reported that *grisea* (large-dark) and *cinerea* (small-pale) had been taken together at three different localities: Viloca (La Paz), Cerro del Juno (Cochabamba), and Padilla (Chuquisaca). A specimen of *cinerea* "was taken on the Cerro del Juno, October 2, where *grisea* was nesting at this time." This record is similar to the one published by Morrison (1939). In Bolivia, as in Huancavelica, it seems surprising that birds should remain as late as October in their winter range. Some individuals may stay longer than most wintering birds, as is well known from migrants in the northern hemisphere. Similarly, in the postbreeding season, some migrants are earlier arrivals than the bulk of the populations. Thus, the "three full-grown but immature specimens [of *cinerea*] . . . taken at Viloca [Department of La Paz], March 25 and 26" (Bond and de Schauensee, 1942: 341) may have been among the first wave of migrants. I believe that immature individuals of the genus *Muscisaxicola* may be migrating earlier than adults. Thus, I have observed immature *M. capistrata*, a species breeding in southern Patagonia, in central Chile on 19 March and in northwestern Argentina on 25 April. By analogy, the arrival of immature birds from Chilean populations of *cinerea* in Bolivia in March would therefore not be surprising.

Two alternative explanations are possible for the above data. The first is that the small-pale populations (taxonomically assigned to Chilean *cinerea*) found in March, April, May, and October in Peru and Bolivia are migrants and do not breed in these last two countries. The second is that, even though the Chilean populations (*cinerea*) may be migratory, there are two morphologically differentiated populations of the *alpina* species-group living sympatrically in parts of the Peruvian and Bolivian Andes. The second alternative implies that *M. alpina* (as understood, for example, by de Schauensee, 1966) consists, in fact, of two largely allopatric species having a narrow zone of overlap in the central Andes.

Between October 1967 and January 1968, I investigated the relationships of the populations of *M. alpina* in the Bolivian Andes. I traveled on the altiplano southwest of the Cordillera Real, and made several trips along the Cordillera Real, the Cordillera de Cochabamba, and, farther south still, in the Cordillera de Mochará. I visited these areas because they were located immediately around, as well as in, the region of possible sympatry of two differentiated populations of *M. alpina*. I wanted to determine in what habitats these birds occur, to collect samples of specimens in breeding condition, and to delimit the ranges of the two populations. Unfortunately, much more time was spent in just traveling large distances on extremely difficult roads looking for these birds in habitats which appeared suitable, than in actually collecting and studying these birds. The extreme shyness of *Muscisaxicola*, combined with their low population density even in the most suitable localities, was a powerful obstacle to collecting large comparative series, which I had hoped to assemble. Furthermore, great physical difficulties were encountered in

TABLE 3. A COMPARISON OF MORPHOLOGICAL CHARACTERS IN POPULATIONS OF THE *MUSCISAXICOLA ALPINA* SUPERSPECIES FROM THE BOLIVIAN ANDES

	M. alpina semispecies	*M. cinerea* semispecies
Character	Range (mean) (sample size)	Range (mean) (sample size)
Mensural characters		
Weight in grams (males and females)	24.9–27.9 (26.61) (7)	17.5–23.3 (20.55) (14)
Weight in grams (males only)	25.8–27.9 (26.92) (5)	18.9–22.7 (21.06) (8)
Wing-length (mm) (males only)	115.5–122.0(119.50) (5)	108.0–114.0 (111.87) (8)
Tail-length (mm) (males only)	78.5–90.5 (82.80) (5)	72.0–78.0 (75.18) (8)
Culmen-length (mm) (males only)	17.5–19.0 (18.30) (5)	17.0–18.5 (17.93) (8)
Tarsus-length (mm) (males only)	32.0–33.5 (32.80) (5)	28.0–30.0 (29.37) (8)
Nonmensural characters		
Superciliary stripe	Whitish supercilium extends slightly beyond the eye	Whitish supercilium does not extend beyond the eye, at least in most specimens
Underparts	Abdomen white, tinged with pale buffy	Abdomen whitish, tinged with pale gray or grayish brown
	Breast gray, darker than the whitish throat	Breast and throat pale gray, almost concolor
Upperparts	Uniform dark grayish brown (mouse-gray or mouse-brown)	Uniform grayish with distinct pale brownish tinge in most specimens
Wing coverts	Brownish gray, without buffy wash	Brownish with pale buffy wash

the pursuit of these elusive birds at altitudes usually over 4000 meters.

In spite of these difficulties, however, my efforts proved successful. I collected a total of 21 specimens of the *alpina* group, as well as other species of *Muscisaxicola*. This number is small, when compared to the yield of similar field endeavors in localities which are easier of access. Yet, the results of this exploratory collection permit the following unequivocal conclusions.

(A) Two populations of the *alpina* species-group occur in the high Andes of Bolivia (Departments La Paz and Cochabamba). One of them comprises large and relatively dark birds, hereafter referred to as "*grisea* phenotype." The second contains small pale birds, referred to below as "*cinerea* phenotype."

The birds of the *grisea* and *cinerea* phenotypes that I collected in Bolivia can be distinguished from each other by a series of characters (see Table 3). Weight alone permits complete separation, since there is no overlap in weight ranges between the *grisea* and the *cinerea* specimens. In other mensural characters, birds of the *grisea* phenotype are consistently larger than those of the *cinerea* phenotype. In color characters, birds of the *grisea* phenotype appear generally darker than those of the *cinerea* phenotype.

(B) Birds of both the *grisea* and the *cinerea* phenotypes breed between October and January. Although no nest could be located, the specimens collected include adult males with enlarged testes and fully ossified skulls for both phenotypes. The females collected did not have enlarged ovaries, however. No nestlings were collected, but two juvenile specimens of *grisea* had largely unossified skulls, either very small or unobservable gonads, and loose, very fresh plumage. All the other specimens, of both *grisea* and *cinerea* phenotypes, had worn plumage, especially remiges and rectrices. Food carrying and display behavior, including display flights, were seen from birds of the *cinerea* phenotype in October, November, and December. (The conditions of the gonads of the other three species collected, *M. rufivertex, M. juninensis,* and *M. albifrons,* were similar to those of the birds of the *grisea* and *cinerea* phenotypes.)

(C) Birds of the *cinerea* phenotype occur both on the altiplano and along the high mountains forming the eastern Andean wall (Cordilleras Real and of Cochabamba) (see Fig. 18). Birds of the *grisea* phenotype, however, were encountered only in the Cordilleras Real and of Cochabamba (see Fig. 18).

(D) In one of the ten localities at which I collected specimens of the *grisea* or *cinerea* phenotypes, I observed both together. Along the road to Morochata, at about 4040 meters altitude in the Cordillera Tunari (Department Cochabamba), I encountered a sparse population of *Muscisaxicola* on gentle, grassy slopes. The birds were foraging in the densely matted, grazed grass or turf, and were very wary. Much stalking and patience permitted me to secure five specimens within a radius of about one kilometer.

Two of these birds proved to be of the *cinerea* phenotype. They had testes 9.0 × 4.5 and 9.0 × 4.0 mm respectively, fully ossified skulls, and slightly worn plumage.

The other three specimens were of the *grisea* phenotype. All three were males, with testes and skull conditions as follows. Testes 5.0 × 3.0 mm, skull with two tiny unossified windows; testes 6.0 × 3.0 mm, skull fully ossified; testes 4.0 × 2.5 mm, skull with a moderately large unossified occipital window. All three had slightly worn plumage, like that of the birds of the *cinerea* phenotype.

The evidence presented above suggests that two allopatric species or semispecies come in contact along the eastern wall of the Andes of Bolivia (Department Cochabamba). An unequivocal decision on whether or not the taxa involved are specifically distinct cannot be made from the present, still insufficient, data. More information is needed on the respective distributional ranges of the *grisea* and *cinerea* phenotypes, on possible differences in ecological preferences, in displays or other behavior, and on the relationships in narrow zones of overlap, as in the Cordillera of Cochabamba. Do the two taxa hybridize? Do they have intra- or interspecific territories, and so forth.

The taxonomic solution adopted here, pending further field work to clarify the situation, is that birds of the *alpina* species-group constitute a superspecies, with two component semispecies, nomenclaturally treated as species: *M. alpina* (including *grisea*), living in the wetter Andes of Colombia, Ecuador, Peru, and northwestern Bolivia (see Fig. 18), and *M. cinerea* (including *argentina*) living in the drier Andes of central and southern Bolivia, northwestern Argentina, and central Chile (see Fig. 18).

5. The albifrons Species-Group

The albifrons Superspecies

Muscisaxicola albifrons. Muscisaxicola albifrons is usually found at higher altitudes than are most other species of the genus, except perhaps *juninensis.* In Chile, Goodall et al. (1957) give the altitudinal range from 4000 to 5000 meters. Their photograph (page 163) shows the habitat of the species in Chile: gently undulating slopes with sparse and overgrazed scrub and bunch-grass. In Peru and Bolivia I saw the species on valley slopes where grazed grasslands were interrupted by cliffs and boulders, between 4300 and 4500 meters. *M. albifrons* ranges from northern Peru to extreme northern Chile and Bolivia; it has not been reported from northwestern Argentina. As far as is known it is a resident species. There is no geographic variation in this species.

Muscisaxicola flavinucha. Muscisaxicola flavinucha is a southern South American species ranging from central Chile and adjacent Argentina to Tierra del Fuego. It occurs up to about 4000 meters, according to Goodall et al. (1957), but in the Andes south of about 40°S its altitudinal limits are lower, because the Andes themselves rarely exceed 3000 to 3500 meters. The habitat of this species consists of barren rocky slopes with small cliffs or boulders, and very little herbaceous vegetation. Goodall et al. (1957) say that *flavinucha* occurs especially near streams and mountain lakes, but in my experience, it also breeds in regions devoid of either streams or lakes.

M. flavinucha is migratory and goes as far north as northern Peru (Libertad) to spend the southern hemisphere winter. This migration seems to take place entirely at high altitudes in the Andes.

There is minor geographical variation in *M. flavinucha*. Olrog (1949b) described the birds of Tierra del Fuego as a distinct subspecies (*brevirostris*) because they have smaller bills and wings, and are darker in color than mainland birds. From an evolutionary point of view, *M. flavinucha* has one weakly differentiated isolate on Tierra del Fuego. It should be pointed out that although the type locality of *brevirostris* is Ushuaia (Tierra Grande, Tierra del Fuego), Olrog (1949b) did not think that these birds bred on this island, but rather on the mountains of Navarino and Hoste Islands and in the Cape Horn archipelago. These populations are probably rare or uncommon. It was not until 1928 that Reynolds (1934) observed and collected this species in Harberton, Beagle Canal. Later (1935) he reported that he might have seen it on Freycinet.

Muscisaxicola frontalis

This species breeds in Chile (Antofagasta) and Argentina (Mendoza) in the north and from there southward to the latitude of Colchagua and Río Negro (Johnson, 1967). Bond and de Schauensee (1942: 340) mentioned four specimens from Viloca and La Cumbre in Bolivia, and Bond (1947: 129) cited one male collected 21 April at Pampa de los Arrieros near Arequipa in southern Peru. I agree with Bond that these birds are migrants from the south. The breeding habitat of *M. frontalis* seems to be stony and rocky slopes with sparse vegetation of small shrubs and bunch-grass. During the nonbreeding season, the species occurs also at very high altitudes, either in bunch-grass steppes or in rocky spots near marshy areas (personal observation). *M. frontalis* does not show any detectable geographic variation.

DISCUSSION

The bush and ground tyrants analyzed in Part II show clear-cut instances of various stages of the speciation process. Thus, at least the most recent events in the adaptive radiation of these birds can be traced. Yet, the earlier episodes of their evolutionary history appear shrouded in uncertainty. Indeed, these flycatchers have a rather large number of both taxonomically isolated species, and taxonomically closely related but extensively sympatric species.

Table 4 shows this evolutionary dichotomy. Of thirty-three species and semispecies, nine (about 27 percent) possess

TABLE 4. STAGES OF THE SPECIATION PROCESS IN THE BUSH AND GROUND TYRANTS

Species and semispecies	Geographical variation: Absent	Geographical variation: Gradual	Geographical variation: Discontinuous (Isolates slightly differentiated)	Member of a Super-species	Second-ary contact	No close relative	Closest relative broadly sympatric
Xolmis striaticollis	—	—	—	—	+[1]	—	+
X. pernix	—	—	—	+	—	—	—
X. fumigata	+	—	+	+	—	—	—
X. fuscorufa	+	—	—	+	—	—	—
X. signata[2]	+	—	—	—	—	+?	—
X. erythropygia	—	—	+	—	—	—	+
X. rufipennis	+	—	—	—	—	—	+
X. pyrope	—	+[3]	+[3]	—	—	+	—
X. cinerea	—	+	—	—	—	—	+
X. velata	—	—	—	—	—	—	+
X. coronata	—	—	—	—	—	—	+
X. dominicana	—	—	—	—	—	—	+
X. irupero	—	+	—	—	—	—	+
X. rubetra	+	—	—	—	—	+	—
Neoxolmis rufiventris	+	—	—	—	—	+	—
Agriornis montana	—	—	+	—	+[4]	—	+
A. albicauda	—	+	—	—	—	—	+
A. livida	—	+?	—	—	—	—	—
A. microptera	—	—	+	—	—	—	—
A. murina	+	—	—	—	—	+	—
Muscisaxicola brevicauda	—	+	—	—	—	+	—
M. maculirostris	—	—	+	—	—	—	—
M. fluviatilis	+	—	—	—	—	—	—
M. macloviana	—	—	+	—	—	—	+
M. capistrata	+	—	—	—	—	—	+
M. rufivertex	—	+?	—	—	—	—	+
M. juninensis	+	—	—	+	—	—	—
M. albilora	+	—	—	+	—	—	—
M. alpina	—	—	+	+	+[5]	—	—
M. cinerea	—	+	—	+	+[5]	—	—
M. albifrons	+	—	—	+	—	—	—
M. flavinucha	—	—	+	+	—	—	—
M. frontalis	+	—	—	—	—	—	+
Totals: 33	13	8	9	9	4	6	14

[1] *X. striaticollis* shows what appears to be a stepped cline in southern Peru and northern Bolivia. The interpretation as "secondary contact" is hypothetical.

[2] *X. signata* may or may not belong in *Xolmis*.

[3] *X. pyrope* shows gradual geographical variation on the continent, but has a subspecifically distinct isolate on Chiloé Island.

[4] *A. montana* shows a phenomenon similar to that of *X. striaticollis* above.

[5] The two semispecies of the *M. alpina* superspecies appear to overlap in a very narrow zone of the Bolivian Andes.

Semispecies belonging in the same superspecies are enclosed in braces.

morphologically differentiated isolates, nine (about 27 percent) are members of superspecies, and four (about 12 percent) have what appear to be secondary contacts suggesting former isolation. At the same time, of thirty-three species (regardless of whether they also show active speciation or not), six (about 18 percent) are taxonomically isolated, and fourteen (about 42 percent) are broadly sympatric with their most closely related congener(s). These two aspects of the evolutionary history of these flycatchers are analyzed further below.

Presently Active Speciation

One of the most important events of geographical speciation is the establishment of isolates within a species' range (see, e.g., Mayr, 1963). The corollaries of geographical isolation are the cessation of gene flow between populations, and the subsequent initiation of genetic divergence in the isolates under different selection regimes. The presence of genetically distinct isolates is therefore an index to the speciation potential of extant species (Prakash, Lewontin, and Hubby, 1969).

In the absence of actual data on the genetics of populations of Andean birds, including the Tyrannidae of the present study, I have of necessity relied on morphological differentiation to make statements about genetic differentiation. My conclusions about speciation are therefore based on the assumption that morphological differentiation between two isolated populations is positively correlated with their genetic differentiation. That this is indeed the case is suggested by the work of Hubby and Throckmorton (1968) on isozyme variability among triads of closely related species of *Drosophila*.

Nevertheless, genetic differentiation can be extensive even in the absence of parallel morphological variation. Thus the bias of my study would be to underestimate genetic differentiation: first, by considering that morphologically similar isolates are also genetically similar, and second, by failing to recognize minor, but real, geographical variation.

The first source of bias may prove very difficult to erase. The second, however, could be eliminated by undertaking exhaustive studies of geographical variation of each of the species treated here, especially, perhaps, those considered to have no, or only gradual, variation (see Table 4). As every systematist knows, such studies are extremely time consuming. Since my goal was to obtain broad comparative data on speciation from a large sample of the entire Andean avifauna (see Vuilleumier, 1969b), I have deliberately chosen breadth at the expense of depth, and can only hope that the many problems uncovered will be taken up as separate projects by others.

The observed instances of presently active speciation fall in two categories: (a) differentiation centered around more or less well-marked geographical and ecological barriers, and (b) differentiation and secondary contacts not centered around such barriers.

Geographical Barriers

In two species and one superspecies of *Xolmis*, one species of *Agriornis*, and four species of *Muscisaxicola*, morphological differentiation can be correlated with the presence of barriers. In all these cases the isolates have been formally recognized taxonomically by previous ornithologists, usually as subspecies, but as species in the *X. fumigata* superspecies.

From an evolutionary point of view, the barriers isolating these populations would therefore seem to inhibit gene flow from other populations, as evidenced by the morphological differentiation. These barriers are listed below in geographical sequence from north to south (several of them have already been cited in Vuilleumier, 1968, 1969a, 1969b).

(1) *César Depression.* The lowlands separating the Santa Marta Mountains of northern Colombia from the Perijá Range seem to affect *Xolmis pernix* and *X. fumigata*, two species or semispecies of the *X. fumigata* superspecies (see Fig. 12). In this case, morphological differentiation is sufficient to suggest that species level has been reached by the populations on either side of the gap. In *Xolmis erythropygia*, a population appears restricted to the Santa Marta Range; it has been separated taxonomically as a subspecies (*orinoma*). The species is absent from the Perijá Range, and also from the remainder of the Colom-

bian Andes, except in the extreme south (Nariño). Whether this patchy distribution means that extinction has occurred in the Andes between Nariño and Santa Marta or whether it is an artifact reflecting insufficient collecting (as a result of the rarity of the species?) cannot be resolved at the present time. *Xolmis striaticollis* has an apparently undifferentiated population in the Santa Marta Mountains.

(2) *Río Torbes Valley.* This arid valley isolates the Andes of eastern Táchira, Mérida, and Trujillo from those of western Táchira in Venezuela. The populations of *Xolmis fumigata* living in the Andes to the east of this valley are clearly distinguishable morphologically from other populations, and have been separated taxonomically as the subspecies *lugubris* (see Fig. 12).

(3) *Río Magdalena Valley.* The Central and Eastern Andes of Colombia are isolated from each other by this dry valley. *Muscisaxicola alpina* has an isolated population in the Central Andes (taxonomically separated as the subspecies *colombiana*) and another in the Eastern Andes (subspecies *quesadae*) (see Fig. 18). The morphological differentiation between these populations is slight.

(4) *Upper Río Magdalena Valley and Southwestern End of Eastern Andes.* The southwestern part of the Eastern Andes appears too low for páramo vegetation to occur, so that there is a distribution gap between the Andes of Nariño in southern Colombia and the central part of the Eastern Andes. *Muscisaxicola maculirostris* has a well-differentiated isolate (subspecies *niceforoi*) in the Eastern Andes, isolated by a very large gap (marked by ? in Fig. 15) from the Ecuadorean population (subspecies *rufescens*). The problem of whether or not the actual barrier corresponds to a gap in the vegetation preferred by this species in Colombia remains to be established in the field, hence my ? in Figure 15. A similar gap exists in the distribution of *Muscisaxicola alpina* (marked with a ? in Fig. 18).

(5) *Upper Río Marañon Valley and Northern Peruvian Low.* In the Andes of northern Peru, the Río Marañon Valley cuts deeply across the relatively low-lying mountains as its course changes from a south–north to a west–east direction. The Andes west of this bend are especially low, and are probably unsuitable for many high altitude birds, because the upper vegetation zones, especially those above the timber line, are either absent or of very small area. This complex barrier separates populations of *Xolmis fumigata* (see Fig. 12), with slight morphological differentiation only. In *Muscisaxicola,* however, two species have well-marked populations on either side of this gap. In *M. maculirostris,* the subspecies *rufescens* occurs north of the barrier, and *maculirostris* south of it (see Fig. 15). In *M. alpina,* the northern subspecies is *alpina* and the southern *grisea* (see Fig. 18). Finally, *Agriornis montana* has weakly differentiated populations separated by this gap (see Fig. 14), taxonomically recognized as subspecies *solitaria* (north) and *insolens* (south). Thus the Marañon gap has various effects on flycatchers living in this area, but is it noteworthy that none of the populations so isolated belong to a superspecies.

(6) *Río Apurimac Valley.* The upper Río Apurimac and some of its tributaries (Río Pampas, Río Mantaro) may constitute a barrier between *Xolmis fumigata* and *X. fuscorufa* of the *X. fumigata* superspecies (see Fig. 12), and between the weakly marked subspecies *erythropygia* and *boliviana* of *Xolmis erythropygia.* In both cases, however, much more collecting is necessary before the precise barrier area between taxa can be ascertained.

(7) *Andes of Western Argentina.* The huge hiatus (over 1000 km) in the distribution of *Agriornis microptera* (see Fig. 13) is difficult to interpret in terms of a single

TABLE 5. SMALL PERIPHERAL ISOLATES THAT SHOW DIFFERENTIATION IN MORPHOLOGICAL CHARACTERS

Species or superspecies having isolate	Geographical isolate (taxonomic rank)	Location of isolate
Xolmis fumigata	*lugubris* (subspecies)	Mérida, Venezuela
Xolmis fumigata	*pernix* (species or semispecies)	Santa Marta, Colombia
Xolmis erythropygia	*orinoma* (subspecies)	Santa Marta, Colombia
Xolmis pyrope	*fortis* (subspecies)	Chiloé Island, Chile
Agriornis montana	*solitaria* (subspecies)	Ecuador and southern Colombia
Muscisaxicola maculirostris	*niceforoi* (subspecies)	Eastern Andes, Colombia
Muscisaxicola maculirostris	*rufescens* (subspecies)	Ecuador
Muscisaxicola macloviana	*macloviana* (subspecies)	Falkland Islands
Muscisaxicola alpina	*columbiana* (subspecies)	Central Andes, Colombia
Muscisaxicola alpina	*quesadae* (subspecies)	Eastern Andes, Colombia
Muscisaxicola flavinucha	*brevirostris* (subspecies)	Tierra del Fuego

"barrier." The habitats favored by this species seem to be zones of xeric, rocky plains, which are largely missing in the Andes, and the foothills between the ranges of the subspecies *andecola* (high Andes) and *microptera* (Patagonia). Range disjunctions similar to the one found in *A. microptera* are also observed in *Pterocnemia pennata, Tinamotis,* and *Diuca.*

(8) *Straits Between Chiloé Island and Mainland.* The Chiloé Island population of *Xolmis pyrope* appears slightly differentiated from the mainland ones.

(9) *Straits of Magellan.* The population of *Muscisaxicola flavinucha* living on Tierra del Fuego or on islands south of the Beagle Canal may be slightly differentiated morphologically. More field work is needed to check whether the variation is truly discontinuous (and if so, whether the barrier is indeed the Straits of Magellan) or merely clinal.

(10) *Straits Separating Falkland Islands From Mainland.* The Falkland population of *Muscisaxicola macloviana* is slightly differentiated from the mainland ones (see Fig. 17).

From an ecological standpoint, the ten gaps listed above are quite variable. Aside from barriers 8–10, which are marine, all others are terrestrial. Barriers 2, 3, 5, and 6 may be roughly equivalent ecologically. They are situated around arid valleys cutting across high mountain ranges. Barrier 1 is a more varied lowland gap. Finally, barriers 4 and 7 are ill-defined interruptions in the continuity of certain habitats.

Of the morphologically differentiated isolates separated by one or another of barriers 1–10, it is interesting to note that eleven may be considered peripheral and of small size (see Table 5). These isolates may have originated as small founder populations that colonized suitable habitats at the periphery of the range of the species (see Mayr, 1954). Eight of the eleven isolates occur north of barrier 5, in the Andes of Ecuador, Colombia, and Venezuela, where the distribution patterns of high altitude habitats, especially páramos, are quite insular (see Vuilleumier, 1970). The potential importance of peripheral isolates as incipient species has been emphasized by Mayr (1963). Recently, Prakash, Lewontin, and Hubby (1969) have demonstrated that genetical differentiation is marked in the small and isolated peripheral population of *Drosophila pseudoobscura* in Colombia.

Absence of Barriers

I have argued that in *Xolmis striaticollis* and *Agriornis montana* (see Fig. 14), and in the *Muscisaxicola alpina* superspecies (see Fig. 18), secondary contacts are responsible for the observed patterns of distribution and variation: hybridization or secondary intergradation, and narrow marginal overlap. Although these interpretations need to be substantiated by more evidence, it is possible to state here that these contacts do not seem to take place in regions that can be called barriers. All three contact zones are located in the Andes between southern Peru and northwestern Bolivia.

In both the *Muscisaxicola albilora* and *M. albifrons* superspecies, a distribution gap appears to exist between the pairs of species or semispecies in the Andes of extreme northern Chile and of western Bolivia. Whether these gaps are real or artificial, resulting from the lack of intensive collecting in these areas is, of course, not possible to ascertain at the present time. In the *albilora* superspecies, the two semispecies (or species) are quite similar morphologically, and secondary contact might conceivably result in hybridization. In the *albifrons* superspecies, however, the differences between the two taxa are well marked, and contact might result in sympatry (as it apparently does in the *alpina* superspecies).

All of the supposed instances of secondary contacts rest, unfortunately, on too few specimens having sufficient label data and on too few field data. The best field evidence, in the *M. alpina* superspecies, comes from my own exploratory field work, so I am better aware than anyone else ot the limitations of the speculations advanced here.

Older Speciation Patterns

The taxa of bush and ground tyrants that do not show evidence of active speciation fall in two categories: (a) taxonomically isolated species, and (b) taxonomically related, sympatric species. In the first group belong *Xolmis pyrope, X. rubetra, Agriornis murina, Neoxolmis rufiventris,* and *Muscisaxicola brevicauda.* Some of these species (e.g., *Xolmis pyrope, Neoxolmis rufiventris,* and *Muscisaxicola brevicauda*) occupy relatively specialized habitats, as I pointed out in Part I. Nothing can be inferred of the history of these species on present evidence.

In the second category (sympatric congeners) belong especially the species of the *Xolmis fumigata, erythropygia,* and *cinerea* species-groups, those of the *Agriornis montana* and *livida* species-groups, and the species of the subgenus *Muscisaxicola.*

Sympatry in Xolmis

If the *Xolmis fumigata* superspecies is considered as one geographical species, it is broadly sympatric with *X. striaticollis, X. erythropygia,* and *X. rufipennis.* These species show various degrees of habitat differentiation, so that habitat co-occupation may only occur between *X. fumigata* and *X. erythropygia,* whereas *X. striaticollis* and *X. rufipennis* are ecologically more distinct. The precise degree of habitat overlap between these species, however, is a problem needing future field work. In any event, this extensive sympatry makes it impossible to deduce anything about past speciation within the Andean species-groups of *Xolmis.*

In the *cinerea* species-group, sympatry is again too extensive for inferences to be drawn about the history of the group in extra-Andean open habitats.

Sympatry in Agriornis

Two species of *Agriornis* (*montana* and *albicauda*) are not only sympatric over large areas of the high Andes from Ecuador to northwestern Argentina, but they can also be found in similar habitats, at least in Bolivia (personal observation). Furthermore, *A. microptera* is sympatric with both *montana* and *albicauda* in parts of the altiplano of Bolivia and northwestern Argentina.

Sympatry in Muscisaxicola

The only species of the subgenus *Muscisaxicola* that lives in complete allopatry is *M. fluviatilis*, a lowland species. In the uplands and high Andes, especially south of central Peru, up to four or five species of this subgenus live sympatrically.

Sympatry in *Muscisaxicola* has long been known to ornithologists, yet no more than passing mention of the phenomenon can be found in the literature. As a result, the following discussion is compiled from my own field notes.

Altitudinal and ecological replacement is obvious in Ecuador between *M. maculirostris*, a species that lives in xeric steppes and brushlands in the inter-Andean region from about 2000 to 3700 meters, and *M. alpina*, a larger species that occurs in moister habitats such as meadows and bunch-grass from about 3500 to well above 4100 meters.

In central Peru, *M. maculirostris* ranges from about 1500 to 4000 meters, and broadly overlaps with *M. rufivertex*, which occurs from about 3000 to 4200 meters. At altitudes above 4000 meters in the altiplano of Peru and Bolivia, *M. alpina* (or *M. cinerea*), *M. juninensis*, *M. albifrons*, and locally also *M. maculirostris* and *M. rufivertex* occur together. Of the five species and superspecies, *M. rufivertex* seems to occur lower down, whereas *M. albifrons* is found only at the highest altitudes. I have seen and collected *M. alpina* and *M. juninensis* (or *M. cinerea* and *M. juninensis*) in the same habitats in Bolivia, and have also observed these two species with *M. albifrons*. In some localities, I have seen *M. cinerea* and *M. rufivertex* together, in others, *M. cinerea* and *M. maculirostris*. Thus true habitat co-occupancy involves usually two, but sometimes three, of the five species listed above.

Further study of these sympatric associations should be made to determine whether these species differ in habitat requirements, foraging sites, nesting habits, or in other details that might reduce competition among them. It is noticeable that the two semispecies of the *alpina* superspecies (*alpina* and *cinerea*) overlap in body size and bill size with *juninensis* and *rufivertex*. Thus food size partitioning may not be an important way of effecting ecological segregation.

This preliminary discussion of sympatry in *Xolmis*, *Agriornis*, and *Muscisaxicola* shows that this phenomenon is quite extensive in these genera. It would therefore seem that they have been present in the high Andes and the extra-Andean open regions of central South America for a long time, so long, in fact, that the early stages of their adaptive radiation have been obliterated by complex patterns of secondary sympatry.

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Chapter II. Behavior of *Muscisaxicola* and Related Genera

W. JOHN SMITH

ABSTRACT. Terrestrial species of tyrannid flycatchers in the genera *Muscisaxicola, Agriornis,* and *Xolmis* appear to be closely related to the less terrestrial species of *Xolmis* and to the essentially nonterrestrial genera *Ochthoeca, Pyrocephalus,* and *Sayornis* on the basis of characteristics assessable in museum skins. Although the ecological span of the group as a whole is great, specific habitat preferences, foraging methods, patterns of locomotion and nesting behavior all vary along continua that transcend generic limits. Further, members of all of the genera are shown to employ in similar ways displays that are alike in various aspects of form, and that do not appear to have converged as the result of selection pressures operating in the semi-open to open habitats. It is concluded that all of the species, both terrestrial and nonterrestrial, belong to one phylogenetic group.

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INTRODUCTION

The markedly terrestrial genus *Muscisaxicola* is one of the most extreme products of the South American radiation of the Tyrannidae. It is not the only genus committed to ground-dwelling, but its trim, longlegged, *Oenanthe*-like species are a close-knit group, strikingly different in aspect from better known tyrannids such as the kingbirds (*Tyrannus*), which perch on vegetation and forage largely by pursuit of aerial prey. A superficial examination of museum skins supports the usual arrangement of taxonomic lists which places *Xolmis* (herein including *Myiotheretes*) and *Agriornis* close to *Muscisaxicola* and suggests relationship to nonterrestrial genera such as *Ochthoeca, Sayornis,* and *Pyrocephalus.* The purpose of this paper is first to describe behavior—primarily foraging behavior, habitat preferences, and display (stereotyped communicative behavior)—in all but the last two genera, which are reported upon elsewhere (Smith, 1969, in press, 1 and 2, and 1967). Secondly, it is to show that this information supports the apparent phylogenetic relationship of all of these genera.

As subjects for a comparative study of behavior patterns, the terrestrial tyrannid genera appear promising, largely because of their open habitats. Easily seen birds are more easily studied than are birds obscured by dense vegetation. Thus, when I began in 1959 a series of comparative behavioral studies of a wide variety of tyrannids, I included a program on this group. Of the many tyrannids with which I eventually worked, however, these proved among the most difficult for reasons which had not been anticipated.

In the case of *Muscisaxicola*, for instance, most of my field work was in the Andes of central Chile. In early spring, several species were grouped into loose flocks at accessible altitudes, frequenting widely scattered good foraging sites where meltwater collected and where a carpet of green vegetation was present. When higher slopes became more open, they moved up in pairs and scattered. In these sparse populations there was relatively little display behavior. Most work in my first spring was on steep slopes where a bird could put itself out of sight by flying 50 meters, leaving me scrambling to locate it again. For my second spring in Chile I found better sites, but had less time available and lost most of that to an unseasonably late snowstorm that closed access to higher altitudes and brought the birds back down into their loose flocks.

An additional problem of work in early spring in central Andean valleys was high wind in at least the early morning hours when birds are most active. This wind made tape recording difficult, yet the recording was essential because accurate distinctions among the various calls in the repertoires of *Muscisaxicola* species cannot be made by the human ear.

Similar problems were met in briefer attempts to study members of this genus in areas other than central Chile, although reasonably dense populations of *Muscisaxicola maculirostris* were found in Ecuador, and of *M. brevicauda* in Peru. Within the other genera, both *Xolmis pyrope* and *Agriornis livida* were much rarer as breeding birds in areas accessible from Santiago, Chile, than I had surmised from the literature. *Xolmis pyrope* was more common on Tierra del Fuego, along with *Muscisaxicola capistrata*, although neither formed dense populations and both were in late phases of the breeding cycle when I was there. Again, Tierra del Fuego is almost continuously swept by high winds, hindering tape recording. Elsewhere, in northern Argentina both *Xolmis* and *Agriornis*, and in southern Brazil *Xolmis* species were not found in dense populations suitable for study of their displays. It seems possible that at least *Agriornis* species may customarily have very thinly scattered populations (see Goodall et al., 1957). Finally, I spent little time in regions where *Ochthoeca* species occur.

Under suitable conditions, there are advantages to comparative behavioral studies of several species in one season. Yet, with relatively undemonstrative species at low population densities, this tactic yields incomplete information. The alternative of studying one or two species at a time requires considerable financial resources and many seasons. In the present case, where the end was taxonomic and the field work was, for the most part, expected to confirm conclusions derived from less expensive methods, large expenditures did not appear justified. Accordingly, I devoted what field time I could allot to continuing a broad approach, even after initial experience showed this would yield quite incomplete results. Granted our nearly complete ignorance of these birds, even incomplete comparative information could be expected to provide useful perspective. I believe the results aid in making phylogenetic interpretations and justify the choice of tactic. It should be noted, however, that the observed sample of display behavior is too small to be of more than limited use in studies of communication per se.

The behavioral information is insufficient, by itself, to support the taxonomic views implied by my assignments of species to genera herein. This information is not intended to stand alone, but to be considered with Vuilleumier's work (Chapter 1, which includes a formal taxonomic conclusion).

This presentation is divided into two main parts; the first comprises nondisplay behavior: habitat preferences, foraging methods, methods of locomotion, and nest structure and placement. This is primarily to facilitate generic comparisons, and much detail about species has been omitted or stated briefly in a general form. While the data at hand would permit much more complete descriptions in some cases, useful species comparisons require even more information, gathered under a greater variety of circumstances.

The second part deals with display behavior, and all available data judged to be useful are presented. Because these data are limited, however, formal names have been assigned to the vocal displays only provisionally, and by comparison with the more thoroughly studied genus *Sayornis* (Smith, 1969, and in press, 1 and 2). These names are often reduced after their first appearance to initials (e.g., Simple Vocalization becomes SV). Illustrations of vocalizations are based on analyses (Sonagrams) made with a Kay Electric Company 6061-A Sona-Graph. In all figures the ordinates represent frequency marked in kilocycles per second, and the abscissae duration in tenths of seconds. In order to illustrate better the detail in the relatively brief vocalizations of the *Muscisaxicola* species, the temporal scales have been doubled (with corresponding halving of the frequency scales) with respect to the species of the other genera.

FIELD SITES

(1) Chile:

Most sites were in the central Andes, in two regions: (*a*) Lagunillas, about 60 kilometers east of Santiago, a relatively well-vegetated region centering around a ridge at about 2300 meters; and (*b*) farther east at the headwaters of the Río Yeso, a tributary of the Río Maipo near the Argentine border; a relatively arid, rocky region. The two main sites on the Río Yeso were the headwater lake at approximately 2500 meters, and about 3 kilometers downstream on a gravelly shelf where a small tributary stream descends from Cerro Morado to the east. In addition, one visit was made to sites at a similar altitude north of Santiago, Farellones and La Parva.

Agriornis livida was studied near Los Molles, Aconcagua Province, along the coast northwest of Santiago. Another coastal site was west of Santiago at Isla Negra, Valparaiso Province. A few observations were made on the outskirts of Santiago at Fundo lo Recabarren on Cerro Manquehue. Other Chilean sites were on Tierra del Fuego at the farm school Las Mercedes and at Cameron sheep station, respectively north and south of Bahia Inutil.

(2) Argentina:

Limited work was done in southern Tucumán Province, near La Cocha, and in the cordillera of western Tucumán above Tafi del Valle (about 2200 to 2500 meters) and in the pass of Infiernillo (3040 meters). A brief stop was made for *Xolmis irupero* on a gravelly river plain (altitude about 1400 meters) about 8 kilometers north of San Salvador de Jujuy.

(3) Brazil:

Observations were made in the interior plains of the state of São Paulo near Pirassununga and Bebedoura, and in savannas of the Territory of Amapá near Porto Platon.

(4) Peru:

My main site was in cotton fields near the coastal town of Lurin, about 35 kilometers south of Lima. Less time was spent in a steep-sided gully ("quebrada") of a tributary of the Río Rimac just west of Surco (about 80 kilometers east of Lima in the arid foothills at less than 2000 meters).

(5) Ecuador:

All sites were reached from Quito. The lowest were all within 5 kilometers of the town of San Antonio, an arid region on the equator about 25 kilometers north of Quito on the northern slopes of Cerro Pichincha. Another set of sites ranged from the pass between Cerro Pichincha and Cerro Atacaso about 5 kilometers southward in the páramo zone along the east face of Atacaso (over 3000 meters), as well as eastward, down from the pass about 4 kilometers to the upper reaches of good montane forest. Finally, two mornings were spent south of Machachi in the páramo on the western slopes of Volcán Cotopaxi, at 3800 meters.

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PART I. NONDISPLAY BEHAVIOR

Habitat Preferences

(1) *Muscisaxicola.* Among the most terrestrial of all tyrannids, these birds inhabit open country in the Andean chain and southern tip of the continent (for a zoogeographic account see Vuilleumier, Chapter I). Some (e.g., *M. capistrata*, *M. macloviana*, and *M. maculirostris*) usually frequent grass or other low vegetation, often among scattered bushes, while others (e.g., *M. cinerea*, *M. flavinucha*, and *M. albilora*) breed in less well-vegetated areas, usually among rocks. Rocks or bushes in all cases offer the birds commanding perches up to a meter or more tall; sometimes riparian trees are used.

The three smallest (*M. maculirostris*, *M. brevicauda*, and an eastern Andean one I have not seen, *M. fluviatilis*) inhabit relatively low altitudes for the Andean species.

Their habitats regularly include bushes and even trees. In coastal Peru, *M. brevicauda* lives in cotton fields, preferring sites with poor growth and foraging from the bushes or on the ground. Most of its natural habitats in Peru are also brushy (Koepcke, 1954, 1958), although on Ecuador's Santa Elena peninsula, Marchant (1960) found it in open country with or without bushes, as well as in "surprisingly thickly wooded places."

M. maculirostris inhabits the lowest altitudes of any *Muscisaxicola* species in the Chilean and Argentine Andes, along the upper edge of the zone of brushy vegetation among bushes up to 2 meters tall (where these are not contiguous), and extending above into rocky areas with fewer, much shorter bushes. In Tucumán Province, Argentina, the one pair found was in a grazed quebrada with few bushes and a riparian line of trees 8 to 10 meters tall; the birds perched within and on top of the trees. Ecuadorean sites varied from open, sparsely vegetated, steep, eroded slopes to brushy quebradas and fields of short corn, comparable to the cotton fields of *M. brevicauda.*

In early spring, all Andean species seen in central Chile frequented upland meadows and river flats with short green vegetation and copious meltwater, or foraged in mud beside melting snow. Such sites are ephemeral, and through most of the breeding season, most species have xeric sites with dusty soil and sparse vegetation. I have seen *M. cinerea, M. albilora, M. maculirostris,* and *M. capistrata* foraging on the banks and gravel bars of rivers and streams, and feeding by water may be common in other species (e.g., *M. fluviatilis*). Goodall et al. (1957) remark that most Andean species occur near lakes, although they also occur elsewhere.

Both Vuilleumier and I noted a tendency for dorsal coloration and/or saturation of color to match general characteristics of the surrounding habitat. Species inhabiting high rock deserts are grayest, those of lower, grassier areas are brown (grass is dry and brown through much of the time the birds are present). The two most southerly species and *M. alpina* in the wet páramo of Colombia and Ecuador are deepest and richest in color, and live in regions of relatively high rainfall. Similar color correlations are known from other tyrannids (e. g., *Tyrannus,* Smith, 1966) and probably reduce the conspicuousness of birds which spend most of their time perched very much in the open.

(2) *Xolmis* and *Neoxolmis.* (a) While terrestrial by general tyrannid standards, most *Xolmis* species are much less so than are *Muscisaxicola* flycatchers. Most perch above the ground and live among bushes or trees commanding a view of grass or swamp vegetation. *X. pyrope* and the more northern species east of the Andes often inhabit edges of woods or such brushy regions as the Brazilian cerrados, although some, like *X. velata,* are found on more open savannas. Species in the Andean foothills will live in brushy stream cuts where the surrounding countryside is open. Even *X. coronata,* which winters on the pampas, "seldom" runs on the ground (Hudson, 1920: 142) and often perches on the tall grasses; this has been confirmed for individuals wintering near Rosario, Argentina, by Dr. Juan Delius (personal communication). Wetmore (1926) reports *X. cinerea, X. coronata, X. irupero, X. pyrope,* and *X. rubetra* as occurring among and perching on bushes.

Even the most terrestrial species, *X. rubetra* and *N. rufiventris,* do not usually breed in fully open plains. Olrog (1959) gives the breeding habitat of the latter as shrubby open country ("campos arbustivos"). P. S. Humphrey (personal communication) found its principal breeding habitat to be "flat or gently rolling country, dotted with . . . shrubs about a foot or so" tall, and it was also common in rolling country with short grass tussocks. Maclean (1969) found the breeding habitat to be "flat, open, wind-swept pampa dotted with occasional *Berberis* bushes."

There is less tendency for dorsal coloration to match the habitat in this genus than in *Muscisaxicola*. *X. irupero*, for instance, is a conspicuous, exposed, white bird. Others are more cryptic. For example, *X. pyrope* and *X. cinerea* are dark gray and live in fairly wooded sites. *X. velata* is paler gray, overlaps with the darker *X. cinerea*, and tends to be in more open habitats. The most richly colored species, *N. rufiventris*, is again the southernmost.

(b) I have had very little field experience with members of the *fumigata* species-group of *Xolmis*. Pairs of *X. fumigata* were seen in Ecuador where plantations of pine or eucalyptus bordered pasture land on steep slopes at about 3000 meters. They perched in the lower limbs of trees or on telephone lines, often about 7 meters above the ground. Koepcke (1954) reports that *X. striaticollis* prefers more densely vegetated areas (around woods and small groups of trees) than do species of *Agriornis* and *Muscisaxicola* in the western Andes above Lima. Todd and Carriker (1922) in the Santa Marta region of Colombia found this species from about 2500 to 3600 meters, also along the edges of forest and in some more open sites with "stunted trees and shrubbery." Olrog (1959) says that *X. striaticollis* inhabits brushy quebradas and larger river valleys up to about 2500 meters in northwestern Argentina. In Ecuador and Argentina, Vuilleumier found the species in "open sites, but in Ecuador also on steep slopes where there were scattered bushes about 2 meters tall, and in eucalyptus plantations by pastures and streams."

Todd and Carriker (1922) also found the rare *X. pernix* at the edge of forest, and in "shrubbery." A single *Xolmis* (apparently related to *X. fuscorufa* and to *X. pernix*, see below) was seen by my wife and me on Volcán Cotopaxi in dense brushy páramo up to about 2½ meters tall in a steep-sided quebrada which extends far up into the grassy páramo at about 4000 meters. The habitat of *X. erythropygia* is given by de Schauensee (1964) as "scrubby open slope" in páramo.

From all accounts, the habitat preferences of this species-group seem to be like those of other *Xolmis* and the higher altitude species of *Ochthoeca*.

(3) *Agriornis*. *Agriornis livida* at Los Molles was in what was perhaps a natural habitat before the introduction of domesticated grazing animals to Chile. This subarid countryside had large patches of bushes, cacti, and bromeliads. Between the patches were relatively small but usually continuous areas of sparse, short, dry grass about 4 to 7 centimeters tall. In the same region the species was also on edges of relatively open, grazed fields with smaller patches of bushes and cacti not more than 3 to 10 meters apart. Perhaps the present scarcity of *A. livida* in Chile is due to the opening of the environment.

On the pass of Infiernillo in Tucumán Province, Argentina, the closely related *A. montana* was in arroyos at about 2200 to 3000 meters (I did not search higher). In these were small streams running amid grass, scattered rocks, and a few bushes. Open, grazed grasslands separated the arroyos, dividing pairs from one another. These grasslands had few rocks and thus lacked elevated perches. In Chile, Goodall et al. (1957) report this species on relatively barren but rocky Andean slopes, and Vuilleumier has found it mostly in rocky areas. On Mt. Pichincha in Ecuador we found *A. montana* in a very open habitat at the lower, shallow end of a large quebrada. There was no grass, and the one individual ran on bare, dry soil much like a *Muscisaxicola* species; it also perched and peered from the tops of scattered agaves and bushes.

Other *Agriornis* (probably also *montana*, see below) individuals were found higher in the same quebrada on Mt. Pichincha, and in another, higher quebrada. In both sites the slopes were well vegetated with bushes, bromeliads, agaves, and grasses, and appeared similar to the coastal *A. livida* habitat. Similar birds were found in even lusher habitat at about 4000 meters on the northwest slopes of Volcán Cotopaxi amid tall, dense grasses.

On the whole, the habitat preferences of this genus probably fall between those of northern lowland *Xolmis* species and the larger *Muscisaxicola*.

(4) *Ochthoeca.* Some dark-colored, relatively low altitude members of this Andean genus (e. g., *O. cinnamomeiventris*, Vuilleumier's observations) live in dense forests, others (e.g., *O. diadema* and *O. rufipectoralis*) in second growth or edge habitats at intermediate elevations, and species such as *O. fumicolor* primarily in the transition between brushy and grassy páramo. The relatively pale *O. leucophrys* inhabits arid, brushy, stream valleys over a wide range of altitudes. Most species apparently do not depend on open habitat and usually forage within and among trees or bushes.

Locomotion and Foraging Behavior

(1) *Flight and Aerial Foraging.* While flying at least several meters, a *Muscisaxicola* alternately flaps and folds the wings, using just one or very few flaps before each very brief fold. The flight is strong and rapid, and not undulating. In all but the longest flights the birds do not usually ascend far above the ground. *Xolmis* species have a similar flight, although they usually begin with a downward plunge from their higher perches and continue close to the ground. In both genera the end of a flight is usually a rapid glide on folded wings, the bird turning abruptly upward on opened wings to land. In short flights, birds of either genus may flap without intermittent folding, but still use the terminal glide.

The flight of *Agriornis* is similar, with fewer wing foldings. Members of this genus look relatively heavy-headed and short-winged in flight, more thrushlike than the previous species.

Both *Ochthoeca rufipectoralis* and *O. fumicolor* have slightly undulating flights with bursts of rapid beats and brief wing folding. In at least *O. rufipectoralis* a conspicuous pump of the tail came at the beginning of each burst of flapping, and occasionally a whirring sound came during a burst. In *O. fumicolor* whirring was much louder in intraspecific fights and in one probably interspecific situation, but was not heard under other circumstances.

All of the species do some aerial flycatching, and when perched, survey the air. In most cases the choice of foraging method appears to be based on availability of prey, but some species seem more prone to aerial flycatching than others. For the very terrestrial *Muscisaxicola* species most pursuit flights are steeply upward, but some extend laterally 20 to 35 meters, as in much more aerial genera such as *Tyrannus.* I have seen *Muscisaxicola maculirostris*, *M. brevicauda*, and *Ochthoeca fumicolor* flight glean (hover in front of a twig or flower head and pluck nonflying prey).

(2) *Perching and Locomotion and Foraging on the Ground.* In country without woody vegetation, the species of *Muscisaxicola* customarily perch stiffly upright on clods of earth, stones, or larger rocks. Where bushes or even trees are present, these provide additional vantage points. After scanning briefly from one point, most individuals dash to another, usually within 3 meters. These rapid dashes may employ running, hopping, or both. Running seems common only if a bird goes at least a meter, and only on quite level, unbroken substrate. Larger species may run much more often than the smaller species, and, also in keeping with the findings of Kunkel (1962) for other passerines, all species seem to use both modes. Even a running dash may begin and end with rapid hopping. I have confirmed some observations by tracking

the birds in light snow or fine earth, showing that even extremely rapid dashes may employ only hopping. Some species (e.g., *M. rufivertex*) often make a short flight instead of a dash, while others (e.g., *M. flavinucha*) almost always dash.

The relatively long tarsi of these species have been thought to permit greater speed in running. That running often gives way to hopping on broken substrates, however, suggests that long tarsi are probably also important in making long hops. Pettingill (personal communication to Vuilleumier) comments that long legs permit *M. macloviana* to stand high and thus see farther above its grassy habitat in the Falklands.

When a *Muscisaxicola* species sees prey, it approaches by a quick flight or dash. Prey was often discovered at the base of plants where litter had gathered. Individuals of at least *M. flavinucha* and *M. frontalis* sometimes proceeded from plant to plant, tossing litter aside with vigorous sideways swipes of the bill and peering at the site after each swipe. Feet and legs were never used for throwing litter.

In *M. albilora* and *M. maculirostris*, individuals have been seen to flash their wings open as they leaned forward after a dash or a flight toward prey. Sometimes this appeared to prevent them from falling forward by helping to check their speed. At other times, particularly if the bird did not lean forward, a very slight wing flick looked like an intention movement of flight (seen in *M. albilora, M. maculirostris, M. frontalis*, and *M. rufivertex*, and by Vuilleumier in *M. macloviana*). At yet other times, however, the movement in *M. maculirostris* appeared to be neither balancing nor intention. It was then very conspicuous, and might be repeated two or three times while standing still after a dash. In these cases it may have been stereotyped for conspicuousness, and probably functionally convergent with the "wing flashing" of other ground foraging birds like the mockingbirds (e.g., *Mimus polyglottos*, with conspicuous white wing markings, see Selander and Hunter, 1960; or *Mimus gilvus*, which lacks conspicuous wing markings, see Haverschmidt, 1953). Convergent evolution of wing flashing techniques has been shown by Cade (1962) for the Northern Shrike, *Lanius excubitor*, which sometimes forages on the ground, and similar techniques should perhaps be expected in other ground foraging birds—with or without conspicuous wing markings. Hailman (1960) has reached a similar conclusion, which he does not restrict to species that forage on the ground.

Muscisaxicola species frequently use intention movements. Most (perhaps especially *M. flavinucha* or *M. frontalis*) may "scissor" the tail open and closed on landing, or before and/or at the end of a dash. At least *M. frontalis* rarely gives a very brief, small amplitude wing flick with the tail movement. The frequency of tail-scissoring varies greatly, even in one individual over a few minutes, being most common if the bird appears nervous, or if other birds are foraging close by. As it often exposes otherwise inconspicuous white outer webs of the outermost rectrices, it makes a good flock signal (see Moynihan, 1960), and may occur primarily during flocking.

One *M. rufivertex* often flicked its half-fanned tail up-down at the end of a dash while foraging alone, usually with a very brief, small amplitude flick of its wings. Wing-flicking, not correlated with tail movements, was seen in a foraging *M. maculirostris*.

Each *Xolmis* species observed spent much less time on the ground than did species of *Muscisaxicola*. As Hudson (1920) says, these birds are "ground-gazers"; they usually perch on tall vantage points and peer downward, dropping to the ground if they see prey, or changing perch. Wetmore's (1926) observations of at least *X. cinerea* and *X. irupero* agree. I have seen *X. irupero* hover above the ground where no bushes were available for perching.

Most species hunt on the ground at least occasionally, though. I have seen both *X. pyrope* and *X. velata* do this, nearly always hopping slowly. Only one pair of *X. pyrope* dashed and paused in the fashion of *Muscisaxicola.* According to Hudson, wintering *X. rubetra* and *Neoxolmis rufiventris* run on the ground much more than the other species. J. Delius (personal communication) is familiar with the latter in winter and says that it does not make the repeated short dashes typical of *Muscisaxicola* species. Wetmore (1926: 302), however, describes *X. rubetra* as running "swiftly along the ground to pause and stand with head erect."

I have never seen *Xolmis* species take prey that was difficult to kill, but Hudson (1920) says they typically grasp beetles or grasshoppers with their feet while struggling to kill them.

Vuilleumier has seen *X. striaticollis* fly down from perches and forage in 30-centimeters tall grass. Little is known of the habits of this or other members of the *fumigata* species-group, but from his observations they appear similar to other species of *Xolmis* or to *Agriornis*, as might be expected from their size and structure.

Foraging of *Agriornis livida* and *A. montana* is similar to that of the previous genera, and in some ways intermediate. Periods of a minute or more are spent peering about from the top of a bush, bromeliad, or a rock, followed by dropping and running to another perch. Sometimes food is taken from the ground during such a dash; this has been large invertebrates in the few cases I have seen. At least *A. livida* sometimes gleans food from branches accessible from its perch. Goodall et al. (1957) say these species take large prey (small mammals, lizards, amphibians, and birds' eggs and nestlings), as well as insects. Goodall's figure of *A. livida* shows a bird holding a mouse under one of its large feet. Peña (1961) recovered seeds, plants, insect remains, and a wing-bone of a small bird from stomachs of *A. montana;* he also observed an *A. montana* killing a "small mouse." Birds of this genus, even more so than those of *Xolmis*, quite likely grasp prey in their feet and beat it with their bills. They appear to be, as Goodall et al. claim, ecological counterparts of shrikes.

The three *Ochthoeca* species I have seen all often pumped the tail (up-down, as in all of the species in this paper) with a simultaneous brief, small amplitude flick of the wings. These movements came on landing or when perched, and their frequency increased if I made a bird nervous. *O. leucophrys* and *O. fumicolor* both did mostly aerial foraging, and the latter several times sallied out to flight glean from the páramo grass or to take prey flying over the páramo. In 1959, while an *O. fumicolor* kept in the edge of a grove or worked over the páramo, an *O. rufipectoralis* worked through the same grove, hopping from twig to twig and gleaning like a *Vireo.* Vuilleumier has seen *O. leucophrys* fly down to the ground for prey.

Although the data are scanty, it appears that *no* known species of these genera is *primarily* an aerial flycatcher. All spend considerable time as gleaners, taking much of their food from the surface of the ground or of the vegetation.

Flocking

In at least central Chile, while lush early spring sites are available and snow-covered higher slopes are not, large numbers of *Muscisaxicola* flycatchers may forage together. The species of large flocks intermingle, to some extent, with less abundant species clumping amid the more numerous individuals of other species. I have never seen a fully stable flock, and there is always some intra- *and* interspecies aggression. Birds of larger species often supplant individuals of smaller species; individuals of different species that are about the same size occasionally fight vigorously.

As higher sites open and the flocks thin out, aggression appears to increase. I have then seen temporary territories in which one individual foraged for some minutes and drove out all intruding conspecific individuals. Individuals of other species might be driven out or tolerated. These appeared to be foraging territories only, and were small—three to seven meters across in most cases—in sites that were exceptionally wet and covered with low, green vegetation.

Hudson (1920) mentions single-species flocks of several wintering species of *Xolmis* in Argentina. Further, *Neoxolmis rufiventris* is said by him to associate with flocks of plovers. Whether these were really mixed flocks or aggregations resulting from patchy distribution of habitat is not clear. The same may be said of the interspecies flocks of *Muscisaxicola.*

I have found no indication that members of the other genera (*Agriornis* and *Ochthoeca*) flock outside the breeding season. Within the breeding season all are reputed to be found only in pairs. Flocking behavior does not seem to be characteristic of this group outside of migration, and may play an important role only in *Xolmis.*

Nest Construction

The open, cup-shaped nests of *Muscisaxicola* species are always placed on the ground in crevices between rocks, or even within a rabbit burrow (e.g., *M. capistrata*, personal observation). Only *M. brevicauda* does not always employ crevices, and where its nests are hidden by grass alone they are often partially roofed with grasses (Marchant, 1960).

Most *Xolmis* species build open cup-shaped nests in bushes or trees, although *X. irupero* hides its in holes in trees (Hudson, 1920; Wetmore, 1926), or appropriates an enclosed nest of *Furnarius rufus* (see Hudson, 1920). *X. cinerea* is said to nest in holes in banks in Argentina, but to build an open nest in trees in Brazil and Uruguay (von Ihering, 1904; Hudson, 1920). *X. coronata* nests either in a bush or in a "large clump of grass" (Hudson, 1920), but apparently not on the ground. The only described nest of *Neoxolmis rufiventris* was on the ground (Maclean, 1969).

The species of *Agriornis* also build cup-shaped nests in bushes, except for *A. montana*, which nests on the ground amid rocks like a *Muscisaxicola* (Goodall et al., 1957). Nests of *Ochthoeca* species and *Pyrocephalus rubinus* are open cups, usually in bushes or trees. Todd and Carriker (1922) report a nest of *Ochthoeca rufipectoralis* that was placed on "a projection on the side of a huge boulder, sheltered by some stunted trees," apparently comparable to the nests of *Sayornis* species.

PART II. DISPLAY BEHAVIOR

The following accounts present what is known about the form and employment of stereotyped signals ("displays") used by these birds in communicating. A detailed description of the display repertoire of *Muscisaxicola albilora* provides a basis for comparison. The displays of two small *Muscisaxicola* species are also described in detail: that of *M. maculirostris* to show its comparable structure, even though it sounds simpler to the human ear, and that of *M. brevicauda* because (*a*) it is at least superficially somewhat aberrant; and (*b*) the species has customarily been placed in the monotypic genus *Muscigralla*, usually not seen to be related to *Muscisaxicola* (Hellmayr, 1927: 94, was not even sure it belonged in the Tyrannidae).

Where possible, comparisons are made with displays of *Sayornis* species, since these are known in much greater detail and provide a coherent frame of reference (see Fig. 11). Occasional comparisons among species are made in this section to facilitate description, but general comparisons follow in the Comparative Summary.

IIa. *Muscisaxicola*

Muscisaxicola albilora

Most individuals of this species were still in loose flocks, although many appeared paired, on 5 November 1961, at

Farellones and La Parva, Chile. On 7 and 8 November those at the Río Yeso sites all appeared paired, but were foraging communally at the best sites and showing only slightly more frequent territorial behavior. Several kilometers farther into the interior of the Andes along the Río Volcán on 8 November there were flocks of over 60 individuals, plus lesser numbers of at least two other congeneric species. By 17 November most snow at the upper Río Yeso site had melted, and much more green vegetation was scattered about. Most pairs had dispersed onto the slope, and I found one nest being built among the boulders on an unstable talus slope. There was some communal foraging at the best local site, however, the edge of a large meltwater pond.

In 1962 the upper Río Yeso site was almost entirely snow-covered on 15 October, and had no *M. albilora*. On this and the subsequent day only three small groups were at the lower site; the individuals associated with almost no display and only occasional supplanting attacks. A few lone individuals occasionally held temporary territories, but with little display.

Vocal Displays

(1) In agonistic encounters increasingly prominent aggressive tendencies are expressed by the more or less graded series: "tseet" and "tseek," "tut," "tsk," "tchk," and "tk." Most are known primarily from males. Both "tseet" and "tseek" (Fig. 1a and b) may occur very early in agonistic encounters, and "tut" (Fig. 2c) and "tsk" (Fig. 1d) at various points, but "tchk" (a more sharply peaked variant of "tsk") and "tk" (Fig. 2d, perhaps a high, brief, extreme variant of "tut" with different harmonic structure, an extended peak, and prominent descending terminal arm) are almost restricted to fighting, as two birds grapple.

(2) As avoidance or escape become more probable, "tseet" or "tsk" calls are replaced by more prolonged vocalizations: "teek" (Fig. 1c) and "seet" (Fig. 1e, and with a slight tendency to show two peaks in Fig. 1f), respectively. During agonistic encounters, fights are often separated by periods in which the quarreling birds stand apart and usually do Wing Raising displays while one individual utters long strings of "seet." In at least some encounters, however, it was this individual which later pressed the attack again.

(3) A bird flying or landing alone may utter a single "tseet." This is more likely to be a "tseek" or especially a "teek" (Fig. 1c) if the communicator is flying toward its mate. The usual reply by the mate is a "tsk," but if both individuals are in flight toward each other there is often a rapid jumble of quite variable calls (e.g., Fig. 1g), perhaps not all uttered by one individual. These include "tseek," "seet," "tsk," and even "tchk," plus special forms such as the third and final in the illustration, which are probably the only ones peculiar to greeting usage. Sometimes in less agonistic situations, however, mates employ a simpler stereotyped greeting (Fig. 1h).

Bursts of a simple, chevron-shaped call, "tuh" (Fig. 2a), have been heard and recorded only from apparently paired birds foraging together when there has been no agonistic activity for at least several minutes. Bursts of a higher form (Fig. 2b) appear intermediate to some greetings. The similar "tut" call (Fig. 2c) is sometimes uttered, singly, from mates while foraging.

(4) In one Aerial Display a loud "clee-ip" (not recorded) was heard; it was quite reminiscent of the corresponding call of *M. maculirostris*, but with a more abrupt termination.

Most of the known vocal displays of *M. albilora* are thus unelaborate calls linked by extensive sets of intermediates. Only the most different forms, such as "tuh" and "tseet" are easily distinguished by the human ear, although many of the others are recognizable with practice. The more agonistic vocalizations resemble in form

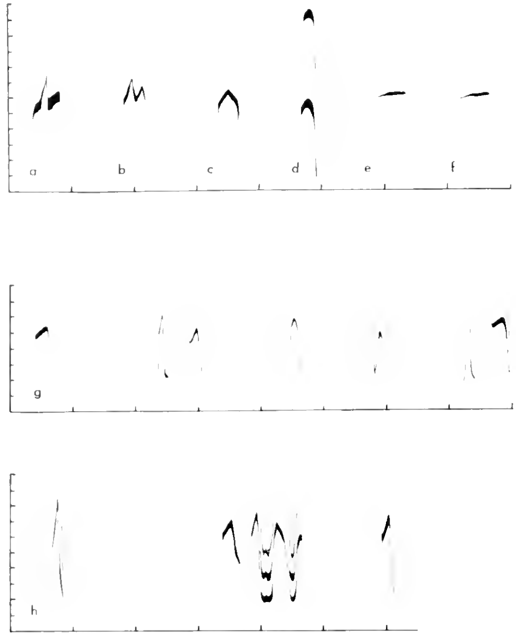

Figure 1. Vocalizations of *Muscisaxicola albilora*: 1a. "tseet"; 1b. "tseek"; 1c. "teek"; 1d. "tsk" (compare with Fig. 11a); 1e. "seet"; 1f. "seet" (note the slight tendency toward two peaks in this case); 1g. an example of a variable greeting; 1h. an example of a greeting in a less agonistic situation.

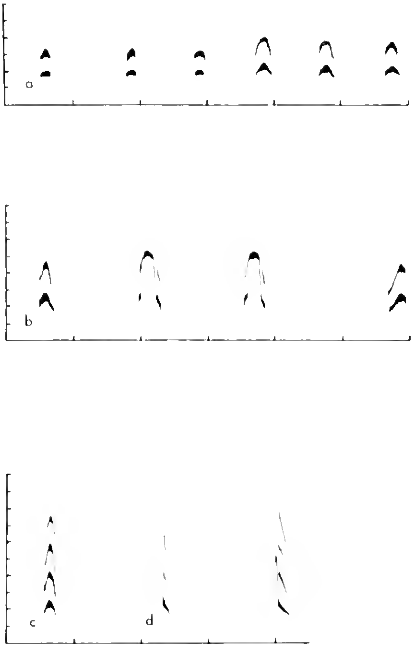

Figure 2. Vocalizations of *Muscisaxicola albilora*: 2a. a burst of "tuh" calls; 2b. a burst of higher "tuh" calls (note general similarity to Fig. 1g); 2c. "tut"; 2d. two examples of "tk."

and usage calls of *Sayornis* species. For instance, "tseet" is comparable to the Initially Peaked Vocalization (IPV) of all *Sayornis* species, "teek" resembles the Simple Vocalization (SV) of *S. nigricans* and "tsk" the SV of *S. phoebe*, and "tseek" somewhat resembles the Bipeaked Vocalization (BV) of *S. phoebe* and *S. nigricans*. As in at least *S. phoebe*, greetings between mates during or shortly after agonistic situations usually involve SVs, BVs, or IPVs, and the special greeting vocalization of *M. albilora* resembles that of *S. saya* and to a lesser extent, that of *S. phoebe*.

None of these possibly homologous calls corresponds exactly to each other in specific usage. The fit is probably least good for the bursts of "tuh" calls of *M. albilora*, which may be only superficially similar to the Chatter Vocalization (CV) of *S. saya*, and the Doubled Vocalization (DV) of *S. phoebe*. (In comparing forms, note that the scale of Figure 11, showing sample *Sayornis* vocalizations, is like that used for the remaining genera of this paper, but proportionately condensed along the time axis and elongated along the frequency axis as compared with the scale used to illustrate the very brief *Muscisaxicola* vocalizations.)

Nonvocal Displays

(1) *Wing Raising*. In prolonged aggressive encounters birds within a meter of one another may raise one or both wings. Encounters in which neither individual is very active usually lack Wing Raising. The minimal form has been seen when two birds, sometimes one member of each of two pairs, approach each other during

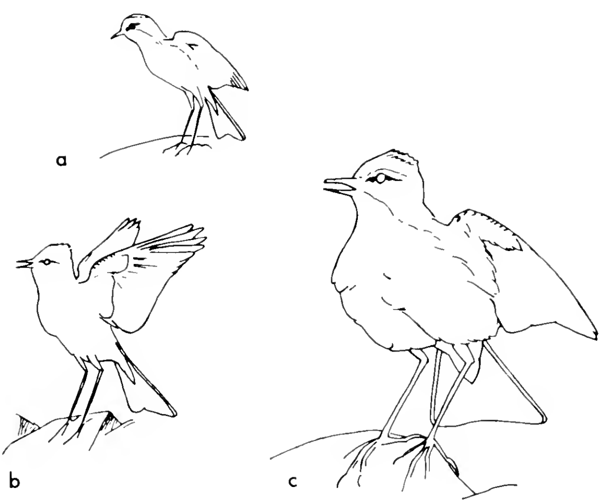

Figure 3. Some Visible Displays of *Muscisaxicola albilora*: 3a. minimal Wing Raising with one wing, and slight Head Bow; 3b. Wing Raising with synchronous fluttering of both wings; 3c. asynchronous Wing Raising with Crown Ruffled, and ruffling of the flanks and chest.

foraging. One or both may "casually" lift one wing very slightly (Fig. 3a) without other display, and not facing its opponent. In such instances no fights result, and the birds usually go their separate ways.

There may be fights, however, when two or more pairs come together after prebreeding flocks have scattered. Simple raising of one wing by one or more individuals comes early in such encounters; later the movement becomes jerky and abrupt, and the second wing begins to be jerked slightly up. Often the two wings are lifted to different extents and asynchronously, or both are raised at once and wagged irregularly in an asynchronous, "semaphoring" pattern emphasized by the pale color of the wing undersurfaces. Less commonly, both are lifted high over the back and fluttered in unison (Fig. 3b). Rarely, a bird in this pose flies perhaps three to five meters between two rocks, still with its wings high and fluttering. This resembles part of the Aerial Display, and it is likely that Wing Raising and that display intergrade, although I have not seen the remaining intermediates. Any flight during a Wing Raising encounter will likely terminate with the wings held high, and partial raising in what appears to be a flight intention movement is common between bouts of Wing Raising. The tail is fully spread in most forms of the display, but not flicked.

The flanks and chest are ruffled during at least some phases, and the Crown Ruffled accompanies all but the simplest forms (Fig. 3c). Thus Wing Raising shows several special plumage features: pale wing linings, pale bases to the primaries on the upper wing surface, and the occipital crown-patch.

Opposing individuals orient variously but usually laterally; a tendency to orient sideways to the opponent seemed strongest when both wings were held high. I could detect no obvious preference to raise, or to raise first the wing closer to or farther from the opponent.

A few times, up to five individuals, apparently including two pairs, partook in an encounter. In the most vigorous periods of activity all used Wing Raising. Rapid and confused chasing and fighting developed, and long chases went beyond effective observing range. In one encounter between two pairs the display of two individuals proceeded as far as two-wing semaphoring with only an occasional "tseet," and no fight or chase resulted. After about a minute of stalemate one individual performed an Aerial Display.

Sayornis saya and probably *S. nigricans* have displays similar in form to Wing Raising and the forms of Aerial Display closest to it, but these appear to function in what is probably pair-bonding. As I have seen neither territorial defense in those two *Sayornis* species, nor pair-bonding in *M. albilora*, the functional comparison is incomplete.

(2) *Aerial Display.* On 5 November 1961, an individual several times silently chased an intruder from what was probably a potential breeding territory. It then began to fly, climbing slowly with wings held high over its back and used in bursts of short strokes. Its long legs dangled and the feet appeared relaxed. The dark tail was held vertically down and fully spread. The bird remained silent. It often simply hovered, sometimes climbed higher, and frequently turned to a new direction, remaining over a limited area. Finally it descended in a long, fast swoop with its wings closed until near landing, and perched stiffly upright atop a group of rocks.

At another site on 17 November 1961, a bird left a stalemated Wing Raising encounter (q.v.) and flew up in a *Tyrannus*-like twisting flight of about 20 to 25 meters, then swung around and dropped quickly to a foraging area. During the flight it uttered several loud, abrupt "clee-ip" calls.

(3) *Crown Ruffled.* During Wing Raising disputes all birds ruffled their crowns, either entirely or just at the rear. This made the head appear larger, and also made very conspicuous the occipital crown-patch, the rusty color of which is species-specific.

Establishment of a temporary foraging territory was watched on 16 October 1962. The owner foraged vigorously for several minutes before a conspecific individual arrived. The intruder was immediately driven to the edge of the area without display, but it persisted in reintruding over the next three minutes. The territorial owner always caused it to retreat by dashing toward it without display. The trespasser never faced toward the owner, and would ruffle the back of its crown as soon as it began to be pressed and on stopping after a chase.

(4) *Head Bow.* On 5 November 1961, two individuals were observed about 60 centimeters apart, oriented almost toward one another and bowing their heads, thus revealing the ruffled patch of color at the back of the crown. Occasionally one or both uttered a barely audible "tseek." Before anything further happened one saw me and ran off, the other following several meters behind.

Muscisaxicola frontalis

In 1961 individuals of this species were observed foraging by a pond where some interacted with *M. albilora.* In 1962 three were observed foraging in loose association.

Actively foraging individuals uttered two different calls: "trit" and "treet" (Fig. 4a and 4b). They resemble, but at much lower frequencies, "tseet" and "seet," respectively, of *M. albilora.* One individual, apparently nest site prospecting while foraging, uttered short bursts comprising several "pt" vocalizations at two frequencies (Fig. 4d); these were like the "tuh" of *M. albilora*, and the usage strengthens the comparison of such calls with the CV of *Sayornis.* Yet another foraging individual used a "tuk" (Fig. 4c, like the "pt" but higher, briefer, and uttered singly instead of in bursts—i.e., resembling the "tut" of *M. albilora*).

I recorded several sharp "t" calls from an *M. frontalis* as, and shortly after, it fought with an *M. albilora.* These resemble the "tk" used by the latter species in fights, but emphasize the initial ascending arm and almost omit the descending arm. All known vocalizations of *M. frontalis* thus correspond in form, and in general usage, to calls of *M. albilora.*

Muscisaxicola flavinucha

Displays were observed only on 26 September 1962, when a heavy spring snowfall at Lagunillas, Chile, brought birds down from higher altitudes. Three *M. flavinucha* appeared on my study area before snow accumulation exceeded 2.5 centimeters. They associated loosely while foraging, and one made occasional silent supplanting flights against the others.

Once the aggressor stopped about 60 centimeters away from another without supplanting. The approached individual stood still with its head withdrawn between its shoulders, and began to call. There were some short bursts such as "tsee tee tsee tseet." Other calls were more irregularly spaced, but sounded similar, and were like calls recorded from *M. albilora* during greetings. Both ruffled their upper backs. The calling one maintained an oblique orientation toward the other for about 90 seconds, then the latter wandered off, and eventually flew away.

Vuilleumier (personal communication) has heard vocalizations from two adults feeding large nestlings at Cerro Llaima (Cautín Province), Chile: high-pitched "seeht" and "seeseeht." A fledgling he watched being fed at Cerro Catedral (Río Negro Province), Argentina, begged with a thin "see . . . . see . . . ."

Muscisaxicola rufivertex

On 12 October 1961, several separate individuals were seen on steep slopes near Lagunillas, Chile. In mid-afternoon two flew from opposite sides of a rocky stream bed out over a gully, somewhat toward one another without approaching closely. Both performed Aerial Displays. Each would fly about 16 meters then rear up until hanging vertically and stall with wings stretched fully above its back, at this point uttering a thin, high-pitched "twee-it." This was repeated several times, then both turned back and repeated it several more times before landing on the slopes. Neither displayed further, and later in the season they apparently ascended to higher altitudes as the snows melted.

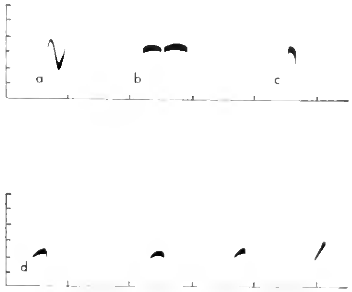

Figure 4. Vocalizations of *Muscisaxicola frontalis*: 4a. "trit" (compare with Fig. 1a); 4b. "treet" (compare with Fig. 1f); 4c. "tuk" (compare with Fig. 2c); 4d. burst of "pt" vocalizations (compare with Fig. 2a and 2b).

On 16 October 1962, two apparent pairs foraged on the rocky outwash plain of a small stream at the lower Río Yeso site. The one pair flew to a bush about 1 meter tall, one perching on top and aligning at right angles to the pair still on the ground. This upper one began occasionally lifting and waving one wing, the wing toward the other pair. It had its chestnut occipital patch conspicuously elevated (i.e., Crown Ruffled). The other pair was then about 10 meters away, the nearer individual facing the bush and Wing Raising vigorously, usually with both wings. Within a minute they flew toward the same bush, landing within 60 centimeters of the first pair. The first individual now aligned slightly more away, but continued to raise its wing. The "aggressor" oriented its body to within five to ten degrees of the first and raised both wings. Both had Crowns Ruffled, and I could hear "tee" vocalizations poorly over the high wind.

Within a minute, the individual which had approached dropped back to a second

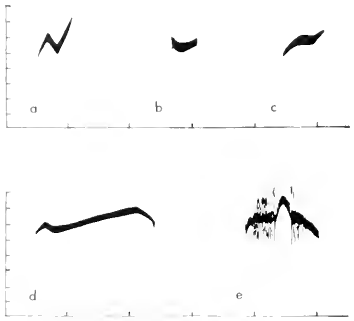

Figure 5. Vocalizations of *Muscisaxicola capistrata*: 5a. "tueee" (compare with Fig. 1a); 5b. "tee" (compare with Fig. 1e and 1f); 5c. a common vocalization, intermediate between the previous two; 5d. clear "seeee" of a nestling, begging; 5e. loud and harsh call of a nestling, in the hand.

bush 70 centimeters farther away, and continued vigorous Wing Raising. The first then flew about 6 meters followed by its apparent mate; the other pair followed to within 2 meters, and all displayed as before. The first pair then flew another 6 meters away, the displaying individual raising both wings over its back and gliding to its perch. This ended the encounter; within 45 minutes all four birds had left the area.

All known displays of this species are comparable in form and usage to displays of *M. albilora*. Note that Wing Raising with both wings characterized the more aggressive bird, and wings raised high in flight appeared in a situation similar to that in which it occurred in *M. albilora*, again resembling an intermediate between the Aerial Display and Wing Raising.

Muscisaxicola macloviana

Hudson (1920) described "low plaintive whistling notes" given by this species when wintering, perhaps what Pettingill (personal communication to Vuilleumier) called a "reedy cheep."

Muscisaxicola capistrata

Observations were made from 4 to 8 December 1961, on the farm "Las Mercedes," Tierra del Fuego, Chile. One nest was located with three young, about a week old. Other local pairs probably had nests, and there were also apparently a few independent fledglings.

Vocal Displays

(1) While I examined nestlings, one adult sometimes called a "tueee" (Fig. 5a), closely similar to the "tseet" of *M. albilora*, but with its two peaks respectively low and high instead of the reverse. It did not approach close to me and usually called only when its mate flew to perch near it.

(2) A variable "tee" (Fig. 5b) was used by both parents while I examined their nestlings, and the one which approached me closer uttered only this call. It is similar to the "seet" of *M. albilora*, the main difference corresponding to that of the previous case: the second peak is higher in *M. capistrata*.

Intermediates between "tueee" and "tee" (e.g., Fig. 5c) were common on each occasion I examined the young. During five consecutive days, however, I heard no other vocalizations from any adults.

(3) Nestlings removed from the nest-burrow uttered two quite variable calls (Fig. 5d and e). One was a simple, clear "seeee" with rising inflection, and the nestlings were sometimes begging when uttering it. It resembles the IPV of *Sayornis saya* nestlings. The other was loud, had an initial ascending arm, terminal descending arm, and often something resembling a chevron between, but with gaps filled with harsh noise separating all three sections.

Nonvocal Displays

(1) *Feather Ruffling*. The parent which approached me closely uttering "tee" remained conspicuously sleeked. Its mate usually perched 3 to 7 meters away, called "tee" frequently, and sometimes ruffled its chest, flanks, and the sides of its head. (At least the first two areas were ruffled

by some *M. albilora* when Wing Raising, but the present species did not Wing Raise in the several intraspecific fights observed.)

(2) *Wing Whirr.* Very loud Wing Whirring was heard in some intraspecific fights, and was likely a display. Loud Wing Whirrs were also produced by the bird hovering near me at the nest. (A Wing Whirr was also heard from one *M. frontalis* in a situation I could not be sure was display, but possibly this sound need never be produced in any wing stroke functioning solely for flight.) Its usage corresponds to that of a similar sound of *Sayornis phoebe.*

(3) *Aerial Display.* On the afternoon of 4 December a lone individual made two silent display flights within three or four minutes. The bird made little headway against a wind of about 30 kilometers per hour. It simply flew up about a meter, raised its wings high over its back, and fluttered briefly until poised in a vertical stall with wings stretched maximally upward. Then it fluttered again, repeating the procedure two or three times per flight. This was probably the sort of intermediate between Wing Raising and full Aerial Display which was missed in *M. albilora.*

Muscisaxicola maculirostris

I observed this small species during several periods: shortly after its arrival on breeding grounds (13 September to 16 October 1962, Chile), during nesting (9 to 17 June 1966, Ecuador, and 28 November 1962, Tucumán, Argentina), late in the breeding season (4 to 6 August 1959, Ecuador), after the breeding season (13 January 1962, Chile), and in midwinter (4 to 6 February 1962, Ecuador). Although at one Chilean site (Lagunillas) and at all Ecuadorean sites near San Antonio population densities were high, there was never much interaction or much displaying.

Vocal Displays

(1) Its basic call is "tek," most variants of which are indistinguishable in the field. Extensive tape recorded samples show that its variations tend to correspond to the various briefer calls of *M. albilora,* but are insufficient to show the limits of each.

The "tek" itself probably corresponds roughly to the "tut" form of *M. albilora,* is often repeated at similar intervals, and has the same chevron shape but not the harmonics (Fig. 6a). Foraging individuals often repeat it for minutes at a time, but are silent for similar periods. Usually it comes at or just after the end of a dash, or while the bird is stopped and peering around.

A bird which has just been fighting, or which has watched a hawk or owl pass by may utter "tek" and slight variations frequently. It was occasionally used in mobbing a small predator such as the Burrowing Owl (*Speotyto cunicularia*) or Sparrow Hawk (*Falco sparverius*), at least in Ecuador where these are common and were often ignored or mobbed in a "desultory" fashion without displays. Sometimes when we appeared to make an individual slightly nervous it would begin to call "tek."

Occasionally, slightly higher pitched forms can be distinguished. These are most often uttered by a bird about to join another (or about to be joined), or one which is foraging near another and appears slightly nervous. They probably correspond to the "teek" of *M. albilora.* Other variants are lower or more prolonged, or have a more prominent tail (like a small "whee-oo" call, q.v.). The prolonged ones may be used primarily by relatively fearful birds. No known vocalization clearly corresponds to either the bi-peaked "tseek" or the "tseet" of *M. albilora.*

(2) I have recorded nothing as flat as the prolonged "seet" of *M. albilora,* but did obtain some relatively long, variable, asymmetrical, squeaky calls (e.g., Fig. 6b) from an apparently partly cowed and indecisive individual. It had begun to crouch after running toward several individuals that were responding to the overflight of a large hawk with Aerial Displays. The area was

the site of several intraspecific encounters and was likely a boundary region among ill-defined territories. Once a grappling fight there terminated on the ground, then the attacked bird crouched low with wings outspread and uttered a "squeal" (probably more prolonged than in Fig. 6b) in the brief interval before it was again attacked.

(3) No greetings were recorded from mates meeting in agonistic circumstances. However, two probably intergrading sorts of calls were found, each with a single peak preceded by a sharply descending arm. The forms resemble BV-types recorded in agonistic greetings of *M. albilora*. The first (Fig. 6c) is relatively prolonged, and was recorded from the individual which next uttered the call shown in Figure 6b, just before it stopped approaching the others. The second (Fig. 6d) tends to occur in agonistic encounters, including fights, and may be repeated in series before an Aerial Display (Fig. 6g shows the end of such a series). Such series, however, usually becomes composed just of "tk."

In relatively nonagonistic meetings mates seldom called, and then usually used "tek" or a closely similar SV variant. I very rarely heard calls that could have been similar to the LHV-type display of *M. albilora*, and obtained no recordings.

(4) The "tk" is slightly briefer and lower than "tek." It may be uttered in series before launching an Aerial Display, or in rapid series while standing and watching a neighbor's Aerial Display. Other uses correspond to the known uses of "tuh" series by *M. albilora*.

The descending arm of "tk" is characteristically more emphasized than is the ascending. From two fights, one in Ecuador and one in Chile, I recorded versions virtually reduced to a prominent descending arm (Fig. 6e and f), and thus comparable to its apparent homologue in *M. albilora*. The Chilean example is much lower in frequency than the Ecuadorean. Shortly after the Chilean fight (between two males establishing territories), one of them did an Aerial Display and upon returning gave a similar burst of low "tk" as he landed alone.

Similar brief "tk" variants, usually at fairly low frequencies and not in series, were also used in fights, and many by an individual standing outside one fight as a spectator. He became the aggressor only when the first aggressor withdrew.

(5) The Aerial Display vocalization has two parts, the second of which commonly occurs alone when the display is used after dawn. The first is a series of "tk" or sometimes "t," which seems to be a very brief "tk." This accelerates toward the end, then rises in frequency either through several units (Fig. 6g) or in one unit (Fig. 6h). The second part is a clear, whistled "clee-oo" or "whee-oo." In one Ecuadorean bird this had a relatively prolonged tail and harmonics (Fig. 6i). When combined, the two parts resemble the Regularly Repeated Vocalization (RRV) of *Pyrocephalus rubinus* (Smith, 1967) and the CV plus IPV of *Sayornis saya* (Smith, in press, 2).

(6) The sole nestling examined repeated almost continuously a faint, rapid series of variable "ti" units (Fig. 6j) as my wife held it in her hand. This is not yet known from congeneric species, but in *Sayornis phoebe* and *S. nigricans* the "tee" of nestlings is very similar and may be used in bursts.

Almost fully grown fledglings sometimes uttered rapid series (probably corresponding to the nestling call) and gaped toward an adult. When they were about to be fed the series seemed to become high pitched. If I approached such a fledgling closely it would usually begin to call "tek."

Nonvocal Display

(1) *Aerial Display*. In the most complex form the bird flies out (or outward and upward if the slope is not steep) and begins a flat, fluttering flight, calling a string of very brief "t" or "tk" units, sometimes

jerking slightly back with each call. As the series accelerates the frequency of the last few units ascends and the bird climbs sharply into a stall. Just before stalling, the tail flicks up, then drops straight downward and spreads. The bird comes to hang vertically in the air, dangling its legs and feet. Its wings stretch over its back and nearly touch together as it utters the clear "whee-oo" and then pitches forward. Regaining speed, it retracts its legs and flutters on in another performance. The flight is straight or twisted, and in the latter cases remains over a small piece of ground. After from one to about fifteen (commonly about five) stalls, the bird flies back to the slope or partly closes its wings, slightly cocks its tail, and dives to the ground. Peters (1923) gave an accurate but much less detailed description.

There are various less complex forms. Just the terminal "whee-oo" may be uttered, which is very like counterparts of the display known in *M. albilora* and *M. rufivertex*. At least in Ecuador in 1966, this was the common form after extensive predawn usage of the full form. Flights were then usually given in response to the passage overhead of an avian predator or in response to Aerial Display by a neighbor. The latter individual might be close to a boundary and the two displaying against one another, or (more commonly) might be responding to an avian predator—the first *Muscisaxicola* to go into Aerial Display when a Sparrow Hawk or *Buteo* passed seemed to precipitate the display from most of his neighbors.

Sometimes a bird calling "tek" would launch into Aerial Display without an introductory series. More commonly, a series of "tk" calls was uttered before the bird took flight—these may have replaced the usual aerial calls. Sometimes such a "tk" series would build up in speed and then slow down, the bird lapsing into "tek" without an Aerial Display. Fully complex Aerial Displays were never preceded by a "tk" series from the ground.

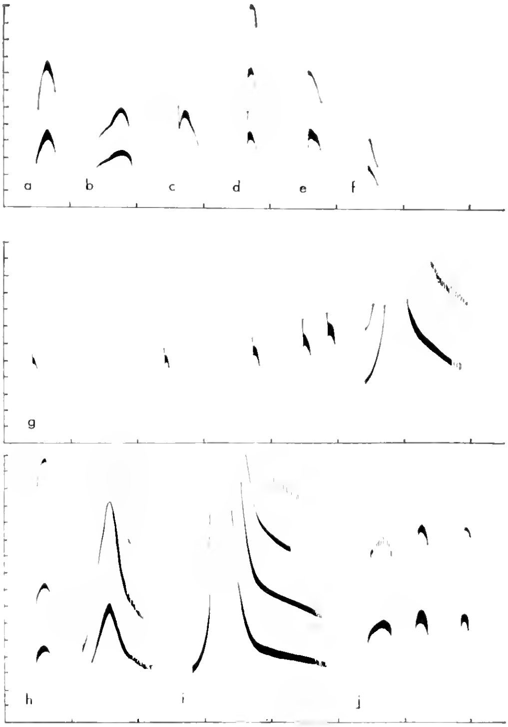

Figure 6. Vocalizatons of *Muscisaxicola maculirostris*: 6a. "tek" (compare with Fig. 1c, and first vocalization of Fig. 1g); 6b. squeaky sounding vocalization (compare with Fig. 1e and 1f); 6c. vocalization recorded from an individual running toward a fight, just before stopping and crouching; 6d. a somewhat similar form, used in fights, agonistic encounters and sometimes in series before an Aerial Display; 6e. "tk," recorded from a fight in Ecuador (compare with Fig. 2c and 2d); 6f. "tk," recorded from a fight in Chile (compare with Fig. 2d); 6g. vocalizations from an Aerial Display: the end of a "tk" series, with the last intervals shortening, and the last several "tk" rising in frequency before the "whee-oo"; 6h. vocalizations from an Aerial Display: the "tk" series is not shown, but ended in a single relatively high unit, followed by the "whee-oo"; 6i. a "whee-oo" vocalization with a relatively prolonged tail; 6j. three successive "ti" vocalizations from a series uttered by a nestling.

In a unique variant the terminal "whee-oo" was omitted and the aerial stuttering series left intact. The bird flew up when a Sparrow Hawk pounced well upslope from him, and did ordinary Aerial Display with five stalls and vocalizations before each. His "t" series accelerated and rose slightly in frequency just before stalling, but at the stall he simply used another "t" of the original frequency. Yet another individual once gave a single performance that was silent except for a sharp "clit" at the stall; shortly later he did an Aerial Display with a "whee-oo" at each of several stalls.

The display's appearance also varies. In the most interesting case, an Ecuadorean bird rose to level with the lip of a quebrada then flew at that height, repeating rapidly "t t t tu-twit" in which the terminal arm of the call seemed foreshortened (not recorded). With each "tu-twit" it arched its back, raised its wings high (but not to the customary extreme), lowered its legs, and partly cocked and partly spread its tail. This cocking of the tail is normally brief and precedes the stall. In this case, the bird did not assume a vertical orientation of its body, but used a form much more like that of *M. brevicauda.*

The Aerial Display may not differ appreciably between the Chilean and Ecuadorean populations observed. The full form most common in Chile was also most common in the predawn twilight in Ecuador. The Ecuadorean vocalizations are apparently slightly lower in frequency, and the terminal "whee-oo" at least sometimes descends less abruptly than in the Chilean sample.

Not all factors governing the use of this display are yet known. It is more common just before and during the nesting season than at other times. It is "infectious" in that males stimulate one another to perform (as in the Tumble Flight of the genus *Tyrannus,* Smith, 1966, and the display flights of *Pyrocephalus rubinus,* Smith, in preparation). It is used during aggressive encounters and is sometimes given by spectators. Perhaps it is used by a "frustrated" aggressor—a bird intimidated but not cowed by his opponent(s) or by an aerial predator, or thwarted by poor visibility in the predawn twilight. Whatever the causation, the display is suited to function as a long distance advertisement and specific identification of a territorial male.

(2) *Wing Raising* cum *Buzz.* A pattern which precedes or replaces Aerial Displays in some agonistic encounters is almost certainly homologous with Wing Raising of the larger congeneric species. Once a bird watched two others fight about 10 meters away for over a minute, calling "tek" frequently. It began to jump up about 30 centimeters while lifting both wings, synchronously, fully over its back into the maximal position typical of the Aerial Display (revealing a large expanse of pale plumage). An abrupt, snapping, mechanical Buzz was produced as the wings either reached their full stretch or started down. After several such displays the bird paused, began Wing Raising *cum* Buzzes again without jumping, then did an Aerial Display with repeated stalls.

In two other cases this Wing Raising *cum* Buzz was used by one participant 30 or more seconds after a fight. In one case it was repeated twice by a perched individual about 30 seconds before giving an Aerial Display, and in the other was given as an Aerial Display when the bird flew up 2 meters, stalled in the usual fashion once but with the Buzz instead of calling. On yet another occasion, Wing Raising *cum* Buzz immediately preceded Aerial Display by an individual responding to the Aerial Display of a neighbor. In several dozen recorded Aerial Displays *with* vocalizations, I have never detected a Buzz. Probably the Buzz relates to the Wing Whirr of some larger species, but in *M. maculirostris* it has a ritualized relationship to Wing Raising.

The wings are sometimes raised synchronously into the full upright position without a Buzz by a bird on the ground in an aggressive encounter, and this is perhaps the minimal form of the display. In the one case seen clearly, the bird gave a "tk" with each wing movement, then attacked its opponent.

(3) *Other Wing And Tail Movements.* Aggressive individuals facing an opponent often droop their wing tips nearly to the ground before and after fighting. The wings, and less often the tail, may be given little flicks. One aggressor cocked its tail up while letting its wing tips droop, without flicking either. Birds in these postures were silent and very likely to attack, darting forward with rapid wing flicks, showing the upper wing surfaces to the opponent.

One was seen to wing quiver slightly with each "tek" after landing from an Aerial Display. Within a minute it flew off—apparently to an agonistic encounter. Usually no wing movements accompanied "tek" calls. A slight and very rapid flick of the tail, however, often accompanied a "tek," especially if calling was rapid. Another tail movement, a quick fanning partially open and shut again, often preceded running.

(4) *Crown Ruffled.* If I approached a fledgling and it called, the adult female might also call "tek" and ruffle her forehead conspicuously. This is the second phase of crown ruffling in the larger species, most of which have an occipital spot of color which *M. maculirostris* lacks.

Muscisaxicola brevicauda

I studied this species (*Muscigralla brevicauda* of authors) at only one site in coastal Peru, from 23 to 26 January 1962. The population was locally dense, and there was much displaying.

Vocal Displays

(1) A loud "tchek" (Fig. 7a) was often heard just as birds landed; it resembles in form and usage the Locomotory Hesitance Vocalization (LHV) of *Sayornis phoebe* (Fig. 11c). The communicators were usually watching as I walked through their territories, and probably most were males, since they also used the prolonged vocalizations described below. In fact, the "tchek" appears to be incorporated into the prolonged vocalization, immediately preceding the ultimate descending series.

A slightly briefer form "tchk" (Fig. 7b), hard to distinguish by ear, occasionally intergraded with "tchek." "Tchk" was sometimes weak, nearly lacking its first element, with emphasis then falling on the third or, sometimes, the second element. It was also uttered on landing, or by perched individuals making flight intention movements, and sometimes preceded landing or was repeated two or three times during a very short flight. But usually it was in a short series as prologue to the prolonged vocalizations given while perched. It may correspond to the Doubled Vocalization (DV) of *S. phoebe.*

Occasionally in fights a harsh "zrrt" was used that may have been a version of "tchek"; it was not recorded. No forms similar to "tchek," "tchk," or "zrrt" are known from other *Muscisaxicola* species, except for the apparently rare LHVs. In usage, however, they at least partially replace the two-peaked calls of *M. albilora* and other large species. The reduced visibility in the brushy habitat of *M. brevicauda* may require more complex calls for at least species identification.

(2) There are at least three briefer vocalizations. One has an initial descending arm preceding a peak (Fig. 7c) that sounds like "tk" and is sometimes repeated two or three times in flight toward a perch, followed by "tchek" on landing. Occasionally, a similar series of "tk" followed by a "tchk" comes just after landing. In a short flight the series may be intermediate between "tk" and "tchk," with the third element of the "tchk" emphasized.

Two other very brief calls sound like "tk" (Fig. 7d and e), but do not seem to form intermediates with it, although they do with each other. They are often interspersed among successive prolonged vocalizations in flight, but do not form long series without having interpolated occasional "tk" calls of the first sort. The more obviously chevron-shaped element

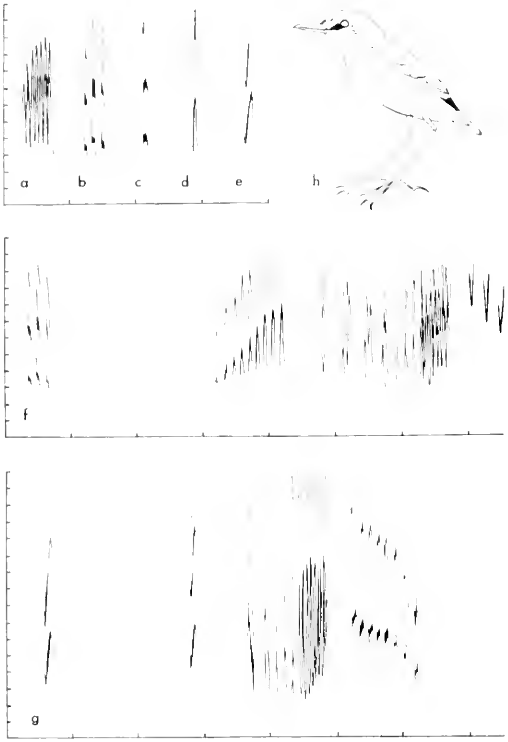

Figure 7. Vocalizations and Pose of *Muscisaxicola brevicauda*: 7a. "tchek" (compare with Fig. 11d); 7b. "tchk" (this occasionally intergrades into the previous vocalization); 7c. "tk" (compare with the elements of a "tchk"); 7d. "tk" (compare with Fig. 6a); 7e. "tk" (compare with Fig. 5a); 7f. prolonged series vocalization uttered while perched (all but the last unit of the introductory series has been omitted); 7g. prolonged series vocalization uttered during Aerial Display (all but the last unit of the introductory series has been omitted); 7h. customary pose while uttering a prolonged series vocalization from a perch.

(Fig. 7d, compare with "tek" of *M. maculirostris*) is sometimes uttered irregularly by a bird which alternates foraging with perching on a bush and uses this and no other calls; it also utters this call sometimes on landing from a short flight. Occasionally a series of this version comes just after landing, followed by one or more "tchk" calls leading to the prolonged vocalization.

Series of the second version (Fig. 7e) may be the more usual among successive prolonged vocalizations of a flying bird, and often continue as a bird completes a relatively long flight. Such long terminal series are broken by an occasional "tk" (Fig. 7c). On the whole, these last two versions of "tk" appear to correspond closely to "tek" and "tk" in the repertoire of *M. maculirostris*, and must be related to Simple Vocalizations.

(3) Prolonged series vocalizations (Fig. 7f) are uttered either from perches atop cotton bushes or during Aerial Displays. Those in flight are usually, but not invariably, less complex (Fig. 7g). All evidence indicates that the prolonged vocalizations correspond at least in part to what is usually called "song" in oscines, or to the Regularly Repeated Vocalizations of *Sayornis* and *Pyrocephalus*. They are used in countercalling among conspicuous individuals remaining within their apparent territories.

Prolonged vocalizations may be stereotyped elaborations of the less complex calls used by the same individuals during flight and landing. A "tchek" or "tchk" preceded by any of the "tk" vocalizations may correspond to a minimal form. The more complex flight form is a "tk" series plus a "tchek" with a harsh section interpolated, and a set of five or more descending elements appended (Fig. 7g). In the most complex (perched) version, the initial series is two to four "tchk" instead of "tk," plus yet another new feature, a section of ascending pitch matching the ultimate descending three elements.

The whole vocalization sounds reminiscent of a slurred version of the Aerial Display call of *M. maculirostris*, but the form of the prolonged vocalization is much more complex. If, however, the audible rise and fall of the second portion is equivalent to the "whee-oo" of *M. maculirostris*, then the prolonged vocalization may be homologous. Perhaps significantly, the "whee-oo" is at least rarely replaced by three chevron-shaped elements, and is in this form more similar. The greater complexity of the prolonged vocalization of *M. brevicauda* is consistent with the greater complexity of each of its other most common calls.

Nonvocal Displays

(1) *Wing Raising.* No display seen was certainly comparable to Wing Raising of the other species. Once, however, after two individuals fought and chased, the pursuer perched and partly opened its right wing several times in rapid succession. Further, one incident before launching into Aerial Display also suggests that a display like Wing Raising exists, although I may not have seen its full form: A bird was repeating "tchek" fairly rapidly. It gradually extended its wings laterally, and without fully spreading the primary feathers, appeared to arch them slightly downward. It ruffled its back, fluffed its chest and crown, and uttered a minimal version of a prolonged vocalization (roughly: "tk-turrk"), then did a low display flight with one prolonged vocalization.

(2) *Aerial Display.* A bird may launch into display silently or after a single prolonged vocalization. Usually he climbs rapidly to about 6 or 7 meters above the vegetation, then flies with very full wing strokes. While flying he utters a prolonged vocalization, holding both wings stretched maximally upward during the final flourish of the call, lifting his head and body axis slightly upward but not into the vertical pose of other *Muscisaxicola* species. Pitching forward slightly, and usually veering at least slightly, he then repeats the performance about three or four more times. Sometimes he climbs continuously throughout, but if only one prolonged vocalization is uttered, the flight usually does not ascend. Except for the lack of full stalling (also omitted, but rarely, in the other species) and the deep wing stroke, the Aerial Display is similar to that of other members of the genus, and to that of *Pyrocephalus rubinus* (which also does not usually stall).

Other Display

About 70 per cent of the prolonged vocalizations heard were from perched birds (the usual stance is shown in Fig. 7h). Their bills open for each call and very widely for the ultimate flourish as the head is thrown back, and the tail and occasionally the wings are slightly flicked. While *M. maculirostris* never gives its full Aerial Display call from a perch, this usage by *M. brevicauda* may correspond to series of "tk" by an *M. maculirostris* before (or while apparently not quite ready to perform) an Aerial Display.

Wing flicks are occasionally given by disturbed birds, and are very frequent if the individual is very excited. These are simple, small amplitude, forward and upward rotations of the wing tips.

The tail of *M. brevicauda* is so short that adults look as if they should be fledglings. Nonetheless, it has a rusty terminal bar which probably has some signal function such as making tail flicks more conspicuous. The only other movement seen to involve the tail is landing atop a bush, when the tail is cocked as if for steering or balance. The tail is probably at least partly fanned in the Aerial Display.

Some plumage display has been mentioned above under Wing Raising.

IIb. *Xolmis*

All *X. pyrope* and *X. irupero* were seen in or immediately before the breeding season, and *X. velata*, *X. cinerea*, and *X. striaticollis* only after the breeding season. Most published accounts report the birds as nearly or wholly silent, and undemonstrative. I heard and saw little display.

Xolmis pyrope

Xolmis pyrope was observed in Chile near Isla Negra, Cerro Manquehue, and on Tierra del Fuego.

Vocal Displays

(1) A simple, chevron-shaped call, "pt" (Fig. 8a), sounds very like "tek" of *Musci-*

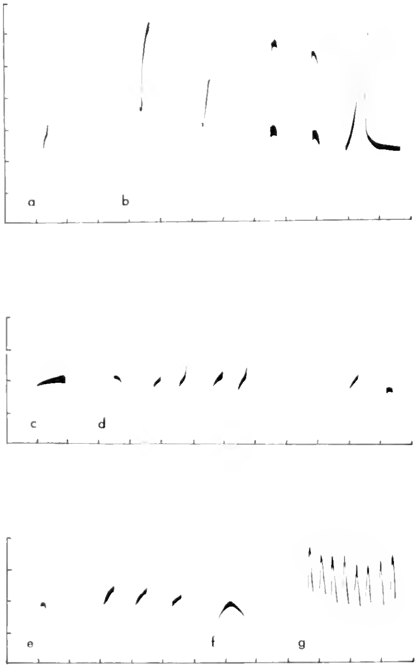

Figure 8. Vocalizations of *Xolmis* species: 8a. "pt" of *X. pyrope*; 8b. prolonged vocalization "wheet whut T-T-wheeoo" of *X. pyrope* (an initial "pt" omitted); 8c. "puh" of *X. irupero*; 8d. several coupled vocalizations recorded in a fight of two *X. irupero*; 8e. vocalizations by one *X. irupero* after chasing another; 8f. "pew" of *X. irupero*; 8g. a nasal vocalization of *X. irupero* (compare with Fig. 11d).

saxicola maculirostris and is probably an SV. I noted uses identical to those of that species (q.v.), except that *X. pyrope* was not seen to mob a predator. This "pt" may be Wetmore's (1926: 301) faint "*tick tick*."

(2) A very brief and relatively high pitched "tseet" was heard several times in a face-to-face aerial fight. Another time, an *X. pyrope* pursued a conspecific bird closely through some bushes, then immediately after perching called: "tseet pwut, pwut pwut, put." These "pwut" and "put" were probably related to the "pt." "Tseet" may correspond to at least the "teek" and "tsk" of *M. albilora;* if so, all are SV forms.

(3) An encounter between an apparent pair and a third individual was seen on the boundary of a transient territory during spring migration. The third individual and one other came to a stand-off, both uttering the brief "pt" frequently and countercalling with bouts of a much more complex, patterned vocalization: "pt wheet whut T-T-wheeooo" (Fig. 8b, which omits the initial "pt"). The ultimate portion is closely similar to the prolonged vocalization of *M. maculirostris*, and the whole follows the basic pattern of a series of brief calls and a flourish.

(4) A weak, low, monosyllabic whistle is said to be characteristic (Goodall et al., 1957: 151). It may correspond to the "tseet" (IPV) of *M. albilora*, but I have not heard it.

Nonvocal Displays

None was certainly identified. In the single stand-off encounter, both participants sometimes raised both wings quickly and slightly above the back, probably a display similar to the Wing Raising of *Muscisaxicola* species. The individual which called after terminating a nonaggressive chase had a conspicuously ruffled throat. During that chase the white in the tail of both individuals was especially conspicuous.

Other *Xolmis* Species and *Neoxolmis*

(a) In northwestern Argentina I found contiguous territories of *Xolmis irupero* in dry, gravelly river beds below the foothills of Salta and Jujuy, and saw several territorial chases. When perched, each participant would utter a "puh" (Fig. 8c) at long intervals; this call is rather prolonged and flat, with a terminal increase in amplitude. The usage suggests the briefer "pt" of *X. pyrope*, but the length suggests the "seet" of *M. albilora*. *Sayornis saya* uses a prolonged and rather flat IPV in many agonistic situations, and it and *S. nigricans* use IPVs in situations in which *S. phoebe* usually uses an SV.

Immediately after chasing an intruder, the victor usually gave variable calls, often suggesting the initial portion of the prolonged vocalization of *X. pyrope* (see Fig. 8e). One such victor landed and gave a prolonged "pweeeeet" plus three couplets of modified "puh" calls resembling the calls of an *X. pyrope* after a chase (see above).

Some calls during fights had coupled elements (Fig. 8d) and one was a broad chevron ("pew," Fig. 8f). These all appear more like SV than the simple "puh," and most differ primarily in duration and slope. Calls recorded from one fight are different, a set of eight very brief, nasal elements (Fig. 8g) quite reminiscent of an LHV.

(b) Little is known about the displays of other *Xolmis* species. Hudson (1920: 142) remarked that *X. coronata* has a "long, low, whistle." Wetmore (1926) has heard a "faint swee" from *X. cinerea,* as well as a "little whistled song," used just at dawn and probably corresponding to the prolonged vocalization of *X. pyrope.* Of *X. rubetra,* he says that males "at intervals flew up to make a metallic rattle with their wings as they turned abruptly and dropped to the ground." This is the only indication of which I am aware of some sort of flight display and Wing Whirr or Buzz in the genus. It may be similar to flight displays in *Knipolegus* and related genera (Smith, in preparation) of a lineage probably fairly closely related to the genera discussed herein.

(c) I have seen *X. fumigata* only in the post-breeding season, and the birds did not display. Vuilleumier (personal communication) has heard a loud "tew" from foraging individuals of *X. striaticollis* in July, in Ecuador. In Argentina he found one individual in April 1965; it uttered a loud "they-tew-thew." Other accounts of the call of this species (e.g., Todd and Carriker, 1922; Koepcke, 1964) resemble his.

One individual of an apparently undescribed population of this species-group was observed by my wife and me on 15 June 1966, at about 4000 meters on the northwest slope of Volcán Cotopaxi in Ecuador. The bird was medium brown above, paler buffy below, pale yellowish on the throat, and had a very faint supercilium. Extremely faint traces of broken streaking marked the lower throat and flanks. The bill was black. The plumage was very fluffed, hiding most of the wings so that it was impossible to tell if these were completely unmarked, but they could not have had prominent bars. In shape, size, and color the bird was very close to specimens I have examined of *X. fuscorufa* of southern Peru and Bolivia, but lacked prominent wing bars. According to Hellmayr (1927), the local *X. pernix* of the Santa Marta range in Colombia is the population phylogenetically closest to *X. fuscorufa,* but it has much less prominent wing bars and a more reddish coloration (I have seen only the one skin of this population in the M.C.Z.). A likely explanation of our bird is that it was a member of a deme intermediate between these two disjunct populations, and that they are extreme members of a linear series of populations. (The genus has another supposed rare and local population, *X. signata,* in addition to *X. pernix* and our bird. As it is an "island" genus, such populations are perhaps to be expected.) I shall refer to this bird as *X.* (*fuscorufa/pernix*?).

It perched silently atop a tall bush for several minutes, then repeated a loud "cleeoo" (Fig. 10a), building quickly to a rate of 29 per minute and maintaining this for over five minutes, like the RRV of a *Sayornis* species. There was slight variation in at least the slope of the terminal arm of the call, which is markedly similar to the RR2 of RRV ("song") of *S. nigricans* (particularly an individual recorded in Panama, Smith, in press, 1). After seven to eight minutes, calling stopped, and the bird dropped to the grass where it stood like a *Turdus* thrush for some tens of seconds before dashing off. We were not able to find it again.

(d) *Neoxolmis rufiventris,* closely related to the species of *Xolmis,* is said to

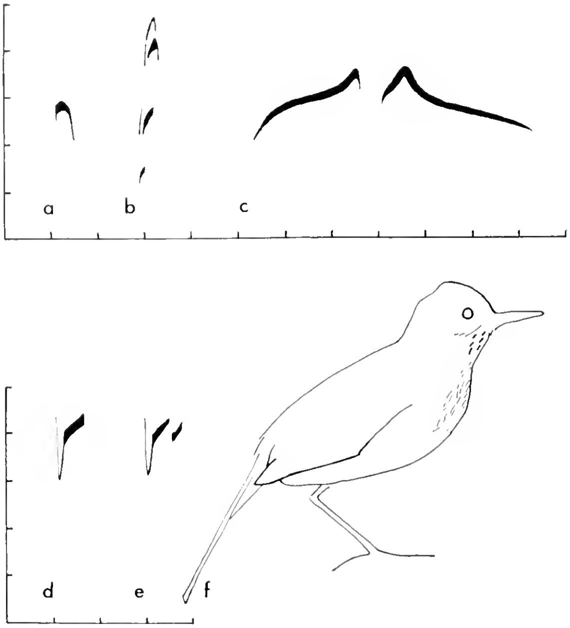

Figure 9. Vocalizations and Pose of *Agriornis* species. 9a. "pyuk" of *A. montana*, Argentina; 9b. "pyuk" of same individual *A. montana*; 9c. "wheet hyou" of gray *Agriornis*, Ecuador, (also *A. montana*?); 9d. "t-eek" of *A. livida*; 9e. "t-eek-ek" of *A. livida*; 9f. pose of *A. livida* while uttering "t-eek" calls.

have a "long, low, plaintive whistle" (Hudson, 1920: 138).

IIc. *Agriornis*

I have seen two of the five species, but never in dense populations. Both have a loud whistle which probably serves some "song" functions, since birds utter it from atop shrubs or other relatively tall vegetation at long, irregular intervals (often about 45 to 80 seconds).

Agriornis montana, recorded in Tucumán, Argentina, has the briefest vocalization, a relatively low pitched "pyuk" of SV form (Fig. 9a and b). Goodall et al. (1957) say this is used in the early morning, which is when I recorded it, and consider the species more vocal than *A. livida* in Chile. Dark gray birds on the northeast slopes of Mt. Pichincha in Ecuador had the longest call (Fig. 9c), a clear "wheet hyou" with a form like a *Sayornis saya* RR1 song unit (see below, and Fig. 11h). A bird using it also foraged while under observation, and sometimes countercalled with another individual using the same vocalization. Vuilleumier has heard a nearly identical call from *A. montana* in the Potosí Department of Bolivia (see his discussion in Chapter 1).

The corresponding vocalization of *A. livida* in central Chile is somewhat like a *Sayornis phoebe* IPV: "t-eek" or "t-eek-ek" (Fig. 9d and e, with pose of bird between calls in Fig. 9f). Fully grown, nearly independent fledglings were found at Los Molles, Chile, from 7 to 9 January 1962. They sometimes perched and called a flatter version lacking a terminal peak: "pwut." It sometimes wavered or was harsh. One perched alone once and uttered a loose series of weaker "peet" calls that became slightly harsher ("pwt") before it flew off. Later it landed near me, looked at me for

20 seconds, then with a faint, harsh "pwt" began to forage. Still later, when an adult came the fledgling gaped toward it and repeated "peet" two to three times per second, the "peet" getting harsher until the adult flew away.

The known vocalizations of adults of these *Agriornis* populations are not closely similar to one another. All, however, resemble different vocalizations of *Muscisaxicola* and *Sayornis* species which are used (at least in part) similarly. The one visible display known is an Aerial Display by an *A. albicauda* seen by Vuilleumier (personal communication) in La Paz Department, Bolivia. The bird circled silently, alternately rising to a partial stall and dropping forward on closed wings, as in an incomplete Aerial Display of a *Muscisaxicola* species.

Wetmore (1926) heard "sharp squeaky notes" (perhaps BVs) from *Agriornis murina* during a pursuit.

IId. *Ochthoeca*

Ochthoeca fumicolor

I observed this species in Ecuador on Cerro Atacaso in 1959 and 1966, and on Volcán Cotopaxi in 1966. The following vocalizations have been recorded.

(1) A very variable, loud, clear, abrupt whistle: "kleeip," "kleeep," or "kleech" (Fig. 10c, d, e, and f). The variations have not been correlated with different usages, but are comparable to variations of the very similar IPV of *Sayornis phoebe*. The call is uttered at long intervals by some foraging birds while perched, or sometimes in flight. Sometimes two countercall with it: e.g., immediately after an agonistic encounter, both participants uttered it before one flew away. An adult repeated it nearly every time it fed its fully grown fledglings, and spanned all of the recorded variations. Most calls of the fledglings (e.g., Fig. 10g) were similar to one sort of the adult's, and much fainter. All usages strongly suggest the IPV of *Sayornis saya*.

(2) A less loud "tee-oo" (Fig. 10b, rarely just the descending arm is uttered) is nearly indistinguishable in sound from the one known call of *Xolmis* (*fuscorufa/pernix*?). At least once, two individuals separated after one agonistic encounter, then countercalled with this before the next. It is very similar in sound and form to the terminal calls of Aerial Displays in *Muscisaxicola* and the prolonged call of *Xolmis pyrope*, as well as somewhat similar to the one known call of the *Agriornis* species recorded in Ecuador. All apparently relate to RRV units of *Sayornis*.

(3) *Ochthoeca fumicolor* also uses patterned series of one to three variable "kleep" vocalizations followed by about eight to ten simpler "klee" calls (Fig. 10h, probably also IPV or RRV forms). The latter are nearly invariable in form, and nearly evenly spaced about 0.4 seconds apart, with a slightly longer pause before the ultimate one. In series that had as few as two "klee" units these sounded more like "tee-oo." In 1966 the only series we recorded were during and after an agonistic encounter, as two participants countercalled at irregular intervals. They eventually shifted from using both "kleeip" and the patterned series to just "kleeip." One individual in 1959 uttered short series while foraging near a calling *O. rufipectoralis* (see below).

(4) Two other vocalizations, recorded during fights, both resemble calls used in fights by at least *M. albilora*. One (Fig. 10i) sounds like "pw-pwt" or "pw-pw-pwt," the other (Fig. 10j) like "twee tik." Both may be uttered in bursts, and at least the former is sometimes used in flight with a Wing Whirr. Both may be LHV forms, and have similarities with the LHV of *S. phoebe* ("twh-t," see Fig. 11e).

Some of *O. fumicolor's* nonvocal displays are also known. During and after agonistic encounters there was much wing and tail flicking that was rapid during series calls, but there was some also with at least "tee-oo" calls. When foraging with or

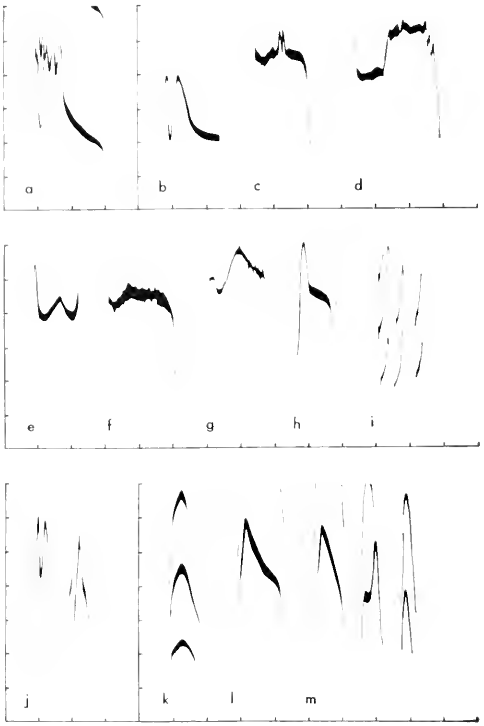

Figure 10. Vocalizations of *Xolmis* (*fuscorufa/pernix?*) and *Ochthaeca* species: 10a. "cleeoo" of *Xolmis* (*fuscorufa/pernix?*); 10b. "cleeoo" of *O. fumicolor*; 10c. through 10f. variations of the abrupt whistle of *O. fumicolor*: "kleeip," "kleep," "kleeeh," and "kleeeh," respectively; 10g. a similar vocalization of a fledgling *O. fumicolor*; 10h. "klee" vocalization of *O. fumicolor*; 10i. a vocalization recorded from a fight of two *O. fumicolor*; 10j. another vocalization recorded from a fight of *O. fumicolor* (compare with Fig. 11d); 10k. "tyeh" of *O. leucophrys* (Peru); 10l. "tyee" of *O. leucophrys* (Argentina); 10m. "tee tee ti," recorded from a fight of two *O. leucophrys* (Argentina).

without occasional "kleep" type calls, there were occasional tail flicks (always up/down), especially on landing. A Wing Whirr in several flights during at least one agonistic encounter had two forms: several single or paired snaps about 0.2 seconds apart, or a quick burst of about seven similar sounds in about 0.4 seconds (analyzed from recordings). The individual foraging near an *O. rufipectoralis* gave very noticeable bursts of whirring every time it flew.

Other *Ochthoeca* Species

A single foraging *O. rufipectoralis* was observed for an hour on 7 August 1959, on Cerro Atacaso. It occasionally uttered a rather faint "cleeoo" (not recorded) which I could distinguish from the "tee-oo" being used by an *O. fumicolor* primarily by amplitude. That these two species and the *Xolmis* (*fuscorufa/pernix*?), all in the same general region, should have such remarkably similar calls is probably due to more than close phylogenetic relationship. The species probably have some organized social relationship (see Moynihan, 1968, for various possible interspecies relationships). Perhaps it is significant that while the only two members of *Ochthoeca* in the copse during that hour were of different species, both kept displaying but had no encounter.

One other vocalization was heard when the *O. rufipectoralis* was especially active: a long, rapid, series of brief "pt" calls, terminating in two "cleeoo" calls. If this corresponds to the series call of *O. fumicolor* the reversed sequence in the two species may be significant in the light of the unusual interspecies similiarity of the aforementioned vocalizations. The brief "pt" calls seem likely to be SVs, and may replace the IPV in this species—such a substitution occurs among the species of *Sayornis*.

Finally, the *O. rufipectoralis* tail flicked less than its slightly larger congeneric associate, and Wing Whirred only twice, faintly. However, all its flights undulated like Wing Whirr flights, being broken into segments by recurrent pumping of the relatively long tail.

I recorded *O. leucophrys* near Lima, Peru (September 1962), and in northwestern Argentina (November 1962). The lone individual in Peru foraged with an occasional abrupt, SV-like "tyeh" (Fig. 10k) when perched or during flights of 6 to 25 meters between bushes. On calling while perched, it would give a slight wing flick and single tail flick. Once it called "tyeh tuh tuh tuh tuh" in flight as it approached a perch.

At the Argentine site two pairs of *O. leucophrys* were in a narrow quebrada, and one individual kept intruding into the area of the other pair. Several times one chased, fought, and expelled the intruder, and in each encounter one used brief bursts of: "tee tee ti" (Fig. 10m). These resemble, respectively, an SV, BV, and SV of *Sayornis phoebe,* and, to a lesser extent, calls recorded from flying *Xolmis* and *Muscisaxicola.* Between intrusions the defender foraged with an occasional "tyee" (Fig. 10l), slightly more prolonged and more IPV-like than the "tyeh" of the Peruvian bird. Vuilleumier watched two individuals foraging near Mitotambo, Peru, on 27 May 1965, and one or both uttered "wheet" and "wheeyet," calls which may correspond to the "tyeh" (SV) and "tyeee" (IPV) I have recorded. (It is very difficult to correlate onomatopoetic descriptions of different observers, since bird vocalizations do not correspond closely to the vowels and consonants we must use to describe them; Vuilleumier and I each heard calls in similar circumstances which fell into two categories by length and were generally similar in pitch.)

Vuilleumier (personal communication) heard an *O. cinnamomeiventris* call occasionally while foraging below the Carpish Pass, Peru, on 28–30 May 1965: "long, high-pitched *seee,* very reminiscent of the call of *Colorhamphus parvirostris.*"

COMPARATIVE SUMMARY AND DISCUSSION

The known behavioral similarities of the above genera are here summarized, and are compared with the behavior of the genera *Sayornis* (for which all references below are to Smith, 1969, and in press 1 and 2) and *Pyrocephalus* (for which references are to Smith, 1967, plus subsequent work in preparation).

Habitat preferences vary along a continuum transcending generic limits. While some *Ochthoeca* species inhabit dense forests, others live on the wooded or bushy fringes of the open, grassy páramo, and devote much of their foraging attention to it. In openess and general distribution of bushes for perching, the latter habitats are comparable to those of *Sayornis* and *Pyrocephalus.* Among Xolmis species, even members of the *fumigata* species-group are not found in dense forest, and range primarily from edge to semi-open habitats with tall perches. Other *Xolmis* species carry this trend further, and at least two are as terrestrial as some *Muscisaxicola* species, although perhaps not identical in their modes of foraging. Extremes of open habitat preference are reached in both *Agriornis* and *Muscisaxicola,* but in all cases some feature provides elevated lookout posts. The less extreme members of even these genera have breeding habitats with abundant bushes or some trees.

Attention in searching tends to be directed downward in some *Ochthoeca* species, in *Sayornis saya,* and at least seasonally in other *Sayornis* species. This feature is particularly obvious in *Xolmis,* most species of which perch relatively high for terrestrial foragers. The larger, ground-dwelling *Muscisaxicola* species direct most of their searching attention downward, although even they have some tendency to scan the air for flying prey. Throughout the group as a whole, locomotory patterns show obvious adaptations to the form of searching, from a tendency to fly close to the ground to the development of rapid hopping and running.

All of the species do some or much foraging by gleaning, and possibly a tendency to glean is necessary in the evolution of terrestrial habits, since most prey in open country is likely to be on the ground or clinging to plants. Particularly where open habitats are windy, flying invertebrates are relatively uncommon. Yet aerial flycatching persists. It may be of major significance only in *Sayornis, Pyrocephalus,* and some *Ochthoeca* species, but all of the species under consideration do it. It is behavior that characterizes the tyrannids among the other terrestrial passerine insectivores which share their habitats. Another such feature is the tendency of *Muscisaxicola* and some *Xolmis* species to alternate short dashes and/or flights with pauses to scan for prey; in central Chile and coastal Peru, *Anthus* species (motacillid), and *Geositta* and other terrestrial furnariids sympatric with one or more *Muscisaxicola* species usually walk continuously while foraging. The Old World flycatching muscicapids (genus *Oenanthe*), with which *Muscisaxicola* species are convergent, use the same foraging tactics, while their sympatric passerine insectivores (at least in Iceland, where these are *Anthus* and *Motacilla* [personal observation]), are also "walkers." It is as if a flycatcher, of whatever phylogenetic affiliation, in taking to terrestrial foraging, preempts this tactic.

All members of the assemblage build open cup nests. They employ available opportunities for concealment, placing their nests in vegetation (grass clumps or bushes), in crevices or burrows, or on partly concealed ledges. *Sayornis* species use only the last, including artificial substitutes like bridges and buildings, and *Ochthoeca rufipectoralis* has been known to use a similar site. *Muscisaxicola* is the only genus restricted to terrestrial nesting (if we consider ledges as being off the ground), and *Agriornis montana* and *Neoxolmis rufiventris* may be the only other species nesting on the ground (some populations of *Xolmis cinerea* may nest in holes in banks). That closely related species should differ in nesting on the ground or in bushes suggests that evolution of ground nesting has not been difficult for open country flycatchers.

The nondisplay behavior patterns do not appear to set any of the genera apart, but show a general trend from some adaptation to open environments in *Sayornis, Pyrocephalus,* some *Xolmis,* and some *Ochthoeca* species, to considerable adaptation in *Muscisaxicola,* other *Xolmis* species, and *Agriornis.* By "trend" I do not mean to imply that any of these genera is a part of the phylogenetic lineage of another. Obviously, all are contemporary end-products of adaptation to different habitats, but they serve to show the nature of possible stages in the evolution of terrestrial forms from less terrestrial ones.

Comparison of the displays is less easy than of the nondisplay behavior. It can best be done by comparison with the displays of the related genus *Sayornis,* in which all displays of at least *S. phoebe* appear to be known, and the relationships among those displays are relatively well understood. No attempt is made here to repeat detailed descriptions of the form and usage of *Sayornis* displays; they are cited below only insofar as is necessary to establish points of comparison or contrast with the other species. Oversimplification is inevitable, and most of the following general statements about form and usage of displays can be qualified by a variety of exceptions. The exceptions do not appear to contradict the conclusions, but a reader wishing a more complete comparison must consult the more detailed papers on *S. phoebe* and the genus *Sayornis.*

One important problem is that the amount of use of different vocalizations almost certainly varies with the stage of the breeding cycle sampled during the field work, as has been shown for *S. phoebe.* Since all the specific display repertoires appear comparable in many respects, seasonal shifts can likely be predicted from what is known about *S. phoebe.*

(1) *Simple Vocalization* (SV). In *S. phoebe* this sounds like "tp" (Fig. 11a). It is used in a variety of circumstances, most of which are agonistic or potentially agonistic: foraging while patrolling, responses to predators, and agonistic or

potentially agonistic interactions of mates. The SV of *S. nigricans* and the "peent" vocalization of *Pyrocephalus rubinus* are full chevrons, similar in most known usages.

In *Muscisaxicola*, at least some larger species divide the SV into a number of intergrading forms, each with its own range of usage. Thus, in *M. albilora*, "teek" (Fig. 1c) is usually used in approach toward an interaction which may be agonistic, whereas "tehk" and "tk" (Fig. 2d) are used in grappling fights, and almost all forms are heard when mates meet during or immediately after an agonistic situation. *M. frontalis* and *M. flavinucha* appear to have similar SVs, *M. rufivertex* and *M. macloviana* may, while *M. capistrata* either lacks such calls or uses them primarily at other parts of the breeding cycle than were observed.

Muscisaxicola maculirostris has a chevron-shaped homologue ("tek," Fig. 6a) which it uses much more abundantly than the SVs of any of its larger congeners. The indistinct variations of "tek" appear to correspond to the different SV forms of *M. albilora*. The yet smaller *M. brevicauda* has only comparable "tk" forms (particularly Fig. 7d), and restricts their usage (see below, under LHV).

All *Muscisaxicola* species employ forms closely related to SVs (and here grouped with them) in short series or bursts in circumstances suggesting Chatter Vocalization (CV) usage of *Sayornis* species. These usages are either by a bird associating with its mate without attempting other activities, or by males before or in Aerial Displays. The one observation of CV-type calls by a lone *M. frontalis* apparently prospecting for a nest site is significant, since it is typical of CV usage in many better known tyrannid genera, and in the three *Sayornis* species and *P. rubinus*. The forms resemble the chevron series CV of *S. nigricans* (Fig. 11d), and similar variants of the CV of *S. saya*.

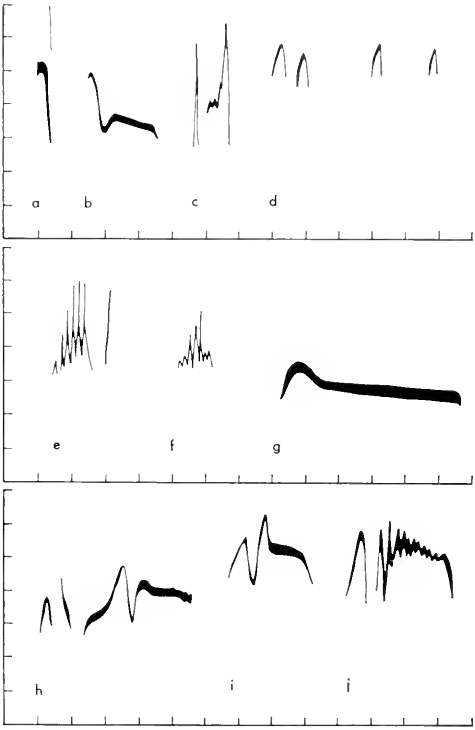

Figure 11. Vocalizations of *Sayornis* species: 11a. Simple Vocalization (SV) of *S. phoebe*; 11b. Initially Peaked Vocalization (IPV, one variant) of *S. phoebe*; 11c. Bipeaked Vocalization (BV) of *S. phoebe*; 11d. A portion of a Chatter Vocalization (CV) of *S. nigricans*; 11e. Locomotory Hesitance Vocalization (LHV) of *S. phoebe*; 11f. A unit of Chatter Vocalization (CV) from a series of *S. phoebe*; 11g. An Initially Peaked Vocalization (IPV) of *S. saya*; 11h. An RR1 of the Regularly Repeated Vocalization (RRV) of *S. saya*; 11i. An RR1 of the RRV of *S. nigricans* (Arizona); 11j. An RR2 of the RRV of *S. nigricans* (Panamá) (compare with Fig. 10a).

Xolmis pyrope has a "pt" (e.g., Fig. 8a) which corresponds to the SV of *M. maculirostris*, and *X. irupero* has similar but more prolonged calls (e.g., "pew," Fig. 8f) as well as coupled elements which are SV or CV. Some calls of other *Xolmis* species described in the literature appear to be SVs.

In *Agriornis*, at least the "pyuk" of *A. montana* is of SV form and usage. Calls recorded from *Ochthoeca leucophrys* during fights ("tee" and variants, Fig. 10m) and apparent patrolling ("tyek," Fig. 10k) are probably SVs.

(2) *Initially Peaked Vocalization* (IPV). In *Sayornis phoebe* IPV (Fig. 11b) is very rare and variable. It is sometimes used by males before going to roost, after an agonistic encounter, or when thwarted in an agonistic situation. *S. nigricans* uses its homologue more than *S. phoebe*, although in similar circumstances as well as in some patrolling and with RRV, and in *S. saya* the IPV (Fig. 11g) virtually replaces the SV. Thus, within *Sayornis* one species uses primarily SV and little IPV, another uses both, and the third primarily IPV. Similar patterns may recur in the other genera.

Muscisaxicola albilora has a slightly bipeaked "seet" (Fig. 1e and f) which occurs between attacks in agonistic encounters like an IPV; its "tseet" (Fig. 1a) is also IPV-like. *M. frontalis* has two corresponding calls (Fig. 4a and b). Both species also have SVs. *M. capistrata* may have only IPV forms (Fig. 5a, b, and c). A "tee" heard from *M. rufivertex* with Wing Raising may be either IPV or SV. But if *M. maculirostris* has an IPV (perhaps the squeak, Fig. 6b, by an individual on ceasing to approach a fight), it is very rarely used, whereas SV is used abundantly.

In *Xolmis irupero*, "puh" (Fig. 8c) is probably an IPV, as is the "t-eek" (Fig. 9d and e) of patrolling *Agriornis livida*. The most *Sayornis*-like IPVs are found in *Ochthoeca*, the genus most like *Sayornis* in habits and plumage. The variable "kleeip" (Fig. 10c to 10f) used in patrolling, countercalling, and after agonistic encounters is the IPV of *O. fumicolor*, a species with no known SV. Some other calls in this genus may be either IPV or RRV forms (see below).

(3) *Calls of Nestlings and Fledglings*. In *Sayornis*, nestlings of *S. phoebe* beg with an SV-like "tee," those of *S. saya* primarily with IPV forms, and those of *S. nigricans* with both, thus roughly corresponding to differences in the frequency of usage by adults of SV and IPV. The begging of young *Muscisaxicola maculirostris* and *M. capistrata* suggests a similar correlation in that genus, and in *Ochthoeca fumicolor* begging fledglings used only IPVs—as did adults. It does appear as if either IPV or SV can serve nearly the same functions in different species, and that which is more prominent is not a generic characteristic.

(4) *Regularly Repeated Vocalization* (RRV). Each *Sayornis* species has a characteristic "song" of two units (called RR1 and RR2) repeated in patterns for up to thirty minutes at a time. In *S. saya*, IPV units make up the bulk of most "song" bouts. The most closely similar performance heard from any of the species described here was the bout in which the single *Xolmis* (*fuscorufa/pernix*?) repeated regularly a "cleeoo" (Fig. 10a) with a form like the RR2 of *S. nigricans* (Fig. 11j). *Ochthoeca fumicolor* has a closely similar call ("cleeoo," Fig. 10b), recorded in countercalling bouts, and a regularly repeated "klee" (Fig. 10h) which is either an IPV variant or a second RRV unit (see Fig. 11i). *O. rufipectoralis* has a "cleeoo," and the "tyee" (Fig. 10l) of *O. leucophrys* is similar to an RRV unit (Fig. 11i). It is likely that the "wheet hyou" (Fig. 9c, compare with Fig. 11h) of gray *Agriornis* in Ecuador is an RRV unit, but it was never heard in series.

The calls referred to as "prolonged vocalizations" in several species of *Muscisaxicola* and *Xolmis pyrope* are like the RRV of *Pyrocephalus rubinus*. Although they are not regularly repeated for long, even in Aerial Displays, they are used in countercalling. Most terminate with "cleeoo" or "clee-ip," and those recorded (Figs. 6g, 6h, 6i, and 8b) appear to be simplified versions of the *O. fumicolor* "cleeoo" (Fig. 10b), preceded by a series of brief vocalizations which are usually SV- or CV-like. The complex prolonged vocalization of *M. brevicauda* (Fig. 7f and g) appears to be a secondary specialization of the common form, convergent in harshness with the RR1 of *S. phoebe*.

Regular repetition, particularly in predawn bouts, as a characteristic RRV usage, seems lost in the terrestrial genera, and its use in an Aerial Display is correspondingly increased. *Sayornis* species sometimes, and *P. rubinus* frequently, use their RRVs in flight displays, and also have predawn calling patterns, and occasional daytime bouts.

(5) *Bipeaked Vocalization* (BV). In *Sayornis phoebe* and *S. nigricans* this has the form of a rather abrupt and multipeaked IPV (Fig. 11c) and sounds like "T-keet." It is uttered by the aggressor in agonistic encounters and occurs in some Flight Displays.

In *Muscisaxicola* the most similar vocalization is also IPV-like, and forms intermediates with IPV. The only larger species it has been recorded from is *M. albilora* ("tseek," Fig. 1b), used by birds flying toward their mates, and in agonistic encounters between pairs. In *M. maculirostris* the closest approximation was a "tek" variant (Fig. 6e) used by a bird approaching a fight with considerable hesitance. Similarly, in *M. brevicauda* a "tk" variant (Fig. 7e) may approximate this call.

In *Agriornis,* only the call described by Wetmore from a pursuit in *A. murina* may be a BV. A "tee" (Fig. 10m) used in a territorial fight by *Ochthoeca leucophrys* appears BV-like.

(6) *Locomotory Hesitance Vocalization* (LHV). *Sayornis phoebe* has a call ("twh-t," Fig. 11e) used primarily on landing when there is a conflict of tendencies to continue flying or to take a perch. In early spring it is used during patrolling, but thereafter most commonly by males approaching their usually aggressive mates, or by males being attacked by their mates. Less commonly, a bird appearing "nervous" in any potentially agonistic situation may sometimes utter it on landing from a short flight. S. *saya* has a similar form known only from male-female disputes. A very similar "twee-tk" (Fig. 10j) heard in fights of *Ochthoeca fumicolor* is the closest apparent homologue in the other genera. A nasal call from a fight between two *Xolmis irupero* (Fig. 8g) may be an LHV.

In *Muscisaxicola albilora*, apparent LHV forms were recorded only in a few greetings between mates. It is not certain that *M. maculirostris* has a homologue, but in my brief field work with *M. brevicauda,* an LHV ("tchek," Fig. 7a) was heard very commonly. It was used by patrolling males, almost always on landing from a flight (as in S. *phoebe*). No greetings were seen. Within their respective genera, both *M. brevicauda* and *S. phoebe* are prominent for having harsh calls. Even the CV of S. *phoebe* is harsh, and intergrades with its LHV. In the other species, CV may replace the LHV in some usages, and the SV and/or IPV in others.

(7) *Doubled Vocalization* (DV). A rare display of S. *phoebe*, this is usually a couplet of brief chevron-shaped calls. It may represent a partial remnant of the CVs of the other *Sayornis* species, and is used in some instances in which an LHV might seem appropriate. Only *M. brevicauda* appears to have a call ("tchk," Fig. 7b) which corresponds in usage, and this species is like S. *phoebe* in having a frequently used LHV.

(8) *Flight Display*. The Flight Display of *Pyrocephalus* is similar both in its form and its usual vocalization to the Aerial Displays of *Muscisaxicola* species. The Aerial Displays of *M. brevicauda* differ primarily in having a very full wing stroke, but DeBenedictis (discussed in Smith, 1967) has seen full wing strokes used by some individuals of *Pyrocephalus*. The conspicuous Flight Display of S. *phoebe* is probably comparable, but may usually be relatively fast and erratic; few detailed observations exist. All *Sayornis* species have fluttering flights with CVs and RRVs and/or IPVs, which differ primarily in lacking stalls and in usually being oriented toward potential nest sites. Aerial Displays may also be found in at least *Xolmis* and *Agriornis.*

(9) *Wing Raising*. The elaborate Wing

Raising displays known in agonistic encounters of *Muscisaxicola* species intergrade with the Aerial Display. *X. pyrope* may also have a Wing Raising display, but there is no evidence for homologous displays in the other genera. *S. phoebe* apparently lacks such a display, although its Wing Fluttering display may assume some of the functions of Wing Raising. Males of both *S. saya* and *S. nigricans* have been seen to Wing Raise briefly at the end of short fluttering display flights, in what appeared to be pair-bonding contexts.

(10) *Wing Whirr.* Abrupt bursts of sound produced by the wings are known in *Sayornis, Pyrocephalus*, two *Ochthoeca* species, three *Muscisaxicola* species, and probably *Xolmis rubetra*. Many other tyrannids, and many other passerines, at least rarely produce similar sounds. Wing Whirrs tend to occur in agonistic situations, sometimes in association with flight displays (e.g., in *Tyrannus*) or with Wing Raising (very regularly in *M. maculirostris*).

(11) *Other Wing and Tail Displays.* The Wing Shuffle of *Sayornis* and Wing Flirting of *Pyrocephalus* appear to correspond closely. Probably *Ochthoeca* has similar displays, but related movements of the other genera may not be ritualized (except as a specialization for foraging in *Muscisaxicola*). Similarly, Tail Wagging in *Sayornis*, Tail Flicking in *Pyrocephalus*, and a tail movement of *Ochthoeca* species correspond closely. Such a display is lacking in at least the more terrestrial genera, where it is to some degree replaced by Wing Raising. Tail movements known in the terrestrial species appear to be primarily balancing movements associated with locomotion.

(12) *Crown Ruffled.* Similar forms of Crown Ruffled are known in at least *Sayornis, Pyrocephalus*, and *Muscisaxicola*. If there are other plumage displays, I have missed them by concentrating on sound recording and by not using binoculars sufficiently.

In sum, this comparison shows that similarities among the displays of all these species are prominent, while widely different displays apparently do not occur. This is not to claim that there are no novel specializations in the group; certainly the Head Bow of *Muscisaxicola* is a novelty, specialized to show the species-specific occipital patches, but it is not an elaborate innovation. Other less novel specializations appear to be modifications of identifiable components, and do not observe generic limits. For instance, at least some species in the most open habitats appear to have lost the use of RRV in bouts while perched, and to have elaborated and stylized the Aerial Display instead. And at least the very terrestrial *Muscisaxicola* species appear to have incorporated in the Aerial Display a Wing Raising which appears to be much rarer and less stylized in two *Sayornis* species.

The displays, to the degree that they are now known, are less useful in delineating the genera than are morphological and plumage characteristics. Some display characteristics may be of some help at this level, however. For instance, very brief vocalizations are typical only of *Muscisaxicola* (including *M. brevicauda*, in which the component elements of displays are very brief); *Xolmis pyrope* may be the most comparable species from this aspect in another genus. Further, the IPV and RRV are most similar in form and usage in the *fumigata* species-group of *Xolmis*, in *Ochthoeca*, and in *Sayornis*, which also intergrade in plumage pattern and coloration, and in habitat choice and many general behavioral features.

Displays vary considerably within each genus, but mostly in ways already known in other genera. For instance, within one or more of the genera described herein, in some species, either the IPV or the SV may be prominent to the virtual exclusion of the other, or both may be common in the same species. This is also the case in the genus *Sayornis*, and shifts of a similar sort (usually involving the RV and CV) are known in the phylogenetically distant tyrannid genus *Tyrannus* (Smith, 1966).

The display behavior of *Muscisaxicola brevicauda* is at the moment the most obvious case of intrageneric distinctness, and the species is undoubtedly not fully typical of the genus *Muscisaxicola*. For a bird which is aberrant in so many ways, however, it is the similarities of its displays with those of other *Muscisaxicola* species that are striking, not the differences. Further, the displays of *M. brevicauda* are more like the known displays of *Muscisaxicola* species than they are like the known displays of any other passerines of the Andean chain. Considered alone, these displays suggest that *M. brevicauda* is at least closely related to the members of *Muscisaxicola,* and differs largely through its emphasis on the LHV and related displays. Considered in the light of ecology and other behavior (see above), plumage, morphology, and geographic distribution (see Chapter 1 by Vuilleumier), they help suggest that the species belongs in *Muscisaxicola,* as its most aberrant member.

Finally, the behavioral similarities among the birds of these genera indicate that they belong to a natural group, the limits of which have not yet been determined. Other tyrannid genera which overlap with some in their habitats (e.g., *Anairetes, Elaenia,* and *Mecocerculus* in the páramo of Ecuador and Peru) are quite different in many aspects of their repertoires (Smith, in preparation). The various *Tyrannus* species have little in common with these species in the detailed forms of their displays, even though there is at least general comparability in the usages (as should be expected for species with basically similar social behavior). In addition, sympatric nontyrannid passerines are generally quite dissimilar from the genera described herein in the forms of their displays, and this is true even of the superficially similar flight displays of some species of *Phrygilus* and *Anthus.* Thus there is little reason to suspect that the many similarities among the displays of the species of *Muscisaxicola, Agriornis, Xolmis, Ochthoeca, Pyrocephalus,* and *Sayornis* are wholly or largely due to convergence in the face of common environmental pressures. The similarities of display behavior, like the similarities of nondisplay behavior, suggest close relationship.

CONCLUSIONS

General behavior patterns of the terrestrial tyrannids in the genera *Muscisaxicola, Agriornis,* and *Xolmis* are similar in many respects, and no strongly divergent behavioral trends are known. In habitat preferences, foraging methods, patterns of locomotion, selection of nest sites and in the structures of the nests they build, they appear to vary along continua that transcend generic limits and relate these species to the less terrestrial members of *Xolmis, Ochthoeca, Pyrocephalus,* and *Sayornis,* all of which they also resemble in structure, coloration, and plumage patterns. Detailed similarities in the form and usages of the displays of members of all of these genera do not appear to be determined primarily by evolutionary pressures related to the habitats of the birds, and indicate that they belong to one phylogenetic group, distinct from many sympatric tyrannids. Some specialized differences in display forms have developed among the genera, but none constitutes a major innovation. The forms of the displays give some clues as to relationships within the group, indicating that the less terrestrial genera may be more closely related to each other than any is to *Muscisaxicola,* and that *Muscisaxicola* is a fairly coherent genus (with the partial exception of the aberrant *M. brevicauda*) that is probably closely related to *Xolmis* through *X. pyrope.* Greater detail of interrelationships can likely be revealed by more detailed studies of display behavior, but it is not clear that this will necessarily aid significantly in the recognition of generic limits within this group.

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Systematics and Natural History of the Mygalomorph Spider Genus *Antrodiaetus* and Related Genera (Araneae: Antrodiaetidae)

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SYSTEMATICS AND NATURAL HISTORY OF THE MYGALOMORPH SPIDER GENUS *ANTRODIAETUS* AND RELATED GENERA (ARANEAE: ANTRODIAETIDAE)

FREDERICK A. COYLE*

CONTENTS

ABSTRACT

A taxonomic section includes a characterization of the family Antrodiaetidae, a key to its three genera (*Antrodiaetus*, *Atypoides*, and *Aliatypus*), a revision of *Antrodiaetus*, and a preliminary study of *Aliatypus*. The family, except for two Japanese species of *Antrodiaetus*, occurs only in North America. Of the 13 species of *Antrodiaetus*, four are newly described: *A. occultus*, *A. cerberus*, *A. stygius*, and *A. apachecus*. Six new synonymies are recognized. Natural history data are reported for all species of the three genera. Antrodiaetid evolution, with emphasis on geographic variation and speciation in *Antrodiaetus* and *Atypoides*, is discussed.

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INTRODUCTION

In general morphology and behavior *Antrodiaetus* (Figs. 109–112) and the closely related genus, *Atypoides* (Coyle, 1968), resemble the stout-bodied burrowing trapdoor spiders of the distantly related mygalomorph family Ctenizidae. All species construct tubular silk-lined burrows in the ground and prey nocturnally upon invertebrates which wander within reach of the burrow entrance. This entrance is well camouflaged and is closed off by a collapsible silken collar (or a rigid turret). The long-legged adult males abandon their burrows during the mating season and wander nocturnally in search of females. Most species are found in humid well-drained soil in forest or woodland habitats.

Antrodiaetus and *Atypoides* together form a distinct monophyletic unit within the atypoid mygalomorph spider family Antrodiaetidae. The 13 species of *Antrodiaetus* and the three of *Atypoides* exhibit in toto a markedly disjunct geographic distribution with species in Japan, western North America, and eastern North America. The center of species diversity in both genera is in far western North America. These are clearly the dominant (most abundant and widespread) mygalomorph spiders above 35° latitude on this continent.

Taxonomic revisions of *Antrodiaetus* are nonexistant. Many species descriptions, particularly pre-1900 descriptions, are based on immature specimens or tiny samples, lack diagnostic characters, and are poorly illustrated. Misidentifications are common in the literature. Little has been written about the natural history of antrodiaetid taxa. Such a state of affairs is largely due to the relatively simple external morphology and covert behavior of these spiders.

I have based the taxonomic revision of *Antrodiaetus*, like that of *Atypoides* (Coyle, 1968), upon a thorough and objective search for diagnostically useful characters, my primary tool being an analysis of variation of quantitative and qualitative morphological characters. Because I believe that many kinds of nonmorphological data provide useful, often vital, and interesting information about populations, taxa, and their past history, I have also made a start at a comparative behavioral, ecological, and life history study of the Antrodiaetidae. Using both morphological and nonmorphological data, I have discussed the evolution of *Antrodiaetus* and *Atypoides*. Included is a preliminary consideration of the relationship of the only other antrodiaetid genus, *Aliatypus*, to these two genera. It is my wish that this paper will stimulate further interest and continued research on these and related spiders.

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NATURAL HISTORY

Only three species of Antrodiaetidae—*Antrodiaetus unicolor*, *Antrodiaetus roretzi*, and *Atypoides riversi*—have had more than a few sentences written about their ecology, life history, or behavior. In this section I shall summarize the natural history literature of the family and add original data. Primarily because of my field studies in 1966, we now know much more about *A. unicolor* than any other antrodiaetid. A comparative summary and discussion of the natural history of the family is placed at the end of this section after the separate consideration of each species. An enormous amount of information is still needed before a valuable comparative biological study of the family can be completed. Hopefully this paper will trigger the search for such information.

My observations were made chiefly in the field during the summers of 1966 and 1967, but I also observed living spiders in the laboratory. Most observations on *Aliatypus* species were contributed by Wendell Icenogle. All specimens are numbered and have been placed in the American Museum of Natural History (AMNH) and the Museum of Comparative Zoology (MCZ); the correspondingly numbered field notes have been placed in the MCZ. Data on burrow architecture refer to adult female burrows unless stated otherwise. In the text many localities are represented by italicized letters; these localities are identified in the records section at the end of the appropriate taxonomic species description.

Antrodiaetus unicolor (Hentz)

Ecology

Geographic distribution and elevation range. Centered in the central and southern Appalachian region of the eastern U. S. with peripheral populations as far west as the Ozark region and south to near the Gulf coast (Map 1). 0–6600 ft (0–2000 m).

Habitat. Optimum conditions for *A. unicolor* are found in humid, cool, densely forested habitats with sandy loam soil. Such habitats are abundant and nearly continuous in the dissected terrain of the central and southern Appalachian Mountains and their foothills and westward over the Appalachian Plateau. The densest and largest burrow aggregations are usually found on the inclined surfaces of slopes and banks along ravines, streams, roads, and trails; at the base of rock (particularly sandstone) outcrops; and in other sheltered spots. Hemlock (*Tsuga*) and *Rhododendron* are often good plant indicators of optimum *A. unicolor* habitats. Over the more peripheral portions of the range of *A. unicolor*, one finds only scattered pockets of favorable habitat separated by larger areas of more or less unfavorable (dry, poorly drained, etc.) habitats. Although sandy loam is optimum, burrows also occur in other soil types, even sometimes in clay soil, decaying logs, etc. Burrows are normally uncommon in rocky, shallow soil that is too well drained.

Within favorable habitats burrows tend to be aggregated where the soil is constantly humid (at least around the lower portion of the burrow) and protected from erosion and flooding. In dry regions burrows are often clumped only near springs, along stream banks, or near seeps at the bases of rock outcrops. Burrow aggregations are seldom found on near-horizontal ground, unless such ground is well sheltered under something such as a rock outcrop, a sandstone shelter cave, or the base of a large tree. Two limiting factors that may contribute to this clumping under shelters are the temporary localized flooding and the buildup of fallen leaf cover on open noninclined ground surfaces. Such flooding and (usually) leaf litter accumulation do not occur on the steeply inclined slopes and banks where *A. unicolor* burrows are common. On these inclined surfaces, burrows are clearly aggregated in stable spots where erosion is minimal, e.g., moss covered areas and bare parts of the bank sheltered under the overhang of ground surface vegetation, exposed rocks, logs, large roots, and tree bases. Branson and Batch's (1968) statement that *A. unicolor* "lives in burrows mostly beneath fallen logs and deep litter" is erroneous.

Population density. The densest and largest populations were found at *C, D, I, J, K, O, P,* and *Q* within the central and southern Appalachian region. Even at such favorable localities, the population consisted of dense aggregations in optimum habitat spots and scattered individuals in intervening areas of less suitable habitat. One of the densest such burrow aggregations covered an area of about 50 m^2 and contained an estimated 80 to 100 adult females and several thousand immatures. Small dense aggregations were common within the larger aggregations in the above localities. A 0.1-m^2 area at *O* contained four brooding females and 25 immatures. An 0.81-m^2 area at *P* contained three adult females and 198 immatures. A 225-cm^2 area at *B* contained two adult females and 31 immatures. In many dissected regions the populations are concentrated and essentially continuous throughout the interconnecting ravines, young valleys, and coves, with the surrounding matrix of dryer ridges and upland areas very sparsely populated. In the peripheral portion of the *A. unicolor* range, aggregations are (like the favorable habitat) discontinuous and generally smaller and less dense.

Associated burrowing mygalomorph spiders. Throughout most of its range, *A. unicolor* is clearly the most abundant mygalomorph spider. Except for areas of overlap with the northern *Antrodiaetus robustus* (Map 1), only in southern and western parts of its range (in lowland habitats and in the Ozark region) is the abundance of *A. unicolor* equaled and sometimes surpassed by other burrowing mygalomorph species. I have found the following such spiders living side by side with *A. unicolor* at the following localities: *Atypoides hadros* Coyle at *F* (These two species have been found together in other southern Illinois localities by other collectors.); *Myrmekiaphila fluviatilis* (Hentz) at *H, O, R, Q,* and Mammoth Cave, Kentucky; *Cyclocosmia truncata* (Hentz) at *Q, R,* and David Crockett State Park, Tennessee; *Ummidia audouini* (Lucas) at Chickasaw State Park, Tenn.; *Ummidia carabivora* (Atkinson) at *N;* and *Ummidia* spp. at *Q* and Blanchard Springs, Arkansas. At *F, A. hadros* was common but not as abundant as *A. unicolor.* At both *Q* and *R, M. fluviatilis* was common but much less abundant than *A. unicolor.* In one low road bank at *Q, A. unicolor, M. fluviatilis, C. truncata,* and *Ummidia* sp. lived together, the latter two species being rare. At all other localities cited above, the other mygalomorph spiders were very rare. *Atypus* species are sympatric with *A. unicolor* but uncommon; I have never observed them at the same locality. I have not found Lycosidae burrows in *A. unicolor* aggregations.

LIFE HISTORY

Males. Males of *A. unicolor* (and all other Antrodiaetidae) closely resemble females in external anatomy and behavior until the striking metamorphosis of the final male ecdysis. Only a few obvious, sexually dimorphic characters—a sclerotized lip at the male genital opening, swollen male pedipalpal tarsi, and well-developed seminal receptacles of the females—appear during the later immature instars. The penultimate male undergoes the final molt within its burrow, and the adult remains there without feeding until certain factors trigger its abandonment of the burrow. Upon emergence, it wanders over the ground surface in search of female burrows, mates, and eventually dies.

The data summarized in Figure 1 indicate that the period of male wandering and mating for the entire species population of *A. unicolor* lasts from late July through late December. Because of occasional long-lived males, the mating season may be shorter than the period during which wandering males have been collected. The high frequency of wandering male records during October indicates that this may be the chief mating season of *A. unicolor*. However, all August records of mature males collected within their burrows were from cooler climate localities (*C*, *I*, and *P*) than the October collections and therefore possibly belong to earlier (September ?) emerging populations.

Evidence indicates that within any given local population the time of male emergence (and probably mating) occurs more nearly synchronously and is probably triggered by local climatic conditions. At *N*, J. Berry conducted a systematic, year-long pitfall trap collection resulting in a relatively complete record of male emergence in that population (J. Beatty, personal communication). Traps were put out for approximately 24-hour periods two times each month (only once a month in the winter) in each of 11 different areas. Fourteen of the 18 adult males collected were taken from 22 to 24 October (ten of these on 24 Oct.) following the first heavy rainfall after a dry summer. The other four males were collected on 1 October, 7 November, and 3 January. Pitfall traps maintained continuously from 7 October to 10 November at *E* by J. Nelson several years later (J. Beatty, personal communication) yielded 11 males during the initial week (7–14 Oct.), two the second week, one the third, one the fourth, and none during the final week (3–10 Nov.). A similar pitfall collection maintained by J. Nelson the following year at *G* from 10 September to 2 November yielded the first male during the week 28 September to 5 October, seven males the next week, one the following week, none the next week, and one during the final week (26 Oct.–2 Nov.). Collections during August revealed a pre-emergence synchrony of adult males at localities *C*, *I*, and *P*. Twenty-one of the 22 adult males collected were within their own burrows. I searched hard for wandering adult males during day and night but found only one. It appears that very few males had emerged and that proper conditions could have set off a large synchronous emergence.

A few winter records exist for wandering males of *A. unicolor*—an early January record from *N* and a literature record from *D* of "males observed on [the] surface during late winter" (Branson and Batch, 1968). I have not seen the latter males (from *D*) so only assume that they are *A. unicolor*. Such records are probably either aberrant late emerging individuals or individuals which have extended their above-ground survival time in particularly protective microhabitats.

Females. Pattern of early postembryonic development. Enough data were obtained from stereomicroscopic examination of each preserved *A. unicolor* brood to establish the following pattern of early postembryonic development. Hatching involves the simultaneous (or nearly so) shedding of the chorion and embryonic or "prelarval" (Vachon, 1958) cuticle. The resulting instar, which I shall call the first instar, is the "first free postembryonic stage" of Holm (1954) or "larva" of Vachon (1958). The second instar corresponds to the "first complete postembryonic stage" of Holm (1954) or "first nymph" of Vachon (1958).

The segmentation and appendages of the late embryo, as well as the dark egg teeth, are visible through the chorion. During hatching, first the chorion splits anteriorly and peels back over the abdomen. Usually the embryonic cuticle splits very soon after the chorion and also peels posteriorly, and the chorion and cuticle are shed simultaneously from the posterior of the abdomen and remain attached to each other. Occasionally, possibly because the interval between the splitting of these two membranes increases, they are shed separately. These conclusions about the timing of hatching are based on the following observations of preserved material: 1) Relatively few spiderlings in any hatching brood were actually in the process of peeling back or shedding the chorion or embryonic cuticle, and, in the great majority of those that were, the chorion was either peeling back or was still attached to the spiderling while the embryonic cuticle was peeling back. 2) Almost all shed chorions observed contained the embryonic cuticle.

The embryonic cuticle is very thin and transparent, lacks setae, has blunt nonfunctional chelicerae, and possesses a dark egg tooth at the base of each pedipalp. The first instar (Fig. 4) possesses several tarsal setae, lacks a rastellum or fang on the chelicera, lacks spinneret spigots, has anterior lateral spinnerets, and lacks pigmentation, except for that which slowly develops around the eyes. The second instar (Fig. 5) has functional chelicerae and spinnerets and can locomote rapidly. The chelicerae possess a few rastellar macrosetae and fully formed fangs, the anterior lateral spinnerets are lost, the other two pairs of spinnerets possess spigots, setae are plentiful, and the body is pigmented.

This pattern of development is the same as that described for *Ischnothele karschi* (Dipluridae) by Holm (1954) and for *Atypus karschi* (Atypidae) and *Heptathela kimurai* (Liphistiidae) by Yoshikura (1955, 1958). It is considered by Holm (1954) to be the most primitive pattern in spiders. Vachon (1958) reviewed these studies and is in agreement on the similarity of patterns in the above three species.

Timing of brood development. The numerous field collections of *A. unicolor* broods yield substantial data on the timing of brood development in nature within the species population as a whole. As shown in Figure 2, the egg stage is found from late June to mid-August, the first instar from mid-July to mid-September, and the second instar from mid-August through at least December. The relatively small number of broods in the process of hatching and molting is apparently a result both of the brevity of hatching and ecdysis in individual spiderlings and of the close synchrony of development within each individual brood. The regular temporal pattern of the brood stages and the absence of more than a single brood in the burrow of any brooding female strongly indicate that *A. unicolor* produces only one brood per year in nature. As Table 1 shows, brood development is not strictly synchronous within a local population, populations *C* and *O* showing the largest amount of variation. These data also indicate little or no lag in timing of brood development at warm climate localities (*N, O, Q, R*) behind that in cooler localities.

Substantial evidence indicates that the spiderlings overwinter in the second instar within the maternal burrow and disperse in the spring. As indicated in Table 1, 15 brooding females were collected between 14 September and 3 December from three localities. Each brood consisted entirely of second instar spiderlings, and none of the broods appeared to be diminished. In the December collection from *Q*, the spiderlings were quite sluggish as a result of the cold weather. During this collection and the September collection at *F*, I searched hard for burrows constructed by second instar spiderlings but the smallest burrows found contained only later instars. Two samples of second instar spiderlings from the December *Q* broods were kept alive at a nearly constant temperature of 12°C. One sample was checked in mid-February and the other in mid-March and both were still 100 per cent second instar broods. These were then released at room temperature into a jar of sand, and they constructed burrows within 24 hours.

Few data exist concerning longevity and the time normally required for an individual to mature. Oviposition to the beginning of the third instar may take nine or ten months. I would estimate at least three or four years from egg to sexual maturity. I have collected two brooding females (384 at Blanchard Springs, Ark., on 11 Sept.; 378 at *F* on 15 Sept.) with new cuticle visible under the old cuticle, thus indicating that females continue to molt after becoming sexually mature and after producing broods. The following evidence indicates that a given female may be capable of producing more than one brood. A number of brooding female burrows were each located in the center of a cluster of homogeneously-sized burrows of small immature spiders. Three of these brooding females (787 at Fort Mountain, Ga., 433 at *Q*, and 448 at *F*) were completely isolated from other large burrows.

Brood size and egg size. The sizes of complete broods collected at different localities are given in Table 2. Brood size statistics for the species as a whole are listed in Table 3. All populations with significant sample sizes show a wide range of variation in brood size and overlap with one another, but the means are often quite different. Table 4 indicates that there is much variation in egg size of *A. unicolor*. Egg size variation within an individual brood is quite small.

BEHAVIOR

Burrow structure. A. unicolor constructs a roughly tubular silk-lined burrow which is widened just below the entrance and at the bottom end (Figs. 6–9). The detailed shape of the burrow, its size, and the thickness of its silk lining vary greatly, depending on the size, sex, and reproductive state of the spider, and especially on soil condition. Tables 5 and 6 show the variation in burrow length and entrance diameter in *A. unicolor*. The latter measurement is more closely related (directly) to body size than is burrow length, which is more influenced by soil conditions. The mean size of penultimate male burrows is markedly smaller than that of adult female burrows, probably because of the smaller body size of the males. Soil with many pebbles, rocks, or roots usually contains crooked and/or shortened burrows. Burrows in hard clayey soil are shorter than those in firm sandy soil. Soil stability (and possibly humidity) appears to have considerable effect on the thickness of the burrow lining. Burrows in loose soil tend to have thicker linings than those of the same population in more stable soil. Usually the upper part of a burrow has the thickest silk lining, this probably being, at least in part, an adaptive response to the relative instability (or low humidity) of surface soil. The rest of the burrow is sometimes only thinly lined with silk. Brooding females (even with unemerged broods) often have thicker burrow linings than adult females without broods. All brooding females at *O* had markedly thicker burrow lining than many brooding females at other localities.

Burrow inclination is strongly correlated with the inclination of the immediate ground surface. The *burrow pitch*—here defined as the angle formed between the mean longitudinal axis of the burrow and the line originating at the entrance and perpendicular to the surrounding ground surface (i.e., the deviation of the burrow from the perpendicular)—of the great majority of *A. unicolor* adult female burrows is 0–15°. Exceptions are often the result of rock or root barriers in the soil. Only one or two burrows sloped upward from the entrance. The probable adaptive significance of such a near-perpendicular burrow pitch is that it removes as much of the burrow as possible from the surface soil, which is structurally and climatically (humidity and temperature) more unstable than the deeper soil layers. This might be particularly important on the steeply inclined banks often inhabited by *A. unicolor* where surface erosion is relatively great. Humidity, structural stability, or temperature gradients are directional cues that might be used in burrow construction.

Occasionally, *A. unicolor* burrows have single, short, dead-end side branches. These are either close to the surface (Fig. 10) or, rarely, at the bottom end. One Y-shaped burrow (389 at *F*) with two entrances was found. Only once have I found a spider in a side branch.

Entrance structure. The silk lining of the burrow is extended above the soil surface to form a flexible collar which is collapsed inward to close off the open end of the burrow (Figs. 11–14, 40–43, 59). This collar is composed of excavated soil particles and materials from the immediate ground surface (such as pieces of twigs, leaves, conifer needles, moss, or just surface soil) held together by silk so that its outer surface is camouflaged and its inner surface silk-lined. The kind and quantity of surface material incorporated into the collar depends on its abundance on the immediate ground surface. When open the collar is more or less erect, and when closed it is roughly flush with the ground surface. The relative height of the collar varies noticeably within populations. Population *O* appears to have collars with the largest height/diameter ratio.

The spider collapses the collar in a bilateral manner by pulling inwardly on two opposing sectors (lateral to the spider), producing a condensation of folding at the two opposing points where these sectors meet. When the burrow entrance opens onto an inclined ground surface, these two points are at the ventral and dorsal sectors of the entrance opening, because of the spider's stereotyped foraging posture orientation. The collar (especially of the larger spiders) is frequently somewhat reduced at these two points, which, if the entrance opening happens to be slightly elliptical, also correspond with the ends of the long axis of such an ellipse. Careless observation of such a collapsible collar by Atkinson (1886) led to his erroneous description: "Each door is a surface of a half circle, is hung by a semicircular hinge, and the two meet, when closed, in a straight line over the middle of the hole. . . . " Unfortunately the majority of subsequent descriptions (Simon, 1892; Comstock, 1912 and 1940; Gertsch, 1949; Kaston and Kaston, 1953; Kaston, 1964 and 1966; Pimentel, 1967) of *Antrodiaetus* burrow entrances are apparently based on Atkinson's inaccurate description.

Under certain conditions, a closed collar may be held shut by a small amount of silk spun over the inside surface of the collar. Such sealing is usually performed before a spider molts. The burrow entrances of brooding females are sometimes similarly sealed. Soil plugs are apparently used much more infrequently to seal the burrow entrance. I have found these soil plugs in only five medium-sized burrows (at *O* and *J*) and one adult female burrow (1115 at *Q*). The immature spiders were molting and the adult female had an egg sac. In each of these, the upper 0.5–1.5 cm of burrow just behind the closed collar was packed tightly with soil (Fig. 8).

Burrow construction behavior. Normally an individual probably occupies and enlarges the same burrow during its entire life span, the burrow site initially being chosen by the second instar spiderling. However, I have collected several medium-sized immatures and one adult female *A. unicolor* on the ground surface away from any burrow and have occasionally observed empty burrows with open collars, no spider remains, and no penultimate male molts. Under laboratory conditions, large immature male and female spiders and adult females are capable of constructing burrows from scratch. These observations indicate that the abandonment of burrows and the founding of new burrows at different sites may not be uncommon in nature.

The following account of burrow construction behavior is based on laboratory observations of ten large immature (male and female) and mature (female) spiders burrowing into humid packed sand; it is incomplete and subject to revision when more detailed observations are completed. The initial step is the construction of a shallow enclosure or cell. Next, sometimes after a period of inactivity, the spider extends this closed cell deeper into the soil until the elongate burrow is formed. Most observations were made on the initial cell construction phase, which lasted from 15 to 30 minutes.

Four rather well-defined behavioral components form cell construction behavior: 1) burrowing, 2) excavating, 3) silk application, and 4) raking. Burrowing consists of pushing into the sand, forcing it apart, and compacting it. An initial depression is made by forcing the palps and first legs into the sand surface. Very soon, however, as the size of the depression increases, the other appendages enter into the burrowing movement. Full-formed burrowing behavior consists of the chelicerae pressing forcibly against the side of the bottom of the depression (or burrow) with the legs flexed over the dorsum of the cephalothorax and abdomen and pressing in the opposite direction against the opposing side of the cavity (Fig. 56). Excavating involves digging sand from the bottom of the depression, transporting it, and releasing it on the soil surface. The chelicerae are elevated and spread apart laterally, and the fangs are extended. These are forced ventrally into the sand, flexed, and then lifted away with the sand held in between. The spider then pivots to reverse its direction and moves up to the top of the cavity. The palps aid in holding the sand in the chelicerae. With its front legs, pedipalps, and chelicerae it reaches out of the cell opening over the soil surface (Fig. 57). It then releases the load by opening its fangs and chelicerae, and pulls away from the load while holding the load against the soil surface with its pedipalps. Silk application includes circular and lateral movements of the abdomen and the entire body (with the spider facing down into the cell) and sweeping movements of the spinnerets (particularly the elongate posterior lateral spinnerets), during which silk is applied to the cell wall and most abundantly to the rim of the cell opening (Fig. 58). In raking, the first legs, the pedipalps, and sometimes the chelicerae and fangs reach out past the rim of the cell opening and pull surface detritus and soil back to the rim of the opening and partially over the opening. This material is often compacted by being pressed against the chelicerae by the first legs and pedipalps. After the spider releases it, it is held in place by silk previously applied to the rim.

Cell construction usually begins after considerable searching behavior in which wandering alternates with mild burrowing, which is usually released by depressions in humid sand. Eventually a series of burrowing movements is repeated in one spot. Burrowing usually continues until a fairly deep depression is formed, and then excavating begins and alternates sporadically with burrowing. The frequency of burrowing decreases, and soon silk application begins and, sporadically, but with increasing frequency, accompanies burrowing and excavating. If it follows excavating, silk is usually applied to the sector of the opening rim and cell wall where the soil load was dropped. When the cell becomes deep enough to contain the spider, raking begins and often follows excavating. Usually only a few instances of raking will suffice to pull the rim of the cell opening shut (or almost shut) and thus end the initial stage of burrow construction.

Burrowing, excavating, and silk application continue during the rest of burrow construction, but the manner in which the load of sand is deposited was quite different in the only two spiders observed after initial cell construction. Instead of being deposited on the ground surface, each load was pressed into the burrow wall just below the top of the closed cell. Apparently the pedipalps held the sand against the wall while the chelicerae and fangs were pulled away, then the sand was pushed into the wall with the rastellar area of the chelicerae. This behavior eventually caused the area around the entrance to bulge outward into a mound. Such internal deposition of soil, if it is normal behavior, would seem to be an effective adaptation for minimizing the exposure of the spider to predation. Collar formation has not been observed.

Atkinson (1886) observed burrow construction behavior in several spiders kept in captivity, and although his description is often difficult to understand, his observations generally agree with those above. He observed too, that after the initial cell is closed over, the excavated soil is deposited and pushed into the wall within the upper end of the burrow. "Dome" apparently refers to the closure over the cell. Atkinson claimed that the spider would apply "viscid liquid" as well as silk to the excavated soil deposited at the rim of the cell opening. It is not clear what he meant by "viscid liquid."

Egg sac structure and position. The egg mass of *A. unicolor* takes the form of a flattened sphere or ellipsoid with a maximum dimension of usually 9–14 mm and a thickness of usually 5–8 mm. Apparently this mass is formed on a portion of the burrow lining which has been thickened with a few additional layers of silk. Several layers or sheets of silk are then apparently applied over the egg mass and hold it firmly against the burrow wall, each sheet larger and attached to the burrow wall slightly farther from the egg mass than the previous sheet (Figs. 6–9). J. R. Tripp, who has recently observed oviposition and egg sac construction in this species, confirms that this is the method of egg sac construction (personal communication). Egg sac silk has the same texture and white color as burrow lining silk.

As shown in Tables 5 and 6, the position of the egg sac in the burrow is quite variable for *A. unicolor.* However, while some population samples exhibit wide variation in egg sac position, others (*Q* and especially *O*) show much less variation and have all egg sacs deep within the burrow. In the populations in which brooding females were often actively feeding (*O*, *Q*, and *R*), egg sacs were well below the surface. It is possible that these two phenomena are adaptively linked, since it is likely that egg sacs near the entrance would be more easily damaged during prey capture than egg sacs attached deep within the burrow. Possible environmental causes should be investigated. All but one of the 101 egg sacs were placed on the ventral sector of the burrow wall. Most egg sacs produced a localized constriction of the burrow lumen, but never so much that the spider could not maneuver past it. In at least most cases this constriction is counteracted, because the burrow is somewhat widened in the vicinity of the egg sac.

Overwintering. On 28 December burrows were observed at *B* on an overcast afternoon (noon temperature = 0°C). Five centimeters of snow lay on the ground except under the shelter of a sandstone wall where most of the burrows were located. The upper 1 cm of the sand soil was dry, loose, and unfrozen; the next 9–15 cm frozen; and below this humid, packed, but unfrozen. No burrows were seen with open collars. Close examination of about 20 small and medium-sized burrows revealed only two entrances sealed inside with silk and none plugged with soil. Four burrows were completely excavated. Two of these had one or two very thin silk septa spun across the narrowed central part of the burrows. Two of the burrows did not extend below the frozen zone, the other two did. All four spiders were quite sluggish but became active after several seconds in my hand.

On the night of 2 December and in daylight the next morning, I observed a burrow aggregation at *Q*. The ground was unfrozen, but the air temperature was 3°C at 9 P.M. and –2°C at 8 A.M. At night, during a light snow and rain, I was surprised to find that most burrows of all sizes were open, and most of these had spiders at the entrance in normal foraging posture. These spiders were more sluggish than usual, however. In the morning (clear weather), a few entrances were still open but no spiders were in the entrances. No sealed entrances could be found. This ability to remain active at relatively low temperatures may contribute to the remarkable success of *Antrodiaetus* in the temperate zone.

Behavior of brooding females and broods. The data summarized in Table 7 show that the broods emerge from the egg sac just before, during, or just after they molt from the first to the second instar. In broods that were emerging when collected, only a few first instar spiderlings (when present) but most of the second instar spiderlings (when present) were found outside the egg sac. Also, in emerging broods and in the few completely emerged broods still with egg sacs, most of the first instar exuviae were found in the egg sac. One exception, 477 at *I*, had these exuviae scattered all over the burrow wall. These data indicate that most emergence is performed by the active second instar spiderlings. There is no evidence indicating how the spiderlings escape from the egg sac or how the egg sac is disposed of. In 59 of the 66 burrows with completely emerged broods, the egg sac was no longer present.

Table 8 indicates that while in some populations (*O*, *Q*, *R*) brooding females with egg sac broods do not seal their burrow entrances and usually continue foraging, in others (*B*, *C*, *J*) they commonly maintain sealed burrows. Such sealing of burrows is in contrast to neighboring contemporary nonbrooding females, which, unless molting, usually kept their entrances unsealed and were actively feeding. How long and for what function such burrows are kept sealed is not known. I was unable to determine whether the sealing of burrows containing emerged second instar spiderlings was initially produced by the adult and thus signifies inactivity or whether it is simply the result of spiderlings trailing dragline silk over the inside of the entrance. At least a number of such brooding females had unsealed burrows and were actively feeding.

First instar spiderlings, extremely slow moving, are sometimes seen moving within the egg sac. Second instar spiderlings are active—they can move quickly in response to stimuli, wander over the burrow wall, and are capable of performing many behavior patterns necessary for independent existence. Several second instar spiderlings released on humid sand in the laboratory constructed individual burrows and assumed normal foraging postures. Second instar spiderlings are capable of spinning draglines and normally appear to do so as they move about. When a brooding female burrow with a closed entrance is first discovered, second instar spiderlings are often found in the upper end of the burrow, but these always retreat to the bottom of the burrow as it is excavated. This may be a photonegative response, but other behavioral controls must be operative in preventing these spiderlings from escaping at night if the burrow entrance is open and the brooding female is feeding (such as at *Q* in September and December). Each of the five broods observed on 2–3 December at *Q* was aggregated in the bottom end of the burrow, several in dense clusters; and all spiderlings were sluggish.

There are no data on whether spiderlings normally feed within the parental burrow before dispersal. An observation of a second instar spiderling which had not yet constructed a burrow but which carried a collembola in its chelicerae, and observations of other second instar spiderlings capturing prey after constructing their burrows, indicate that they are at least capable of feeding before dispersal. Intrabrood cannibalism is possible, but the broods observed in fall and winter did not appear to be smaller on the average than those collected earlier.

Molting behavior. Fragmented remains of one and occasionally two old exuviae were often found to be bound with silk and compacted into the bottom end of burrows. I collected (in July, August, and September) ten immature spiders each with an incompletely sclerotized cuticle and a freshly fragmented exuvia mashed into the bottom of its burrow. Seven of these recently molted individuals had sealed their entrances with silk, and three were discovered by scraping the soil (whether the entrances were sealed could not be determined). Four other immatures (also collected during the summer) were found just after ecdysis; they were much less sclerotized and could not move quickly. These were at the bottom end of their burrows, and the intact exuviae were attached lightly to the ventral sector of the wall of each burrow at one-half to three-fourths of the distance from the entrance to the bottom end. One exuvia was attached with its venter against the burrow wall, and its anterior end heading up the burrow. The orientations of the other three were not recorded. The entrances of three of these burrows (133 at *J*, 951 at *C*, and 747 at Brasstown Bald, Ga.) were sealed with silk, the fourth (355 at *J*) was filled with a soil plug. Another medium-sized immature spider (7040 at *Q*) was excavated shortly before ecdysis, which it underwent within a glass vial kept humid by a moist piece of paper towel. Ecdysis lasted ten minutes. Within four days of ecdysis, the spider had thoroughly fragmented the exuvia and formed it into a compact mass bound together with a small amount of silk.

Twenty-seven burrows of recently molted adult males were excavated. All burrow entrances were closed, but 23 were discovered by scraping the soil surface; whether they were sealed could not be determined. Three of the other four were sealed with silk; the fourth was unsealed. In all but two of these 27 burrows the penultimate exuvia was partly broken up, bound with a little silk, and packed lightly into the bottom end of the burrow. Sometimes this exuvia and the end of the burrow were covered with several thin sheets of silk. The other two burrows each contained a pale unsclerotized male resting motionless at the bottom end of the burrow. In each the freshly shed exuvia was attached—venter against the wall, anterior end heading up the burrow—to the silk lining of the ventral sector of the wall, two-thirds (409 at *F*) and three-fourths (450 at Blanchard Springs, Ark.) of the distance from the entrance to the bottom end.

Apparently, molting behavior in penultimate males and other immatures is similar. In summary, ecdysis usually takes place in a sealed burrow on the ventral sector of the burrow wall in the lower half of the burrow (but above the bottom end). Shortly after ecdysis, the spider moves to the bottom end. After sclerotization reaches a certain point, the spider detaches the exuvia from the burrow wall, breaks it up, and compacts it into the bottom end of the burrow, adding silk. Adult males do not usually fragment the molt as thoroughly or pack it into the end of the burrow as compactly as do females or immature males. The sealing of burrows before molting may help protect the molting spider from predation and may maintain a higher, more constant humidity within the burrow.

Defensive behavior. When spiders in normal foraging posture are disturbed by light, substrate vibration, or prodding with a stick, they sometimes retreat down the burrow without closing the collar or may quickly close the collar, often remaining for a time just below the collar holding it closed. During the later stages of excavating to expose a burrow, one finds most adult female spiders at the bottom end of the burrow in an aggressive defensive posture. The spider faces up the burrow with its cephalothorax reared backwards at an angle to the abdomen. Legs IV and III and possibly II hold onto the burrow wall to anchor the spider. The other legs and pedipalps are raised and spread apart. The chelicerae are also raised and spread apart laterally with the fangs extended. If prodded, the spider strikes forcibly with a sudden downward movement of the cephalothorax and chelicerae. Such a defensive posture within the confines of the bottom end of the burrow limits the approach of an attacker to that part of the spider protected by its chelicerae. Younger individuals and adult males tend to be less aggressive and often do not exhibit such defensive behavior while being excavated. Medium and large spiders will often exhibit similar defensive behavior outside their burrows if prodded.

Predators and parasites. Observations show that females and immature males of *A. unicolor* are preyed upon and parasitized by centipedes, pompilid wasps, acrocerid flies, and mites. Adult males have been collected several times from the ground webs of theridiid spiders.

Four instances of apparent centipede predation have been observed. At Clifty Falls, Indiana, a 50–70 mm long scolopendromorph centipede escaped from a burrow containing a recently killed spider. At *L* a scolopendromorph centipede, *Theatops postica,* was found in a burrow with spider remains. At both *O* and Blanchard Springs, Arkansas, a *Theatops spinicauda* centipede was found in an empty *A. unicolor* burrow. One instance of unsuccessful centipede predation was observed at *C* where a nearly dead *Lithobius forficatus* centipede (lithobiomorph) was found in the burrow of a large immature *A. unicolor.* The centipede had probably entered the burrow through the soil; the burrow entrance was sealed shut.

Twenty-one cases of predation by pompilid wasps have been observed (Table 9). No larvae could be reared to adulthood, thus no specific or generic identification could be made. More than one species is probably involved since variation in cocoon size is great. Spiders with attached eggs or early instar larvae were found in the bottom of their burrows dorsal side up and partially paralyzed. Leg jerking was the chief response to disturbance. The wasp egg was always attached centrally on the abdominal dorsum. Soil plugs apparently constructed by the ovipositing female wasp sealed the spider and larva into some burrows (Fig. 15). Cocoons were usually attached to the burrow wall some distance from the burrow end, where the spider remains were usually found. The hollow usually found in the burrow wall just above the soil plug appears to be the source of the plug.

One tiny, recently hatched pompilid larva and its paralyzed food source from *C* were placed in a narrow glass vial and observed through cocoon formation. Feeding lasted four days. The spider remains consisted of a small packet of compacted spider cuticle. On the fifth day, the larva had moved away from the spider remains. It first spun a loose maze of silk threads between the walls of the tube and then constructed the cocoon within this maze. Cocoon construction took less than 24 hours.

Population *P* was parasitized by the dipteran *Eulonchus marialiciae* Brimley of the Acroceridae. Observations were made on 1 and 2 August. This is presently the only host record for the genus *Eulonchus,* which, because its distribution is otherwise limited to western North America (Schlinger, 1966), and, because it is similar to that of the antrodiaetids, may be an important parasite of other antrodiactid species. Considering that collected specimens of *E. marialiciae* are extremely rare (C. W. Sabrosky, personal communication), the population discovered at *P* was surprisingly dense. One freshly emerged adult was collected vibrating its wings just inside an *A. unicolor* burrow entrance. One pupa was collected from a burrow and kept for several hours until the adult emerged. Several other burrows were found with abandoned pupal skins and spider remains. A total of about 18 adult acrocerids were seen hovering near *A. unicolor* burrow aggregations.

The adults appeared to fly only during the daytime. The largest aggregation of adults (about 12) formed rather quickly as I was excavating several burrows and hovered close to the ground where I was digging, as if attracted by some chemical released by my digging. Twice I observed adults hovering over and momentarily landing near (or on?) a closed burrow entrance. It is probable that, as in other acrocerids, the first instar larva actively searches out the spider, penetrates the cuticle, and develops as an endoparasite. My observations indicate that the larva, after feeding on the spider in the bottom end of the burrow, climbs up the burrow wall, attaches somewhere above the bottom end, and completes development in this spot. (One pupa and three pupal skins were attached here.)

Immature parasitic mites have been found on 18 adult females from nine different localities scattered over the species range. These were usually attached to appendages as well as to the body proper. It is likely that mite parasites on other specimens have gone unnoticed.

Prey capture behavior. The normal foraging posture of *A. unicolor* is as follows (Fig. 59): The spider is positioned inside the burrow just below the opened collar and faces out the entrance with its pedipalps and first legs extended slightly forward and touching the inner surface of the open collar. Usually the spider's venter is against the ventral-most sector of the burrow wall. Sometimes a spider may be in this posture with the collar only partly opened. Often prey capture behavior is also released in spiders which are positioned farther down the burrow or which have their collars closed. Such individuals, however, appear to respond more slowly to prey stimuli.

Larger immature spiders and adult females usually open their collars and assume the typical foraging posture only in very reduced daylight and in darkness. Younger spiders, particularly the youngest, frequently leave their collars open and often assume the foraging posture during daylight hours as well. The less light (heavily shaded habitats, overcast days, early morning and late afternoon hours) and the greater humidity, the more likely a given spider will be found with an open collar or in a foraging posture. *A. unicolor* is thus primarily a nocturnal feeder with some tendency to feed also during daylight hours, depending upon environmental conditions, age, and probably nutritional condition.

Observations indicate that the prey sensing radius of *A. unicolor* does not exceed several centimeters. Substrate vibration transmitted via the burrow lining and collar is apparently the only stimulus used by the spider to determine the presence and location of prey. This conclusion is indicated by numerous observations (in nature and in the laboratory) of prey capture behavior being released simply by the observer gently vibrating the collar or adjacent ground surface with forceps or sticks, thus eliminating visual and chemical cues. Additional evidence also rules out visual signals. In the typical foraging posture, the spider's field of vision is only a limited inverted cone of space projecting out from the burrow entrance; when the great majority of prey is caught, it has not entered this cone. I have frequently observed spiders within closed collars sensing and capturing ground surface prey. Prey capture is commonly performed in the dark; moreover, the eyes of antrodiaetids are quite small.

Casual observation in nature and in the laboratory, as well as motion pictures of prey capture behavior in lab animals, indicate the following pattern for prey capture behavior. After having determined the approximate location of the prey by tactile stimuli, the spider lunges from the burrow entrance at the prey. Legs IV and, usually, III remain within the burrow anchoring the spider to the burrow wall. The pedipalps and legs I are held out in front of the spider, and legs II also usually leave the burrow. The tarsi and penultimate segments of the pedipalps and legs I contact the prey and hold it against the substrate (Fig. 60). Lateral rows of strong suberect macrosetae on the tarsus and tibia of the pedipalps and on the metatarsus of legs I and II aid in holding the struggling prey and probably also provide important sensory input. Sometimes legs II aid in holding the prey. While the prey is held against the substrate, the chelicerae spread apart laterally, the fangs are extended, and the spider strikes forward and down at the prey with the chelicerae. The fangs contact the prey at two well-separated points (Fig. 61). There may be one to several more such strikes and maneuvering of the prey with the pedipalps and legs before the prey (usually still struggling) is quickly pulled down into the burrow by the pedipalps and legs I (Fig. 62). The spider does not usually close the collar until later, presumably after the prey has been subdued. Sometimes, however, friction of the prey or spider legs against the collar as the prey is being pulled into the burrow partly or completely closes the collar. The time from the beginning of the lunge to the disappearance of the captured prey into the burrow for seven filmed prey captures of seven different spiders ranged from 0.8 to 4.5 seconds, with a mean of 1.8 seconds. The time from the beginning of the initial lunge until contact was made with the prey for four of these spiders ranged from 1/32 to 1/16 of a second.

Atkinson (1886) described the capture of an ant. After detecting the ant, the spider quickly closed the collar, leaving it open only a crack. When the ant crossed this opening, the spider threw open the doors and caught the ant. Such behavior was observed several times, and Atkinson concluded that the spider did not strike until it could see the ant through the opening. That vision actually did play such an important role is doubtful.

Prey composition. Records obtained from prey rejectamenta and freshly killed prey found in burrows in nature indicate that *A. unicolor* is markedly unselective in its choice of prey. It appears to capture and feed upon any arthropod that it is capable of catching and killing (speed, strength, and size of the potential prey probably being important factors) that chances to enter within the prey-sensing radius of the burrow entrance. The prey records in Table 10 indicate that ants and beetles form a large part of this species' diet. This is not surprising considering the abundance of these arthropods on the ground surface. However, thinner-cuticled arthropods are probably more common prey than these records indicate; the rejectamenta records are strongly biased toward such thick exoskeleton forms as ants, beetles, and millipedes which are not as finely fragmented by the spider.

The ants consisted of both formicine and myrmicine species, with the large-bodied formicine genus *Camponotus* common. Numerous beetle families were represented. Three millipede families were found: Parajulidae (five individuals), Xystodesmidae (two individuals), and Polydesmidae (one *Scytonotus granulatus*, one *Pseudopolydesmus serratus*, and two *Pseudopolydesmus* sp.). One of the spider prey was a conspecific male; another was a male *Agelenopsis.* Two phalangids belonged to *Leiobunum.* One wasp was a *Vespula.* In the laboratory, *A. unicolor* readily captures and eats *Porcellio* isopods and *Tenebrio* beetle larvae. Small immatures take wingless *Drosophila.* Identifiable prey ranged in length from about 2 mm to a 16-mm carabid beetle and a 25-mm *Pseudopolydesmus* millipede. It is noteworthy that *A. unicolor* is capable of killing and digesting arthropods (ants, wasps, and millipedes) well known for their stings and/or chemical defenses.

Disposal of prey remains. Exoskeletal remains of digested prey are apparently disposed of in two ways: 1) packed into the burrow wall, 2) discarded on the ground surface outside the burrow. In most burrows, prey rejectamenta is found mixed with a small amount of silk and compacted into the bottom end of the burrow. All except the toughest exoskeletal portions (ant heads and thoraxes; beetle heads, thoraxes, and elytra) are usually fragmented. Sometimes similarily compacted rejectamenta is also present in parts of the burrow wall closer to the entrance. These trash packets possibly mark previous positions of the bottom end of that particular burrow. Some burrows with large amounts of rejectamenta in the bottom end had collembola aggregated on and near the trash.

Occasionally spiders kept in the laboratory disposed of pieces of prey remains by placing them on the soil surface outside their burrows. At least some of these pieces were only partly digested and were decaying; this disposal behavior may be an adaptive response to such decay. Other evidence indicates that prey remains are disposed of outside the burrow: many burrows lack or have very little rejectamenta in their walls; a large amount of fragmented insect cuticle lay on the ground surface in the midst of a dense concentration of burrows at *B.* The periodic excavation to enlarge a burrow and the concomitant disposal of trash packed into the burrow end very likely explain both of these latter types of observations. In summary, the primary method of trash disposal *could* involve two steps: 1) packing the fragmented exoskeleton into the bottom end of the burrow and 2) discarding this compacted rejectamenta on the ground surface during burrow enlargement (or after a sufficient amount of trash collects in the burrow end). Such a method might mean less exposure to predation than would the surface disposal of each prey exoskeleton separately.

Mating behavior. Only a single observation exists on the time of day of male wandering; I collected a wandering male (637 at *P*) on 3 August at 9 P.M. (after dark), 90 minutes after a heavy rain. The mostly digested remains of an adult male *A. unicolor* were found in the burrow of a conspecific female (543 at *I*).

Antrodiaetus robustus (Simon)

ECOLOGY

Geographic distribution and elevation range. Eastern Ohio east through Pennsylvania, northern Virginias, and Maryland (Map 1). 0–1500 ft (0–460 m).

Habitat. I have observed *A. robustus* in only one locality; Caledonia State Park in southern Pennsylvania. Small clusters of burrows were scattered over steep, well-shaded banks on a hillside near a stream in mixed conifer-hardwood forest. White pine and hemlock were dominant near the burrow sites. Most burrows were under the shelter of trees, tree trunks, or exposed rocks and roots, and were as common in spots with a thick surface mat of pine needles as where surface litter was absent. The soil consisted chiefly of firmly packed light tan loam with pebbles.

LIFE HISTORY

Males. The data in Figure 1 indicate that male wandering and mating occur during September and October.

Females. The second instar morphology of *A. robustus* is like that of *A. unicolor.*

Four records (Fig. 2) indicate that the timing of brood development may be similar to that of *A. unicolor.* The presence of a fully sclerotized second instar brood within a parent burrow at Canton, Ohio, on 19 October weakly indicates that broods may overwinter within the parent burrow before dispersing. The sizes of the two completely collected broods are given in Table 3.

BEHAVIOR

Burrow structure. The five adult female burrows observed (Table 6) were similar in structure to *A. unicolor* burrows. They were widened just below the entrance and at the bottom end, and entirely or almost entirely lined with silk. The silk lining was thickest at the upper end. Burrow pitch ranged from 0 to 10°. All burrows sloped downward from the entrance. The burrow of one immature had a dead-end side branch near the bottom end, another immature burrow had a similar side branch near the surface.

Entrance structure. The silk lining of the burrow is extended above the soil surface to form a flexible collar like that of *A. unicolor.* This collar is well camouflaged and is opened and closed in the same manner as that of *A. unicolor.*

Egg sac structure and position. Both egg sacs observed were constructed and positioned like *A. unicolor* egg sacs. Both were in the bottom half of the burrow on the ventral sector of the burrow wall (Table 6).

Behavior of brooding females. Both females with egg sacs (collected near midnight) had their collars closed and sealed lightly on the inside with silk.

Molting behavior. Fragmented exuviae were sometimes found to be bound with silk and compacted with prey rejectamenta into the bottom end of burrows.

Defensive behavior. All individuals in foraging posture at night retreated down the burrow when disturbed by light or vibrations. Adult females and often immatures assume an aggressive defensive posture like that of *A. unicolor.* Both brooding females were particularly aggressive.

Feeding behavior. The foraging posture of *A. robustus* is like that of *A. unicolor.* Individuals assumed this stance (with the collar open) only in twilight and at night. Fragmented prey cuticle (primarily of ants and beetles) was found packed into the bottom ends of most burrows.

Antrodiaetus pacificus (Simon)

ECOLOGY

Geographic distribution and elevation range. The Pacific Coast of North America from San Francisco Bay north to southern Alaska, with outlying, perhaps isolated, populations in the montane areas of western Idaho, northeastern Oregon, and adjacent Washington (Map 2). 0–7500 ft (0–2280 m). The range of *A. pacificus* extends much farther north than that of any other North American mygalomorph spider.

Habitat. The habitat requirements of this species appear to be similar to those of *A. unicolor.* Optimum conditions for *A. pacificus* are apparently found in humid, cool, rather densely forested habitats with deep loam or sandy loam soils. Such habitats are particularly abundant in the moist lowlands and mountains along the Pacific Coast from northern California into Alaska (Fig. 63), but are less continuous inland, there to be found in the mountains of Idaho, eastern Washington, and eastern Oregon.

A. pacificus also occurs in the volcanic "sand" soil of the Cascade Mountain Range, and even constructs burrows in decaying logs in Douglas fir forest. Burrows are sparse in rocky areas with shallow, fast drying soils. The densest aggregations were discovered in soil that was humid and firm at or just below the surface. Within favorable habitats, burrows tend to be clustered in sheltered spots protected from erosion and flooding. Such spots are found on the stable parts of slopes and banks along ravines, streams, trails, and narrow roads. Moss-covered bank surfaces, or portions under the shelter of root, log, rock, or tree overhangs are, as in *A. unicolor*, common sites of burrow aggregations.

The densest and largest population was found at *I* where one burrow cluster contained four adult females, one adult male, and 36 immature spiders within 0.25 m^2. The largest and densest population in the eastern part of this species' range was found at *U*.

LIFE HISTORY

Males. The data in Figure 1 indicate that male wandering and mating occur between early June and early November, with peak activity perhaps from late July to late September. Records from a few relatively well-collected localities hint that, as in *A. unicolor*, male emergence is more nearly synchronous in any given locality and is controlled by local climate.

Females. Close examination of the four *A. pacificus* broods indicate that the pattern of early postembryonic development is the same as in *A. unicolor*. Almost all of the shed chorions examined contained the embryonic cuticle, and very few of the spiderlings actually in the process of hatching had lost the chorion but not the embryonic cuticle. Therefore hatching involves the splitting and peeling back of the chorion and then the embryonic cuticle in close succession, followed by the (usually) simultaneous shedding of these membranes. The morphology of the embryonic cuticle and the first instar is as in *A. unicolor*.

The few data (Fig. 2) indicate that the timing of brood development of *A. pacificus* in nature may be similar to that of *A. unicolor*. Evidence that spiderlings may overwinter in the second instar and that adult females are long-lived was provided by an adult female (2246 at *R*) collected on 3 July. Although she was rearing no brood that year, her burrow was in the center of a 30 cm diameter aggregation of 36 burrows of spiderlings that matched the size and morphology of second instar *A. unicolor* spiderlings. Since she was isolated from other adult burrows, these spiderlings almost certainly belonged to her brood of the previous year. Data on brood size and egg size are given in Tables 3 and 4.

BEHAVIOR

Burrow structure. A. pacificus burrows (Figs. 16 and 17) are very similar in structure to *A. unicolor* burrows. The tubular burrow is slightly widened just below the entrance and at the bottom end and is narrowed between. The silk lining is thickest in the upper end, is often nearly imperceptible in the lower portion of the burrow, and tends to be thicker in less stable or dryer soil. There is considerable variation in burrow length among adult spiders (Table 6). These burrows tend to be longer in dryer soil, but many other factors also affect burrow length. Penultimate male burrows average smaller than those of adult females. Adult female burrow pitch ranged from 0 to 35° with most burrows between 0° and 15°. No burrow sloped upward from the entrance.

Entrance structure. This species possesses at its burrow entrance a flexible silken collar identical to that of *A. unicolor* (Figs. 18, 19, and 44). The only burrows observed with the collar closed and sealed on the inner surface with a small amount of silk (as is fairly common in *A. unicolor*) were those of three penultimate males apparently ready to undergo the final molt. Two burrows were found with soil plugs. In one burrow (2994 at Catherine Creek State Park, Ore.), the plug was in the entrance under the closed collar, but in the other (2970 at *V*), the plug was positioned one-third of the way down the burrow.

Egg sac structure and placement. All

four egg sacs examined were like those of *A. unicolor* (Fig. 16). Of the three egg sacs which I excavated, one (2825 at *S*) was near the top of the burrow, and the other two (at *I*) were in the bottom half (Table 6). All were attached to the ventral sector of the burrow wall.

Molting behavior. Fragmented exuviae were often found compacted like prey exoskeletons into the bottom end of burrows. Only two recently molted spiders were observed; two mature males each had the final exuvia packed lightly into the bottom end of its burrow. The exuvia of one male (2628 at *V*) was slightly broken, and the nature of the entrance closure could not be determined. The exuvia of the other (L-1 at *I*) was unbroken, and the collar was closed and lightly sealed inside with silk.

Defensive behavior. The behavior of foraging individuals of *A. pacificus* when disturbed by strong light and substrate vibrations is like that of *A. unicolor.* Adult females, when prodded, often assume an aggressive defensive posture like that of *A. unicolor.* Five large immature spiders at *R* were observed at the bottom end of their burrows spinning a thin septum of silk across the burrow lumen between themselves and the entrance as I excavated their burrows. When I broke the septa and prodded them, they exhibited the typical aggressive defensive posture.

Predators and parasites. Three recently digested males were found hanging in the webs of theridiid spiders at *G*. One male from Washington was taken "from the stomach of *Bufo boreus*," a western toad. Three large immature specimens (2249 and 2640 at *R*, and 2114 at *M*) each had large nematode worms filling their abdomens. A pompilid wasp larva was found on the abdominal dorsum of a female *A. pacificus* on 26 July near Friday Harbor, Washington.

Prey capture behavior. Adult females were observed in foraging position within their open burrow entrances only after nightfall, or, rarely, in very dim light; the burrow entrances are normally closed during the daytime. Immatures usually assumed foraging postures earlier in the evening. Very young spiders frequently had collars open during the daytime and were often in foraging postures then. The foraging posture of this species is similar to that of *A. unicolor.*

Prey composition. Recently captured prey and identifiable prey rejectamenta found in the bottom of burrows include ants, beetles, spiders, hymenoptera (one vespid wasp and one Argidae), and Hemiptera. Ant and beetle remains were far more abundant than those of other groups. A 15-mm long carabid beetle (Broscinae) and *Camponotus* major worker ants were the largest prey found.

Disposal of prey remains. Fragmented exoskeletons of digested prey were frequently found mixed with a small amount of silk and packed into the bottom end of burrows as in *A. unicolor.* The thicker the cuticle, the less fragmented the remains. Live collembola were observed on such trash in a few burrows.

Mating behavior. Males of *A. pacificus* apparently wander in search of mates only at night. I have observed 12 wandering males, seven at *L* and five at *K*, all after nightfall. Considerable daytime collecting at both localities failed to turn up wandering males. Four male specimens from *W* are accompanied by the label "on ground at night." Wandering males usually stop moving when light is shown on them.

At *L*, two captured males were released near female burrows, and each stopped suddenly when it came close to a burrow. In one encounter, the female closed her collar just as it was discovered by the male, which then used his pedipalps and first legs in an apparent attempt to open the collar. After about 30 seconds it wandered away. In the second encounter, a female lunged out of her entrance toward the other male, made contact with its front legs, and both remained motionless for a few seconds. Then the female retreated quickly into her burrow and closed the collar. The male moved to the entrance, briefly handled the collar with its pedipalps and first legs, and then wandered away. Because of the handling of the males and the dim light used for observation, both encounters were probably abnormal. At *I*, the discovery of the first leg of a male *A. pacificus* on the soil surface at the burrow entrance of adult female 2232 suggested a male-female struggle. No male remains were found within this burrow.

Antrodiaetus occultus new species

ECOLOGY

Geographic distribution, elevation range, and habitat. This species appears to be limited to the relatively dry and warm valleys of the Willamette and Umpqua Rivers of western Oregon (Map 2). 0–600 ft (0–180 m).

LIFE HISTORY

Males. Adult males of this species apparently wander and mate during late September and October (Fig. 1). The data in Figure 3 indicate that there may be a partial temporal separation of the mating season of *A. occultus* from that of sympatric populations of *A. pugnax* and *A. pacificus.*

Antrodiaetus pugnax (Chamberlin)

ECOLOGY

Geographic distribution and elevation range. Northern Oregon, southern Washington, and northwestern Idaho (Map 2). 0–3500 ft (0–1100 m).

Habitat. I have observed *A. pugnax* at only two localities. At *B* on 8 July, a large population was located in a deciduous woods with a dense understory of shrubs and herbs along a small, flowing stream. Surrounding the woods was nonforested land, chiefly farmland. Although burrows were scattered throughout the woods on both horizontal and inclined ground, dense aggregations were found only beneath the densest vegetation. The soil was hard-packed brown loam with a high organic content, and was dry at the surface but slightly humid below 10-cm depth. The densest aggregation was found under the shelter of a large shrub on horizontal ground covered with scattered leaf and twig litter. Ten adult females, five penultimate males, and about 150 immatures were present in a 1-m^2 area. The habitat at Lewis and Clark Trail State Park, Washington (Fig. 64)—a dense deciduous riparian woods located at the bend of a river and surrounded by wheat fields—was very similar to the above habitat. The understory vegetation was dense, and the burrows were found in the more sheltered spots on both horizontal and sloping ground. The soil was firmly packed light brown silty loam with a slightly greater moisture content than at *B*.

Most of the other locality records for *A. pugnax* are in dry regions at low elevations near rivers or streams and therefore presumably in riparian woods similar to those described above. The only wooded habitats in the immediate vicinity of *C* are such riparian woods. *H* has similar habitats. However, one collection of *A. pugnax* at *E* was made in Douglas fir forest, a more humid habitat. Thus it appears that *A. pugnax* is chiefly found in the low elevation riparian deciduous woodlands of the dry interior portions of Washington and Oregon, and in the low, relatively dry forest of the valleys between the Coast Range mountains and the Cascade Range mountains.

LIFE HISTORY

Males. Collection data (Fig. 1) indicate that male wandering and mating occur within the period from late July to October.

Females. The limited data (Fig. 2) indicate that the timing of brood development in *A. pugnax* may be similar to that in *A. unicolor.* All individuals from which the brood size (Table 3) and egg size (Table 4) data were obtained are from *B* and Lewis and Clark Trail State Park, Washington. The second instar morphology is like that of *A. unicolor.*

BEHAVIOR

Burrow structure. (All observations on burrow and entrance structure and egg sacs were made at *B* and Lewis and Clark Trail St. Pk.) The burrow structure is similar to that of *A. unicolor.* The burrow is roughly tubular and slightly widened just below the entrance and at the bottom end (Fig. 20). The entire burrow is silk-lined, with the thickest lining in the upper portion. The lining is thicker in burrows with egg sacs, at least in the vicinity of the sac. Burrows vary considerably in size but are usually relatively small (Table 6). The longer burrows were in softer soil. All burrows but one were in horizontal ground; all these were vertical except for a slight turn at the bottom end of some. The burrow pitch of the burrow on sloping ground was 10°. The five penultimate male burrows observed averaged considerably smaller than the female burrows, were completely and rather heavily lined with silk, and had 0–5° burrow pitches. No burrows sloped upward from the entrance.

Entrance structure. Small immature spiders have flexible collar entrances similar to those of *A. unicolor.* The silk lining of the burrow is extended above the soil surface, stands erect when open, and collapses inward to close off and camouflage the entrance. Soil particles and ground litter fragments are incorporated into this collar. The burrow entrances of older spiders were sealed and plugged with soil (Fig. 20), making it difficult to determine the exact nature of the unsealed entrance. The closure varied from a thin septum of soil and silk only a few millimeters thick to a hard plug up to 15 mm thick, mainly of soil. Such a sealed entrance is very difficult to discover visually. The inside surface of the closure is covered with a lining of silk continuous with the burrow lining.

Egg sac structure and position. The egg sac structure of this species is very similar to that of *A. unicolor* (Fig. 20). The egg masses varied from 7 to 9 mm maximum diameter and 4 to 6 mm in thickness. Six of the eight egg sacs were positioned on the ventral sector of the burrow wall, the other two on lateral sectors. The egg sac silk appears to have the same texture and whiteness as burrow lining silk. All egg sacs but one were positioned just above the bottom end of the burrow (Table 6).

Behavior of brooding females. Like the large immature and nonbrooding adult spiders, all females with egg sacs had plugged and sealed entrances.

Predators. A female specimen collected at *G* on 15 April is accompanied by a label saying that she was the "prey of *Dinocnemis,*" a pompilid wasp.

Feeding behavior. Many young immature spiders were in foraging postures within their open burrow entrances during daylight, although more exhibited such behavior at night. Fragmented prey exoskeletons held together with small amounts of silk were found packed into the bottom ends of several burrows. Such rejectamenta from the burrow of a brooding female at *B* contained parts of two beetles.

Mating behavior. A label accompanying a male from *B* reports that the male was wandering over the ground surface at night.

Antrodiaetus montanus (Chamberlin)

ECOLOGY

Geographic distribution and elevation range. Primarily the Great Basin region from Utah and Nevada north to Washington (Map 2). 2500–7200 ft (750–2200 m).

Habitat. I have observed *A. montanus* in two localities. Near Pocatello, Idaho, on 26 July, a small aggregation of burrows was located in the bank of a dry ravine in juniper-sagebrush habitat at 4500 ft (Fig. 65). Burrows of three adult females and several immatures were found in an uneroded portion of the bank under a large juniper. The soil surface was covered with a thin layer of pieces of dead grass and juniper. The soil was extremely dry hard-packed loam down to 25 cm and dry looser gravel and loam below that. The bottom ends of the large burrows were about level with the ravine bed. At Crater Lake, Oregon, on 30 July, I observed a sparse population of *A. montanus* in open and dry lodgepole pine, fir, and spruce forest at 6000 ft. The two burrows observed were in rather unsheltered spots, one on horizontal ground. The soil was composed of volcanic "sand," very dry and loose at the surface, becoming firm at 5 to 10-cm depth and slightly humid below 15 cm. Scattered burrows of *A. pacificus* and *Atypoides gertschi* were also found at this locality.

The locality records in the Salt Lake City, Utah, area indicate that *A. montanus* is there found in dry, non- or sparsely wooded habitats along the lower portions of canyons and in the foothills of the mountains. All other locality records for this species are likewise from relatively xeric habitats similar to those described above.

LIFE HISTORY

Males. Collection data (Fig. 1) indicate that male wandering and mating occur within the period from early August through early November. Chamberlin and Ivie (1935, 1945) observed males wandering "in the autumn."

Females. Very limited data for *A. montanus* (Fig. 2) indicate that the timing of brood development may be similar to that of *A. unicolor*. The brood size and egg diameter of the single known brood of *A. montanus* (2160 at Pocatello) are given in Tables 3 and 4.

BEHAVIOR

Burrow structure. (Based on observations of three adult female burrows from Pocatello and one large immature female burrow from Crater Lake.) Burrow structure is quite similar to that of *A. unicolor*, except for a considerably greater average length (Fig. 21, Table 6). Two of the burrows were completely silk lined with the thickest lining in the upper part of the burrow. In the other two burrows, the lining below the upper 5 cm was barely perceptible. Burrow pitch ranged from 5 to 25°, and all burrows sloped downward. Chamberlin and Ivie (1933), who found a female *A. montanus* without a distinct burrow and under a cottonwood log, later (1935) erroneously stated that females of *A. montanus* "ordinarily do not have burrows." Their observation in a later paper (1945) was more accurate: "The female lives in burrows which extend about a foot or more straight down into the soil. The upper part of the burrow is lined with silk; the bottom is slightly enlarged, but not bent."

Entrance structure. (Based on observations of two adult female burrow entrances at Pocatello and one large immature female entrance at Crater Lake.) *A. montanus* constructs a flexible silken collar like that of *A. unicolor*.

Egg sac structure and position. The structure and means of attachment to the burrow wall of the single egg sac observed (2160 at Pocatello) were like those of *A. unicolor* egg sacs. Egg mass dimensions were 14 × 10 × 7 mm. The sac was positioned on the ventral sector of the burrow wall deep in the burrow (Fig. 21, Table 6). Chamberlin and Ivie (1945) also found egg sacs only in the lower portion of the burrow.

Behavior of brooding females. When collected in the evening before dark, the single brooding female (2160 at Pocatello) had a closed but unsealed collar.

Parasites. The abdomen of a large immature *A. montanus* (0174) from Steens

Mountain, Oregon, was filled with a nematode worm.

Feeding behavior. The two large immature *A. montanus* females from Crater Lake were collected after dark in foraging positions just inside their open collars. Fragmented prey exoskeleton was found mixed with silk and packed into the bottom ends of the burrows of all three adult females from Pocatello. Two of these trash packets contained the remains of 12 medium to large-sized beetles.

Mating behavior. Apparently *A. montanus* males wander in search of mates at night and remain under the shelter of various objects during the day. One male from Verdi, Nevada, was collected walking over the ground at night. Chamberlin and Ivie (1945) often collected adult males "under stones, sticks, [and] bunches of grass" presumably during daylight hours. A label with the holotype male notes that it was resting under a piece of sagebrush.

Antrodiaetus hageni (Chamberlin)

ECOLOGY

Geographic distribution and elevation range. South-central British Columbia, eastern Washington, and eastern Oregon (Map 2). 1000–4000 ft (300–1200 m).

Habitat. I have observed *A. hageni* at only one locality—at Trail, British Columbia, on 13 July on the slopes along a dry stream bed in a large nonforested ravine one mile from its junction with the Columbia River (Fig. 66). The vegetation consisted of scattered young poplar trees and large deciduous shrubs. Much of the soil surface was without plant or litter cover. The soil was chiefly deep sand with a few rocks and very little organic material. The upper 3–8 cm of the sand was hot, dry, and loose; below that it was humid, well packed, and much cooler. Burrows were found in both steeply inclined and horizontal ground, but were usually clustered in more sheltered spots where the soil surface was stable, such as under trees and shrubs. *A. hageni* was not found in the cooler, humid forest habitats near Trail.

Near Baker, Oregon, where *A. hageni* has been collected, I unfortunately searched only in humid forest habitats and there found only *A. pacificus*, evidence that *A. hageni* is here found in the drier habitats (with sparser vegetation) at and below 4000 feet. An adult female *A. hageni* from near Oliver, British Columbia, was collected on a dry "sandy-rocky slope" covered with bunch grass and sagebrush (E. Thorn, personal communication). All other British Columbia records of *A. hageni* are in low river valleys where dry habitats similar to this and to that along the Columbia River at Trail are common; it is probably safe to assume that the habitat at Trail is an approximately normal *A. hageni* habitat.

LIFE HISTORY

Males. Adult male wandering and mating apparently occur within the period from late July through October (Fig. 1).

Females. Two records (Fig. 2) weakly indicate that the timing of brood development is similar to that of *A. unicolor*.

BEHAVIOR

Burrow structure. (Based on observations of two adult female and two immature female burrows.) The burrow architecture (Fig. 22, Table 6) is similar to that of *A. unicolor*. The roughly tubular burrow is somewhat enlarged just below the entrance and at the bottom end. All burrows were entirely silk lined, with the lining of the collar and upper part of the burrow much thicker than the rest of the lining. The two penultimate male burrows observed were similar to the female burrows in structure. Burrow pitch ranged from 0 to 35°, and all sloped downward.

Entrance structure. (Based on observations of one adult female and two large immature female burrow entrances.) *A. hageni* constructs a flexible silken collar very similar to that of *A. unicolor* (Figs. 45–46).

Molting behavior. An immature spider which molted within a glass tube in captivity fragmented its shed exuvia several days after ecdysis.

Predators. A large immature female of *A. hageni* was collected together with a pompilid wasp, *Priocnemis oregona* Banks (identification, H. E. Evans), on 7 April at Baker, Oregon. Unfortunately, no other data was included with the specimens. It is probable, however, that *A. hageni* is a host of this wasp, since the three other host species records for this wasp are mygalomorph spiders, one being *Atypoides riversi* (Wasbauer and Powell, 1962).

Feeding behavior. All burrow entrances were closed during the afternoon of observation. Prey remains were found packed into the bottom end of the burrow of one large immature female. The prey exoskeletons were fragmented (the thinner the cuticle the smaller the fragments) and held together with a small amount of silk. Identifiable prey consisted of 12 ants, two beetles, one dipteran, and two adult male spiders (*Tegeneria domestica* and *Xysticus* sp.).

Antrodiaetus cerberus new species

ECOLOGY

Geographic distribution, elevation, and habitat. Known only from the type locality in coniferous forest in northeastern Washington. Approximately 2000–2500 ft (600–750 m).

LIFE HISTORY

Males. All four examined males of this species were collected in pitfall traps sometime during May, 1962 (Fig. 1). Three more males were collected sometime during April and May, 1962 (W. Ivie, personal communication). It is thus likely that *A. cerberus* males wander and mate only during the spring.

Females. Two records (Fig. 2) weakly indicate that brood development timing may be similar to that of *A. unicolor.*

Antrodiaetus yesoensis (Uyemura)

ECOLOGY

Geographic distribution and habitat. Known only from the northern Japanese island of Hokkaido, where it is presumably found in the conifer forest of that cool temperate climate (Map 3).

LIFE HISTORY

Males. The few records (Fig. 1) indicate that the period of male wandering and mating occurs during the summer months.

Antrodiaetus lincolnianus (Worley)

ECOLOGY

Geographic distribution and elevation range. Eastern Kansas and eastern Nebraska (Map 1). 700–1200 ft (210–360 m).

Habitat. In 1928, Worley stated that the holotype male and the three paratype males were collected "on clay banks near deciduous forest" at Lincoln, Nebraska. Later (Worley and Pickwell, 1931), he stated that these males were found "under logs in woods" apparently in their own burrows. H. S. Fitch (personal communication) collected a wandering male near Lawrence, Kansas, about 35 m from a large patch of deciduous forest through which ran an intermittent stream with high banks. This limited evidence, in addition to the fact that no specimens of *A. lincolnianus* have been collected in localities removed from the western lobes of the eastern deciduous forest, indicates that this species is probably found in somewhat humid forest habitats.

LIFE HISTORY

Males. Male wandering and mating in *A. lincolnianus* apparently occur during late winter and early spring. The seven adult males indicated in Figure 1 were collected by four different collectors on seven different dates during four different years. Also, two other males, which I have been unable to examine but which are almost certainly *A. lincolnianus*, were collected by yet a different collector, Scheffer (1906), in Manhattan, Kansas, on 5 April during yet another year. Such a scattering of individual collecting events makes it more likely that these dates indicate the actual wandering and mating period of this species.

Females. The single gravid female record (Fig. 2) for *A. lincolnianus* hints that the timing of brood development may be similar to that of *A. unicolor.*

BEHAVIOR

Burrow structure. Worley and Pickwell (1931) state that "this species is very similar in habits to *B. pacificum* Simon [=*A. pacificus*] of the Pacific Coast, constructing burrows in the ground six to ten inches deep and lining them with silk."

Antrodiaetus stygius new species

ECOLOGY

Geographic distribution and elevation range. Missouri and northern Arkansas (Map 1). 400–1500 ft (120–460 m).

Habitat. I have observed *A. stygius* only at Bennett Springs State Park, Missouri, on 4 September. An aggregation of approximately 100 adult and immature burrows in a 4-m^2 area was found on a 20–35° slope 3–5 m from the edge of a large spring-fed stream in the heavy shade of a mixed deciduous forest (sycamore, elm, and oak trees common). The ground surface had a sparse to dense cover of leaf litter. The hard-packed dark brown loam soil was slightly humid at the surface and increasingly humid downward. A wandering adult male was collected near a stream near Warrensburg, Missouri, in a similar deciduous forest of oak, sycamore, and elm (Peck, 1966).

LIFE HISTORY

Males. The limited data (Fig. 1) indicate that adult males wander and mate during the fall.

Females. All three broods observed had developed beyond the hatching stage, but every shed chorion contained the embryonic cuticle, an indication that the pattern of early postembryonic development is similar to that in *A. unicolor.* Also the morphology of the embryonic cuticle, the first instar, and the second instar is very similar to that of *A. unicolor.* The limited data (Fig. 2) indicate that the timing of *A. stygius* brood development in nature resembles that of *A. unicolor.* The size of the only complete brood is given in Table 3.

BEHAVIOR

Burrow structure. The three brooding female burrows observed were completely silk-lined and shaped much like *A. unicolor* burrows: roughly tubular and slightly widened just below the entrance and at the bottom end (Fig. 23, Table 6). Three penultimate male burrows were shaped similarly but had thinner silk linings and were shorter (Table 6). All six of these burrows were slightly sinuous and nearly vertical, with burrow pitches of 15–30°.

Entrance structure. All burrows discovered—even those of immatures—had their entrances sealed over and usually plugged with soil (Fig. 23), making it difficult to determine the exact nature of an unsealed entrance, which appeared to consist of a flexible collar. The upper 4–10 mm of the larger burrows was packed with soil. The bottom of this plug was lined with silk continuous with the burrow lining, and the upper exposed surface closely matched the surrounding soil surface in texture and color.

Egg sac structure and position. The shape and structure of the two *A. stygius* egg sacs observed appeared similar to those of *A. unicolor.* Both were positioned on the ventral sector of the wall in the bottom half of the burrow (Table 6). The burrow diameter at the region of egg sac attachment may have been greater than normal, but the sacs still produced a slight localized constriction of the burrow lumen. The silk lining was thicker in the vicinity of the egg sac than elsewhere below the upper end of the burrow. Egg sac silk appears to have the same texture and white color as burrow lining silk.

Behavior of brooding females and broods. The burrow entrances of brooding females, like those of nearly all other individuals, were sealed with soil plugs. The brood composed of first instar spiderlings was still enclosed within the egg sac, while both second instar broods were entirely outside the sac. In one of these latter two broods, the egg sac was no longer present; in the other it contained all the first instar exuviae, indicating that the spiderlings emerged from the egg sac after molting into the second instar. The second instar spiderlings were quite active.

Defensive behavior. Some adult females assumed a defensive posture in the bottom of their burrows similar to that of *A. unicolor.*

Predators. A pompilid wasp cocoon containing a larva was found in one medium-sized *A. stygius* burrow. Small pieces of spider exoskeleton were attached to the outside of the cocoon.

Disposal of prey remains. Fragments of prey cuticle were found packed into the bottom end of one adult female burrow.

Antrodiaetus apachecus new species

ECOLOGY

Geographic distribution and elevation range. Mountains of Arizona and New Mexico (Map 4). 6100–8500 ft (1850–2600 m).

Habitat. I have collected *A. apachecus* at only one locality, near La Cueva, New Mexico, at 7800 ft in a somewhat open forest of yellow pine, spruce, and fir. An aggregation of six burrows was found under the overhang of a large rock on the slope of a wide ravine. Aspen and scrub oak were common in the ravine. The ground surface under the rock lacked leaf litter, and the soil was humid dark sandy loam with some pebbles. All other locality records for this species are either from transition zone forest or low Canadian zone forest. Because it is restricted to such high elevation habitats, the species population is presently fragmented into several geographically isolated populations each on a forested montane "island" surrounded by unfavorable nonforested habitats at lower elevations.

LIFE HISTORY

Males. Collection data (Fig. 1) indicate that male wandering and mating occur from midsummer to early fall.

BEHAVIOR

Burrow structure. The burrows of only four medium- to large-sized immature spiders were observed. The burrow shape appeared similar to that of *A. stygius*, i.e., tubular but slightly widened just below the entrance and at the bottom end. The silk lining was very thin and possibly absent over most of the burrow, but slightly thickened at the upper end. The burrows were slightly sinuous and nearly vertical, with a burrow pitch of 10–20°.

Entrance structure. The burrow entrance of only one immature spider was observed and appeared to consist of a short thin flexible collar.

Feeding behavior. A medium-sized immature *A. apachecus* was found at the bottom of its burrow feeding upon a dead, partly digested, 20-mm long lepidoptera larva covered with urticating setae. This was at 11:00 A.M. and the collar was closed.

Antrodiaetus roretzi (L. Koch)

ECOLOGY

Geographic distribution. Central portion of the Japanese island of Honshu (Map 3).

Habitat. According to Yaginuma (1962), *A. roretzi* is usually found in humid, often heavily shaded habitats. Yamamoto (1942) found a sizeable burrow aggregation scattered over a very steep bank composed of reddish soil. Bamboo was growing over the upper part of the bank. Komatsu (1942) reported that this species is found in shaded humid habitats, often on inclines or banks. Uyemura (1936) found a burrow on a steep slope in moss-covered soil at the base of a pine tree. Ohe (1966) found burrows chiefly on inclines (40–90°) of banks along a trail. Such burrows were frequently in the shelter of exposed tree roots near the top edge of these banks or were under the overhang of exposed rocks. All but a few burrows were located on the upper two-thirds of such banks. He found burrows both in heavily shaded moss-covered portions of banks and in less well-shaded spots where the surface soil was rather dry. Burrows are also often found in caves (Yaginuma, 1962; Komatsu, 1961) near the entrances. Komatsu (1942) found an aggregation of over 100 burrows on an inclined surface in humid reddish soil in dim light just inside the entrance of one cave.

LIFE HISTORY

Males. The small amount of data in Figure 1 indicates that male wandering and mating may occur during winter and early spring. More data are needed.

Females. Ohe (1966) observed spiderlings in parent burrows "from September on."

BEHAVIOR

Burrow structure. Yamamoto (1942) observed the burrows of two adult males and several adult females (Table 6). These were tubular and silk lined. Burrows in soft soil free of obstacles were longer than those in harder soil with roots, and male burrows averaged shorter than adult female burrows. The burrow pitch of the two male burrows was apparently about 0–10°. Komatsu (1942) observed several vertical burrows in inclined ground, but most were roughly perpendicular to the soil surface. Ohe (1966) described and illustrated the variation observed in the inclination, shape, and length of a large number of *A. roretzi* burrows (probably both adult and immature). Most burrows apparently were not strongly curved and were roughly perpendicular to the plane of the adjacent ground surface. Exceptions were the result of root or rock obstacles. Most burrows were approximately 20 cm long or shorter, but a few reached 30 cm.

Entrance structure. A pair of photos of an *A. roretzi* burrow entrance has been published twice (Komatsu, 1937 and 1961). Drawings of the entrance can be found in Komatsu (1961), Yamamoto (1942), Yaginuma (1960), and Ohe (1966). Descriptions, all very brief, are found in Yamamoto (1942), Komatsu (1942), Yaginuma (1962), and Ohe (1966). All these describe the structure as a "double door entrance." After studying the fine photos and drawing of Komatsu, it appears to me as though the double door nature of the entrance has been overemphasized and that the entrance structure is more accurately described as a collapsible collar which is reduced at two opposing portions, leaving two lateral flap-like sectors that operate roughly as separate doors. Such a structure is quite similar to that of the collars of some adult *A. unicolor* burrows. Clearly, additional careful field observations are required. Komatsu (1942) and Ohe (1966) observed that, in entrances on an inclined ground surface, the collar is reduced at its ventral and dorsal sectors with both lateral flaps "hinging" on opposing dorsoventral axes. Such an orientation is common in *A. unicolor.* The collar in Komatsu's photos is constructed of silk and soil, well camouflaged exteriorly, and silk lined on the inner surface, this silk lining apparently being continuous with the burrow lining. Ohe found that collars in moss-covered soil were constructed partly of moss and were difficult to discover. Although Ohe (1966) observed a few burrow entrance openings as large as 1.5-cm diameter, most were roughly 1 cm in diameter.

Molting behavior. Yamamoto (1942) collected two adult males in their own burrows. In one, the shed exuvia lay on the ventral sector of the burrow wall about one-third of the way down the burrow, and a maze of silk threads occupied much of the lower half of the burrow, with the male in the bottom end. The second male had spun a thin silk septum across the inside of the entrance, and no exuvia or silk thread mazes could be found in the burrow. Yamamoto did not say whether either collar was closed or open. Possibly the second spider had sealed the inside of the collar shut. Clearly, additional observations are needed to clarify behavior during the final male molt of *A. roretzi*.

Atypoides riversi O. P.-Cambridge

ECOLOGY

Geographic distribution and elevation range. A coastal population in northern California west of the Central Valley as far south as the Monterey Peninsula, and a Sierran population in the Sierra Nevada Mountains and their foothills (Coyle, 1968). These populations are probably geographically isolated. 200–1800 ft (60–550 m) (coastal population). 2000–8000 ft (600–2400 m) (Sierran population).

Habitat. Coastal population: Rivers (1891; O. P.-Cambridge, 1883) found *A. riversi* burrows in both pine and deciduous forests, often in stream banks. Smith (1908) found burrows "abundant along shaded streams and in thickets in the foothills and mountains" of the Coast Range. Gertsch's (1949) habitat description was similar. I have collected coastal *A. riversi* in three localities, and will summarize my observations below.

A. riversi is found in the foothills and mountains of the Coast Range, chiefly in shaded forest habitats. These may be deciduous, pine, or mixed deciduous-pine forests. Interestingly, *A. riversi* is uncommon or absent from the famous "basin forest" of predominately coast redwood and Douglas fir; I searched hard in such habitats at three localities unsuccessfully. *A. riversi* burrows are common in the next highest vegetation zone, the tan oak-pacific madrone forest containing only scattered coast redwood trees (Fig. 67). Burrows are found chiefly on rather steep inclines of banks along trails, roads, and streams. The surface litter in these spots ranges from absent to quite thick. The soil varies from compact sandy loam to clay loam, sometimes with a high pebble content. These soils are usually dry at the surface during the summer, but below about 10-cm depth are at least slightly humid. The densest burrow aggregations are found on stable, noneroding banks. Three adult females and 29 immatures were found in a 0.30-m^2 area at *C*.

Sierran population. I have observed *A. riversi* in three different locations above 6500 ft in the Sierra Nevada Mountains. The habitat ranged from open pine-fir forest to dense pine-fir or California red fir forest. The densest and largest population was found in the red fir forest at *G*. Burrows are found on both steeply sloping stream and road banks and on gently inclined ground. The surface litter varied from absent to very thick. The soil was brown sandy loam, dry and loose at the surface but becoming humid and packed at from 3 to 15 cm deep. The lower the rock content of the soil, the greater is the burrow density.

LIFE HISTORY

Males. Coastal populations: Male wandering and mating in these populations may not normally begin until September, October, or November (Fig. 1), and may coincide with the onset of the fall and winter wet season. At *D* and *F* on 14 and 15 August, I searched both day and night in areas of dense burrow concentrations for adult males but found none. *Sierran populations*: In at least the higher populations

(6500–8000 ft), male wandering and mating commence earlier and probably (because of harsh winter weather) terminate earlier (Fig. 1).

There is some evidence to indicate that the palpal tarsi of immature males of *A. riversi* may be swollen during more than just the penultimate instar and that many of the immature males with swollen palpal tarsi found in late summer or fall may not mature until one year later. The shed exuvia of an immature male collected at *H* on 8 August had swollen palpal tarsi like those of the newly formed instar. The exuvia of a recently molted immature male collected at the same locality and time had unswollen palpal tarsi, whereas those of the new instar were swollen. Thirteen actively foraging immature males with swollen palpal tarsi were collected at *G*, *H*, and *I* from 6 to 9 August when adult males were wandering. At *D* and *F* on 14–15 August, 14 immature males with swollen palpal tarsi were trapped in foraging postures in their burrow entrances at night, and seven were dug out of closed and usually (five) sealed burrows. All 21 were kept cool and humid in an ice chest, but only the latter seven molted to maturity.

Females. Coastal populations: The pattern of early postembryonic development of *A. riversi* appears to be similar to that of *Antrodiaetus unicolor*. All of the many shed chorions observed in each of the six egg sacs with first instar spiderlings have the embryonic cuticle attached, indicating that both the chorion and embryonic cuticle split and peel off simultaneously or in close succession and are then shed together. The morphology of the embryonic cuticle, the first instar, and of the second instar of *A. riversi*, is also quite similar to that of *A. unicolor*, with the obvious exception that the anterior lateral spinnerets are not lost in the second instar of *A. riversi*. The data on the timing of brood development in *A. riversi* (Fig. 2) indicate that eggs are laid in summer, that brood development reaches the second instar by mid-autumn, and that the spiderlings abandon the parental burrow before the following summer. Rivers (1891) observes without further comment that "there is a period of aestivation, but the cause is not yet investigated." Data on brood size and egg size are given in Tables 3 and 4. *Sierran populations:* Only a single Sierran brood was collected (at *I*). Its size and egg size are given in Tables 3 and 4.

BEHAVIOR

Burrow structure. A. riversi has a roughly tubular silk-lined burrow which normally increases slightly in diameter from the top to near the bottom end where there is usually a decrease in diameter so that the last 2–4 cm are narrow (Figs. 24 and 25). In the Sierran populations, this terminal constriction was less noticeable at *H* and *I* but was well developed at *G*. The white silk lining is usually quite thick in the turret and upper part of the burrow, becoming thinner in the bottom portion, and may be nearly imperceptible for the last few centimeters. Burrows with egg sacs usually had thicker silk linings than those without. Burrow dimensions, which show considerable variation, are given in Table 6. As might be expected, larger individuals within a population have larger burrows, and this correlation is shown in the lower mean burrow dimensions of the Sierran populations, which have, on the average, smaller mature individuals than the coastal populations. Also, penultimate male burrows average smaller than adult female burrows. Burrows ranged from vertical to near horizontal, but the burrow pitch ranged within 0–15°. Rivers (1891) also observed that the burrows "were more or less perpendicular" to the ground surface.

The descriptions of coastal *A. riversi* burrow structure by Rivers (1891), Smith (1908), and Gertsch (1949) are in agreement with my observations, except for the statement by Rivers that an adult female burrow "is more roomy at the base than at the opening." He apparently overlooked the terminal constricted portion. Smith, like myself, observed that "the tunnels are commonly considerably reduced in diameter for the last two centimeters. . . ."

Entrance structure. The silk lining of the burrow is extended above the soil surface to form a rather rigid elongate collar or turret (Figs. 26, 47–50), hence the common names "Californian turret builder" (Rivers, 1891) and "the turret spider" (Gertsch, 1949). This turret is smooth white silk on its inner surface and is camouflaged and kept erect by attached soil particles and usually also organic materials (from the ground surface litter) such as pieces of twigs, leaves, needles, bark, and moss. Normally the turret wall is supported at its base by the thickest accumulation of soil and other materials and becomes thinner distally. The opening at the top of the turret is roughly circular, and the rim is slightly expanded to form a lip. The entrance is closed off by collapsing or folding in only the distal end of the turret. Sometimes, as when a spider is molting, this closure is sealed on the inside with a small amount of silk.

There is considerable intrapopulation variation in turret height, as well as a marked tendency for individuals of the Sierran populations to have shorter turrets than those of the coastal populations (Table 6). A possible reason for this difference (other than geographic variation in genetically determined turret building behavior) is that snow accumulation may annually destroy the Sierran turrets, whereas coastal turrets are probably accumulations of several years' additions. A few turrets in the Sierran populations incorporated needles, twigs, or leaves consistently attached by their ends and radiating out roughly horizontally from the turret (Fig. 50). This radial arrangement closely resembles the "twig-lining" arrangement found in some of the Australian aganippine trapdoor spiders (Main, 1957a), but at present there is no evidence that in *A. riversi* it has a similar functional significance in prey detection.

The descriptions of coastal *A. riversi* turret structure by O. P.-Cambridge (1883), Rivers (1891), Smith (1908), and Gertsch (1949) are in agreement with my observations. Both Rivers and Smith describe considerable variation in the litter material used in turret construction. Smith includes two photographs illustrating some of this variation. Rivers observed turrets as tall as 3 inches (= 7.6 cm).

Egg sac structure and position. The egg sac structure (Fig. 24) and egg mass shape of *A. riversi* is very similar to that of *Antrodiaetus unicolor.* Mean dimensions for the three egg masses are 10 × 9 × 6 mm. Egg sac silk appears to have the same texture and whiteness as burrow lining silk. In each of the nine burrows with egg sacs, the sac was positioned about half way down the burrow (Table 6). In five burrows the egg sac was on the ventral sector of the burrow wall, in three on the dorsal sector, and in one on a lateral sector. Some burrows may have been widened somewhat in the region of egg sac placement, but each sac produced a localized constriction of the burrow lumen.

Behavior of brooding females and broods. All of the first instar broods were completely enclosed within egg sacs, but the thickness of the silk of three of these egg sacs had been much reduced and the spiderlings could be seen moving around very slowly within. It would be interesting to know whether these spiderlings (or the parent) possibly possess silk-digesting enzymes. All nine burrows with egg sacs had open turrets. Three of these were found at night, each with the female in foraging position in the top of the turret. It therefore appears that brooding females remain active at least until the spiderlings emerge from the egg sac.

Molting behavior. Molting behavior in *A. riversi* appears similar to that of *A. unicolor.* Four recently molted immature spiders were collected during the second week of August. In each case the top of the turret was closed and the edges held together by a thin layer of silk spun over the inside of the closure. The recently shed exuvia was attached to the ventral sector of the burrow wall two-thirds to three-fourths of the way down the burrow, venter against the wall, anterior end heading up the burrow, and with legs and pedipalps extended on the wall. The unsclerotized spiders were in the very bottom end of the burrows. Five penultimate males (from *D* and *F*) that later molted in captivity and several other immature males with swollen palpal tarsi were collected at other localities in similarly closed and sealed burrows. A fully sclerotized adult male ready to emerge was collected at *I* in a sealed burrow with the last exuvia packed into the bottom end of the burrow.

Defensive behavior. When spiders in foraging positions were disturbed by light or substrate vibrations, they retreated rapidly down the burrow without closing the top of the turret. During the later stages of excavating to expose a burrow, one finds the spider backed up tightly into the narrowed bottom end of the burrow in a stereotyped defensive posture. The cephalothorax is tilted backwards at approximately a 45° angle with the abdomen and is therefore in contact with the sector of the burrow wall dorsal to the spider. Legs IV and III, and possibly II, hold onto the burrow wall to anchor the spider, and the other legs and pedipalps are spread apart laterally. The chelicerae are also elevated and spread apart laterally with fangs extended. If prodded, the spider strikes with a sudden downward movement of the cephalothorax and chelicerae. Penultimate males also exhibit this same behavior. Such a behavior pattern, like that of *A. unicolor,* obviously confines the approach of an attacker to that part of the spider protected by its chelicerae, but the narrowed burrow end of *A. riversi* probably provides more effective protection for its abdomen than the enlarged burrow ending of *A. unicolor.* Smith (1908) observed that the terminal constriction makes "a snug fit for the spider, and here it usually snuggles down tightly when the digging [of the collector] has reached the limit necessary to secure the specimen."

Predators. Wasbauer and Powell (1962) observed predation on *A. riversi* at Felton (Santa Cruz Co.), California, on 5 May, by the pompilid wasp *Priocnemis oregona* Banks. (See *Antrodiaetus hageni* predator records.)

Feeding behavior. The foraging posture of *A. riversi* appears similar to that of *A. unicolor;* the spider is within and facing up the turret with the pedipalps and legs I extending forward, touching the silk lining on or below the turret lip. No adult spider was ever found in this foraging position until the arrival of full darkness. Unlike other species of *Atypoides* and *Antrodiaetus,* most individuals of *A. riversi* were found to leave their turrets open both day and night.

A. riversi, like *A. unicolor,* apparently detects prey primarily, if not solely, through the substrate vibrations transmitted via the silk lining of the turret and burrow. I was able to elicit prey capture responses by gently vibrating with forceps the ends of turret litter. The needles, twigs, leaves, and other somewhat linear litter that are often incorporated into the turret of *A. riversi* probably extend the prey-sensing radius of the spider even when, as is usually the case, this litter is not arranged radially. However, it remains to be shown whether or not attaching linear litter to the turret is a result of selection for improved prey sensing.

Fragmented prey cuticle is often found packed into the bottom end of the burrow and sometimes in other parts of the burrow wall as well. A cursory examination of trash indicates that ants may make up a large part of the prey of this species. Identifiable portions of several *Camponotus* workers were found.

Smith (1908) briefly commented on the

feeding behavior of young immatures of *A. riversi* collected from coastal populations and kept in the laboratory. These accepted both small ants and aphids, and always maintained a hold on the lip of the turret with the claws of legs IV during the lunge for prey.

Courtship and mating behavior. There are no published observations of courtship or mating in the family Antrodiaetidae. I was fortunate enough to witness a portion of mating behavior between a pair of *A. riversi* at *G* on 8 August 1967, at 9:45 P.M., about 45 minutes after nightfall. When first discovered, the male was positioned within and just below the rim of the female's turret facing down into the burrow with the tarsi of legs IV on the turret rim (Fig. 27). The female was immediately below the male and facing up the burrow in a posture very similar to the normal defensive posture, except that her fangs were unextended. The male's cephalothorax was raised slightly and its cheliceral apophyses were positioned as a unit between the outspread chelicerae of the female (Fig. 28). It appeared as though the male was applying substantial pressure with his chelicerae, but the female did not struggle. I could not observe exactly how the pedipalps and legs I, II, and III of the male were positioned, but the pedipalps appeared to be extended beneath the female and legs III and probably legs II were holding onto the burrow wall below legs IV. After two minutes in this position the female struggled and was forced down the burrow by the male, which appeared to maintain his hold with his cheliceral apophyses. I am not certain that the pair was actually copulating when discovered.

Adult males apparently wander in search of mates only at night. Even though I searched during both daylight and evening hours, the Sierran males were found wandering on the ground only after 9:30 P.M., at least half an hour after nightfall, and the largest numbers were found between 10:30 P.M. and midnight, when the searching ended.

Atypoides gertschi Coyle

ECOLOGY

Geographic distribution and elevation range. Cascade Mountain Range and foothills from southern Oregon south and east into the northern end of the Sierra Nevada Mountains of California (Coyle, 1968). 2000–7500 ft (600–2300 m).

Habitat. The densest and largest populations of *A. gertschi* were found above 6000 ft in the open California red fir forest at *N* and *P* (Fig. 68). In this habitat, ground cover vegetation is nearly absent and the surface litter generally sparse. The soil is volcanic "sand" or sandy loam, dry and loose at the surface, but becoming humid and packed 5–15 cm below. Burrows were found both on level ground and inclined surfaces. At lower elevations burrows are often common in open forests with little ground vegetation or in nonforested areas of manzanita chaparral in volcanic "sand" soil, as long as the soil is humid below 5–15 cm. For instance, at *O* I found a dense population in manzanita chaparral only along the edge of the lake. The habitat at *M* is rather artificial because of the great variety of imported vegetation, but it is wooded and the soil is sandy. Most of the burrows there were along the side of a stream (W. J. Gertsch, personal communication).

LIFE HISTORY

Males. The collecting data in Figure 1 indicate that male wandering and mating occur during the summer.

Females. Only a single brood of *A. gertschi* (from *N*) has been collected (Fig. 2). The absence of broods with the many other females that I excavated is puzzling, but it is possible that brooding females of this species tend to keep their entrances closed nocturnally and were missed because of the difficulty of spotting closed entrances. Many females—all collected in late summer—contained small developing eggs that appeared to be timed for spring or summer oviposition. The morphology of the first instar is very similar to that of *A. riversi.* All of the shed chorions examined contained the embryonic cuticle, an indication that hatching is also similar to that in *A. riversi.* The size of the known brood is shown in Table 3.

BEHAVIOR

Burrow structure. (See Table 6 for burrow measurements.) The burrow is roughly tubular, with a slight expansion in diameter just below the entrance and a larger increase in diameter at the bottom end (Figs. 29–30). It is well lined with silk just below the entrance in the usually dry, loose surface soil, but the thickness of the lining decreases with depth as the soil increases in humidity and stability so that there is usually only a very thin lining over much of the rest of the burrow. The long axis of the upper portion of all burrows was nearly perpendicular to the plane of the adjacent ground surface. Almost every burrow curved to nearly horizontal at the bottom end.

Entrance structure. The tubular silk lining of the burrow extends above the ground surface to form a rather thick but flexible collar which is collapsed inward to close off the entrance (Figs. 31–34; 51–53). The collar is composed chiefly of soil particles and small bits of surface litter held together by silk so that a closed entrance is remarkably well camouflaged. When open, this collar normally does not remain erect, but collapses outwardly so that it is roughly parallel to the ground surface. Usually only the proximal portion of the inner surface of the collar is a clean white extension of the burrow lining. The burrow entrance opening is often slightly elliptical. As in *Antrodiaetus unicolor,* a closed collar usually gives the appearance of a "double door" (which it is not) because the spider collapses the collar in a bilateral manner by pulling inwardly on two opposing (lateral) sectors, producing a condensation of folding at the two opposing points where these sectors meet. The collar is often somewhat reduced at these two opposing points, which correspond to the ends of the long axis of an elliptical entrance opening. No sealed collars were found.

Egg sac structure and position. The only *A. gertschi* egg sac collected appeared to be very similar in size, shape, and construction to those of *A. riversi* (Fig. 29). It was attached to the ventral sector of the burrow wall less than one-third of the way down the burrow at a point where the burrow appeared to have been slightly enlarged, but the sac produced a localized constriction of the burrow lumen.

Molting behavior. A recently molted female spider (2016 at *M*) was collected on 31 July. The burrow entrance was closed but unsealed, and a plug of soil had been placed one-third of the way down the burrow. The weakly sclerotized spider was in the bottom of the burrow. The exuvia, heading up the burrow and with legs extended, was lightly attached to the silk lining of the ventral sector of the burrow wall several centimeters from the bottom end.

Defensive behavior. When a female in foraging position was disturbed by light or substrate vibration, she either rapidly withdrew down the burrow without closing the entrance or suddenly closed the collar with her pedipalps and anterior legs and held the collar shut without retreating.

Feeding behavior. Burrow entrances were closed during daylight hours. The youngest spiders opened their entrances and assumed a foraging posture earlier than older spiders, often as soon as it became twilight. Mature females usually opened their entrances well after nightfall. The foraging posture of *A. gertschi* appears similar to that of *A. riversi,* with pedipalps and anterior legs resting on the basal portion of the collar. If the plane of the burrow opening is not horizontal, the spider usually orients this stance with its venter against the lowest sector of the burrow opening, which is also usually the long end of an oval entrance opening. The exoskeletons of two freshly digested *Camponotus* worker ants were found in one adult female burrow, and ant pieces were observed on the ground surface next to another burrow. Only occasionally was prey cuticle found in burrows.

Courtship and mating behavior. Males of *A. gertschi* apparently wander only after dark. All wandering males (14) that I have collected were found after 10 P.M. even though collecting included both daylight hours and the period from 8 to 12 P.M. A female at *O* was discovered at 11 P.M. feeding on a recently killed conspecific male several centimeters below her burrow entrance.

Atypoides hadros Coyle

ECOLOGY

Geographic distribution and elevation range. Southern Illinois and eastern Missouri (Coyle, 1968). 400–1100 ft (120–330 m).

Habitat. I have observed *A. hadros* at only two localities. At Ferne Clyffe State Park, Illinois, burrow aggregations were found in shallow shelter caves cut into the base of steep limestone bluffs. Mixed hardwood forest extended along the base of these bluffs. Burrows were found only in those shelter caves kept moist by water seepage in late summer. The largest aggregation of burrows was found on the floor of the most humid shelter, where males, females, and immatures of both *A. hadros* and *Antrodiaetus unicolor* lived side by side. The soil was a moist to wet mixture of soft clay-loam and pebbles. Surface litter was absent. Burrows were present both at the well-lighted edges of the shelter caves and in the dimly lit areas. Except in the most humid shelter cave, *A. unicolor* was more abundant than *A. hadros.* At Montauk State Park, Missouri, burrows of both *A. hadros* and *Antrodiaetus* were found side by side in moist reddish clay-loam with very little surface litter at the base of a high rock outcrop on the bank of the Current River in mixed hardwood forest.

The other three localities where *A. hadros* has been collected (Little Grand Canyon, Pine Hills, and Lusk Creek, Illinois) are also in forested areas where ravines, rock outcrops, and other sheltered spots are common. An adult female from Little Grand Canyon was taken from a burrow in a drier, less sheltered spot than the shelter caves of Ferne Clyffe State Park (J. Beatty, personal communication). *A. unicolor* is also apparently more abundant at each of these three localities than is *A. hadros.*

LIFE HISTORY

Males. Collecting data (Fig. 1) indicate that penultimate males molt to maturity during late summer or early fall and wander and mate during the first half of fall. Two mature males were collected on 13–14 September in their burrows shortly after the final ecdysis. Pitfall traps planted at Pine Hills by J. Nelson in 1967 collected one wandering male during the first week the traps were set out (7–14 October), nine males during the next week, none during the next week, three during the next week (27 October–3 November), and none during the next week, the final week traps were put out.

Females. The limited data (Fig. 2) hint that timing of brood development in *A. hadros* may be similar to that in *A. unicolor.* Second instar morphology is like that of *A. riversi.* The size of only one brood could be determined (Table 3).

BEHAVIOR

Burrow structure. The burrows were roughly tubular and completely lined with silk. The lining of several adult female and both adult male burrows were especially thick and white. Most burrows were widened slightly just below the entrance and at the bottom end (Fig. 35). Burrows of adult males averaged smaller than those of adult females (Table 6). Probably because of the pebbly soil, many burrows had abrupt curves, with the slope of the bottom end varying from vertical to horizontal.

Entrance structure. The entrances of only two adult females and two immatures were observed. The tubular silk lining of the burrow was extended slightly above the ground surface to form a very short and thin collar (Figs. 36–37). Soil particles were incorporated into the collars so that the external surface had the same texture and color as the surrounding soil surface. The height of each collar was quite strongly reduced at two opposing points on its circumference. When the collar is collapsed, the folding is concentrated at these two points, and the opposing higher sectors or flaps of the collar meet and overlap in the center along the line connecting the two reduced points.

Brood behavior. No egg sac remnants were present in the four burrows with second instar broods collected from Ferne Clyffe State Park. These spiderlings reacted quickly to stimuli and could move about rapidly. They were clustered in the bottom of two burrows, and were more scattered in the other two but retreated down to the burrow bottom as I exposed each burrow.

Molting behavior. The burrows of both recently matured males were heavily lined with silk. Both spiders were sufficiently sclerotized to be active. The recently shed exuviae had been pushed into the very bottom ends of the burrows and covered over with a thin layer of silk. Since both burrows were discovered by scraping the soil surface, I could not determine whether the closed collars had been sealed with silk.

Feeding behavior. Burrow entrances were closed during the daytime. Burrows of several immature *A. hadros* observed 90 minutes after nightfall had the collars open only a crack, while adjacent *A. unicolor* immatures had their collars wide open. Fragmented prey exoskeletons were packed into the bottom ends of a few burrows. Such trash from two immature burrows was examined and found to consist of ant and beetle parts.

Aliatypus californicus (Banks)

Ecology

Geographic distribution and elevation range. West central California from the San Francisco Bay region to the Monterey Peninsula. 1000–2900 ft (300–880 m).

Habitat. I have collected only three specimens, all these near Felton, California, between 1000 and 1600 ft in or near aggregations of *Atypoides riversi. Actinoxia* burrows were also present but as uncommon as those of *A. californicus.* All burrows were found on steeply inclined road banks in rather dense mixed deciduous-coniferous forest (tan oak, pine, and some coast redwoods). The soil varied from clay to sandy loam, was quite rocky, and was dry at the surface.

The holotype specimen was collected at the side of a stream (Banks, 1896). Smith (1908) collected *A. californicus* in the foothills and mountains on both sides of the Santa Clara Valley, finding burrows most commonly along banks of streams and roads in "fine compact sandy soil." Occasionally burrows were found in "sandy adobe" soil. These banks with burrow aggregations "usually have little or no vegetation upon them other than short scattered moss." Smith found *A. californicus* "commonly associated with *Eutychides* [= *Actinoxia*] and *Atypoides* [*riversi*]."

Life History

Males. Smith (1908) collected the only two known males of *A. californicus* during October (Fig. 1), but failed to indicate whether they were taken from burrows or collected wandering.

Females. Smith (1908) observed that most burrows (at least of those found in exposed banks) were sealed shut from June to "the first rains in December." "None were found with sealed doors from the end of December to the end of April." At least some burrows in shaded stream banks were not sealed for such a long time. Such estivating behavior during the dry season may be common to other species of *Aliatypus.*

BEHAVIOR

Burrow structure. Smith (1908) states that "the burrow is comparatively long, [and] simple. . . ." "I have seen no evidence of branches of any type, nor any suggestions of extensions above the surface. The silk lining is so meagre as to be practically indiscernible. The burrows of small specimens are not easy to distinguish from those of certain mining bees, tiger beetles, etc. . . ." Gertsch (1949) notes that "the silken lining is quite thin, but thickens around the opening. . . ." I have observed only two burrows. One was an adult female burrow which was well lined with silk in the upper half but with very little or none in the lower half. The burrow was nearly straight, sloped downward with a burrow pitch of 15°, and the bottom end was somewhat enlarged. The other (immature) burrow was straight, sloped downward with a burrow pitch of 30°, was roughly of equal diameter its entire length, and was detectably lined with silk only near the entrance. (See Table 6 for dimensions.)

Entrance structure. Banks (1896) reported that the holotype burrow entrance was covered with a trapdoor. Smith (1908) observed that the entrance structure was a "simple trapdoor" constructed of silk and soil, sometimes with bits of moss or grass attached. Spiders inactive during the dry season had the trapdoors "plastered down firmly with soil." "Doors sealed up in this way are harder to see, as a rule, than when normally fastened at the hinge only." Smith gives the dimensions of two of the largest trapdoors he examined: 21 × 15 mm and 18 × 13 mm. Gertsch (1949) described the trapdoor as being "of the wafer type." I have observed the entrance of only one medium size immature burrow. The trapdoor was thin and waferlike but quite tough, and was joined broadly to the burrow lining by a wide hinge. The outside surface of the door matched the immediate ground surface, and the inside surface was silk continuous at the hinge with the silk lining of the burrow. The trapdoor was closed and the entrance sealed by a 1 cm thick hardened plug of soil just inside the door.

Trash disposal. Both burrows which I observed had fragmented prey rejectamenta packed into their bottom ends.

Aliatypus no. 1

ECOLOGY

Geographic distribution and elevation range. A small area in southern California between Riverside and Palm Springs. 1000–4000 ft (300–1200 m).

Habitat. A population of *A.* no. 1 was observed in a xeric habitat in the foothills of the Box Springs Mountains on the edge of Riverside, California. Burrows were scattered over the 30–80° inclines of ravine banks covered only with dry scattered vegetation of grass and shrubs. The dominant larger plants were wild buckwheat (*Eriogonum*) and sagebrush (*Artemesia*). The soil was chiefly orange sandy loam with a rather high content of decomposed granite. Two other genera of burrowing mygalomorph spiders (*Bothriocyrtum* and *Aptostichus*) were found in this same location and habitat.

LIFE HISTORY

Males. The data (Fig. 1) indicate that males of this species may wander and mate with the coming of humid weather in late fall or winter.

Females. Examination of the contents of four egg sacs containing first or second instar spiderlings indicates that the pattern of early postembryonic development in this species is similar to that in *Antrodiaetus unicolor.* The morphology of the embryonic cuticle, first instar, and second instar is also similar to that of *A. unicolor*, with the exception of those differences in the second instar that are present in older instars as well. The four brood records (Fig. 2) indicate that the cycle of brood development in this species may begin later than that of *Antrodiaetus unicolor* and other species of *Antrodiaetus* and *Atypoides.* The two first instar broods collected on 5 October and one of the first instar broods collected on 10 October were kept alive and had reached the second instar stage by the end of October. Brood sizes are given in Table 3.

BEHAVIOR

Burrow structure. The burrows of four adult females, several immatures, and one adult male were observed. They were tubular and relatively long (Table 6) and straight. Variation in diameter along their length was not recorded. The adult female burrows had a thick silk lining near the entrance and usually a thin silk lining over most of the rest of the burrow. The walls in the vicinity of the egg sac were more thickly lined with silk. Immature burrows were silk lined near the entrance but very thinly or not at all elsewhere. The burrows of two adult females sloped downward with pitches of 0–10°. The male burrow was considerably smaller than the adult female burrows.

Entrance structure. The burrow entrance is provided with a wafer type trapdoor (Figs. 38–39 and 54–55) composed of soil and silk and often particles of ground surface materials. The trapdoor of adult females is 1–2 mm thick. The outer surface is well camouflaged and the inner surface is silk lined, this lining being continuous with the burrow lining at the hinge. The hinge is almost as wide as the maximum diameter of the entrance. The rim of the burrow opening is usually flared outward slightly to form a narrow lip against which the trapdoor fits snugly when closed. Many of the spiders collected in September and early October had sealed their trapdoors shut with silk seals and/or soil plugs applied to the inside of the door. The adult male's trapdoor was sealed shut with silk applied to the inner surface of the door and the adjacent burrow wall.

Egg sac structure and position. The structure of the egg sac is poorly known. The thickness of the sac wall appears similar to that of *Antrodiaetus* and *Atypoides* egg sacs. The egg sac is apparently firmly and broadly attached to the burrow wall, and at least somewhat flattened, as in *Antrodiaetus* and *Atypoides* species. The sacs were positioned in the bottom of the burrow (Table 6).

Molting behavior. The penultimate exuvia of the nearly fully sclerotized adult male lay slightly broken up in the bottom end of the burrow. Its trapdoor was sealed shut with silk.

Feeding behavior. Broken prey cuticle was found in the bottom end of several burrows. Identifiable prey included several tenebrionid beetles, ants, and a mutillid wasp.

Aliatypus no. 2

ECOLOGY

Geographic distribution and elevation range. Southern California in the vicinity of Los Angeles. 500–2500 ft (150–760 m).

Habitat. A dense burrow aggregation of this species was found at Placerita State Park, California, on a north-facing road bank. Burrows of three adult males, five brooding females, and another adult female were found within a 0.2-m^2 area.

LIFE HISTORY

Males. Collecting records (Fig. 1) indicate that adult males of this species wander and mate during the wet season in late fall and in winter.

Females. An examination of the single first instar brood and the second instar broods indicates that the pattern of early postembryonic development is similar to that of *Antrodiaetus unicolor.* Almost all of the shed chorions examined contained the embryonic cuticle. The morphology of these stages is similar to that of *A. unicolor,* except for the larger rastellar macrosetae and retention of the anterior lateral spinnerets in *A.* no. 2. Brood records (Fig. 2), like those of *A.* no. 1, indicate that the cycle of brood development may begin later than in *Antrodiaetus unicolor.* Only one complete brood was collected (Table 3).

BEHAVIOR

Egg sac structure. The single preserved egg sac had a similar shape and the sac wall thickness appeared similar to that of *Antrodiaetus unicolor.*

Behavior of brooding females and broods. The spiderlings apparently emerge from the egg sac early in the second instar or possibly very late in the first. Only the first instar brood was still within the egg sac.

Aliatypus spp.

Several other *Aliatypus* populations have been sampled, but few natural history observations have been recorded. A few of these populations probably belong to the above pair of undescribed species; others represent new species. These samples are scattered widely in Southern California from Yosemite National Park south to the Los Angeles area. Their total elevation range is 1000–7000 ft (300–2130 m). Almost all samples were collected in dry nonforested habitats similar to those of *A.* no. 1 and *A.* no. 2. One population (possibly conspecific with *A.* no. 2) was found along the 30–60° incline of a 2-meter deep ravine in Water Canyon in the Tehachapi Mountains, California. Grasses and willow bushes (*Salix*) were the dominant vegetation. The soil was dark friable clay-loam that became humid at about 20 cm below the surface (on 7 September). Burrows of the ctenizid genus *Aptostichus* were present in the same ravine. All male records (Fig. 1) indicate that wandering and mating occur during the winter wet season. When observed, entrances have always been trapdoors.

Summary and Discussion

So many gaps exist in our present knowledge of these spiders that it is not possible to do much more than briefly summarize and discuss the above data where it is plentiful or of special interest.

ECOLOGY

Habitat. Throughout the major part of their ranges, the genera *Antrodiaetus* and *Atypoides* are clearly the most successful (in terms of abundance) mygalomorph spider genera. Apparently few other mygalomorph groups are so successfully adapted for life in the cool temperate zone. The different species of *Antrodiaetus* occupy a variety of habitats—at one end of the spectrum *A. unicolor* and *A. pacificus* are found in humid forest habitats and at the other end *A. montanus* lives in dry, often nonforested, habitats—but the genus is basically adapted to fairly humid forest or woodland habitats. In the northwestern United States, where a number of species are sympatric, there is evidence for habitat segregation among the closely related species *A. pacificus, A. hageni, A. montanus,* and *A. pugnax*, i.e., ecological isolating mechanisms may be operative.

There is considerable evidence (described above) that *A. hageni* is found in relatively dry unforested habitats that are often distinct from the more humid forest habitats of sympatric *A. pacificus* populations. These two species have not yet been collected together in mixed burrow aggregations. *A. montanus* occurs in unforested or thinly forested habitats usually too dry for *A. pacificus*. It apparently occurs in mixed populations with *A. pacificus* only in open montane forests such as at Crater Lake, Oregon. (This is apparently marginal habitat for both species.) In the eastern portions of Washington and Oregon, the low, riparian, deciduous woodland habitats of *A. pugnax* are usually separated by wide expanses of wheatland or sagebrush-grassland from the higher montane forest habitat of *A. pacificus*. Except for possible contact of these two habitats along streams in the foothills of mountains, these two species may be effectively separated in this region. However, in the Willamette River Valley and the lowlands to the north, both species have been collected at the same localities. (Adult males of both species have been collected in Douglas fir forest at Olympia, Washington, and in a single pitfall collection at Eugene, Oregon.) Apparently habitat segregation in this region is at least imperfect. I have yet to find mixed species populations of any pairing of *A. hageni*, *A. montanus*, and *A. pugnax*.

The species of *Atypoides* are, like most *Antrodiaetus* species, usually found in relatively humid forest or woodland habitats. Even though *Atypoides gertschi* is sometimes found in manzanita chaparral, it is found only where the subsurface soil is humid. All three species are sympatric with *Antrodiaetus* species. *Atypoides hadros* is commonly found in mixed species populations with *Antrodiaetus unicolor*, with no evidence yet of habitat segregation. Over much of its range *A. gertschi* is sympatric with *Antrodiaetus pacificus* and probably *Antrodiaetus montanus*. One or both of these species was often found in low numbers in *A. gertschi* aggregations. On the slopes of Mt. Shasta, California, above 5500 ft, only a single *Antrodiaetus* specimen was found among the dense *A. gertschi* populations, but, at 4950 ft at McBride Springs, *A. gertschi* and *Antrodiaetus* exhibited habitat segregation. *Antrodiaetus* (immature, probably *A. pacificus*) burrows were found only in the dark, humid, organically rich loam soil of the stream bank immediately below the spring in the heavy shade of a small dense stand of young fir and pine trees. *A. gertschi* burrows were present only in the volcanic "sand" soil (dry and loose at the surface, humid and packed below 5–7 cm depth) along the edge of the same stream in an extensive area of chaparral only 10–20 m downstream of the spring.

The habitats of *Aliatypus* species are poorly known, but are relatively dry and usually nonforested. Most species are found within the Californian Province as defined by botanists (Gleason and Cronquist, 1964) and experience the long annual dry season characteristic of southern California. *Aliatypus* species are found competing in the same habitats with several genera of Ctenizidae, the trapdoor spider family towards whose niche *Aliatypus* has converged.

LIFE HISTORY

Males. In most species of *Antrodiaetus* and *Atypoides*, the males emerge from their burrows, wander, and mate sometime during the summer and fall, primarily during the second half of summer and early fall (Fig. 1). One exception is *Antrodiaetus lincolnianus*, which apparently mates in early spring. Two other possible exceptions are *Antrodiaetus cerberus* and *Antrodiaetus roretzi*. The partly sympatric species *A. lincolnianus* and *Antrodiaetus stygius* appear to be separated by an effective temporal isolating mechanism. Other pairs of *Antrodiaetus* that are possibly separated in part by temporal isolating mechanisms are *A. pacificus* and *A. occultus*, *A. pacificus* and *A. cerberus*, and *A. occultus* and *A. pugnax*. The studied species of *Aliatypus* appear to mate during late fall or winter.

Climate appears to have an important influence on the time of wandering and mating. High elevation populations (*Antrodiaetus apachecus,* the Sierran populations of *Atypoides riversi,* and *Atypoides gertschi*) often tend to mate earlier than low elevation relatives. There seems to be considerable selective pressure for male wandering to occur during relatively humid periods. Some evidence exists for the triggering of *A. unicolor* male wandering by humid weather. *Aliatypus* species do not mate until the California wet season commences. Coastal populations of *Atypoides riversi* probably do not mate until the long dry season ends in the fall.

Females. The pattern of early post-embryonic development appears to be similar in all three genera, although many species are unstudied. The timing of brood development in nature is reasonably well known for only one species, *Antrodiaetus unicolor* (Fig. 2). The small amount of data for a few other species of *Antrodiaetus* and *Atypoides* indicate that these have a somewhat similar schedule of brood development. In some species of *Aliatypus* the brood cycle may be shifted slightly toward the beginning of the winter wet season, but more information is needed. Some species (*Antrodiaetus pugnax*, *Antrodiaetus stygius*, and *Aliatypus californicus*) may commonly seal their burrow entrances for rather long periods of time during the summer. Such inactivity may be primarily an adaptation to prevent desiccation during dry periods, or possibly to reduce parasitism.

Antrodiaetus unicolor and *Antrodiaetus pacificus* have markedly larger mean brood sizes than any other species of *Antrodiaetus* and *Atypoides* studied (Table 3). This ability to produce large broods may be an important factor in the success of these two abundant species. *Aliatypus* is poorly studied. The egg size of *A. unicolor* and *A. pacificus* averages smaller than that of the other species studied (Table 4). It would seem advantageous for an individual spider to be able to reduce egg size as much as possible without reducing offspring survival ability and thereby maximize the egg number. Why have *A. unicolor* and *A. pacificus,* the adult females of which average slightly smaller than *Antrodiaetus montanus* and larger than *Antrodiaetus pugnax* and *Atypoides riversi,* been most successful in reducing egg size? Perhaps a lower probability of egg and spiderling desiccation in their more humid habitats is an important factor. Much more and other kinds of data are needed to attack this problem effectively.

BEHAVIOR

Burrow structure. There are numerous factors such as substrate environment and body size that cause intraspecific variation in burrow shape and size and in the condition of the burrow lining. However, some aspects of burrow structure are rather constant within species and show interspecific differences. (The three *Atypoides* species can be easily distinguished from each other by differences in burrow and entrance structure.) The burrows of all studied *Antrodiaetus* and *Atypoides* species are roughly tubular and more or less enlarged at the bottom end and just below the entrance, with the exception of *Atypoides riversi,* in which the very bottom end of the burrow is usually narrowed. *Aliatypus* is poorly studied. Adult female burrow length varies considerably within species, but species of smaller body size (*Antrodiaetus pugnax, Atypoides hadros*) tend to have shorter burrows, and those in habitats with particularly dry soil (*Antrodiaetus montanus, Aliatypus* no. 1) apparently tend to have longer burrows (Table 6). All studied species line their burrows with silk, with the thickest lining in and near the entrance, where the substrate is usually the least stable. Some species frequently have very little lining silk in the rest of the burrow.

The burrow pitches of the studied species in all three genera fall within 0–35° and average between 0° and 15°. Only rarely do the burrows of any studied species slope upward from the entrance. The probable adaptive significance of such a nearly perpendicular burrow inclination is that as much of the burrow as possible is removed from the unstable environment of the surface soil. *Atypoides gertschi* burrows tend to turn toward the horizontal at their end. Burrow construction behavior has been observed in only one species, *Antrodiaetus unicolor.* More complete studies of this behavior, particularly of entrance construction, are essential for tracing the evolution of burrow and entrance structure in the Antrodiaetidae.

Entrance structure. All studied species of *Antrodiaetus* have flexible collar entrances that stand erect when open. However, the collar of *Antrodiaetus roretzi* is apparently markedly reduced at two opposing sectors so that it consists essentially of two opposing flaps. *Atypoides hadros* and *Atypoides gertschi* both have flexible collar entrances, but that of *A. gertschi* is rather thick, and when opened, collapses outward instead of remaining erect. *Atypoides riversi* constructs a rigid elongate collar or turret, the opening of which is normally kept open both day and night. All studied species of *Aliatypus* construct wafer type trapdoors.

Probably the two chief functions of the entrance closure of these spiders are to prevent the entry of predators and parasites (by providing camouflage and structural resistance) and to help maintain a favorable environment within the burrow (by preventing rain and runoff from entering and by maintaining higher humidity and moderate temperature). Without more behavioral and ecological data, it is difficult to say what special functional advantages each type of closure mentioned above has. The trapdoor closes automatically when the spider retreats from the entrance, and probably a trapdoor more effectively seals out external climate and flooding than a collar. Perhaps the *Aliatypus* trapdoor originated as a key adaptation for relatively unsheltered habitats in climates such as that of southern California, where occasional torrential rainfall with runoff and flooding and where long dry summers are characteristic. The possible functional significance of the turret of *Atypoides riversi* is particularly puzzling. Possibly it involves an enlargement of the prey sensing surface area. Possibly its rigidity and height serve to protect the burrow during runoff in heavy rain. A better understanding of the special functions of these closure types is needed for a clearer understanding of their evolutionary history.

I strongly suspect that both the turret entrance of *Atypoides riversi* and the double flap collar of *Antrodiaetus roretzi* have been derived from collar entrances resembling those of the other species of these two genera. It is possible that the trapdoor entrance of *Aliatypus* has been derived from a collar via the development of a dominant flap. It presently seems just as likely that both this trapdoor and the collar were derived independently from a simpler, more generalized ancestral type of entrance. It seems much less likely that the collar has been derived from a trapdoor entrance.

There appear to be two methods (perhaps not always distinct) used for sealing an entrance: 1) sealing inside with silk only, or 2) sealing inside with a plug of soil and usually silk combined. Both methods have been observed in each of several species (*Antrodiaetus unicolor*, *Antrodiaetus pacificus*, and *Aliatypus* no. 1). The first method is commonly employed by *Antrodiaetus unicolor* and *Atypoides riversi*, the second method by *Antrodiaetus pugnax*, *Antrodiaetus stygius*, *Aliatypus californicus*, and *Aliatypus* no. 1. Sealing is performed by molting spiders, some brooding females, and spiders which appear to become somewhat inactive during part of the summer. Both sealing methods, particularly the second, probably considerably improve the climate control and predator and parasite defense functions hypothesized above for the unsealed entrance closure.

Egg sac structure and position. Egg sac structure is similar in all studied species of *Antrodiaetus* and *Atypoides*, whereas in *Aliatypus* it remains undescribed. Egg sac position in the studied species of *Antrodiaetus* and *Atypoides* (Table 6) often varies considerably within species, but in all these species, except possibly *Atypoides gertschi*, the egg sac is usually positioned between 0.4 and 0.8 of the distance down the burrow and usually on the ventral sector of the wall. The only species of *Aliatypus* studied (*A.* no. 1) appears to position its egg sac at the very bottom of the burrow. Those species found in habitats with the dryest soil (*Antrodiaetus montanus*, *Antrodiaetus pugnax*, and *Aliatypus* no. 1) appear to place their egg sacs deepest in the burrow, probably because of the greater humidity there.

Brood behavior. In studied species of all three genera, the brood emerges from the egg sac either in the second instar or late in the first instar. There is substantial evidence that in *Antrodiaetus unicolor* the second instar brood overwinters in the parental burrow and disperses in the spring. This might greatly increase the winter survival of offspring of species living in areas with cold winters. The second instar of all studied species is quite active, morphologically equipped for most adult functions, and, in *A. unicolor* at least, is capable of constructing burrows.

Molting behavior. In *Antrodiaetus unicolor*, *Antrodiaetus pacificus*, and *Atypoides riversi*, molting commonly occurs in sealed burrows and is performed on the burrow wall above the bottom of the burrow. After ecdysis the spider rests in the bottom end while sclerotization proceeds. Eventually the exuvia is removed from the burrow wall and packed into the bottom end of the burrow. Data for other species in all three genera appear to fit this scheme. Scanty data indicate that *Antrodiaetus roretzi* may behave differently.

Defensive behavior. When prodded, several species of *Antrodiaetus* and *Atypoides riversi* assume an aggressive defensive posture similar to that of *Antrodiaetus unicolor* at the bottom end of the burrow. Other species of these two genera and *Aliatypus* are unstudied. The bottom end of the *A. riversi* burrow is uniquely narrowed, resulting in a tighter fit for the abdomen when in this defensive posture, and is thus probably more effective protection. Probably pompilid wasps and possibly centipedes are two important predators against which such defensive behavior is employed.

Feeding behavior. In the few species of *Antrodiaetus* and *Atypoides* studied, adults forage chiefly at night, and the foraging posture of each species appears similar. Considerable evidence for *Antrodiaetus unicolor* and *Atypoides riversi* indicates that prey is detected solely by substrate vibrations. *A. unicolor* appears to be an unselective predator. Many species commonly pack fragmented prey exoskeletons into the bottom end of the burrow. Very little data exist on the feeding behavior of *Aliatypus*.

Mating behavior. Evidence from several species of *Antrodiaetus* and *Atypoides* indicates that males wander in search of mates only at night. Certainly such nocturnal behavior would reduce the threat from visual predators and desiccation. Presumably at least the first stages of courtship or mating also take place then, with vision playing no part. Mating behavior has been observed only once, in *Atypoides riversi*. However, with this observation, with knowledge of antrodiaetid male morphology, and with observations on the functional morphology of male mating structures in other groups of mygalomorph spiders, it is possible to form a predictive hypothesis about mating behavior in the Antrodiaetidae.

In *Atypoides riversi,* the cheliceral apophyses of the male are placed between the outspread chelicerae of the female to hold her in position during mating. The similarly well-developed male cheliceral apophyses of the other *Atypoides* species almost certainly perform the same function. Perhaps the male first legs aid in holding the female, but only *A. hadros* males possess a fairly strongly modified first leg (with macrosetae grouped at the proximal end of the tibia).

Males of all species of *Antrodiaetus* lack cheliceral apophyses. (The anterior-dorsal prominence on the chelicerae of *Antrodiaetus* males is apparently a vestigial cheliceral apophysis.) However, most species possess first leg modifications analogous to the tibial spurs and other first leg structures, which, in males of many mygalomorph groups, function in holding the female during mating (for example see Buchli, 1962; Petrunkevitch, 1911a; and Todd, 1945). In the *unicolor* species group and in *Antrodiaetus roretzi,* there are clusters of strong macrosetae on the prolateral and, often, ventral surfaces of the male first tibia and sometimes a sharp bend in the male first metatarsus. Presumably these structures contact some part of the female and hold her in position during mating. The male first legs of the *lincolnianus* species group are only weakly modified, possessing a presumably homologous group of enlarged setae on the prolateral surface of the first tibia. Probably *Antrodiaetus* males hold the females during mating primarily with the modified first legs. The weakly modified chelicerae are probably less important.

Males of all *Aliatypus* species lack cheliceral apophyses and possess no special holding modifications on their legs. However, the pedipalps, unlike those of the other two genera, are extremely elongate. Perhaps in *Aliatypus* the male, when mating, contacts the female only lightly at a distance and reaches the greater distance to her genital opening with his long pedipalps. Studies of mating behavior should receive high priority among the different approaches used to unravel the evolutionary history of the Antrodiaetidae and the other atypoid mygalomorph families.

TABLE 1. TIMING OF BROOD DEVELOPMENT IN *ANTRODIAETUS UNICOLOR* POPULATIONS. (The number of broods collected in a given developmental stage at each locality are recorded chronologically by collection date.)

Date		Locality	Large maturing eggs in abdomen	Eggs in egg sac	Hatching	First instar	First ecdysis	Second instar
April	1	Ohio, Adams Co.	1					
May	18–19	W. Va., *H*	2					
	20	W. Va., Pocahontas Co.	1					
June	11–27	Ala., *R*	7					
July	2	W. Va., Raleigh Co.		1				
	6	Ohio, *B*		2				
	21–22	Ky., *K*		7				
	23–25	Tenn., *O*	2	18	4	5		
	27–28	Ala., *R*	1	3				
	29	Ga., Murray Co.			1			
	31	Ga., Towns Co.		1				
Aug.	2–3	N. C., *P*			4	10		
	7–8	N. C., *N*		2				
	14–16	W. Va., *C*			3	4	1	3
	21–23	Va., *I*				3	2	5
	25–26	Va., *J*				2	4	9
	28–29	N. C., *M*					1	9
	31	Tenn., *L*						2
Sept.	1	Tenn., *O*				2		7
	5–7	Ala., *Q*				6	1	22
	11	Ark., Stone Co.						1
	14–16	Ill., *F*						6
	22	Ohio, *B*						3
Dec.	2–3	Ala., *Q*						5

TABLE 2. BROOD SIZE (NUMBER OF OFFSPRING PER BROOD) OF *ANTRODIAETUS UNICOLOR* POPULATION SAMPLES.

Sample	N (broods)	Range	Mean	Std. dev.
B	2	127–155	141.0	
C	9	79–185	120.2	±36.5
I	4	90–209	127.0	
J	5	99–318	189.0	±87.1
K	6	84–241	142.9	±54.2
M	1	102		
N	2	111–154	132.5	
O	31	38–236	144.1	±49.8
P	14	96–256	169.8	±52.3
Q	7	66–125	100.4	±18.6
R	3	114–160	134.6	

TABLE 3. BROOD SIZE (NUMBER OF OFFSPRING PER BROOD) OF ANTRODIAETID SPECIES.

	N (broods)	Range	Mean	Std. dev.
Antrodiaetus				
unicolor	87	38–383	145.7	±57.0
robustus	2	86–94	90.0	
pacificus	4	107–328	192.2	
pugnax	8	40–75	52.1	±12.1
montanus	1	78		
stygius	1	79		
Atypoides				
riversi (coastal)	7	43–80	63.1	±13.5
riversi (Sierran)	1	81		
gertschi	1	78		
hadros	1	80		
Aliatypus				
sp. no. 1	3	66–104	85.0	
sp. no. 2	1	139		

TABLE 4. EGG SIZE OF ANTRODIAETID SPECIES. (Ten eggs measured in each brood.)

	N (no. of broods)	Egg diam. in mm		Time (months) in 80% EtOH between collecting and measurement
		Range	Mean	
Antrodiaetus				
unicolor	15	1.02–1.75	1.30	12–28
pacificus	3	1.13–1.46	1.32	9
pugnax	8	1.20–1.58	1.44	9
montanus	1	1.78–1.95	1.81	9
Atypoides				
riversi (coastal)	2	1.54–1.73	1.63	5
riversi (Sierran)	1	1.36–1.51	1.47	5

TABLE 5. BURROW DIMENSIONS AND EGG SAC POSITION OF *ANTRODIAETUS UNICOLOR* POPULATION SAMPLES. (Only adult female or adult or penultimate male burrow dimensions included. Sample size, range, and mean given for each sex of each sample. Burrow length is length in cm of longitudinal axis of burrow from ground surface to bottom end. Entrance diameter is maximum inside diameter in mm of burrow entrance opening. Egg sac position is a ratio: length of longitudinal axis of burrow from ground surface to upper end of egg sac/burrow length.)

Sample		Burrow length			Entrance diam.			Egg sac position		
B	♀	19	14–25	19.6	18	11–17	13.3	3	0.13–0.56	0.28
	♂	2	16	16.0	2	8–9	8.5			
C	♀	21	15–30	20.7	14	10–18	13.9	8	0.07–0.78	0.21
	♂	5	14–24	18.4	1	9				
Clifty Falls, Ind.	♀	2	27–38	32.5	2	12–17	14.5			
D	♀	9	11–29	19.5	9	11–20	14.7			
Grandview St. Pk., W. Va.	♀	2	13–19	16.0	2	9–11	10.0	1	0.38	
F	♀	9	14–30	20.3	6	10–13	12.0			
	♂	2	10	10.0	1	10				
I	♀	29	12–30	20.4	17	12–16	13.8	7	0.11–0.67	0.33
	♂	9	6–15	10.3	2	9–10	9.5			
J	♀	37	15–38	24.6	30	12–20	15.1	8	0.05–0.76	0.34
K	♀	14	14–31	20.9	10	12–17	14.7	7	0.06–0.72	0.49
L	♀	4	17–36	23.7	3	12–16	14.3			
	♂	1	4							
M	♀	20	10–30	20.9	10	11–15	12.9	3	0.56–0.67	0.61
N	♀	3	11–18	15.3	2	11–13	12.0	2	0.56–0.73	0.64
O	♀	48	9–33	20.6	45	11–14	12.5	31	0.48–0.83	0.66
	♂	1	15							
P	♀	35	10–29	20.9	22	11–15	13.5	15	0.08–0.75	0.40
	♂	6	11–16	14.0						
Q	♀	35	10–29	20.1	22	10–14	12.3	12	0.35–0.85	0.65
R	♀	8	16–33	24.0	8	11–13	11.8	3	0.48–0.67	0.59
Blanchard Springs, Ark.	♀	2	11–21	16.0						
	♂	1	8							

TABLE 6. BURROW DIMENSIONS AND EGG SAC POSITION OF ANTRODIAETID SPECIES.
(Variables and samples defined as in Table 5. Turret height is length in mm of longitudinal axis of turret from ground surface to top of turret.)

		Burrow length		Entrance diam.		Turret height		Egg sac position	
Antrodiaetus									
unicolor	♀	307	9–38(21.2)	226	9–20(13.4)			101	.05–.85(.51)
	♂	28	4–24(12.7)	6	8–10(8.8)				
robustus	♀	5	18–34(26.8)	4	10–13(11.3)			2	.67–.80(.74)
pacificus	♀	22	16–44(27.6)	18	11–13(12.3)			3	.13–.67(.48)
	♂	8	14–36(24.4)	4	10–11(10.3)				
pugnax	♀	13	9–23(13.8)	12	7–13(9.0)			8	.47–.85(.78)
	♂	2	7–9 (8.0)	2	8 (8.0)				
montanus	♀	3	31–46(38.3)	2	14 (14.0)			1	.71
hageni	♀	2	22–40(31.0)	1	13				
	♂	2	22–32(27.0)						
stygius	♀	3	20 (20.0)					2	.60 (.60)
	♂	2	14–16(15.0)						
roretzi	♀	?	10–15 —from Yamamoto (1942)						
	♂	2	6–10(8.0)—from Yamamoto (1942)						
Atypoides									
riversi (coastal)	♀	11	15–32(23.8)	8	11–14(12.6)	10	13–60(31.8)	8	.43–.59(.50)
	♂	5	18–21(19.8)						
riversi (Sierran)	♀	10	18–27(21.4)	8	9–14(11.3)	10	5–25(14.7)	1	.47
	♂	4	8–20(16.5)						
gertschi	♀	15	18–36(29.6)	13	13–16(14.0)			1	.25
hadros	♀	5	8–15(11.2)	2	9–10(9.5)				
	♂	2	7–8 (7.5)						
Aliatypus									
californicus	♀	3	16–25(19.0)—2 measurements from Smith (1908)						
sp. no. 1	♀	4	31–46(38.0)	4	11–13(12.0)			4	.90–.95(.92)
	♂	1	23	1	7				

TABLE 7. THE INSTAR COMPOSITION OF PRE-EMERGENT, EMERGING, AND EMERGED (FROM EGG SAC) BROODS OF *ANTRODIAETUS UNICOLOR* POPULATION SAMPLES.
(Numbers represent number of broods in each category in each sample.)

	Brood entirely within egg sac			Brood emerging from egg sac			Brood entirely outside egg sac		
Instar of brood	1	1+2	2	1	1+2	2	1	1+2	2
Sample									
B									2
C	5	1		1	1				3
F									6
I	3				1	1		1	4
J	1	2		1	2	1			8
L									2
M					2				8
O	10			1					7
P	13			1					
Q	6	1				3			24
Total	38	4		4	6	5		1	64

TABLE 8. FREQUENCY OF BROODING FEMALES WITH SEALED AND UNSEALED BURROW ENTRANCES IN *ANTRODIAETUS UNICOLOR* POPULATION SAMPLES.
(Asterisk signifies that majority of females had collar open or collar was open and spider was also in foraging posture.)

	Before brood emerges from egg sac		After second instar spiderlings begin emerging from egg sac	
Sample	Unsealed	Sealed	Unsealed	Sealed
B		3		2
C		2		1
F			1	2
I				1
J		2	3	6
K	1	1		
L			2	
M				3
N		1		
O	32*			6
P	1			3
Q	4*	2	14*	4
R	4*			

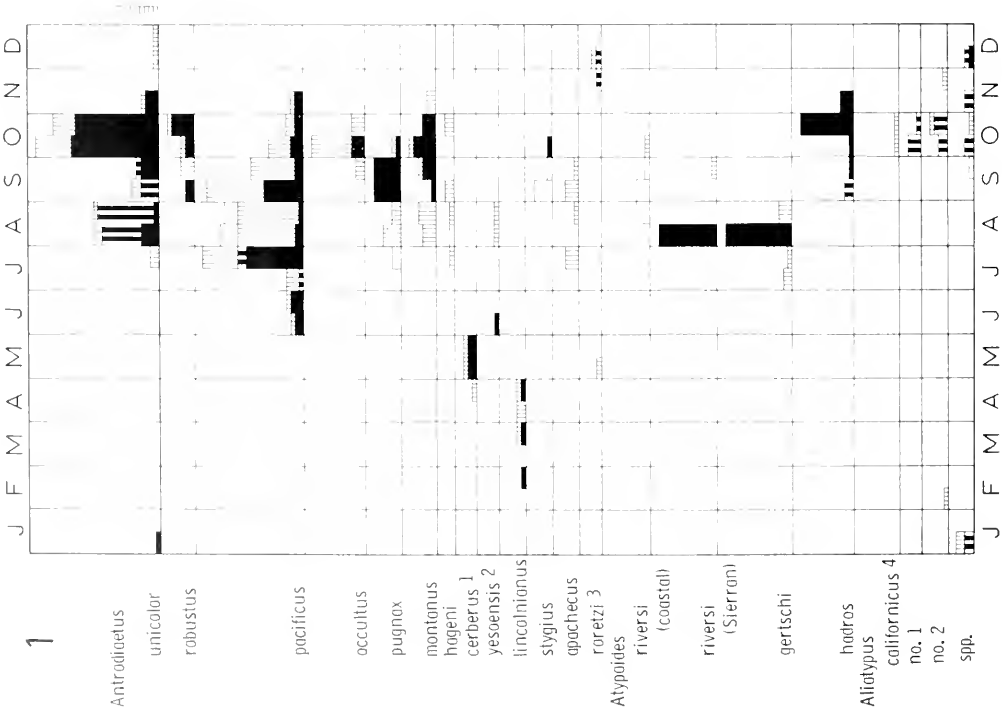
TABLE 9. RECORDS OF POMPILID WASP PREDATION ON *ANTRODIAETUS UNICOLOR.*

		Developmental stage of wasp				
Locality	Date	Egg	Early instar larva	Larva in cocoon	Abandoned cocoon	Soil plug in burrow
Summers Co., W. Va.	July 3			1		?
Jefferson Co., Ind.	July 17	1	1			no
D	July 20	1				no
R	July 27			1		yes
Towns Co., Ga.	July 31				1	
N	Aug. 7				1	
C	Aug. 14–16		1	7		yes—4, no—4
J	Aug. 25	1				yes
M	Aug. 28			1		yes
Q	Sept. 6	1				no
Johnson Co., Ark.	Sept. 10			1		no

TABLE 10. PREY FOUND IN *ANTRODIAETUS UNICOLOR* BURROWS.

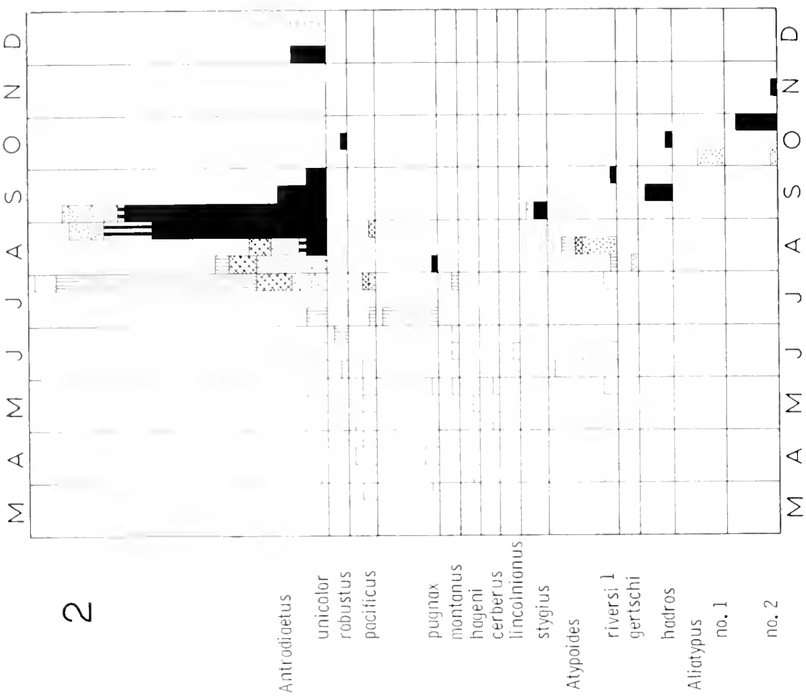
(Numbers indicate in how many of 102 burrows each prey taxon was found. The great majority of these are prey rejectamenta records; very few are records of freshly killed prey.)

Ants (Formicidae)	65
Beetles (Coleoptera)	64
Millipedes (Diplopoda)	11
Flies (Diptera)	4
Spiders (Araneae)	4
Harvestmen (Opiliones)	4
Sow bugs (Isopoda)	4
Snails (Gastropoda)	3
Wasps (Vespidae and Scolioidea)	2
Crickets (Gryllidae)	1
Caterpillars (Lepidoptera: Sphingidae)	1



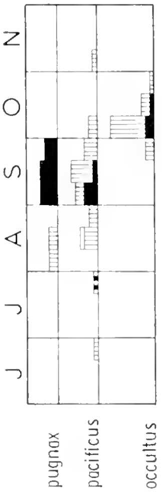
1

J
F
M
A
M
J
J
A
S
O
N
D
Antrodiaetus
unicolor
robustus
pacificus
occultus
pugnax
montanus
hageni
cerberus 1
yesoensis 2
lincolnianus
stygius
apachecus
roretzi 3
Atypoides
riversi (coastal)
riversi (Sierran)
gertschi
hadros
Aliatypus
californicus 4
no. 1
no. 2
spp.



2

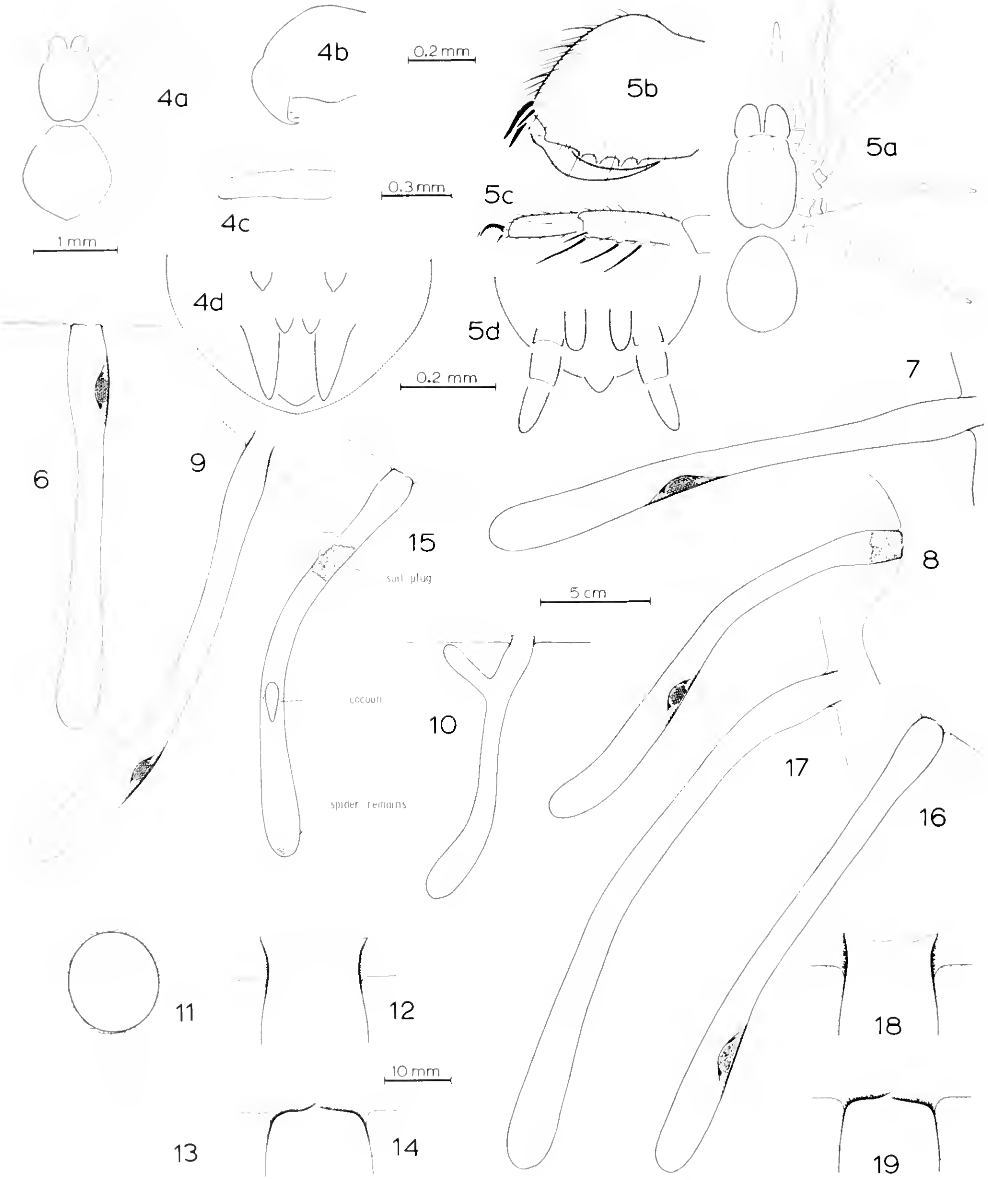
M
A
M
J
J
A
S
O
N
D
Antrodiaetus
unicolor
robustus
pacificus
pugnax
montanus
hageni
cerberus
lincolnianus
stygius
Atypoides
riversi 1
gertschi
hadros
Aliatypus
no. 1
no. 2



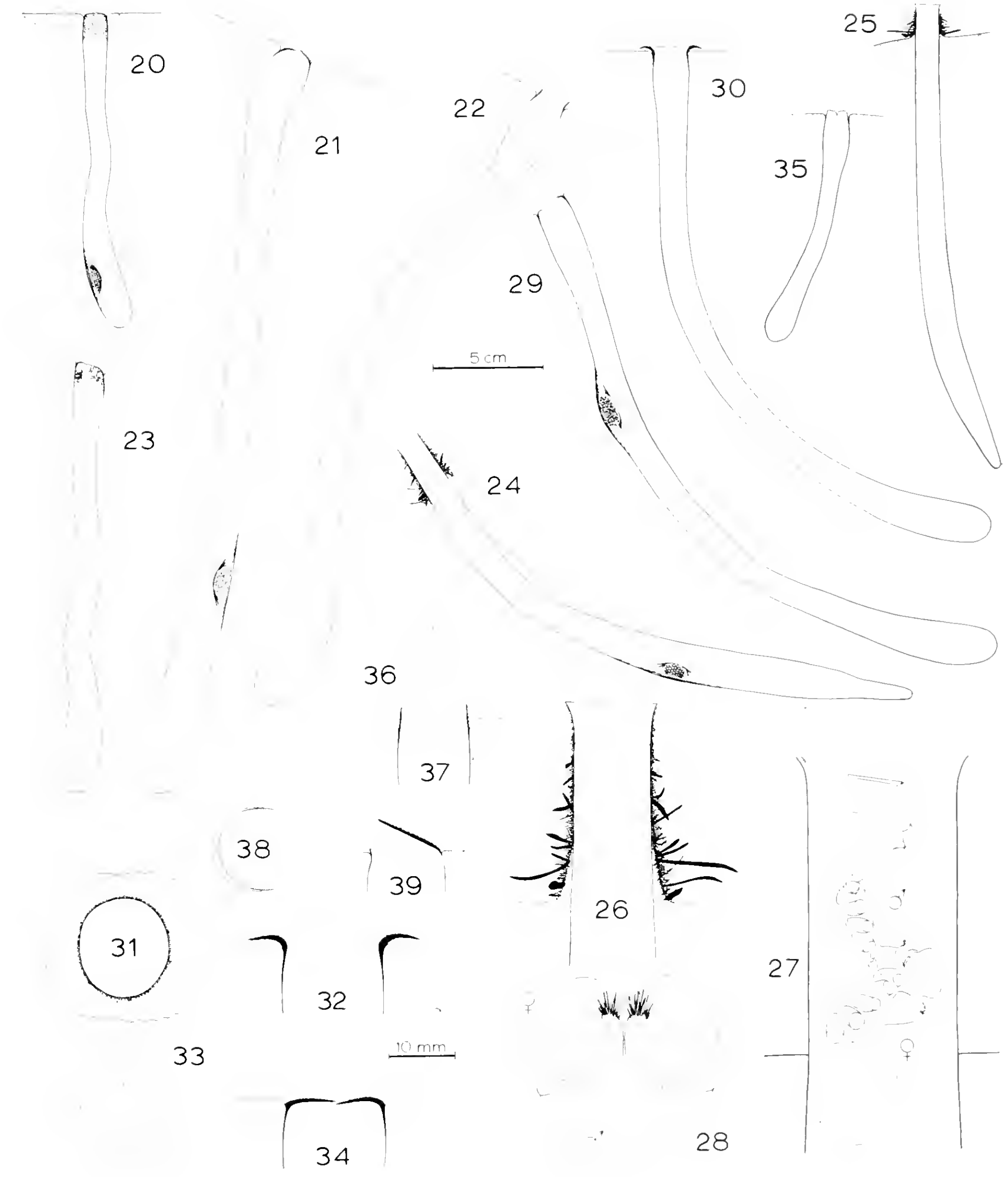
3

J
J
A
S
O
N
pugnax
pacificus
occultus

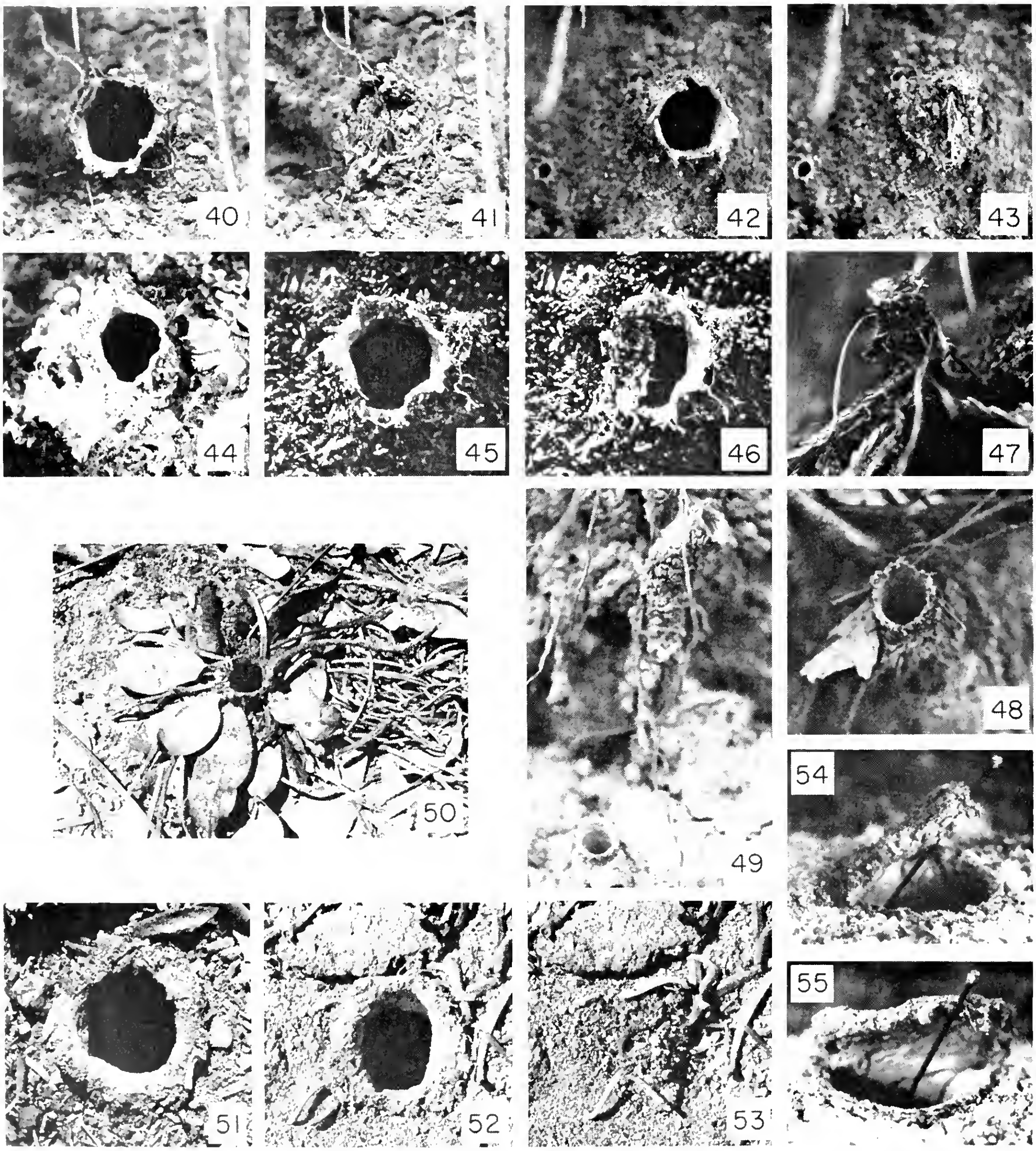
Figure 1. Collection dates of adult male antrodiaetids. Records grouped into $^1/_2$ month periods. One unit of vertical scale represents one male. Solid black represents adult male collected after leaving its burrow. Two vertical bars represent adult male collected within its burrow before abandoning it. Vertical lines represent adult male collected either before or after leaving its burrow; inadequate data accompanies specimen. Empty rectangle represents date on which a male, collected in the penultimate instar, molted to maturity in captivity. All records are from examined specimens with the following exceptions indicated by superscript numbers: (1) 3 records from W. Ivie (personal communication), (2) June record is holotype collection date (Uyemura, 1942), (3) November record and one December record from Yamamoto (1942), (4) Both records from Smith (1908). Figure 2. Timing of brood development in antrodiaetid species. Collection dates and developmental stages of broods collected in the field. Records grouped into $^1/_3$ month periods. One unit of vertical scale represents one brood. Broods in the form of large maturing eggs within abdomen are represented by an empty rectangle, broods consisting of eggs in egg sac by vertical lines, hatching broods by crosshatching, first instar broods by stippling, broods during first ecdysis by 2 vertical bars, and second instar broods by solid black. Note: (1) All *Atypoides riversi* broods are from coastal populations except for a single Sierran brood collected in the first $^1/_3$ of August. Figure 3. Collection dates of adult males of *Antrodiaetus occultus*, *Antrodiaetus pacificus*, and *Antrodiaetus pugnax* in the Willamette and Umpqua River valleys from Roseburg, Ore., north to the Columbia River. Same symbols and scale as in Fig. 1. Records grouped into $^1/_3$ month periods.



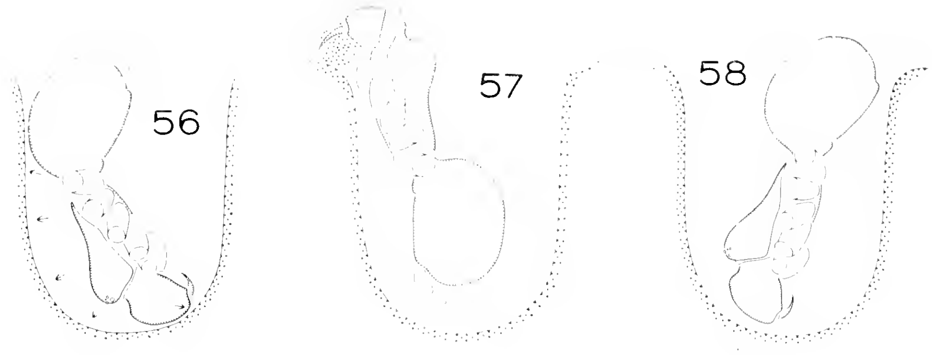
Figures 4–5. Early instars of *Antrodiaetus unicolor*. 4. First instar. 4a. Dorsal view. 4b. Chelicera, retrolateral view. 4c. Leg I metatarsus and tarsus, retrolateral view. 4d. Spinnerets and anal tubercle, ventral view. 5. Second instar; same views and scales as in Fig. 4. Figures 6–15. *Antrodiaetus unicolor* burrow structure. 6–9. Adult female burrows; *P, J, Q,* and *O* respectively. 10. Immature burrow, *D*. 11–14. Burrow entrance. 11–12. Open collar, frontal and sagittal views. 13–14. Closed collar, same views. 15. Burrow attacked by pompilid wasp, *C*. Figures 16–19. *Antrodiaetus pacificus* burrow structure. 16–17. Adult female burrows; *I* and *U* respectively. 18–19. Open and closed collar, sagittal view. (5 cm scale for burrows. 10 mm scale for collars.)



Figures 20–23. Adult female burrows of *Antrodiaetus* spp. 20. *A. pugnax*, *B*. 21. *A. montanus*; Pocatello, Ida. 22. *A. hageni*; Trail, B. C. 23. *A. stygius*, paratype. Figures 24–28. *Atypoides riversi*. 24–25. Adult female burrows; *D* and *I* respectively. 26. Open turret, sagittal section. (Modal form for coastal population. Dotted line indicates form of closed turret.) 27–28. Mating posture observed at G. (Drawn from field sketch and notes.) 27. Lateral view. 28. View looking down burrow. Figures 29–34. *Atypoides gertschi* burrow structure. 29–30. Adult female burrows; *N* and *O* respectively. 31–32. Open collar, frontal and sagittal views. 33–34. Closed collar, same views. Figures 35–37. *Atypoides hadros* burrow structure. 35. Adult female burrow; Ferne Clyffe St. Pk., Ill. 36–37. Collar of same burrow. 36. Closed, frontal view. 37. Open, sagittal view. Figures 38–39. *Aliatypus* no. 1 adult female burrow entrance; frontal and sagittal views with trapdoor open. (5 cm scale for burrows. 10 mm scale for entrances.)



Figures 40–55. Antrodiaetid burrow entrances (adult females only). 40–43. *Antrodiaetus unicolor.* 40–41. *J,* collar open and closed. 42–43. *Q,* collar open and closed. 44. *Antrodiaetus pacificus; U,* collar open. 45–46. *Antrodiaetus hageni;* Trail, B. C. 45. Collar fully open. 46. One lateral sector of collar collapsed by author. 47–50. *Atypoides riversi.* 47. *D.* 48. *I.* 49. *D.* 50. *I.* 51–53. *Atypoides gertschi.* 51. *O,* collar open. 52–53. *N,* collar open and closed. 54–55. *Aliatypus* no. 1; Riverside, Calif. Trapdoor propped open.



Figures 56–58. Drawings of *Antrodiaetus unicolor* burrow construction behavior. Sketched from frames of 16 mm movie film. 56. Burrowing. Arrows indicate general direction of forces produced by legs and chelicerae against cell wall. 57. Releasing load of soil onto rim of cell opening. 58. Silk application.

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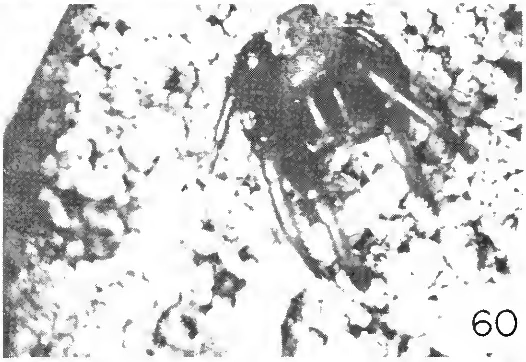

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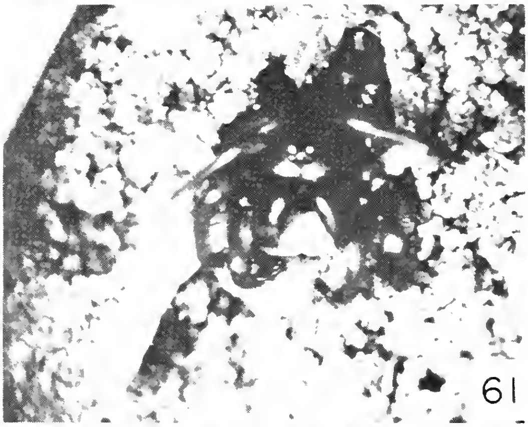

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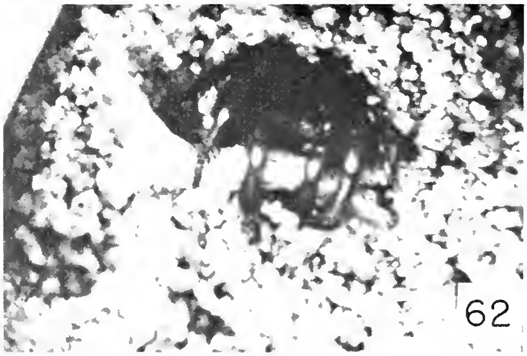

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Figures 56–58. Photos (16-mm movie frames) of *Antrodiaetus unicolor* burrow construction behavior. 56. Burrowing. 57. Releasing load of soil onto rim of cell opening. 58. Silk application. Figures 59–62. *Antrodiaetus unicolor* prey capture behavior. 59. Foraging posture (Photo by R. Ball). (Figs. 60–62 are 16-mm movie frames.) 60. Initial contact with prey (*Tenebrio* larva) at end of lunge from burrow entrance. 61. Fangs imbedded in prey. 62. Spider retreating into burrow with prey.


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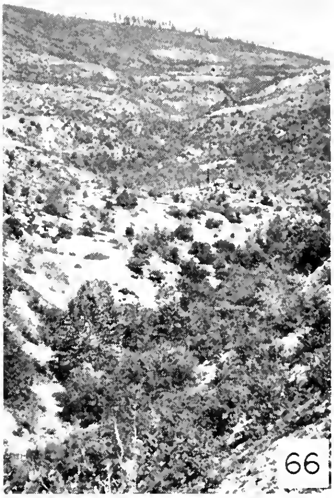
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Figure 63–68. Habitat photos. 63. Conifer forest habitat occupied by *Antrodiaetus pacificus* in Cascade Mtn. Range near L. 64. Riverbank woodland habitat occupied by *Antrodiaetus pugnax* at Lewis and Clark St. Pk., Wash. 65. Juniper-sagebrush habitat occupied by *Antrodiaetus montanus* at Pocatello, Ida. 66. Nonforested habitat occupied by *Antrodiaetus hageni* at Trail, B. C. 67. Tan oak pacific madrone forest habitat occupied by *Atypoides riversi* at D. 68. California red fir habitat occupied by *Atypoides gertschi* at 7,400 ft at N.

TAXONOMIC METHODS

Analysis of Variation

I have approached the species level taxonomy of *Antrodiaetus* with two principal and interrelated aims: to discover morphological characters of high value in distinguishing between species, and to study geographic variation. Difficulty in achieving the first goal in many groups of mygalomorph spiders (including the Antrodiaetidae) is primarily a result of the relatively simple morphology of the male palpus and female genitalia, the difficulty of obtaining samples of adequate size, and the instar heterogeneity (and therefore greater variation) of adult female samples. The second difficulty has been overcome for many antrodiaetid species and the third has been reduced by the use of ratio characters. The study of geographic variation, also affected by the latter two difficulties, is particularly important for mygalomorph species, which often exhibit much geographic variation within a relatively small area. Both aims were pursued by an analysis of variation of numerous quantitative and qualitative characters. Initially, variation in a large number of characters was briefly surveyed, and from these the diagnostically most promising were selected and their variation studied in depth.

Variation of quantitative characters (measurements, meristic characters, and ratios formed from these) was analyzed with the aid of a 7094 IBM computer. A Fortran II program directed the computer to calculate the mean and standard deviation of each character for each local population sample of each sex and for certain groupings of local samples plus individual specimens into larger infraspecific or species samples. The computer then compared these samples pairwise in any desired combination, giving for each character for each comparison a value of the distinctness of the two samples. This "distance" value equals the difference between the means of the two samples divided by the sum of their standard deviations. I could then quickly select those quantitative characters of greatest diagnostic value, those showing the most marked geographic variation, and those infraspecific samples that were most divergent.

This analysis of variation was performed on the following number of quantitative characters: 14–15 measurements, 6 meristic characters, and 35 ratios for males; 17 measurements, 9 meristic characters, and 49 ratios for females. These characters were defined so as to be well delimited. Their definitions and abbreviations are as follows (see Figs. 71–75):

CL	Maximum length of carapace (between lines tangent to anteriormost and posteriormost parts of carapace) along line parallel to median longitudinal axis, with lateral border of carapace horizontal.
CW	Maximum width of carapace along line perpendicular to median longitudinal axis.
OQW	Maximum width of eye group (ocular quadrangle) on line perpendicular to median longitudinal axis of carapace. All eye measurements are made in dorsal view with lateral border of carapace horizontal.
ALS	Minimum distance between anterior lateral eyes.
ALD	Maximum diameter of left anterior lateral eye.
AMS	Minimum distance between *pupils* (light colored saucer-shaped central area of eye) of anterior median eyes.
AMD	Transverse diameter of left anterior median eye pupil.
SL	Maximum length of sternum on line parallel to median longitudinal axis. Anterior border of sternum is its pointed anterior extension lateral to labium.
SW	Maximum width of sternum perpendicular to line defining SL.
IFL	Length of femur I taken as length of straight line connecting the proximal and distal points of articulation. All leg and pedipalp segment length measurements were made in side view along retrolateral surface of appendanges after removing them from spider.
ITL	Length of tibia I taken as length of straight line connecting proximal and distal points of articulation.
IML	Length of metatarsus I taken as length

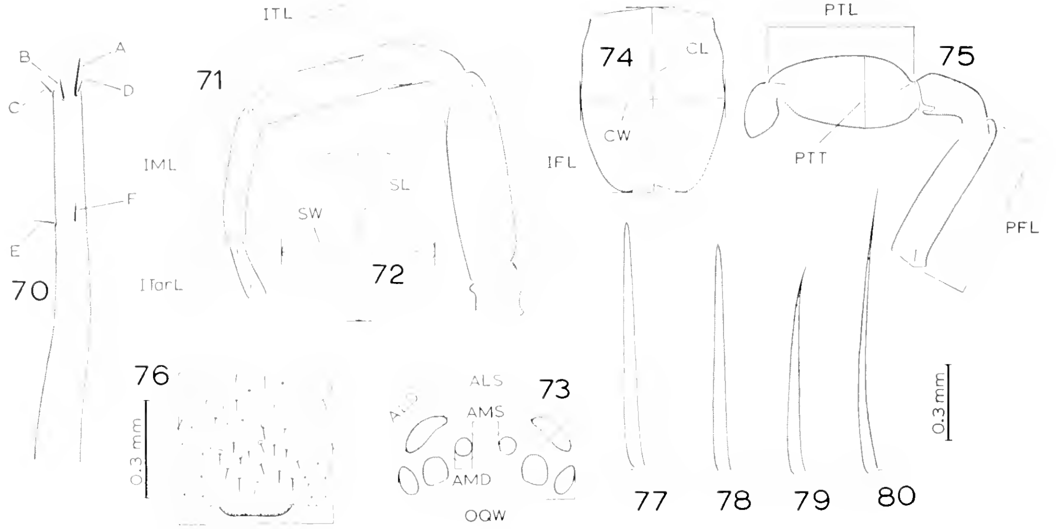


Figure 70. Macrosetae positions on metatarsus I of adult males of *Antrodiaetus*. Figures 71–75. Measurements. Figure 76. Area around genital opening of *Antradiaetus unicolor*, showing epiandrous gland spigots. 0.3 mm scale. Figures 77–80. Macrosetae types. 77–78. Ensiform. 79–80. Attenuate. 0.3 mm scale.

	of straight line connecting proximal point of articulation with distalmost point of segment.
ITarL	Length of tarsus I taken as length of straight line connecting most proximal exposed point of tarsus with distalmost point of dorsal surface.
IVFL, IVTL, IVML, IVTarL	Leg IV segment lengths measured in same manner as corresponding leg I segments.
ITD, IMD	Diameter of male tibia (metatarsus) I at ventral swelling in lateral view (*A. pugnax* only).
PFL	Length of pedipalpal femur measured same as IFL.
PTL	Length of pedipalpal tibia measured same as ITL.
PTT	Maximum diameter, taken perpendicular to line defining PTL, of pedipalpal tibia in lateral view.
ETL	Distance which tip of inner conductor sclerite extends beyond tip of outer conductor sclerite (*A. unicolor* and *A. robustus* only).
CT	Number of cheliceral macroteeth (per chelicera).
CMT	Number of cheliceral microteeth (per chelicera).
PTSP	Number of ensiform macrosetae on prolateral surface of tarsus of female pedipalp.
PTSR	Number of ensiform macrosetae on retrolateral surface of tarsus of female pedipalp.
IMS	Number of ensiform macrosetae on metatarsus of leg I of female.
IVMT	Number of trichobothria in row on dorsal surface of metatarsus IV. As these usually vary greatly in size, some care must be taken to count small ones also.
IVMCR	Number of setae in large comb on retrolateral surface at distal end of metatarsus IV.
IVCTR	Number of teeth on retrolateral claw of tarsus IV. Claw tooth count includes even the reduced proximal teeth. Counts must be made carefully under high magnification in strong light.
EGS	Number of epiandrous gland spigots. These are located just anterior to genital opening on abdomen of adult males (Fig. 76).

All measurements and counts were performed by myself with the same stereomicroscope and eyepiece micrometer scale. Five specimens were remeasured five times for each character during the course of this study; this sampling indicated that the measurements are accurate to one micrometer unit for each of the four different powers of magnification used. One micrometer unit had the following value for the following characters: 0.0753 mm for CL; 0.0377 mm for CW, SL, SW, and all leg and pedipalp segment lengths; 0.0182 mm for PTT, ITD, and IMD; and 0.0092 mm for all eye group measurements and ETL.

Many of the quantitative characters studied proved to be diagnostically useful. Tables 12–14 record for all species the variation found in the measurements, meristic characters, and diagnostically most valuable ratios. Male measurements of greatest diagnostic value are those of leg I segments, pedipalp segments, and anterior median eye diameter and separation. Ratios formed from these are even more useful. Male leg I macrosetae counts are also particularly useful. Females are much more difficult to diagnose with quantitative characters; ratios are usually much more useful than nonratio characters.

Variation in qualitative characters (those not defined strictly quantitatively) was recorded as carefully as possible and is usually described with the aid of figures. Color variation of *A. unicolor* females was quantified as follows. The color of the lateral slope of the pars cephalica was recorded because of the even coloration, ease of observation, and rather wide range of color variation of this area. All specimens studied had fully sclerotized fangs and had been collected and preserved in 80 per cent ethanol four to six months earlier. The total range of color variation was represented by a rectangular grid (Fig. 92) of 30 squares with the vertical scale representing a basic hue change from yellow to orange and the horizontal (grayness) scale a change in the amount of black in the color. The limits of this range are pale yellow (1A) and dark brown (5.5C). Ten specimens separated by uniform grayness intervals along the A (1A–5A) and C (1C–5C) rows were selected as standards and arranged in a shallow tray of alcohol under the even light of two cool white F15T8-CW fluorescent bulbs. All other specimens were compared individually in the tray with these and each was assigned a value corresponding to its position on the color grid.

The diagnostically most useful male qualitative characters are the shapes and macrosetation of tibia I and metatarsus I, the pedipalpal tibia shape, and the shapes and spatial relationships of the palpus sclerites. Females are considerably more difficult to separate with qualitative characters than are males. Cheliceral and carapace setation, coloration, cheliceral microtooth size and arrangement, and seminal receptacle form are the most useful female characters in species diagnoses.

Species sample sizes are given in Tables 13 and 14, and population sample sizes are indicated in the Dice-Leraas diagrams. Each locality from which a significant sample of *A. unicolor*, *A. pacificus,* or *A. pugnax* was obtained is labeled on the maps of Figures 85, 98, and 104 and identified in the records sections and in the text by an italicized capital letter.

No external structure or characteristic gross change in seminal receptacle form has been found that indicates when a female antrodiaetid has reached sexual maturity (or what instar an adult female may be). Therefore a female specimen was included in a population sample only if it had a longer carapace than the smallest reproductively active female in that sample. Exceptions were made for a few rare species for which no reproductively active females were available. (See species sample sizes given in Table 14.) A reproductively active female is defined as one with large ripening eggs in her abdomen or a brood in her burrow. Other females included in a sample therefore represent first adult instar females collected in the summer, fall, or winter before or soon after their initial mating, some later adult instar females, and occasionally an immature female.

MATERIAL

This study is based upon the following material examined: nearly 370 *Antrodiaetus* males (about 250 are *A. unicolor* and *A. pacificus*), approximately 500 *Antrodiaetus* females (almost 420 are *A. unicolor* and *A. pacificus*), 28 *Aliatypus* males, 55 *Aliatypus* females, and roughly 2000 immature specimens. Approximately half of this material I have collected. The rest was loaned to me by the following people and institutions: Personal collections—J. A. Beatty, J. Carico, P. Craig, H. Exline Frizzell, R. Hoffman, W. Icenogle, R. E. Leech, J. MacMahon, B. J. Marples, F. J. Moore, P. Nelson, W. Peck, V. D. Roth, W. A. Shear, R. Snetzinger, M. Thompson, B. Vogel, A. A. Weaver, T. Yaginuma. Institutions—American Museum of Natural History (W. J. Gertsch); British Columbia Provincial Museum (E. Thorn); British Museum (Nat. Hist.) (J. G. Sheals, D. J. Clark); California Academy of Science; Canadian National Collection (A. L. Turnbull); University of Kansas; Museum of Comparative Zoology (H. W. Levi); University of Nebraska (P. C. Peterson); Muséum National d'Histoire Naturelle, Paris (M. Vachon, M. Hubert); Peabody Museum Natural History, Yale (W. Hartman, C. Remington); and, University of Utah (G. Edmunds).

COLLECTING METHODS

The uncommonness of antrodiaetids in collections is due to their covert behavior. Concentration on particular collecting strategies greatly improves one's chances of finding these spiders. Burrow aggregations are best discovered by locating promising habitats during daylight and searching these habitats for open burrow entrances at night with a headlamp. One can then trap and collect the spiders at their burrow entrances by quickly thrusting a knife blade through the soil and across the burrow lumen just below the spider. More information is gained by excavating the burrow, preferably in daylight after marking it at night. As one accumulates experience, it becomes possible to efficiently locate closed entrances in the daylight by carefully examining and delicately picking at likely microhabitat surfaces with a knife blade. During the mating season, one can (with a headlamp) readily spot adult males as they nocturnally wander over the ground surface in the vicinity of burrow aggregations. Pitfall traps are excellent collectors of wandering males. Careful searching for sealed or nocturnally closed burrow entrances early in the mating season will often reveal penultimate males and recently molted adult males. Penultimate males, easily recognized by their swollen pedipalpal tarsi (Coyle, 1968, fig. 45), will frequently molt to adulthood if maintained in a cool, humid, and dark environment.

MORPHOLOGICAL TERMINOLOGY

Eyes. The abbreviations AME, ALE, PME, and PLE designate the following eyes respectively: anterior median eyes, anterior lateral eyes, posterior median eyes, and posterior lateral eyes.

Chelicerae. A variable prominence, probably homologous to the cheliceral apophysis of *Atypoides*, is found on the anterior-dorsal surface of the chelicerae of *Antrodiaetus* males (Figs. 145–157). This is referred to as the *anterior-dorsal cheliceral prominence.* The *cheliceral macroteeth* are the large teeth forming a single prolateral row (Fig. 158) (and a second more retrolateral row in *Aliatypus*). The *cheliceral microteeth* are the much smaller teeth scattered retrolaterally along part of the prolateral macrotooth row. In the descriptions of microteeth position, the term "last" means most proximal. The presence or absence of a setaless area on the upper ectal (=retrolateral) surface of the chelicera is a useful character in the *unicolor* group of *Antrodiactus* (Figs. 170–172). The always setaless ectal and dorsal surface proximal of the dorsal gibbosity is *not* part of this character.

Palpus. In *Antrodiaetus,* as in *Atypoides* and *Aliatypus,* the conductor of the palpus consists of two sclerites (Fig. 207), an *inner conductor sclerite* (i.c.s.), which tapers and at least partly envelops the *embolus* distally, and an *outer conductor sclerite* (o.c.s.), which lies outside and cradles these structures.

Male leg I. An *ensiform* macroseta is one which tapers abruptly at its terminal end and is therefore rigid for its entire length (Figs. 77, 78). An *attenuate* macroseta tapers gradually and is therefore very slender distally and often easily bent (Figs. 79, 80). At least 90 per cent of all male tibia I macrosetae can be definitely assigned to one or the other of these two categories. Attenuate macrosetae with broken tips are readily recognized if one is cautious. The macrosetae pattern of male metatarsus I is diagnostically quite useful. Six such differently positioned macrosetae occur in *Antrodiaetus* and are identified by the letters A through F (Fig. 70). When present, each is in nearly the same position in every species and therefore probably homologous throughout the genus, i.e., macroseta A of *A. unicolor* is homologous to that of *A. pugnax,* etc. However, macroseta B shows some position variation, but it seems to vary as much within *A. pugnax* as between other species. In *A. unicolor, A. montanus, A. stygius,* and *A. apachecus* on most male metatarsi I which are recorded as lacking macrosetae in Table 12, macroseta A is represented by a rather prominent enlarged seta.

Abdomen. The abbreviations AL, PM, and PL designate the following spinnerets respectively: anterior lateral, posterior median, and posterior lateral. The anterior half of the abdominal dorsum of *Antrodiaetus* is provided with constantly positioned, segmentally arranged patches of more heavily sclerotized cuticle (Fig. 109), presumably vestigial abdominal tergites. These may be continuous, i.e., fused to one another at adjacent borders. The second patch (from the anterior end), which is always present in both sexes, is smooth, platelike, and most heavily sclerotized; it is called a *tergite* in this paper.

Female genitalia. The general morphology of the female genitalia in *Antrodiaetus* (Fig. 275) is like that of *Atypoides* (see Coyle, 1968).

METHODS OF PRESENTATION

Descriptions. Only the most important literature references are cited. Complete citations are given in Coyle, 1969. Each description is a composite of all adult specimens at hand. Any characters in which the holotype or lectotype is markedly variant are noted. Only characters of diagnostic value are included. The quantitative characters recorded in Tables 12–15 are an integral part of each description. Colors are described from fully sclerotized specimens immersed in ethanol under strong fluorescent light. Only specimens which have been dead in ethanol from six months to five years were used for color descriptions, with a few exceptions as noted.

Diagnosis. The diagnosis lists characters most useful in identifying a given species. These characters are listed in the approximate order of their diagnostic value. Since I often have not repeated characters in the diagnoses of all of several (or a pair of) closely related species, one should examine the diagnoses of all these possibilities when attempting a difficult identification. The absence of female characters with high diagnostic value in many species calls for extreme care when identifying females. It must also be kept in mind, when using a diagnosis based upon a small sample, that the known variation range is probably considerably less than that of the whole species population.

Illustrations. Illustrations were carefully constructed on translucent paper over a squared grid template with the aid of a squared grid reticle in the eyepiece of the stereomicroscope. Figures of female genitalia are always drawn from reproductively active females unless otherwise noted. The thin-walled ducts leading from the seminal receptacle bases to the bursa copulatrix roof are usually incompletely drawn; their openings into the bursa copulatrix are difficult to see under normal illumination.

Records. Unless otherwise noted, only specimens that I have examined are listed in the records section. States and counties (and Japanese prefectures) are given in alphabetical order. Within each county citation, all records from a given locality are separated from those of other localities by a dash. Collection dates are listed only for males. "(♂)" means that the specimen was collected as a penultimate instar on the date indicated and matured later in captivity. When no "♂" or "♀" follows a record, this means that only immatures were collected.

TAXONOMY

ANTRODIAETIDAE Gertsch, 1940

Brachybothriinae Simon, 1892, Histoire Naturelle des Araignées, 1(1): 193. Type genus *Brachybothrium* Simon, 1884 (=*Antrodiaetus* Ausserer, 1871).

Brachybothriidae Pocock, 1903, Proc. Zool. Soc. London, (1): 346.

Acattymidae Kishida, 1930, Lansania, 2(13): 34. Type genus *Acattyma* L. Koch, 1878 (=*Antrodiaetus* Ausserer, 1871).

Antrodiaetinae Gertsch, 1940, *in* Comstock (rev. ed.), The Spider Book, p. 236. Type genus *Antrodiaetus* Ausserer, 1871.

Antrodiaetidae Kaston, 1948, Connecticut Geol. Nat. Hist. Surv. Bull., (70): 48.

Note on family names. Although the name Brachybothriidae is older than either Acattymidae or Antrodiaetidae, Antrodiaetidae has clearly won general acceptance. Antrodiaetidae (and -inae) has been used more frequently (in approximately 17 publications) than either Brachybothriidae (and -inae) (in approximately 14 publications) or Acattymidae (in approximately 7 publications). Antrodiaetidae is the only name used since 1957 (in approximately 14 publications). It is the only name used in works presently reaching a relatively large audience of both professionals and amateurs (Comstock, 1940; Kaston, 1948; Kaston and Kaston, 1953; Yaginuma, 1960; Kaestner, 1968; Levi and Levi, 1968), with the exception of Gertsch's (1949) use of Acattymidae. In accordance with Article 40 of the recent (1961) International Code of Zoological Nomenclature, both the present general acceptance of the name Antrodiaetidae and the replacement before 1961 of the two older names by Antrodiaetidae because of the synonymy of their type genera with the senior synonym *Antrodiaetus* (Kaston, 1948; Yaginuma, 1962) clearly justify rejection of the older names and adoption of Antrodiaetidae.

Characteristics. Carapace: Pars cephalica elevated above pars thoracica. Eyes grouped on a median prominence. ALE's largest; form a slightly procurved transverse row with AME's. PLE's form lateral limits of eye group. PME's widely separated; close to respective PLE's. *Sternum:* Four pairs of sigilla; anterior pair large, just behind labium and sometimes indistinct; posterior pair larger than second or third pairs. Labium well defined but fused to sternum; inclined from plane of sternum. *Chelicerae:* Female chelicerae very robust; strongly gibbous dorsally. Rastellum well developed on females. One row of macroteeth on prolateral side of closed fang; sometimes a macrotooth row also on retrolateral side of closed fang. Microteeth on retrolateral side of prolateral macrotooth row. *Pedipalps:* Coxal endite very small. Female tarsus with 2 rows of macrosetae (on prolateral and retrolateral aspects of ventral surface). Male tibia swollen. Palpus with well defined o.c.s., i.c.s., and embolus. I.c.s. at least partly envelops embolus distally. *Legs:* Female legs relatively stout and with many macrosetae. *Abdomen:* Males with 1 to 4 segmentally arranged (sometimes fused) sclerotized patches dorsally; second patch most heavily sclerotized, tergitelike, and always present. Females possess only this second tergite; rarely other patches also. Epiandrous gland spigots clustered just anterior to male genital opening. AL spinnerets 2-segmented and functional; reduced and unsegmented; or absent. PM's unsegmented and functional. PL's 3-segmented and functional; distal segment length not over 1½ that of middle segment. *Female genitalia:* Genital opening broad slit shared by uterus exit; not markedly sclerotized externally. Four seminal receptacles with stalk and apical enlarged portion open into chamber (bursa copulatrix) just inside genital opening.

Diagnosis. Males of this family can be separated from those of the Mecicobothriidae and Atypidae by the possession of a strongly sclerotized i.c.s. which is distinct from the o.c.s.; or, if the i.c.s. is not strongly sclerotized, then by the possession of either only two pairs of spinnerets or a pedipalpal patella almost as long as the tibia. Antrodiaetid females can be distinguished from both mecicobothriid and atypid females by the presence of a rastellum, from the former group by the strongly elevated pars cephalica and a proportionately much shorter distal PL spinneret segment, and from atypids by the two rows of pedipalpal tarsus macrosetae.

Provisional inclusion of Aliatypus. As is emphasized in the discussion of phylogeny, *Antrodiaetus* and *Atypoides* form a monophyletic group distinct from *Aliatypus.* A number of character states which these two distinct groups share could be the result of convergence or at least parallel evolution rather than indicators of recent common ancestry. In heavily weighted genitalia characters, *Aliatypus* strongly resembles the family Mecicobothriidae; it is possible that *Aliatypus* is more closely related to this family than to *Antrodiaetus* and *Atypoides.* Perhaps *Aliatypus* will prove sufficiently distinct phylogenetically and ecologically to merit consideration as a separate family. (The resulting four small relict atypoid taxa [Liphistiidae not included] might for convenience's sake be reduced to subfamilies under a single family name.) Only after close study of *Aliatypus* and the mecicobothriids can the approximate phylogenetic position and proper classification of *Aliatypus* be resolved. I shall provisionally retain *Aliatypus* within the family Antrodiaetidae.

KEY TO GENERA OF ANTRODIAETIDAE

1a. Thoracic groove longitudinal. AL spinnerets absent (Fig. 318) or unsegmented with at most one spigot apically. No cheliceral macroteeth on retrolateral side of closed fang (Fig. 158). Female IVMT = 5–21. Male pedipalpal patella much shorter than tibia (Figs. 173–187). Burrow entrance a collar or turret (Figs. 12, 26, 32) 2

1b. Thoracic groove an irregular deep pit, a shallow rounded depression, or absent. AL spinnerets 2-segmented (may be indistinctly segmented) with at least several spigots clustered apically (Fig. 328). Female with small row of cheliceral macroteeth on retrolateral side of closed fang (Fig. 322). Female IVMT = 1–4 (rarely more than 1). Male pedipalpal patella nearly as long as tibia (Fig. 324). Burrow entrance a trapdoor (Fig. 39) .... *Aliatypus*

2a. 2 pairs of spinnerets (AL's absent) (Fig. 318). Male without cheliceral apophysis. (Do not mistake anterior-dorsal prominence for apophysis.) (Figs. 145–157) .... *Antrodiaetus*

2b. 3 pairs of spinnerets (AL's present; may be extremely reduced in some specimens of *A. gertschi.*). Adult male with cheliceral apophysis .... *Atypoides*

Antrodiaetus Ausserer, 1871

Antrodiaetus Ausserer, 1871, Verh. zool.-bot. Ges. Wien, 21: 136. Type species by monotypy *Mygale unicolor* Hentz (See *Antrodiaetus unicolor* description for discussion of identity of this species.). –Bonnet, 1955, Bibliographia Araneorum, 2: 335.

Acattyma L. Koch, 1877, Verh. zool.-bot. Ges. Wien, 27: 760. Type species by monotypy *Acattyma roretzi* L. Koch. –Bonnet, 1955, Bibliographia Araneorum, 2: 141.

Brachybothrium Simon, 1884, Bull. Soc. Zool. France, 9: 314. Type species by subsequent designation (Simon, 1892) *Brachybothrium pacificum* Simon. –Bonnet, 1955, Bibliographia Araneorum, 2: 906.

Nidivalvata Atkinson, 1886, Ent. Amer., 2: 129. Type species here designated *Nidivalvata marxii* Atkinson.
Anthrodiaetus: Simon, 1890, Actes Soc. Linn. Bordeaux, 44: 312.

Notes on synonymies. Simon (1890) first synonymized *Nidivalvata* and *Brachybothrium.* Although he later (1892) suggested that *Antrodiaetus* and *Brachybothrium* might be synonymous, such a synonymy was not designated until 1930 by Kishida and later by Gertsch and Jellison (1939) before receiving general acceptance. Both Pocock (1903) and Simon (1903) first suggested that *Acattyma* and *Brachybothrium* might be synonymous, but this synonymy was not proposed until 1960 by Yaginuma (see also Yaginuma, 1957). As I stress in the discussion of antrodiaetid phylogeny, *Antrodiaetus roretzi* (type species of Koch's monotypic genus *Acattyma*) is an evolutionary relict distinct from, but clearly related to, other species of *Antrodiaetus* and *Atypoides.* Its distinctness may justify re-establishment of the monotypic genus, but until it is more thoroughly studied, I believe it advantageous to retain it within *Antrodiaetus.*

Descriptive diagnosis. Carapace: Thoracic groove longitudinal. *Sternum*: Labium slightly to moderately inclined from plane of sternum. *Chelicerae*: Female with single row of 8 to 17 macroteeth along prolateral side of closed fang; microteeth along posterior portion of and retrolateral to this macrotooth row. Larger microteeth predominantly in retrolateral portion of microtooth group. Male with anterior dorsal prominence of varying size. *Pedipalps:* Male patella much shorter than tibia; tibia swollen, elongate to short and thick. O.c.s. of palpus tapers distally or very wide (*A. roretzi*). I.c.s. clearly separate from o.c.s. distally. *Legs:* 5 to 21 trichobothria dorsally on female metatarsus IV. Zero to 6 teeth on each of prolateral and retrolateral claws of female tarsus IV. Male tibia I with prolateral group of macrosetae or enlarged setae; metatarsus I without macrosetae or with one to few macrosetae distal of midpoint. *Spinnerets:* Only 2 pairs (PM, PL); both functional. *Genitalia:* Seminal receptacle stalks not sinuous; stalk and bowl markedly more sclerotized than bulb. *Behavior:* Burrow entrance a collapsible collar.

Misplaced species. Accatima cunicularia Simon, *Accatima davidi* Simon, and *Acattyma cryptica* Simon, all Ctenizidae, were incorrectly placed in the genus *Acattyma* L. Koch (Simon, 1886, 1892, 1897). Pocock (1901) recognized this error and listed diagnostic features of *Acattyma* L. Koch after describing a new ctenizid genus, *Latouchia,* which he felt was equivalent to *Acattyma* Simon. Simon (1903) later acknowledged his error and placed the three species in *Latouchia.* Crome (1955) describes and illustrates the abdominal anatomy of an "*Acattyma* spec.," but the very short 2-segmented PL spinnerets show that this is not an antrodiaetid.

Species groups and key. Antrodiaetus consists of three monophyletic species groups: the *unicolor* group (9 species), the *lincolnianus* group (3 species), and the *roretzi* group (1 species). The following key first separates the species groups and then the species of each group. The males of each of these taxa are morphologically more distinct than the females and can be much more quickly and confidently identified. *A. occultus* females are unknown but will likely key out to *A. pacificus.*

KEY TO SPECIES OF *ANTRODIAETUS*

Males

1a. O.c.s. of palpus very broad distally (Fig. 233). Prominent tibia I prolateral macrosetae group centered just proximal of midpoint; these macrosetae erect and quite elongate (Fig. 268). Japan (island of Honshu) .... (*roretzi* group) *roretzi*
1b. O.c.s. much narrower distally (Figs. 188–232). Tibia I prolateral macrosetae group, if prominent, centered at or distal of midpoint (Figs. 234–267). N. America or Japan (island of Hokkaido) 2
2a. Relatively inconspicuous group of enlarged setae on prolateral surface of tibia I (Figs. 262–267). Pedipalpal tibia rel-

atively slender (PTT/PTL = 0.23–0.34); greatest diameter in lateral view distal of midpoint (Figs. 184–186) .... (*lincolnianus* group) 3

2b. Prominent tibia I prolateral macrosetae group (Figs. 234–261). Pedipalpal tibia more swollen (PTT/PTL = 0.33–0.54); greatest diameter in lateral view proximal of midpoint (Figs. 173–183) .... (*unicolor* group) 5

3a. Tips of i.c.s. and o.c.s. of palpus about even and very weakly sclerotized; sperm reservoir looped loosely (Figs. 224, 225). Pedipalpal tibia very elongate (PTT/PTL =0.23–0.25) (Fig. 184). AME very small (AMD/AMS = 0.27–0.37) (Fig. 127). Abdomen dark. Central U. S. (Nebraska, Kansas) .... *lincolnianus*

3b. Tip of i.c.s. extends well beyond o.c.s. tip; both well sclerotized; sperm reservoir looped tightly (Figs. 226–232). Pedipalpal tibia not as elongate (PTT/PTL = 0.29–0.34) (Figs. 185, 186). AME not as small (AMD/AMS = 0.36–0.78) (Fig. 128). Abdomen paler yellow-gray. Central or southwestern U. S. 4

4a. O.c.s. tip thin, spatulate, bent away from i.c.s. (Figs. 226–228). IFL/ITarL =2.12–2.29. Central U. S. (Arkansas, Missouri) .... *stygius*

4b. O.c.s. tip moderately thickened and erect (Figs. 229–232). IFL/ITarL = 2.29–2.54. Southwestern U. S. (Arizona, New Mexico) .... *apacheeus*

5a. Eastern U. S. (east of Great Plains) 6

5b. Western N. America (Rocky Mtns. or westward) or Japan 7

6a. More than 20 per cent of macrosetae in tibia I prolateral macrosetae group are ensiform (Figs. 234–240). Metatarsus I macroseta B almost never present. Distalmost macroseta on retrolateral aspect of ventral surface of tibia I almost always less than 3/4 of distance from proximal to distal end (Figs. 234–240) .... *unicolor*

6b. Less than 20 per cent of macrosetae in tibia I prolateral macrosetae group are ensiform (Fig. 241). Metatarsus I macroseta B usually present (Fig. 243). Distalmost macroseta on retrolateral aspect of ventral surface of tibia I 3/4 or more of distance from proximal to distal end (Fig. 241) .... *robustus*

7a. Less than 30 per cent of macrosetae in tibia I prolateral macrosetae group are ensiform (Figs. 244–247). ITL/IML= 0.65–0.81. O.c.s. tip closely appressed to i.c.s. (Figs. 197–203) .... *pacificus*

7b. More than 30 per cent of macrosetae in tibia I prolateral macrosetae group are ensiform (Figs. 248–263). ITL/IML = 0.81–0.99. O.c.s. tip may or may not be closely appressed to i.c.s. (Figs. 204–225) 8

8a. Metatarsus I with strong retrolaterally and ventrally produced "elbow" just proximal of midpoint, *and* macrosetae group on distal half of ventral aspect of retrolateral surface of tibia I (Figs. 256, 257) .... *hageni*

8b. Metatarsus I lacking such a protuberance (Figs. 258–261); *or* protuberance keellike and macrosetae group on retrolateral aspect of ventral surface of tibia I proximal of distal 1/3 of segment (Figs. 250–252, 101) 9

9a. Tibia I and metatarsus I shapes and macrosetation similar to Figs. 258, 259. ITL/ITarL = 1.64–1.66. AME small (AMD/CL = 0.016–0.018) (Fig. 126). Side of i.c.s. against o.c.s. translucent (Fig. 220) .... *cerberus*

9b. Tibia I and metatarsus I not as above. ITL/ITarL = 1.31–1.64. AME larger (AMD/CL = 0.020–0.033). I.c.s. not partly translucent (Fig. 213) 10

10a. ITL/IML greater than 0.93. Tibia and metatarsus I shapes and macrosetation similar to Figs. 260, 261. Japan (island of Hokkaido) .... *yesoensis*

10b. ITL/IML less than 0.93. Tibia I and metatarsus I not as above. Western N. America 11

11a. Tibia I and metatarsus I with ventral swellings of varying prominence (Figs. 250–252, 101); small group of large macrosetae positioned on tibia I ventral swelling. Metatarsal macroseta A always present .... *pugnax*

11b. Tibia I and metatarsus I shapes and macrosetation not as above 12

12a. Pedipalpal tibia strongly swollen (PTT/PTL = 0.44–0.49) (Fig. 178). ITL/CL = 0.57–0.63. Tibia I and metatarsus I shapes and macrosetation similar to Figs. 248, 249. Large setaless area on upper ectal cheliceral surface .... *occultus*

12b. Pedipalpal tibia not as swollen (PTT/PTL = 0.35–0.41) (Fig. 180). ITL/CL = 0.66–0.77. Tibia I and metatarsus I shapes and macrosetation similar to Figs. 253–255. Setae distributed over entire upper ectal cheliceral surface (Fig. 150) .... *montanus*

Females

1a. Bursa copulatrix distinctly divided into 2 lateral pouches by a median partition (Figs. 310–312). Seminal receptacles closely paired, stalks long and slender, bowls weakly developed. Setae absent (or very rare) on labium except for anterior and lateral edges. Japan (island of Honshu) .... (*roretzi* group) *roretzi*

1b. Bursa copulatrix without median partition. Seminal receptacles not or only weakly paired, *or* stalks short to moderately long, *or* bowls moderately to strongly developed (Figs. 270–309). (Some eastern *A. pacificus* individuals are exceptions.) Setae scattered over much of labium. N. America or Japan (island of Hokkaido) 2

2a. From southwestern U. S. (Arizona, New Mexico) or central U. S. (Arkansas, Missouri, Kansas, Nebraska). If from central U. S. then AMD = 0.09–0.13 mm (Figs. 135, 136). IVCTR usually 0 to 2, cheliceral microteeth proportionately large (Figs. 166, 167) ... (*lincolnianus* group) 3

2b. Elsewhere or if from central U. S. (*A. unicolor*) then AMD = 0.11–0.22 mm (Fig. 130), IVCTR usually 3 or more, cheliceral microteeth proportionately smaller (Fig. 158) .... (*unicolor* group) 5

3a. Stalk and bowl portion of seminal receptacles weakly sclerotized and small, border with bulb poorly defined (Figs. 304, 305). Abdomen rather dark yellow-gray or medium brown. CMT/IVMT greater than 2.50. Central U. S. (Nebraska, Kansas) .... *lincolnianus*

3b. Stalk and bowl portion well sclerotized and slightly larger, border with bulb well defined (Figs. 306–309). Abdomen lighter. CMT/IVMT = 1.00–2.25. Southwestern or central U. S. 4

4a. IVML/IML = 1.36–1.38. IFL/IVFL = 1.04–1.05. Carapace narrower (CW/CL = 0.76–0.77) (Fig. 118). Central U. S. (Arkansas, Missouri) .... *stygius*

4b. IVML/IML = 1.21–1.26. IFL/IVFL = 1.09–1.13. Carapace broader (CW/CL = 0.78–0.82). Southwestern U. S. (Arizona, New Mexico) .... *apacheens*

5a. Japan (island of Hokkaido) .... *yesoensis*

5b. North America 6

6a. Eastern U. S. (east of Great Plains) 7

6b. Western N. America (Rocky Mtns. and westward) 8

7a. Combined presence of minute AL spinneret vestiges (Fig. 317), rather short densely distributed dorsal abdominal background setae (Fig. 316), *and* thin elongate setae dorsally just posterior of pedicel (Fig. 314). Seminal receptacle stalks not expanded basally (Figs. 280–283). SL/SW = 1.08–1.16 .... *robustus*

7b. Lacking one or more of first 3 character states above; usually no AL spinneret vestiges, usually longer more sparsely distributed dorsal abdominal background setae (Fig. 315), usually shorter thicker setae dorsally just posterior of pedicel (Fig. 313). Seminal receptacle stalks usually expanded basally (Figs. 270–279). SL/SW = 1.13–1.27 .... *unicolor*

8a. Setae distributed over entire upper ectal surface of chelicera (Figs. 171, 172). Carapace pale to medium dark gray-yellow 9

8b. Small to large setaless area on upper ectal surface of chelicera (Fig. 170). Carapace usually darker 11

9a. CL over 6.2 mm, IFL/IML less than 1.69, posterior abdominal dorsum without darkly pigmented area, IVTL/CL = 0.40 or more, *and* seminal receptacles unpaired (Figs. 292–302) 10

9b. CL under 6.2 mm or IFL/IML = 1.69 or more *or* abdominal dorsum dark *or* IVTL/CL = 0.41 or less *or* seminal receptacles paired (Figs. 288–291) 11

10a. Seminal receptacle stalks not expanded basally (Figs. 299–300). SL/SW=1.20–1.37 (Fig. 141) .... *hageni*

10b. Seminal receptacle stalks expanded basally (Figs. 295–298). SL/SW = 1.06–1.19 (Fig. 140) .... *montanus*

11a. IVTL/IVTarL = 1.90 or more. IVML/IML = 1.42 or more .... *cerberus*

11b. IVTL/IVTarL less than 1.90. IVML/IML = 1.09–1.50 12

12a. ITarL usually more than 1.28 mm. IVML/IML = 1.09–1.38 .... *pacificus*

12b. ITarL usually less than 1.28 mm. IVML/IML = 1.31–1.50 .... *pugnax*

THE *UNICOLOR* GROUP

Descriptive diagnosis. Male: AMD usually proportionately medium to large; AME's narrowly to widely separated (AMD/AMS, AMD/CL; Table 13). Setae scattered over much of labium; setaless area just posterior of labium relatively small. Pedipalpal tibia moderately to strongly swollen (PTT/PTL, Table 13); greatest diameter in lateral view proximal of midpoint. O.c.s. of palpus heavily sclerotized; surface very rough (filelike); relatively narrow apically. Group of strong macrosetae on prolateral surface of tibia I centered at or distal of midpoint; macrosetae also scattered or clustered on retrolateral aspect of ventral surface of tibia I

(Table 12). *Female:* Carapace relatively narrow to moderately broad (CW/CL, Table 14). Labium setation as in male. Cheliceral microteeth proportionately small to large; few to many (CMT, Table 14). Tarsus IV claws (both prolateral and retrolateral) usually with 3 or more teeth (IVCTR, Table 14). Leg IV segments usually proportionately long (IVML/CL, Table 14). Bursa copulatrix lacks median partition. Seminal receptacles medium to large in proportion to body size, stalk generally of moderate length, bowl usually well developed, and receptacles usually not closely paired.

Antrodiaetus unicolor (Hentz)

Figures 113, 120, 130, 138, 145–146, 158, 173–174, 188–194, 234–240, 270–279, 313, 315, 318. Map 1.

Mygale unicolor Hentz, 1841, Proc. Boston Soc. Nat. Hist., 1: 42. Holotype female from Alabama; destroyed. –, 1842, Jour. Boston Soc. Nat. Hist., 4: 57, pl. 7, fig. 5.

Mygale gracilis Hentz, 1841, Proc. Boston Soc. Nat. Hist., 1: 42. Holotype male from Alabama; destroyed. NEW SYNONYMY. –, 1842, Jour. Boston Soc. Nat. Hist., 4: 56, pl. 7, fig. 4.

Antrodiaetus unicolor: Ausserer, 1871, Verh. zool.-bot. Ges. Wien, 21: 136. –Roewer, 1942, Katalog der Araneae, 1: 189. –Bonnet, 1955, Bibliographia Araneorum, 2: 335.

Closterochilus gracilis: Ausserer, 1871, Verh. zool.-bot. Ges. Wien, 21: 142. –Roewer, 1942, Katalog der Araneae, 1: 190.

Eurypelma bicolor: Marx, 1883, *in* Howard (ed.), Invertebrate Fauna of South Carolina, p. 24.

Eurypelma gracilis: Marx, 1883, *in* Howard (ed.), Invertebrate Fauna of South Carolina, p. 24.

Brachybothrium accentuatum Simon, 1884, Bull. Soc. Zool. France, 9: 315. Holotype an immature female from North Carolina; in the Muséum National d'Histoire Naturelle in Paris; examined. NEW SNYONYMY. –Roewer, 1942, Katalog der Araneae, 1: 189. –Bonnet, 1955, Bibliographia Araneorum, 2: 906.

Nidivalvata marxii Atkinson, 1886, Ent. Amer., 2: 130, 110, 111, 113, 116, 131, pl. 5, figs. 8–10, 13, 17, 18, 23. Holotype female (immature ?) from North Carolina, probably Chapel Hill; either in the U. S. National Museum or in the Cornell University collection (see comment below); "Type" from Cornell examined. NEW SYNONYMY.

Nidivalvata angustata Atkinson, 1886, Ent. Amer., 2: 130, 113, 117. Two female syntypes from North Carolina, probably Chapel Hill; in the U. S. National Museum and/or the Cornell University collection (see comment below); "Type" from Cornell examined. NEW SYNONYMY.

Brachybothrium marxi: Simon, 1890, Actes Soc. Linn. Bordeaux, 44: 310. –Roewer, 1942, Katalog der Araneae, 1: 190. –Bonnet, 1955, Bibliographia Araneorum, 2: 906.

Brachybothrium angustatum: Simon, 1890, Actes Soc. Linn. Bordeaux, 44: 310. –Roewer, 1942, Katalog der Araneae, 1: 190. –Bonnet, 1955, Bibliographia Araneorum, 2: 906.

Anthrodiaetus unicolor: Simon, 1890, Actes Soc. Linn. Bordeaux, 44: 312.

Brachybothrium pacificum: Barrows (not Simon, 1884), 1918, Ohio Jour. Sci., 18(8): 298. –Barrows, 1925, Ann. Ent. Soc. America, 18(4): 493, pl. 37, figs. 17–22.

Missulena gracilis: Petrunkevitch, 1939, Trans. Connecticut Acad. Arts Sci., 33: 213. –Bonnet, 1957, Bibliographia Araneorum, 2: 2939.

Antrodiaetus bicolor: Vogel, 1962, Ent. News, 73 (9): 246.

Comments on synonymy and descriptions. Hentz's (1841, 1842) poor descriptions have caused much uncertainty and some confusion concerning the placement of his two species (Ausserer, 1871; Marx, 1883; Simon, 1892; Petrunkevitch, 1911b and 1939). Unfortunately, no one redescribed Hentz's type specimens before their destruction. (Apparently the types were part of a pinned collection housed by the Boston Society of Natural History and destroyed by insects [H. W. Levi, personal communication].) Simon (1892) first indicated that *Mygale unicolor* might be similar to species of *Brachybothrium*, but not until Gertsch and Jellison's (1939) brief statement have authors generally acknowledged this similarity. Although Simon (1892) also indicated the similarity of *Mygale gracilis* to *Brachybothrium* species, no author has subsequently expressed this opinion.

Hentz describes or illustrates sufficient diagnostic characters to show that *Mygale gracilis* belongs to the taxon *Antrodiaetus* as presently defined. In addition to an antrodiaetid body form, eye arrangement, and pedipalp shape, a conductor is illustrated on the palpus, the spinnerets are long, and metatarsus I is sinuous. (Hentz presumably misinterpreted this curvature as a "notch.") Unfortunately the identity of *Mygale unicolor* is less certain. The eye arrangement is strange, no thoracic groove is illustrated, and spinneret form is not mentioned. The reduced endites and general body form are antrodiaetidlike. To avoid upsetting the generic and familial nomenclature, I have decided that—as the meager evidence in Hentz's descriptions indicates—these two names are synonymous, and as first reviser I select *Mygale unicolor* as the senior synonym.

Atkinson (1886) did not indicate the type deposition of the two species he described. Simon (1890), who was loaned the type of *Nidivalvata marxi*, reported that the Atkinson types were in the U. S. National Museum. However, a small adult female labeled "Type *Brachybothrium angustata*" and a probably immature female labeled "Type *Brachybothrium marxii*" are in the Cornell University collection presently housed in the AMNH. Unfortunately the USNM "types" are presently unavailable for study. The Cornell specimens do not match the carapace dimensions recorded by Atkinson for the specimens he described. Although unable to examine the syntypes of *Nidivalvata angustatum*, Simon (1890) stated that this was perhaps a synonym of *Brachybothrium accentuatum*. He examined the type of *N. marxi* and noted its great similarity to *B. accentuatum*. He described the pedipalpal tarsus as being swollen (an indication that the specimen may be a penultimate male), using this as the diagnostic character of *B. marxi* in a key to species.

Description. See Tables 12–14, which contain measurements, meristic data, and diagnostic ratios for a sample of the species.

Male. Carapace: Figure 120. Setae very sparse on pars thoracica, sometimes moderately dense along lateral border. *Chelicerae:* Figures 145, 146. Large setaless area on upper ectal surface. *Pedipalps:* Figures 173–174, 188–194, 81. Tibia moderately to strongly swollen in lateral view; greatest diameter in lateral view at approximately 1/3 of distance from proximal to distal end. Tip of o.c.s. of palpus usually blunt (occasionally rather pointed); closely appressed to i.c.s. I.c.s. tip well sclerotized; often slightly curved; usually tapered to relatively narrow point. *Leg I:* Figures 234–240. Group of macrosetae (33% to 100% are ensiform) centered at 1/2 to 2/3 of distance from proximal to distal end of tibia on prolateral surface. Fewer more scattered macrosetae (0% to 100% are ensiform) along retrolateral aspect of ventral surface of tibia; distalmost macroseta of this group positioned at 2/3 or less (rarely at 3/4) of distance from proximal to distal end. Zero to 8 macrosetae (0% to 100% are ensiform) scattered between these groups, mainly along prolateral aspect of ventral surface. Tibia nearly cylindrical except sometimes swollen at prolateral macrosetae group. One to 3 (rarely none) macrosetae ventrally at distal end of metatarsus; rarely a macroseta present at 2/3 of distance from proximal to distal end on prolateral surface. Metatarsus weakly to moderately sinuous in ventral view. *Abdomen:* 3 dorsal heavily sclerotized usually continuous patches. Posterior patch smaller than anterior 2; occasionally reduced to bilateral pair of sclerotized spots. *Coloration:* Carapace pale gray-yellow to brown. Sternum pale yellow to gray-yellow; pedipalpal coxae similar to or slightly darker than sternum; labium markedly darker than sternum. Patella, tibia, and metatarsus of leg I light gray-orange to dark red-brown, usually darker than carapace; femur dorsally slightly lighter than more distal segments, ventrally even lighter. Pedipalps and other legs dorsally similar to carapace, ventrally lighter. Abdomen pale yellow-gray to gray-brown or purple-gray; dorsal sclerotized patches slightly darker except sclerite of second patch usually similar to carapace.

Female. Carapace: Figure 130. Setae sparse to moderately dense on pars thoracica; densest along lateral border. *Sternum:* Figure 138. *Chelicerae:* Figure 158. Microteeth positioned beside last 9 to last 3 macroteeth; frequently extend beyond last macrotooth. Microteeth usually proportionately small to medium size. Large setaless area on upper ectal surface. *Abdomen:* Figures 313, 315. Dorsal background setae sparsely to moderately long. Convergent median dorsal setae just posterior to pedicel usually short and rather stout; occasionally long and slender. *Genitalia:* Figures 270–279. Seminal receptacles with well-sclerotized stalk and bowl; vary from moderately long and moderately thick to quite stout. Stalk usually expanded (sometimes slightly) at base. Bowl well developed; its border with bulb sharply defined. Floor of bursa copulatrix weakly sclerotized. *Coloration:* Carapace pale yellow to dark brown; pars cephalica usually darker than pars thoracica. Sternum similar to pars thoracica; labium much darker, often similar to chelicerae; pedipalpal coxae usually slightly lighter than labium. Chelicerae pale gray-yellow to dark red-brown, usually darker than pars cephalica. Pedipalps and legs dorsally similar to adjacent portion of carapace, ventrally lighter. Abdomen pale yellow-gray to dark brown, sometimes with faint chevron pattern dorsally behind tergite; tergite usually similar to pars thoracica.

Diagnosis. Males. The shapes and macrosetae distribution patterns of the tibia and metatarsus of leg I (Figs. 234–240; Table 12) are distinctive for this species and include the best diagnostic characters. *A. unicolor* has a proportionately long metatarsus I (Fig. 235), a proportionately short pedipalpal femur, and relatively large AME's (Fig. 120) so that ITL/IML, PFL/CL, and AMD/CL (Table 13) are sometimes useful in distinguishing this species from other *unicolor* group species. *Females.* Characters useful in separating *A. unicolor* females from those of the sympatric *A. robustus* are listed in the *A. robustus* diagnosis. If *A. unicolor* were not geographically separated from the other *unicolor* group species, identification of females would be difficult or impossible. Because of a proportionately short femur I and a fairly small mean CMT number, *A. unicolor* females differ most from *A. pacificus* and *A. cerberus* females in IFL/CL and some other IFL ratios (Table 14) and from *A. pacificus* and *A. montanus* in CMT number (Table 14).

Variation. Males. Although most characters studied exhibit large variation, only a small number of these vary discontinuously. Strong geographic variation occurs with the following ratios (listed in order of degree of discontinuous variation): PTT/PTL (Fig. 81), IML/ITarL (Fig. 83), IML/CL (Fig. 82), ETL/CL (Fig. 84), PFL/CL, ALD/CL, and ITL/IML. In these, all samples (*B*, *C*, *E*, *F*, *G*, *I*, *P*, *Q*) (Fig. 85) except two (*A*, *N*) are connected to others by broadly overlapping variation ranges. Sample *A*, clearly the most divergent sample, is particularly divergent in ratios IML/CL (Fig. 82), ETL/CL (Figs. 84, 188–194), PFL/CL, and PTT/PTL. Sample *N* is also divergent, especially in PTT/PTL (Figs. 81, 174), IML/ITarL (Fig. 83), and IFL ITarL. Sample *A* is much more similar to *N* in most characters with strong geographic variation than to other samples, whereas *N* is usually only slightly more similar to *A* than to other samples. Individuals of both samples usually have a more swollen pedipalpal tibia and a proportionately shorter metatarsus I and pedipalpal femur than other males. Sample *A* individuals have a particularly small ETL. Sample *N* males have a proportionately long tarsus I.

ITL, IML, PTL, and PFL have the least continuous geographic variation of any measurements, but other measurements correlated with body size show similar patterns of weaker geographic variation in which the small-bodied sample *A* is somewhat divergent and the slightly larger-bodied males from *N* are less divergent from the rest of the samples (Figs. 81, 82). Among meristic characters the strongest geographic variation occurs in the number of prolateral tibia I ensiform macrosetae (Figs. 87, 234–240). Sample *N*, with few such macrosetae, is divergent, but its variation overlaps that of other samples. Sample *Q* and several males at *E* possess a distinctly higher number of ensiform macrosetae on the prolateral aspect of the ventral surface of tibia I (Fig. 240) than do most other *A. unicolor* males. Male carapace color varies in a geographic pattern similar to that in the females (see below), but the variation is continuous.

The single male from *O* is particularly divergent in two characters; the pedipalpal tibia is strongly swollen like that of males at *A* and *N* (Fig. 81), and metatarsal I macrosetae are absent (Table 12). The single male from *L* is extremely small (Fig. 82) but in all ratios and other nonmeasurement characters closely resembles most males (except those from *A* and *N*).

Noteworthy continuous variation occurs in several characters. The o.c.s. tip, usually blunt and rounded (Figs. 189, 191), is rarely almost pointed (Fig. 194). Extremely wide variation occurs in EGS number (Fig. 86), which is correlated with body size. The relative size and shape of the anterior-dorsal cheliceral prominence varies considerably. Figure 146 illustrates an exceptionally small prominence, Figure 145 a slightly larger than normal prominance. The metatarsus I macrosetae pattern also varies widely (Figs. 234, 236; Table 12).

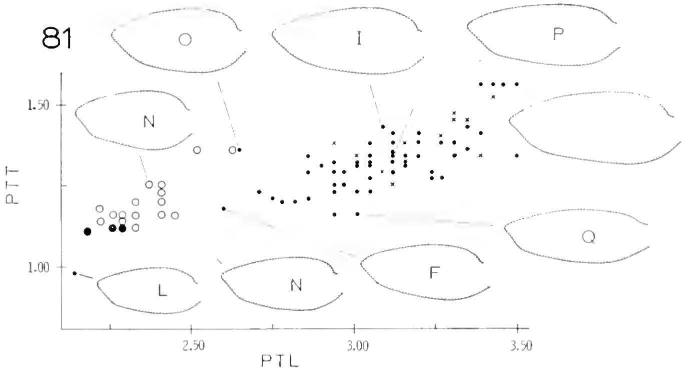
Females. Strong geographic variation occurs in five ratio characters (listed in order of approximate degree of discontinuity): IFL/IVFL (Fig. 88), IVML/CL, IVTL/CL (Fig. 93), ALS/CL, and IVML/IML (Fig. 89). Samples *I* and *D* are each divergent from many other samples in some of these characters. No measurements or meristic characters exhibit strong geographic variation.

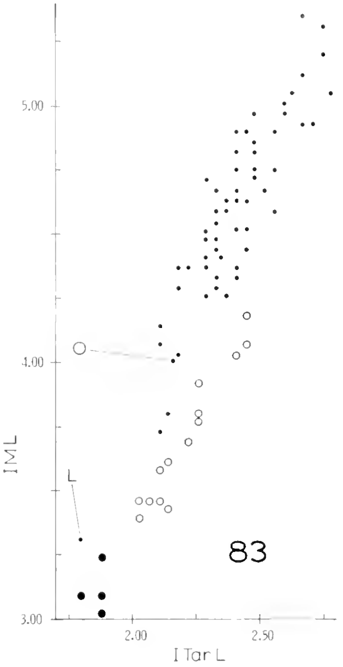
Unlike the males, in which each population sample is homogeneous, some female samples show discontinuous variation within. One of the strongest and, to the casual observer, most obvious instances of discontinuous variation in this species is in coloration, particularly female carapace coloration (Fig. 92). Most samples are homogeneously either light or dark with little overlap between these light and dark samples. In a few localities (*I, K, L*), however, distinct light and dark individuals were found living sympatrically. Although light populations appear to be more common in the south and west part of the species range, dark females have been collected in the western parts of Tennessee and Kentucky and in Arkansas.

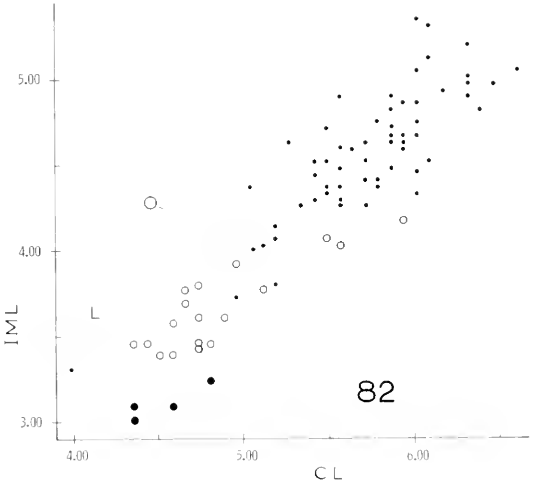
An extensive search was made for characters (other than color) which might also distinguish dark and light samples. Several ratio characters separated light and dark specimens in each of samples *I, K,* and *L*, but only SW/SL exhibits such nearly discontinuous variation in all three samples.

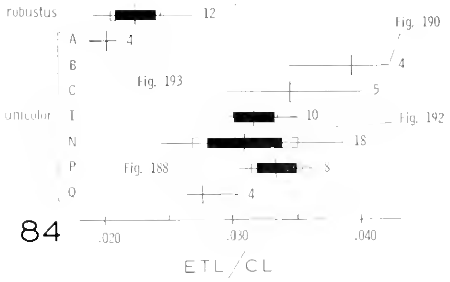
→

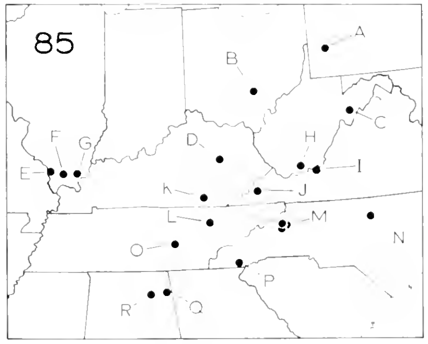
Figures 81–87. Geographic variation in *Antrodiaetus unicolor* males. (All measurements in mm. For scatter diagrams, large black dots represent sample A, circles sample N, and small black dots rest of species sample.) 81. Scatter diagram of PTT and PTL; representative specimens illustrated. (X's represent *Antrodiaetus robustus* males.) 82. Scatter diagram of IML and CL. 83. Scatter diagram of IML and ITarL. 84. Modified Dice-Leraas diagram of ETL/CL variation compared with that of *A. robustus*. (Horizontal line represents the observed range, vertical line the mean, open rectangle the standard deviation, solid black rectangle the 95 per cent confidence interval for the mean, number to right of range line the sample size, and letter in left column the sample locality.) 85. Map of population sample localities. 86. Histogram of EGS number compared with that of *A. robustus*. (One unit of vertical scale represents one specimen.) 87. Histogram of number of ensiform macrosetae on prolateral surface of tibia I. (One unit of vertical scale represents one tibia.) Right column contains percentage of ensiform macrosetae out of total number of macrosetae in this group.

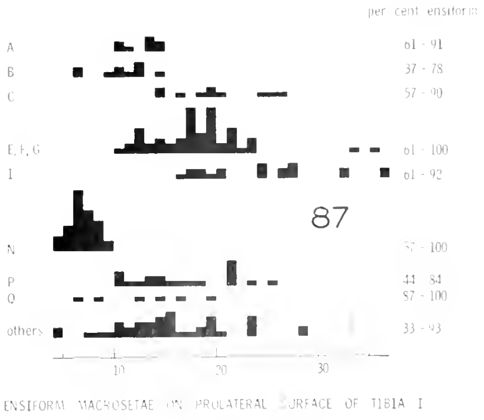

81
O
I
P
N
1.50
1.00
PTT
Q
L
N
F
2.50
3.00
3.50
PTL

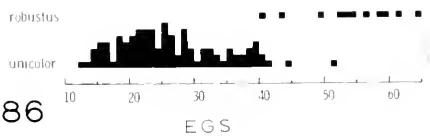

5.00
4.00
3.00
O
L
IML
83
2.00
2.50
I Tar L


5.00
4.00
3.00
IML
O
L
82
4.00
5.00
6.00
CL


robustus
12
A
4
B
4
C
5
Fig. 190
Fig. 193
unicolor
I
10
Fig. 192
N
18
P
Fig. 188
8
Q
4
84
.020
.030
.040
ETL/CL


85
A
B
C
D
F
G
E
H
I
J
K
L
M
N
O
P
Q
R


per cent ensiform
A
61 - 91
B
37 - 78
C
57 - 90
E, F, G
61 - 100
I
61 - 92
87
N
57 - 100
P
44 - 84
Q
57 - 100
others
33 - 93
10
20
30
ENSIFORM MACROSETAE ON PROLATERAL SURFACE OF TIBIA I


robustus
unicolor
86
10
20
30
40
50
60
EGS

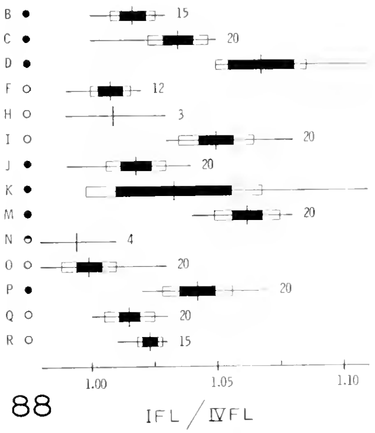
(In all subsequent population sample comparisons, dark individuals were excluded from sample *I* and light individuals from sample *K*.) Marked genetic heterogeneity within the light specimens is indicated by the divergence of sample *I*. This sample is clearly distinct from all other light samples in IVML/IML (Fig. 89), markedly different in a few other ratios (IVTL/CL, Fig. 93), and more similar in most characters to several of the dark samples. (Male sample *I*, which matches the light female *I* sample in color, is not divergent in any character studied.) Light samples *F*, *O*, *Q*, and *R* are quite similar to each other in almost all characters, and as a group differ most from the dark samples in ratios IFL/IVFL (Fig. 88) and IVML/IML (Fig. 89). However, at least one of these light samples exhibits considerable overlap with one or more dark sample in every character. Sample *O* is clearly the light sample most distinct from the dark samples. Sample *N*, which is intermediate in coloration (Fig. 92), more closely resembles dark samples in some characters and light samples in other characters and is not divergent in any character.

As with color, two setation characters revealed discontinuous intrapopulation variation. Three females from *K* differ distinctly from all other females in possessing extremely thick and short background setae on the posterior 1/3 of the abdomen. In addition, these three females have a distinctly lower IML/ItarL (Fig. 90), lower IVML/IVTarL, higher CMT/IVMT, longer thinner setae medially on the abdominal dorsum just behind the petiole, shorter denser abdominal background setae, and slightly more robust chelicerae than the other *K* females. Also the seminal receptacle stalk bases are not expanded (Fig. 277) as in the rest of sample *K* (Fig. 272). These three specimens even differ considerably from the rest of the species sample in IML/ITarL (Fig. 90), IVML/IVTarL, and the shape of the seminal receptacle stalks. The large variance of the whole of sample *K* in several characters (Figs. 88, 89) further illustrates its marked heterogeneity.

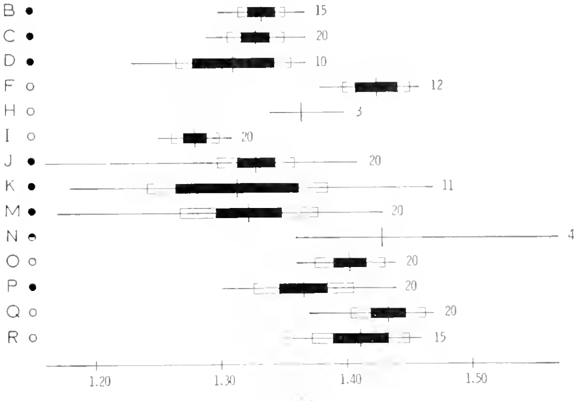
Females with very thick short setae on their sternum are found within several population samples (*M*, *P*, *L*, *D*) and as scattered individuals over a large part of the species' distribution range. Most other individuals possess only slender sternal setae; however, there are a few individuals intermediate in this character. Stout sternal setae are not found on light colored individuals. Comparisons of the stout sternal setae subsample to the slender setae subsample within each of samples *M* and *P*, and comparisons of the entirely stout setae sample *D* against each dark slender setae population sample were performed to discover if these sternal setae forms are distinct in other characters. Within each comparison at least a few ratios separated the two forms (Fig. 91), but few of these characters were common to all comparisons. Sample *D* is markedly divergent in several ratio characters from many other *A. unicolor* population samples (Figs. 88, 93). When all stout sternal setae individuals are compared to a large sample of dark colored slender sternal setae individuals, only IVFL/CL yields rather distinct separation (Fig. 91).

→

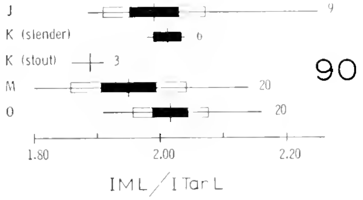
Figures 88–93. Geographic variation in *Antrodiaetus unicolor* females. (Dark colored samples identified by black dot, light samples by circle, and intermediate colored sample by half-blackened circle.) 88. Mod. Dice-Leraas diagram of IFL/IVFL variation. 89. Mod. Dice-Leraas diagram of IVML/IML variation. 90. Mod. Dice-Leraas diagram of IML/ITarL variation in sample with stout posterior abdominal background setae and samples with normal (slender) abdominal setae. 91. Mod. Dice-Leraas diagram of IVFL/CL variation in samples with stout sternal setae and samples with slender sternal setae. 92. Color variation. Frequency of pars cephalica color values given for each sample. (Key to color grid at lower right. Full explanation in Methods section.) 93. Mod. Dice-Leraas diagram of IVTL/CL variation.



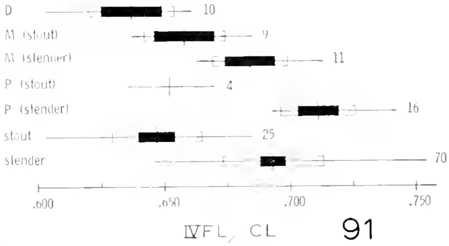
88



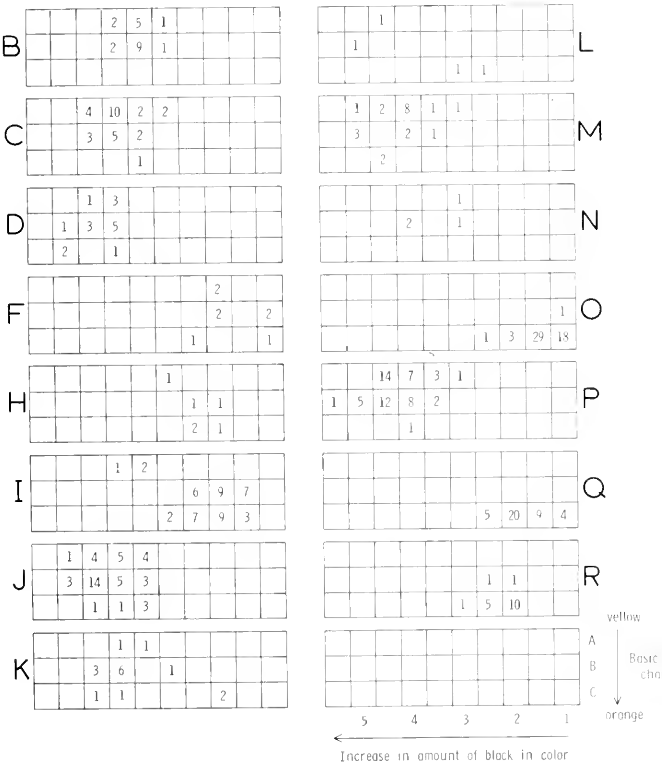
89



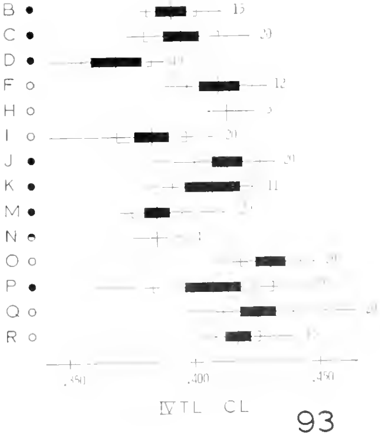
90



91



92



93

Noteworthy variation without a clear geographic pattern occurs in two other qualitative characters. While the great majority of females have short converging setae medially on the abdominal dorsum just behind the pedicel (Fig. 313), a few have here long slender setae (as in *A. robustus*, Fig. 314) or setae of intermediate length. Such aberrant individuals are scattered in several distantly separated dark population samples and are rare in light samples. No other characters vary concordantly with this one. Female genitalia are quite variable in this species, but the variation is continuous with a few exceptions. Figures 274 and 275 illustrate the wide variation apparently common even in a genetically relatively homogeneous population. Figures 270–279 illustrate much of the total variation found, and do not necessarily represent the modal structure for each population sample. Divergent seminal receptacle form was found only in the three *K* specimens with stout posterior abdominal background setae and in both dark specimens at *L*. In these, all seminal receptacles lacked expanded stalk bases (Fig. 277) and also resembled *A. robustus* receptacle form in some qualitative aspects.

Discussion. Variation in *A. unicolor* is somewhat complex and difficult to interpret. In addition to strong geographic variation patterns, there are also instances of different forms occurring sympatrically. It is conceivable that further studies may reveal convincing evidence that this series of populations consists of several reproductively isolated gene pools.

The two clearly divergent population samples (*A* and *N*) exposed in the analysis of variation of male characters are apparently genetically quite different from the other samples (and less different from each other) and each can be readily characterized by a combination of several characters. Both are clearly geographically peripheral populations presumably exchanging genes only at a relatively slow rate, with the sampled populations located in the region of greatest population density. A study of geographically intermediate populations is necessary to determine to approximately what degree (if any) gene exchange is occurring.

The possibility was examined that character divergence might be occurring between *A. unicolor* and *A. robustus* populations in the vicinity of *A* and that this might be partly responsible for the divergence of sample *A*. Sample *A* is markedly more different from the sympatric (Allegheny Co. and Westmoreland Co.) *A. robustus* males than are allopatric samples *B* and *C*—the pattern that could result from character divergence—in 10 ratios including PTT/PTL (Fig. 81), PFL/CL and OQW/CL. Several of the characters that best separate sample *A* from the other *A. unicolor* samples (IML/CL, ETL/CL [Fig. 84], IML/ITarL) either do not show this pattern or show the reverse pattern, and two other characters also show the reverse pattern. Thus, while some of sample *A's* uniqueness could be the result of character divergence, some cannot.

The significance of the color variation, discontinuous in the female samples, is difficult to determine. Considerable genetic heterogeneity exists within the total light sample and the entire dark sample. Upon removing the more divergent elements, the remaining light and dark samples are each still genetically rather heterogeneous and they differ, but are still not distinct in any character except color. It appears unlikely that the color forms are either geographic variants or ecophenotypes, since they are found together in the same general habitat in at least three localities. It is possible that these color forms are distinct species, but the absence of any other character which in many samples consistently matches the discontinuity in coloration argues against this. Perhaps the most feasible explanation is genetic polymorphism; if so, there would appear to be a surprisingly large number of populations in which fixation of one morph has occurred. Analysis of larger samples from localities where the forms are sympatric, close observation for microhabitat differences and local spatial separation of the forms, a study of color variation of adults reared from single broods, and a comparison of the physiological basis of coloration in the two forms are kinds of studies needed to solve this problem.

The specimens from *K* with stout posterior abdominal background setae are so distinct from the rest of the local sample that they may be reproductively isolated. The possibility of genetic polymorphism involving several characters or of ecological races cannot be ruled out presently. It is unlikely that age differences could produce discontinuity in so many characters in this sample and not in other samples. The divergence of sample *D* and the other specimens with very stout sternal setae from the rest of the dark specimens is assumed to represent simple intraspecific genetic variation because of the occurrence of a few intermediate individuals and because only one other character separates most of the individuals of these two forms. These divergent setation forms require further study along the lines suggested above. Particularly helpful would be collections of males from *K* and *D*.

Distribution. Centered in the central and southern Appalachian region of eastern United States with populations extending peripherally in all directions, as far west as the Ozark region and apparently south to near the Gulf Coast (Map 1).

Records. ALABAMA. *De Kalb Co.:* De Soto St. Pk. [*Q*], near Fort Payne, July–Aug. 1937, 2♂; Oct., ♂; Dec., ♂; 1800–1900 ft, 38♀. *Madison Co.:* Monte Sano St. Pk., Dec. 1940, ♂. *Marshall Co.:* Little Mtn. St. Pk. [*R*], 600–700 ft, 24♀. — 0.8 mi. N of Grant, ♀. ARKANSAS. *Stone Co.:* Blanchard Springs Rec. Area (USFS), 11 Sept. 1966, ♂, 2♀. GEORGIA. *Fulton Co.:* Atlanta, 14 Nov. 1945, ♂. *Murray Co.:* Fort Mtn. St. Pk., approx. 2400 ft, ♀. *Rabun Co.:* Rabun Bald, 15♀. *Towns Co.:* Brasstown Bald Mtn., 4700 ft, ♀. ILLINOIS. *Jackson Co.:* Little Grand Canyon, ♀. *Johnson Co.:* Ferne Clyffe St. Pk. [*F*], approx. 800 ft, 13–14 Sept. 1966 (♂), ♀; 1 Oct. 1967, 2♂; 12♀. *Pope Co.:* Lusk Creek [*G*], 28 Sept.–5 Oct., ♂; 5–12 Oct., 7♂; 12–19 Oct., ♂; 26 Oct.–2 Nov., ♂ (all in 1968). *Union Co.:* Pine Hills [*E*], 7–14 Oct., 11♂; 14–20 Oct., 2♂; 20–27 Oct., ♂; 27–30 Nov., ♂ (all in 1967). INDIANA. *Jefferson Co.:* Clifty Falls St. Pk., 2♀. KENTUCKY. *Edmonson Co.*: Mammoth Cave Natl. Pk., 600 ft, 2♀. *McCreary Co.:* Cumberland Falls St. Pk. [*K*], 5♀. *Powell Co.:* Natural Bridge St. Pk. [*D*], 12♀. *Whitley Co.:* Cumberland Falls St. Pk. [*K*], 7♀. MARYLAND. *Montgomery Co.:* Plummers Island, 24 Oct. 1909, ♂. NEW JERSEY. *Bergen Co.:* Closter, ♀. NEW YORK. *Bronx:* Bronx Park, 21 Oct. 1954, ♂. NORTH CAROLINA. *Avery Co.:* between Edgemont and Linville along Gragg Prong Cr. [*M*], 2300 ft, 5♀. *Burke Co.:* Linville Falls [*M*], 3100 ft, 15♀. *Caldwell Co.:* 5 mi. E of Mortimer [*M*], 1500 ft, 4♀. *Durham Co.:* Duke Forest [*N*], approx. 500 ft, 1 Oct., ♂; 22 Oct., ♂; 23 Oct., 2♂; 24 Oct., 11♂; 7 Nov., 2♂; 3 Jan., ♂ (all in 1963–64); 4♀. *Haywood Co.:* Mt. Pisgah, Frying Pan Gap, 13 Oct. 1926, ♂. *Jackson Co.:* 5 mi. E of Bryson City, 2 Oct. 1960, ♂. *Macon Co.:* Highlands [*P*], 1–3 Aug. 1966, 4300 ft, 8♂, 53♀; 24 July 1962, ♂. — Whitesides, Cove Church [*P*], 22 Aug. 1962, ♂. *Transylvania Co.:* Bear Wallow, 2♀. OHIO. *Adams Co.:* Long Lick Hollow, 2♀. *Hocking Co.:* Ash Cave St. Pk. [*B*], approx. 800 ft, 30 Sept. 1962, ♂; 22 Sept. 1966 (♂); 6 July 1966 (♂); 18♀. — Cantwell Cliffs St. Pk. [*B*], 6 July 1966 (♂), 6♀; ♂. PENNSYLVANIA. *Allegheny Co.:* Penn Hills [*A*], 12–13 Sept. 1963, 2♂; 26 Sept. 1963, ♂; 2♀. — Pittsburgh [*A*], Oct. 1960, ♂. SOUTH CAROLINA. *Oconee Co.:* Five Point Cave, 4 mi. N of Westminster, ♀. TENNESSEE. *Anderson Co.:* on rt. 116, 12–24 mi. W of Lake City [*L*], 30–31 Aug.

1966, ♂, 4♀. *Chester Co.:* Chickasaw St. Pk., 600–700 ft, ♀. *Cocke Co.:* Great Smoky Mtn. Natl. Pk., near Cosby Camp, 2200 ft, 5–14 Aug. 1966, 2♂. *Hamilton Co.:* Signal Mtn., ♀. *Lawrence Co.:* David Crockett St. Pk., 700–900 ft, 2♀. *Sevier Co.:* Great Smoky Mtn. Natl. Pk., Laural Creek, ♀. — Elkmont, ♀. — Clingmans Dome, 6000–6600 ft, 10–14 Aug. 1966, 2♂. — Greenbrier Cove, 7–8 mi. NE of Gatlinburg, 2 Oct. 1960, 2♂. *Sullivan Co.:* Bristol, 5 Oct. 1926, ♂. *Van Buren Co.:* Fall Creek Falls St. Pk. [*O*], 1500–1600 ft, 1 Sept. 1966, ♂, 48♀. VIRGINIA. *Dickenson Co.:* Breaks Interstate Pk., ♀. *Fairfax Co.:* on bank of Potomac R. opposite Plummers Island, Sept. 1918, ♂. *Giles Co.:* Mountain Lake [*I*], 3900 ft, 21 Aug. 1966, 9♂; 14 Aug. 1948, ♂; 45♀. *Montgomery Co.:* Radford, Oct. 1967, ♂. — Blacksburg, 23 Oct. 1961, ♂; 28 Oct. 1956, ♂. *Wise Co.:* few mi. S of Tacoma [*J*], approx. 2400 ft, 28♀. — Several mi. S of Tacoma, Osborne Rock [*J*], approx. 3600 ft, 20♀. WEST VIRGINIA. *Mercer Co.:* Brush Creek Falls, 3 Oct. 1966, ♂. — Athens [*H*], 2400 ft, 3♀. *Pendleton Co.:* Briggs Run near Smoke Hole [*C*], 1500 ft, 14–16 Aug. 1966, 5♂, 24♀. *Pocahontas Co.:* Cranberry Glades Nat. Area (USFS), ♀. *Raleigh Co.:* Grandview St. Pk., 23 Sept. 1967, ♂; 3♀. *Webster Co.:* 1 mi. S of Cleveland, ♀. *Wyoming Co.:* Mullins, ♂.

The following geographically important records of immature specimens, probably *A. unicolor*, are indicated on Map 1 with circles. ALABAMA. *Clark Co.:* 2 mi. N of Jackson. *Conecuh Co.:* W Fort Sapulga R. *Coosa Co.:* Hatchet Creek. LOUISIANA. *E. Feliciana Parish.* NORTH CAROLINA. *Yancey Co.:* Mt. Mitchell, 6600 ft. SOUTH CAROLINA. *Greenville Co.:* Paris Mtn. St. Pk. TENNESSEE. *Bedford Co.:* outside Reese Cave. *Madison Co.:* Bonwood. VIRGINIA. *Grayson Co.:* Mt. Rogers, 5000–5600 ft. *Page Co.:* Stony Man Mtn. *Pittsylvania Co.:* Smith Mtn. Gorge, N of Sandy Level.

Antrodiaetus robustus (Simon)

Figures 139, 159, 195–196, 241–243, 280–283, 314, 316–317. Map 1.

Brachybothrium robustum Simon, 1890, Actes Soc. Linn. Bordeaux, 44: 311. Male and female syntypes (one each). The female specimen, which I have examined, is here designated and labeled the lectotype and is in the U. S. National Museum. The male paralectotype may be in the U. S. National Museum or may be lost. (See comments below on the designated type localities.) –Roewer, 1942, Katalog der Araneae, 1: 190. –Bonnet (in part), 1955, Bibliographia Araneorum, 2: 907.

Brachybothrium shoemakeri Petrunkevitch, 1925, Ann. Ent. Soc. America, 18: 318, pl. 20, figs. 3, 5, 6, 11. Five male syntypes and an immature female syntype from "different localities near Washington, D. C., on the Virginia bank of the Potomac River"; 2 males examined. The male collected on the Virginia bank of the Potomac River a short distance above Georgetown (Washington, D. C.), 27 Sept. 1911, by C. R. Shoemaker, is here designated and labeled the lectotype and is in the Yale Peabody Museum. The one examined paralectotype male is in the American Museum of Natural History. (See comments below on these specimens.) NEW SYNONYMY. –Roewer, 1942, Katalog der Araneae, 1: 190. –Bonnet, 1955, Bibliographia Araneorum, 2: 907.

Antrodiaetus robustus: Gertsch and Mulaik, 1940, Bull. American Mus. Nat. Hist., 77: 311.

Antrodiaetus shoemakeri: Muma, 1944, American Mus. Novitates, (1257): 1; examined.

Antrodiaetus unicolor: Vogel, 1966, Jour. New York Ent. Soc., 74(1): 56; examined. –Vogel, 1968, Jour. New York Ent. Soc., 76(2): 101; examined.

Antrodiaetus accentuatum: Snetsinger and Whitmyre (in part), 1967, Science for the Farmer, 14(4): 5, 2 photos; examined. –Whitmyre and Snetsinger (in part), 1967, Melsheimer Ent. Series, No. 1, p. 1, figs. 1–7; examined.

Comments on the descriptions. The male paralectotype of *B. robustum* is not in the Muséum National d'Histoire Naturelle in Paris where all types of the other *Antrodiaetus* species described by Simon are deposited. Simon's (1890) description does not help to identify the male. The designated type locality for the female is almost certainly wrong. Simon listed together two localities, "Virginia, Occoquan Falls (G. Marx); Texas: Rio-Grande (G. Marx)," after the type descriptions and failed to indicate which specimen came from which locality. Since the locality on the label with the female is "Columbus, Texas," the male is presumably from the Virginia locality. Why Simon designated Rio Grande rather than Columbus is unclear. Gertsch and Mulaik (1940), who cited this record, assumed that Simon meant the town of Rio Grande City in Starr County, Texas, about 270 miles southwest of Columbus. Since these Texas localities are at least 1100 air miles southwest of the nearest known population of this species, since the habitats in this area are extremely different from the known northern habitat, and since George Marx (who accumulated and sent the specimens to Simon) often gave specimens wrong locality labels (H. Levi, personal communication), I shall assume that both the label with the female lectotype and the type locality designated by Simon are wrong. The real locality is most likely near Washington, D. C., which is in the known species range, is near the designated locality for the male specimen, and is near Marx's home.

Since Petrunkevitch (1925) did not designate a holotype for *B. shoemakeri*, I have designated as lectotype the specimen on whose label he wrote "Type." The only other paralectotype known to me is accompanied by a label with the word "cotype" in Petrunkevitch's handwriting. This paralectotype male is a misidentified *A. unicolor.*

Figures 1, 2, and 3 in Whitmyre and Snetsinger (1967) are definitely of *A. robustus.* The sternal sigilla, described and figured as being "lighter colored areas," are normally slightly darker than the surrounding cuticle as in all other antrodiaetids. The i.c.s. tip in Figures 6 and 7 is apparently broken off.

Description. See Tables 12–15, which contain measurements, meristic data, and diagnostic ratios for a sample of the species and for the lectotype.

Male. Carapace: Very few setae on pars thoracica except along lateral border. *Chelicerae:* Rather large setaless area on upper ectal surface. *Pedipalps:* Figures 195, 196. Tibia moderately swollen in lateral view; greatest diameter in lateral view at approximately 1/3 of distance from proximal to distal end. Tip of o.c.s. of palpus pointed; closely appressed to i.c.s. Tip of i.c.s. relatively wide; well sclerotized except for translucent area on side against o.c.s. *Leg I:* Figures 241–243. Group of attenuate (occasionally 1 is ensiform) macrosetae centered at 1/2 to 2/3 of distance from proximal to distal end of tibia on prolateral surface. Fewer, more scattered, attenuate (occasionally 1 is ensiform), frequently larger macrosetae along retrolateral aspect of ventral surface; distalmost macroseta of this group positioned at 3/4 or more of distance from proximal to distal end of tibia. One to 8 attenuate macrosetae scattered on ventral surface between these two groups. Tibia nearly cylindrical. One to 3 macrosetae (usually 2) ventrally at distal end of metatarsus. Metatarsus slightly sinuous in ventral view. *Abdomen:* 3 dorsal heavily sclerotized patches. First and second large and usually continuous; posterior patch smallest and usually reduced to transverse row of 2 or 4 small patches. Minute sclerotized scar or bump usually located anterior and ectal of each PM spinneret. *Coloration:* Carapace gray-yellow to brown; pars cephalica usually darker than pars thoracica. Sternum and pedipalpal coxae pale gray-yellow to pale gray-orange; labium darker gray-yellow to brown. Chelicerae similar to or slightly darker than pars cephalica. Patella, tibia, and metatarsus of leg I gray-orange to dark red-brown; femur slightly lighter dorsally and much lighter ventrally. Pedipalps and other legs dorsally similar to carapace, ventrally lighter. Abdomen yellow-gray to medium gray-brown; dorsal sclerotized patches darker except sclerite of second patch often similar to pars thoracica.

Female. Carapace: Setae sparse on pars thoracica, denser along lateral border. All pars thoracica setae very slender. *Sternum:* Figure 139. Relatively broad. *Chelicerae:* Figure 159. Microteeth positioned beside last 6 to last 4 macroteeth; usually extend beyond last macrotooth. Microteeth proportionately large. Large setaless area on upper ectal surface. *Abdomen:* Figures 314, 316, 317. Dorsal background setae densely distributed; moderately short and basally somewhat thickened. Convergent median dorsal setae just posterior to pedicel long and slender. Minute sclerotized scar or bump (probably a vestige of AL spinnerets) located anterior and ectal of each PM spinneret; usually a setaless area posterior of bump. *Genitalia:* Figures 280–283. Seminal receptacles with well-sclerotized stalk and bowl; vary from moderately long and moderately thick to quite stout. Stalk not expanded at base. Bowl well developed; its border with bulb sharply defined. Floor of bursa copulatrix moderately well sclerotized. *Coloration:* Carapace gray-orange to chestnut brown; pars cephalica usually darker than pars thoracica. Sternum similar to pars thoracica; labium and pedipalpal coxae slightly darker than pars cephalica. Chelicerae medium brown to dark red-brown; darker than pars cephalica. Pedipalps and legs dorsally similar to carapace, ventrally lighter. Abdomen light brown to medium brown; tergite similar to pars thoracica.

Diagnosis. Males. The shapes and macrosetae distribution patterns of the tibia and metatarsus of leg I (Figs. 241–243; Table 12) are distinctive for this species. The three important differences in these characters from the similar sympatric species *A. unicolor* are: 1) 8 per cent or fewer of the prolateral tibial macrosetae are ensiform. 2) The distalmost macroseta on the retrolateral aspect of the ventral surface of the tibia is 3/4 or more of the distance from the proximal to distal end (only rarely this near the distal end in *A. unicolor*). 3) Metatarsus I macroseta B is almost always present. The partly translucent i.c.s. tip (Fig. 195) helps identify *A. robustus.* Also the i.c.s. tip is usually wider and usually extends proportionately less beyond the o.c.s. tip (Fig. 195) than in *A. unicolor,* but *A. robustus* cannot be separated from the sympatric Pittsburgh, Pennsylvania, area *A. unicolor* population with these two characters (Fig. 84). High EGS number is also an aid in identifying *A. robustus* (Fig. 86). No other quantitative characters studied help separate these two species. The same measurements and ratios useful in separating *A. unicolor* from the other *unicolor* group species are likewise useful in distinguishing *A. robustus* from these species. The presence of vestiges of AL spinnerets may be diagnostically useful, but a few *A. robustus* males appear to lack these and occasionally *A. unicolor* males have these vestiges.

Females. The combined presence of AL spinneret vestiges (Fig. 317), rather short densely distributed dorsal abdominal background setae (Fig. 316), and thin elongate setae medially and dorsally just posterior of the pedicel (Fig. 314), distinguish this species from other *unicolor* group species. The seminal receptacle stalks are not expanded basally (Figs. 280–283) as is common in *A. unicolor* and some other species. The sternum is proportionately wide, so that SL/SW (Fig. 139; Table 14) helps separate this species from *A. unicolor* and several others. Also metatarsi I and IV and tibia I are proportionately shorter than in *A. unicolor* and some other *unicolor* group species. Therefore IFL/IML, IML/CL, and IVML/CL are diagnostically useful (Table 14). *A. robustus* females usually have larger cheliceral microteeth than do *A. unicolor* females (Fig. 159).

Variation. Only moderate variation occurs in most characters studied for both sexes of *A. robustus. Males.* All specimens have an ETL/CL of .023 or less except one male (from Whitehall, Pennsylvania), which has an ETL/CL of .027 (Fig. 84). There is wide variation in the total number of macrosetae on the prolateral surface of tibia I, but the proportion of these which are ensiform varies only slightly (Table 12). *Females.* Relatively wide but continuous variation occurs in the thickness of the seminal receptacle stalk relative to bowl diameter (Figs. 280–283). The shape of the bursa copulatrix floor also varies considerably.

Discussion. *A. robustus* is extremely similar to *A. unicolor* in nearly all characters studied; these constitute the most morphologically similar pair of *Antrodiaetus* species and perhaps deserve to be called sibling species. Were these two populations allopatric, I probably would conclude that they are conspecific. That they are sympatric (intimately so in at least the Pittsburgh, Pennsylvania, and Washington, D. C., areas) and appear to remain distinct in the several diagnostic characters is strong evidence that they are reproductively isolated populations. However, the possibility that *A. robustus* is a northern genetic variant form of *A. unicolor* cannot be confidently ruled out without more data, chiefly from studies of variation on larger samples of both species from additional localities in the area of sympatry.

In this context, the following instance of variation within an otherwise homogeneous population sample of *A. unicolor* is noteworthy. One aberrant male in a Lusk Creek (Pope Co.), Illinois, sample with nine other *A. unicolor* males has an i.c.s. tip width, an ETL/CL value, a distalmost ventral-retrolateral tibia I macroseta position, A and B metatarsal macrosetae, and a pointed o.c.s. tip all as in *A. robustus*. The part of the i.c.s. tip against the o.c.s is very slightly translucent and therefore intermediate. However, over 50 per cent of its prolateral tibia I macrosetae are ensiform, and 50 per cent of its ventral-retrolateral tibia I macrosetae are ensiform, both diagnostic *A. unicolor* character states.

Distribution. Pennsylvania, Maryland, northern Virginias, and eastern Ohio (Map 1).

Records. MARYLAND. *Allegheny Co.:* Hagerstown, ♀. *Montgomery Co.:* Chevy Chase, ♀. *Prince Georges Co.:* College Park, 15 Oct. 1942, ♂. OHIO. *Stark Co.:* Canton, 28 Sept. 1941, ♂, ♀. PENNSYLVANIA. *Adams Co.:* Caledonia St. Pk., 5♀. *Allegheny Co.:* Whitehall, Sept. 1966, ♂. — Penn Hills, 3♀. — Baldwin, ♀. — Verona, ♀. — Mt. Troy, ♀. *Westmoreland Co.*: Powdermill Nature Reserve, 3 mi. S of Rector, 6 Sept. 1962, ♂; 11 Oct. 1962, ♂; 19 Oct. 1966, 4♂; 19 Oct.–13 Nov. 1966, ♂. — 2 mi. NE of Ligonier, 12 Sept. 1963, ♂. VIRGINIA. *Fairfax Co.:* on bank of Potomac R. a short distance above Georgetown (Washington, D. C.), 27 Sept. 1911, ♂. *St. Marys Co.:* Tall Timbers, 24 Oct. 1927, ♂. WEST VIRGINIA. *Ohio Co.:* Wheeling, Oct. 1947, ♂.

Antrodiaetus pacificus (Simon)

Figures 121–122, 131, 147–149, 160, 170, 175–177, 197–203, 244–247, 284–291. Map 2.

Brachybothrium pacificum Simon, 1884, Bull. Soc. Zool. France, 9: 314. Syntypes (1 male and 1 possibly immature female) from Washington Territory in the Pacific Northwest; in the Muséum National d'Histoire Naturelle in Paris; examined. The male specimen is here designated the lectotype and the female the paralectotype, and they are so labeled. –Worley, 1928, Ann. Ent. Soc. America, 21(4): 619, fig. 2. –Roewer, 1942, Katalog der Araneae, 1: 190. –Bonnet (in part), 1955, Bibliographia Araneorum, 2: 335.

Antrodiaetus hageni: Gertsch and Jellison (not Chamberlin, 1917), 1939, American Mus. Novitates, (1032): 1.

Antrodiaetus pacificus: Chamberlin and Ivie, 1941, Bull. Univ. Utah, 31(8): 3. –Thorn, 1967, British Columbia Prov. Mus. Annual Report, p. 1. (*Antrodiaetes*).

Comment on lectotype. The lectotype male clearly matches in all characters the males in the western (coastal) populations of *A. pacificus*. It was therefore probably collected in western Washington as Simon (1884) apparently meant to indicate by adding "(Pacifique)" to his type locality designation.

Description. See Tables 12–15, which contain measurements, meristic data, and diagnostic ratios for a sample of the species and for the lectotype. In order to avoid contamination of the female *A. pacificus* species sample by *A. occultus* females (which probably are very similar to *A. pacificus*), no females from the area of sympatry of these two species are included in the *A. pacificus* sample studied (except for females from two burrow aggregations containing only *A. pacificus* males).

Male. Carapace: Figures 121, 122. Setae sparse on pars thoracica except usually moderately dense along lateral border. *Chelicerae:* Figures 147–149. Usually a large setaless area on upper ectal surface; occasionally this area small. *Pedipalps:* Figures 175–177, 197–203. Tibia moderately swollen in lateral view; greatest diameter in lateral view at between 1/3 to 1/2 of distance from proximal to distal end. Tip of o.e.s. of palpus rounded (blunt) and closely appressed to i.e.s. I.e.s. tip well sclerotized; usually weakly to moderately curved. *Leg I:* Figures 244–247. Dense, often large group of macrosetae (usually none, rarely a few, ensiform) on prolateral surface of tibia, centered at between 1/2 to 2/3 of distance from proximal to distal end. Other macrosetae (usually none or 1, rarely most, ensiform) scattered along retrolateral aspect of ventral surface of tibia with distalmost macroseta positioned at 3/4 or more (usually more) of distance from proximal to distal end. Often 1 to a few macrosetae scattered ventrally between these two groups. Tibia usually slightly swollen at prolateral macrosetae group. No macrosetae on metatarsus (very rare exceptions). Metatarsus elongate; usually weakly sinuous in ventral view. *Abdomen:* Usually 3 noncontinuous dorsal heavily sclerotized patches; posterior usually smallest and varies greatly in size. *Coloration:* Carapace gray-yellow to medium red-brown; pars cephalica often slightly darker than pars thoracica. Sternum pale gray-yellow; pedipalpal coxae slightly darker; labium darker yellow-gray to brown. Chelicerae similar to or slightly lighter than carapace. Patella, tibia and metatarsus of leg I medium to very dark red-brown, much darker than carapace; femur dorsally almost as dark as these segments, ventrally much lighter. Pedipalps and other legs dorsally similar to carapace, ventrally lighter. Abdomen pale gray-yellow to dark purple-gray; often darkest dorsally posterior of sclerotized patches. Occasionally this dark area chevron patterned. Sclerotized patches often similar to, sometimes darker than, carapace.

Female. Carapace: Figure 131. Setae sparse to moderately dense over most of pars thoracica; moderately dense to dense along lateral border. *Chelicerae:* Figures 160, 170. Microteeth positioned beside last 8 to last 3 macroteeth; often extend beyond last macrotooth. Microteeth proportionately small to medium size. Large to medium size setaless area on upper ectal surface. *Abdomen*: Background setae on dorsum distributed sparsely to moderately densely. *Genitalia:* Figures 284–291. Seminal receptacles evenly spaced or paired; with well-sclerotized stalk and bowl; stout to slender (much variation). Stalk base sometimes expanded. Bowl usually well developed; its border with bulb sharply defined. Floor of bursa copulatrix moderately to very weakly sclerotized; sometimes constricted medially. *Coloration:* Carapace pale gray-yellow to chestnut brown; pars cephalica usually slightly darker than pars thoracia. Sternum similar to pars thoracica; pedipalpal coxae similar to pars cephalica or darker; labium dark gray-orange to dark brown. Chelicerae gray-orange to dark red-brown; darker than pars cephalica. Pedipalps and legs dorsally similar to carapace, ventrally lighter. Abdomen light yellow-gray to dark purple-gray; sometimes much darker dorsally than elsewhere; occasionally this dark area chevron patterned. Tergite similar to pars thoracica.

Diagnosis. Males. The shapes and macrosetae distribution patterns of the tibia and metatarsus of leg I (Figs. 244–247; Table 12) are distinctive for this species and include some of the best characters for identification. *A. pacificus* (especially the western populations) has a proportionately long metatarsus I and short tibia I, so that ITL/IML (and often IFL/IML, ITL/ITarL, and IML/ITarL) provides clear separation from several other *unicolor* group species (Figs. 94, 244; Table 13). Because of a proportionately long pedipalpal femur, *A. pacificus* can be separated from some species by the ratio PFL/CL (Table 13). The o.c.s. tip of the palpus is much more rounded than that of *A. pugnax* or *A. hageni,* and much more closely appressed to the i.c.s. than that of *A. occultus* (Figs. 197–203).

Females. As described in the *A. hageni* and *A. montanus* diagnoses, cheliceral and carapace setation, cheliceral microteeth size, and coloration are usually helpful in separating *A. pacificus* females from these two species (Figs. 160, 170). IVML/IML (Table 14) helps distinguish *A. pacificus* from *A. pugnax* and *A. cerberus;* metatarsus I is relatively longer and metatarsus IV relatively shorter in *A. pacificus.* Because IFL is proportionately long and IVFL relatively short in *A. pacificus,* IFL/IVFL and occasionally related ratios (Table 14) are diagnostically helpful. *A. pacificus* has a significantly lower IVTL/CL value (Table 14) than *A. hageni* or *A. montanus.* The paired nature (Figs. 288–291) of the seminal receptacles in eastern *A. pacificus* specimens is not found in any other *unicolor* group species.

Variation. Numerous characters exhibit marked geographic variation, and in nearly every case the general pattern is the same —the population samples (*R–W*) from the Blue Mountains of northeastern Oregon and adjacent Washington are similar to one another and divergent from the western (*A–M*) samples, while the Idaho samples (*X–Z*) are either intermediate or similar to one of these two groups of samples (Fig. 98).

Males. Much of the strongest and most nearly discontinuous geographic variation is found in the ratio characters ITL/IML (Fig. 94), IFL/ITL (Fig. 95), ALD/CL, AMS/CL, ALD/ALS, ITL/CL, AMD/AMS, and AMD/CL (listed in order of degree of discontinuity). Sample *W* and usually also samples *R–V* and *X* are clearly divergent from the other samples, particularly in the first six of these ratios. Individuals in these samples usually have a proportionately longer ITL (Figs. 244, 247) and proportionately smaller and more widely separated ALE and AME (Figs. 121, 122) than males of other samples. In a few of these ratio characters, samples *R–V*, *Z*, and *M* are intermediate between sample *W* and the western samples, but in most characters samples *Z* and *M* are similar to the western samples. Several measurements, particularly ITL (Fig. 94) and CL (Fig. 97), exhibit rather strong but continuous geographic variation; most exhibit similar geographic patterns presumably because of strong correlation with body size. Several characters—PTT/PTL (Fig. 96), ALD/ALS, and ALD/CL—exhibit the variation pattern that could result from character divergence between *A. pacificus* and *A. occultus.*

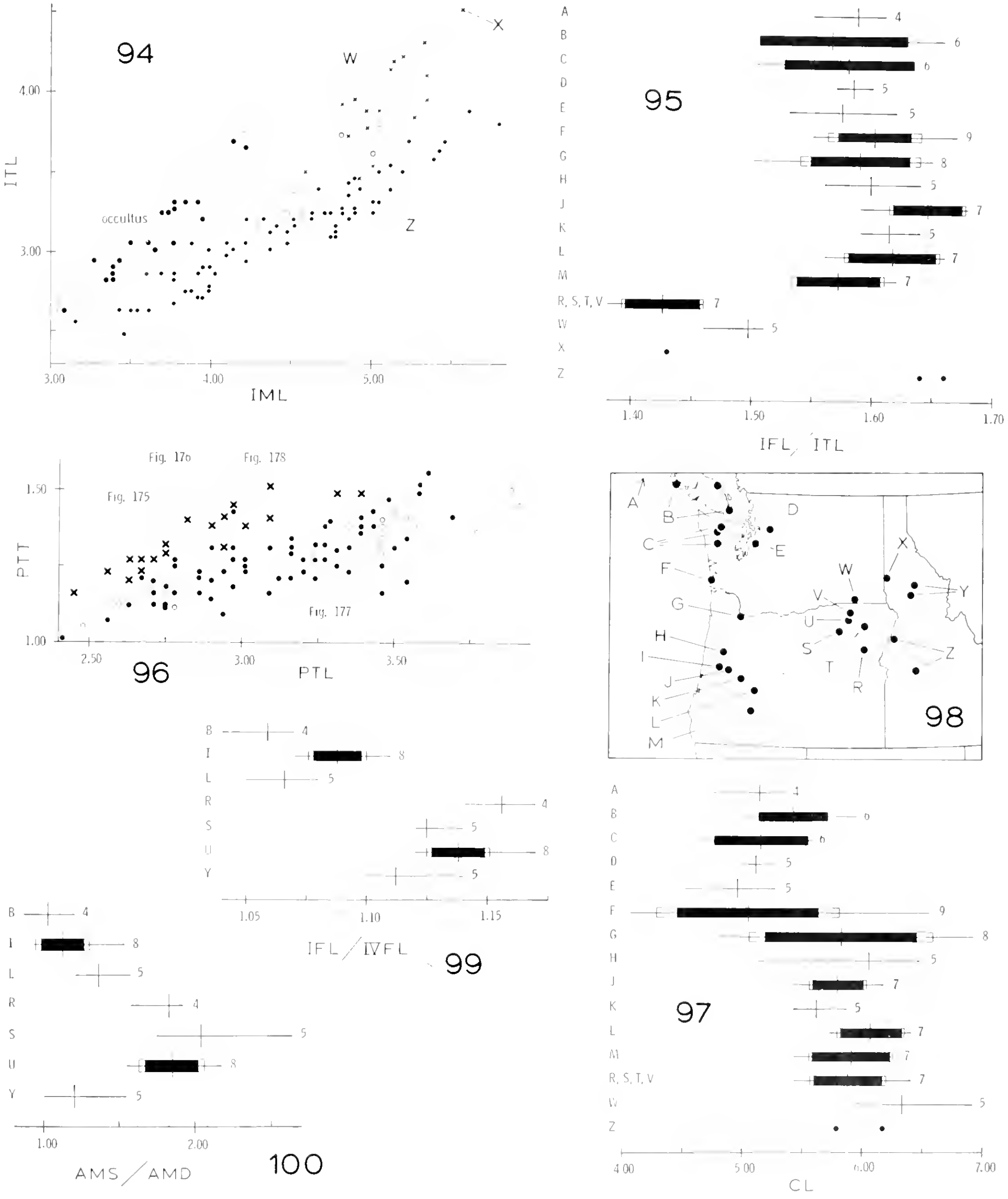
Individuals of samples *R–X* usually have a greater percentage of ensiform macrosetae in both the prolateral (0–27% ensiform vs. 0–3%) and ventral-retrolateral (8–100% ensiform vs. 0–33%) tibia I macrosetae groups than do individuals of all other samples (Figs. 244, 247). The tibia I prolateral macrosetae group is positioned slightly more proximally in samples *R–X* than in all other specimens (Figs. 244, 247). Individuals from *R–W* lack macrosetae on the ventral surface of tibia I between the two macrosetae groups, whereas specimens from *X* and *Z* and the majority of the rest of the samples have scattered small macrosetae in this position (Figs. 244, 247). The only three *A. pacificus* specimens with metatarsal macrosetae (Fig. 246) are from samples *T* and *X*. The i.c.s. tip of the palpus is usually more curved and more slender, the o.c.s. always wider, and the sperm reservoir often narrower in samples *R–W* than in the western samples (Figs. 201–203). The two *Z* males match the western males in palpus structure, whereas the *X* male is clearly intermediate in these characters. Specimens from *R–W* have smaller setaless areas on the upper ectal cheliceral surface than do all other individuals.

Females. The ratios IFL/IVFL (Fig. 99), AMD/CL, ALS/AMS, and AMS/AMD (Fig. 100) exhibit strong, nearly discontinuous geographic variation with samples *R*, *S*, and *U* differing considerably from the western samples (*B*, *I*, and *L*) and with sample *Y* either intermediate or similar to the western samples. Femur I is longer relative to femur IV length and the AME's are proportionately smaller and more widely separated in the Blue Mountain area samples (*R*, S, and *U*) than in the others. A few nonratio quantitative characters, particularly AMD, IVMT, and ITarL, also exhibit rather marked geographic variation, usually of a pattern similar to that of the above ratio characters.

There is remarkably strong variation in female genitalia morphology; much of it is geographic, with the Idaho and eastern Oregon females differing from the western specimens in the following ways (Figs. 288–291): 1) Seminal receptacles usually more or less distinctly paired with the ducts of the two inner receptacles not joining versus seminal receptacles not paired and ducts of inner receptacles usually joining. 2) Outer receptacles usually smaller than inner receptacles versus outer and inner receptacles same size or almost so. 3) Seminal receptacles usually more slender with proportionately longer stalk versus seminal receptacles stout with relatively short stalk. 4) Bursa copulatrix usually bilobed anteriorly versus not bilobed. However, there is much variation within sample S (Figs. 288–290), including two (Fig. 288) individuals with intermediate, nearly western-type genitalia. The females from eastern Oregon have markedly smaller setaless areas on the upper ectal surface of the chelicerae than do those of both the western and Idaho samples, which are similar in this character.

This analysis of variation strongly suggests that the Blue Mountains population (represented by samples *R–W*) and the western population of *A. pacificus* are genetically quite different; there is apparently little gene exchange between these two major populations. Also, records indicate that these populations are geographically isolated. It is doubtful that connecting populations could now exist in the dry, unfavorable region to the south, west, and directly north of the Blue Mountains population. If the Idaho populations were unknown, there would be little hesitancy in describing the Blue Mountains population as a distinct species, cognate with *A. pacificus*. However, the intermediate and frequently near-western phenotype of the Idaho samples is evidence that the Idaho populations are (or, until recent times have been) exchanging genes with both the Blue Mountain population and the western populations. If the eastern and western populations are presently connected, it is probable that the connecting populations will be found in a northern are in the mountains of northern Idaho and along the British Columbia-Washington border where the habitat appears favorable for *A. pacificus* and where there has been very little searching for *Antrodiaetus*. Clearly these populations are worthy of further study.

Noteworthy, largely nongeographic variation occurs in several characters. The form of the male anterior-dorsal cheliceral protuberance is highly variable. Nearly the entire species variation range occurs within several single population samples.



Figures 94–100. Geographic variation in *Antrodiaetus pacificus*. (All measurements in mm.) 94–97. Males. 94. Scatter diagram of ITL and IML. (X's represent samples *R–Z*, circles sample *M*, small black dots rest of samples, and large black dots *Antrodiaetus occultus* males.) 95. Mod. Dice-Leraas diagram of IFL/ITL variation. 96. Scatter diagram of PTT and PTL. (Circles represent *A. pacificus* males sympatric with *A. occultus*, black dots rest of *A. pacificus* males, and x's *A. occultus* males.) 97. Mod. Dice-Leraas diagram of CL variation. 98. Map of population sample localities. 99–100. Females. 99. Mod. Dice-Leraas diagram of IFL/IVFL variation. 100. Mod. Dice-Leraas diagram of AMS/AMD variation.

Figure 147 illustrates a prominent protuberance (one which might function like the apparently homologous cheliceral apophysis of *Atypoides*), Figure 148 illustrates a modal *A. pacificus* cheliceral protuberance, and Figure 149 represents the low end of the range of variation in this character. Figures 96 and 175–177 illustrate the continuous variation in the shape of the pedipalpal tibia. Usually there are three noncontinuous sclerotized patches on the male abdominal dorsum, with the posterior patch smallest but varying greatly in size. Occasionally this third patch is reduced to a bilateral pair of sclerotized spots; on rare occasions it is absent. Occasionally in the western samples and usually in the Blue Mountains samples the three sclerotized patches are continuous.

Distribution. The Pacific coast of North America from San Francisco Bay north to southern Alaska, with outlying, perhaps isolated, populations in the montane areas of western Idaho, northern Oregon, and adjacent Washington (Map 2). Noteworthy locality records (not shown on Map 2) of immatures that are almost certainly *A. pacificus* are: Marin and Sonoma Counties, California, and Terrace, British Columbia (near the southern tip of Alaska).

Records. ALASKA. Ketchikan [*A*], 18–28 July 1951, ♂; 23 Aug. 1952, ♂; 27 July 1951, ♂; summer 1937, ♂. BRITISH COLUMBIA. *Vancouver Island* [*B*]: Victoria, 17 Aug. 1966, ♂; 30 July 1967, ♂; 3 Sept. 1966, ♂; 27 Oct. 1934, ♂; 18 Nov. 1928, ♂; 2♀. — Sidney, 10 Sept. 1967, ♂. — Esquimalt, 30 Aug. 1947, ♂. — Tofino, 7–15 Aug. 1953, ♂; 22 June–12 July 1950, ♂; 2♀. — Wellington, 15–31 Aug. 1951, 5 Oct. 1949, 15 Aug. 1949, 3♂; 2♀. — Nanaimo, 13 Sept. 1935, ♂. — French Creek. 6 Sept. 1949, ♂. — Caledonia, Kyuquot Sound, ♀. — Kyuquot, ♂; 29 July 1931 (♂); 17 Aug. 1958, ♂, ♀; 31 Sept., ♂. — Kyuquot, Weave's Island, 2♀. — Kyuquot, Spring Island, ♀. *Queen Charlotte Islands:* Frederick Island, 2♀. — Yalcoun River, 11 Aug. 1961, ♂. CALIFORNIA. *Humboldt Co.:* Miranda, 3 June 1936, ♂, ♀. *Mendocino Co.:* Piercy, ♀. — Russian Gulch St. Pk. near Mendocino, 2♀. *Trinity Co.:* Carrville, July 1934, ♂. IDAHO. *Adams Co.:* Bear [*Z*], ♂. *Boise Co.:* Lost Lake [*Z*], 27 July 1939, ♂. *Clearwater Co.:* Pierce [*Y*], 3♀. *Idaho Co.:* Kamiah [*Y*], 2000 ft, 2♀. *Latah Co.:* Moscow Mtns. near Moscow [*X*], June 1936, ♂. OREGON. *Baker Co.:* Marble Creek Picnic Area (USFS) [*R*], 7 mi. W of Baker, 4600 ft, 2–3 July 1967 (♂), 4♀. — Washington Gulch [*R*], 5 mi. W of Baker, 4000 ft, 2–4 July 1967 (♂). *Benton Co.:* Corvallis [*H*], 13 Sept. 1940, 2♂; 31 Aug. 1951, ♂; 7 Oct. 1952, ♂; ♂. — 9 mi. W of Philomath, 1 Sept. 1949, ♂. *Coos Co.:* Charleston, 9 Aug. 1941, ♂. *Curry Co.:* 2 mi. N of Brookings, ♀. — Pistol River, 17 Sept. 1956, 2♂. *Douglas Co.:* Yoncalla, 1939, ♂. *Jackson Co.:* Ashland, Lithia Park, ♀. — Crater Creek [*M*], 4500 ft, 18–21 Aug. 1950, ♂♀. — Union Creek [*M*], 3300 ft, 1–15 Sept. 1950, 2♂. — Beaver Sulphur Forest Camp near Applegate River, 9 Oct. 1964, ♂. — Siskiyou, 5 July 1951, ♂. *Klamath Co.:* Odell Lake at outlet [*L*], 28 July 1967, 7♂, 5♀. — Willamette Pass Summit, 5130 ft, 17 Aug. 1968, ♂. — Lake of the Woods, 13 Aug. 1935, ♂. — Crater Lake Natl. Pk. [*M*], Headquarters, 21 July 1951, 13 Aug. 1950, 2♂; Sleepy Hollow, 7 Aug. 1950, ♂; Annie Springs, 6000 ft, ♂; ♀. *Lane Co.:* Alderwood St. Pk. [*I*], 200 ft, 29 July 1967, ♂ (♂), 8♀. — Black Canyon Camp (USFS) at SE end of Lookout Point Reservoir [*K*], 29 July 1967, 5♂. — Eugene [*J*], Sept. 1941, 4♂; 12 Aug. 1941, 2♂; 2–23 Nov. 1941, ♂. *Linn Co.:* House Rock Camp, 13 mi. E of Cascadia, 23 July 1949, ♂. *Marion Co.:* Silver Creek Falls, 27 Sept. 1959, ♂. *Multnomah Co.:* Portland [*G*], 9 Sept. 1947, 2♂; June 1948, ♂; 3 Oct. 1948, ♂; 20 Sept. 1935, ♂; 31 Aug. 1935, ♂; Summer 1934, ♂; Sept. 1934, ♂; 2♂. *Tillamook Co.:* Tillamook, summer 1933, ♂. — Bay Ocean, 3 Sept. 1932, ♂. *Umatilla Co.:* Bear Wallow Camp (USFS) [*S*], 10 mi. NE of

Ukiah, 4000 ft, 7 July 1967 (2♂), 5♀. — Emigrant Springs St. Pk. [*U*], 3900 ft, 8♀. — 3 mi. NE of Gibbon at Umatilla River [*V*], 1800 ft, 7 July 1967, ♂, ♀. *Union Co.:* 4–5 mi. W of Cove [*T*], 4600 ft, 5 July 1967 (2♂), 2♀. — Catherine Creek St. Pk., 3600 ft, ♀. *Yamhill Co.:* McMinnville, Aug. 1930, fall 1934, 2♂, ♀. WASHINGTON. *Clallam Co.:* Olympic Natl. Pk., Olympic Hot Springs [*C*], 27 July 1968, ♂; 8 Aug. 1968, 2♂. — Crescent Lake [*C*], 10 Sept. 1965, ♂. *Grays Harbor Co.:* Quinalt [*C*], 21 July 1952, ♂, ♀. *Jefferson Co.:* Olympic Natl. Pk., Ho River, Jackson Forest Camp [*C*], 19 Aug. 1956, ♂. *King Co.:* Seattle [*E*], Oct. 1951, ♂; 3 and 12 Sept. 1934, 2♂; 2♂, ♀. *Lewis Co.:* Chehalis, ♀. — Packwood Lake, 11 Aug. 1931, ♂. *Pacific Co.* [*F*]: 1952, 3♂. — Ocean Park, 11 Sept. 1929, 2♂. — Bay Center, 1 Sept. 1933, Aug. 1931, 2♂. — Nahcotta, 20 Aug. 1954, 2♂. *Pierce Co.:* Puyallup, 1931, ♂. — Mt. Ranier Natl. Pk., Longmire, 2000 ft, 1 July 1934, ♂. *San Juan Co.:* Blakeley Island, ♀. — Browns Island, ♀. — Friday Harbor, 2 Aug. 1927, ♂; 20 July 1935, ♂. *Snokomish Co.:* Chase Lake [*D*], 25 Sept. 1954, ♂; June 1956, 4♂. *Thurston Co.:* Olympia, 26 Aug. 1959, ♂; 2♀. *Walla Walla Co.:* Walla Walla [*W*], Nov., ♂; Oct. 1926, 4♂; 10 Oct. 1927, 2♂.

Antrodiaetus occultus new species

Figures 123, 178, 204–206, 248–249. Map 2.

Type specimens. Holotype male from Corvallis, Linn Co., Oregon, 7 October 1951 (V. Roth), in the American Museum of Natural History. Seven males from type locality with same date designated as paratypes and deposited in AMNH and MCZ. The specific name is a Latin adjective meaning "hidden."

Description. See Tables 12, 13, and 15, which contain measurements, meristic data, and diagnostic ratios for a sample of the species and for the holotype. Females of this species, if present in the material which I have examined, were not distinct enough for me to separate from *A. pacificus* females and therefore remain undescribed.

Male. Carapace: Figure 123. Setae scattered sparsely over pars thoracica except denser along lateral border. *Chelicerae:* Large area on upper ectal surface without setae. *Pedipalps:* Figures 178, 204–206. Tibia strongly swollen in lateral view; greatest diameter in lateral view at approximately 1/3 of distance from proximal to distal end. Tip of o.c.s. of palpus roundly pointed; not closely appressed to i.c.s. but bent away from it. Tip of i.c.s. rather well sclerotized and curved (often rather strongly). *Leg I:* Figures 248, 249. Dense group of macrosetae (over 1/3 are ensiform) occupying most of distal 2/3 of prolateral surface of tibia. Small number of scattered macrosetae (usually most attenuate) on retrolateral aspect of ventral surface of tibia; distalmost macroseta not over 3/4 (usually less) of distance from proximal to distal end of tibia. Rarely any macrosetae on ventral surface between these two groups. Tibia thick; swollen at proximal macrosetae group. No macrosetae on metatarsus. Metatarsus sinuous in ventral view. *Abdomen:* 3 dorsal noncontinuous heavily sclerotized patches (sometimes nearly continuous); posterior patch smallest. *Coloration:* Carapace gray-orange or light brown. Labium similar to carapace; sternum and pedipalpal coxae lighter gray-yellow. Chelicerae usually slightly lighter than, sometimes similar to, carapace. Patella, tibia, and metatarsus of leg I medium to dark red-brown; femur lighter but slightly darker than carapace. Pedipalps and other legs dorsally similar to carapace, ventrally lighter. Abdomen pale gray-yellow laterally; dorsally posterior of sclerotized patches pigmented light to rather dark gray-brown in dense chevron pattern; sclerotized patches similar to carapace.

Diagnosis. The shapes and macrosetae distribution patterns of the tibia and metatarsus of leg I (Figs. 248, 249; Table 12) are distinctive for this species. The numerous ensiform macrosetae in the prolateral macrosetae group of the tibia (and often the more proximal position of the distalmost macroseta on the retrolateral aspect of the ventral tibial surface) allow clear separation of *A. occultus* from *A. pacificus*. Since metatarsus I of *A. occultus* is proportionately short, IML/CL, IFL/IML, and ITL/IML (Figs. 248, 249; Table 13) distinguish this species from *A. pacificus* (Fig. 94) and several other *unicolor* group species. The pedipalpal tibia of *A. occultus* is markedly more swollen than in many other *unicolor* group species so that PTT/PTL and PTT/CL (Figs. 96, 178; Table 13) are also excellent diagnostic ratios. Its proportionately large AME's (AMD/CL and AMD/AMS, Table 13; Fig. 123) separate *A. occultus* from several *unicolor* group species. The flexion of the o.c.s. tip away from the i.c.s. (Fig. 204) is a particularly distinctive feature not found in *A. pacificus* and some other species.

Variation. The variation in all characters studied is continuous and usually not wide. Figures 205 and 206 illustrate most of the range of variation observed in o.c.s. tip shape.

Distribution. Western Oregon in the valley between the Coast and Cascade mountain ranges (Map 2).

Records. OREGON. *Benton Co.:* Corvallis, 7 Oct. 1951, 8♂; 7–9 Oct. 1912, 3♂; 8 Nov. 1895, ♂; winter 1936, ♂; 10 Oct. 1947, ♂; 21 Oct. 1934, ♂. *Clackamas Co.:* 3 mi. N of Marguam, 26 Sept. 1964, ♂. — Oregon City, 30 Sept. 1950, ♂. *Douglas Co.:* Roseburg, 22 Sept. 1946, ♂. — Yoncalla, 1939, ♂. *Lane Co.:* Eugene, Oct. 1927, ♂; 12 Oct. 1941, ♂.

Antrodiaetus pugnax (Chamberlin)

Figures 109–112, 124, 132, 161, 179, 207–212, 250–252, 292–294. Map 2.

Brachybothrium pugnax Chamberlin, 1917, Bull. Mus. Comp. Zool., 61(3): 73. Holotype collected by Charles Bendire; in the Museum of Comparative Zoology; examined. (See comments below on sex of holotype and designated type locality.) –Roewer, 1942, Katalog der Araneae, 1: 190. –Bonnet, 1955, Bibliographia Araneorum, 2: 907.

Brachybothrium shoshoneum Chamberlin, 1925, Proc. California Acad. Sci., 14(7): 105, figs. 1–3. Holotype male from Troy, Latah Co., Idaho, 16 August 1908; in the Museum of Comparative Zoology; examined. NEW SYNONYMY. –Roewer, 1942, Katalog der Araneae, 1: 190. –Bonnet, 1955, Bibliographia Araneorum, 2: 907.

Comments on original description. The holotype of *Brachybothrium pugnax* is clearly a mosaic gynandromorph with at least some intersexual tissue, but has enough diagnostic male structures to show its conspecificity with the holotype male of *B. shoshoneum.* Although Chamberlin (1917) described the abnormal right pedipalp and the differences between the holotype chelicerae, he did not state that the specimen was gynandromorphic or teratological. Such a description published even today would not violate Article 1 of the present International Code of Zoological Nomenclature (1964) which states that "names given . . . to teratological specimens . . . as such . . . are excluded" from the Code.

There is considerable evidence to indicate that the type locality which Chamberlin designated for *A. pugnax*—Tucson, Arizona—is in error. All other records for this species are clustered in the Pacific Northwest (Map 2) over 1100 air miles from Tucson, even though numerous specimens of other antrodiaetid species have been collected from the intervening area. Both labels accompanying the holotype are in Chamberlin's handwriting. The stated locality, written on both pieces of paper, reads "Arizona: Tucson (Bendier coll.)" and "Tucson, Ariz. Bendier coll." Chamberlin's handwriting and the misspelling of the collector's (Charles Bendire) name indicate that this information was transferred from some source. Errors may have been present in the source and/or committed during the transfer. (The type localities of five of the 34 new species described by Chamberlin in the same publication were either unknown or followed by a question mark.)

Charles Bendire, who collected the specimen, was a U. S. Army officer and prominent naturalist who collected and gave, chiefly to the U. S. National Museum, large quantities of natural history specimens (primarily bird eggs, birds, and other vertebrates) from the western U. S. (Merriam, 1897; Merrill, 1898; Mearns, 1902). Not until about 1870, while stationed in Idaho, did he begin collecting large numbers of specimens (Merrill, 1898). While earnestly collecting in the West (1870–1886), he was stationed in Oregon, Washington, and Idaho for about 10.5 years, in Arizona for only 1.5 years, and elsewhere about 4 years (Merrill, 1898). He therefore spent the great majority of his collecting time within or near the Pacific Northwest distribution range of *A. pugnax*. In summary, the evidence suggests both an error in the designation of the type locality and that the real type locality is somewhere in Oregon, Washington, or Idaho.

Description. See Tables 12–15, which contain measurements, meristic data, and diagnostic ratios for a sample of the species and for the holotype.

Holotype. Since the holotype of *A. pugnax* is a mosaic gynandromorph with some portions of the body also exhibiting intersexuality, it is not included in the species population sample for which quantitative character values are summarized in Tables 12–14, but its measurements are given in Table 15. The holotype is larger than other known *A. pugnax* males and females except for one somewhat shrivelled and unmeasured male lacking a locality label. The left chelicera of the holotype is composed of male tissue; it is small, possesses a typical anterior-dorsal protuberance, and lacks a rastellum. The highly diagnostic tibia and metatarsus of the left leg I, which is also composed of male tissue, match those of males from the eastern portion of the species range. (The other leg I and the left pedipalp are missing.) At least much of the abdomen, with a male genital opening and 3 heavily sclerotized patches dorsally, is composed of male tissue, but the EGS are abnormally numerous (Table 15). The sole demonstrable female structure is the right chelicera, which is much larger than the left one, lacks a male protuberance, and possesses a well-developed rastellum. Possibly a substantial part of the cephalothorax is also female tissue. The right pedipalp is intersexual. Its tibia is partially swollen and possesses some (but fewer than the normal female complement of) ensiform macrosetae. The tarsus is also swollen, possesses some ensiform macrosetae, is somewhat hollowed out ventrally on the distal half, and the claw is slightly enlarged and partly sheathed in a rudimentary o.c.s. At least some of the legs and possibly much of the cephalothorax also contain intersexual tissue.

Male. Carapace: Figures 109, 124. Setae sparse to moderately dense on pars thoracica; always moderately dense along lateral border. *Chelicerae:* Usually a large to small setaless area on upper ectal surface; occasionally setae cover entire upper ectal surface. *Pedipalps:* Figures 179, 207–212. Tibia moderately swollen in lateral view; greatest diameter in lateral view at approximately 1/3 of distance from proximal to distal end. Tip of o.c.s. of palpus pointed and closely appressed to i.c.s. I.c.s. tip well sclerotized (occasionally side against o.c.s. nearly translucent) and straight or only weakly curved. *Leg I:* Figures 101, 250–252. Dense group of macrosetae (majority ensiform) on prolateral surface of tibia, centered just distal of midpoint. Another smaller group of macrosetae (50% or more are ensiform) on retrolateral aspect of ventral surface of tibia; distalmost macroseta positioned at 2/3 or less of distance from proximal to distal end; distalmost macrosetae of this group very large. No macrosetae between these groups. Tibia swollen at ventral macrosetae group. One to 4 macrosetae ventrally at distal end of metatarsus; occasionally a macroseta also positioned ventrally at 2/3 distance from proximal to distal end. Metatarsus with keellike swelling on retrolateral aspect of ventral surface at between 1/3 to 1/2 of distance from proximal to distal end; weakly sinuous in ventral view. *Abdomen:* 3 (occasionally 2) frequently continuous, dorsal, heavily sclerotized patches; third (posterior) patch varies from absent to nearly as large as others. *Coloration:* Carapace pale gray-yellow to gray-orange. Sternum and pedipalpal coxae paler gray-yellow; labium yellow-gray. Chelicerae similar to carapace, often slightly lighter. Patella, tibia and metatarsus of leg I orange to red-brown; femur lighter. Pedipalps and other legs dorsally similar to carapace, ventrally lighter. Abdomen pale yellow-gray to gray-brown; usually darkest pigment dorsally and lighter laterally; dorsal sclerotized patches gray-yellow to gray-brown, usually darker than rest of abdomen.

Female. Carapace: Figures 110, 132. Setae density on pars thoracica as in male. *Chelicerae:* Figure 161. Microteeth positioned beside last 5 to last 2 macroteeth and often extend beyond last macrotooth. Microteeth small to medium in size. Setae sometimes scattered over entire upper ectal surface, sometimes absent from small to large part of this surface. *Abdomen:* Background setae on dorsum moderately slender and distributed moderately densely. *Genitalia:* Figures 292–294. Seminal receptacles with well-sclerotized stalk and bowl; usually of moderate length and breadth. Stalk frequently expanded basally. Bowl usually well developed; its border with bulb sharply defined. Floor of bursa copulatrix weakly to moderately well sclerotized. *Coloration:* Carapace gray-yellow to light brown; pars cephalica frequently slightly darker than pars thoracica. Sternum similar to pars thoracica; labium and pedipalpal coxae darker than carapace. Chelicerae light brown to brown, markedly darker than carapace. Pedipalps and legs dorsally similar to carapace, ventrally lighter. Abdomen pale gray-yellow, sometimes with darker gray-brown pigmentation dorsally; tergite similar to pars thoracica.

Diagnosis. Males. The shapes and macrosetae distribution patterns of the tibia and metatarsus of leg I (Figs. 101, 250–252; Table 12) are distinctive for this species and include the best characters for identification. Because of the proportionately long tarsus I and a proportionately shorter metatarsus I than in some species, IML/ITarL, ITL/ITarL, ITL/IML, and occasionally other ratios (Table 13) separate *A. pugnax* from several *unicolor* group species, particularly *A. pacificus.* ITL, IFL, PFL, and other measurements (Table 13) help separate *A. pugnax* with its small mean body size from the larger species *A. hageni* and *A. montanus. Females. A. pugnax* has a significantly smaller mean body size than most other *unicolor* group species; many appendage and carapace measurements (Table 14) are diagnostically useful, giving particularly good separation from the large sympatric species, *A. hageni* and *A. montanus.* As a result of the proportionately long tarsus IV and other leg IV segments that are relatively short, IVML/IVTarL and IVTL/ IVTarL (Table 14) help distinguish *A. pugnax* from *A. hageni* and *A. cerberus.* The best ratio for separating *A. pugnax* from *A. pacificus* is IVML/IML, and from *A. montanus* is IFL/IML (Table 14). The small cheliceral microteeth (Fig. 161) of *A. pugnax* help distinguish this species from both *A. hageni* and *A. montanus.*

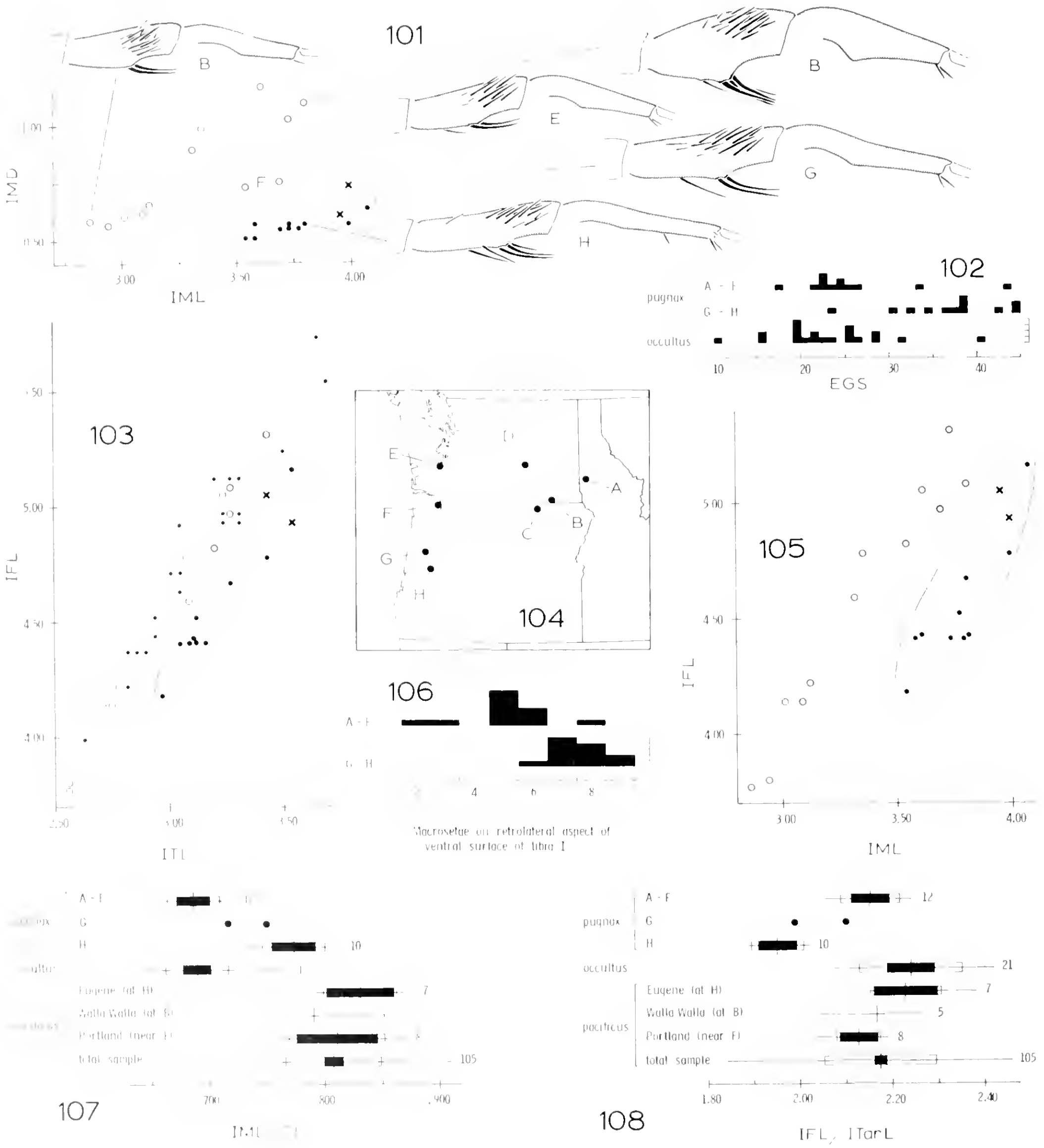
Variation. A number of characters exhibit strong geographic variation in male *A. pugnax.* On the other hand, comparisons of four female samples (from Corvallis, Ore., and from Ft. Lewis, Walla Walla, and Lewis and Clark St. Park, Wash.) reveal no marked geographic variation. Male quantitative characters with the strongest geographic variation are (in approximate order of the degree of discontinuity of variation): IFL/IML, IFL/ITL, IML/CL, IFL/ITarL, IMD/IML, ITD/ITL, metatarsus I macrosetae number, tibia I macrosetae number, EGS, and ALD/CL.

For the first four of these characters, population sample *H* is distinct from the northern and eastern samples, which have a proportionately shorter leg I tibia, metatarsus, and tarsus (Figs. 103–108). Sample *G* is similar in these characters to sample *H* or is intermediate. The geographic patterns of IMD/IML (Fig. 101) and ITD/ITL variation are very similar to each other and resemble those of the above characters. However, this variation appears somewhat clinal, with sample *F* intermediate. The thickest tibiae and metatarsi I (also with the most prominent protuberances) are in the northeastern part of the species range and are the most slender in the southwestern portion (Fig. 101). All sample *H* specimens have on metatarsus I a macroseta F (Fig. 252), not present on other males except the one from *A*. Also there is a much greater tendency for sample *H* individuals to have metatarsal macrosetae C and D (Fig. 252) and for macroseta B to be ensiform. The southwestern samples (*G, H*) have a significantly higher mean number of EGS (Fig. 102) and of macrosetae on the retrolateral aspect of the ventral surface of tibia I (Fig. 106) than northern and eastern samples. ALD/CL exhibits a different pattern of geographic variation, with samples *E* and *F* having markedly smaller mean values of this character than samples *B* and *H*, but only small gaps separate the variation ranges of these small samples.

Clearly population *H* is genetically divergent and could be satisfactorily distinguished from the known northern and eastern samples by most of the above (male) characters. However, present evidence does not justify concluding that population *H* is reproductively isolated from the rest. Geographically intermediate and larger samples need to be studied. The intermediate position of sample *G* and (occasionally) sample *F* in the variation pattern of some markedly varying characters is some evidence that populations *H* and *G* are exchanging genes, but perhaps at a reduced rate, with the more northerly known populations. Perhaps favorable *A. pugnax* habitat is discontinuous in the Willamette River Valley area of northwestern Oregon, thus hindering gene exchange with northern and eastern populations. Another factor possibly involved is character divergence.

It seems highly unlikely that character divergence between *A. pugnax* and *A. pacificus* could cause such geographic variation in *A. pugnax*, since *A. pugnax* is throughout its entire range sympatric with *A. pacificus* (Map 2), unless possibly an uncommon situation of strong local competition exists between *A. pacificus* and semi-isolated *A. pugnax* populations only in the Eugene, Oregon, area (samples *G* and *H*) where their habitats are spatially intermingled. An examination of all characters for variation patterns that could result from such character divergence reveals that 1/6 do have such a variation pattern (one in which the *A. pugnax* population samples *G* and *H* are markedly more distinct from the Eugene [sympatric] *A. pacificus* sample than are the other *A. pugnax* samples). But almost as many characters had just the opposite pattern. IFL/ITarL, ITarL/CL, PFL/CL, and IFL/ITL show the former type of pattern most strongly (Fig. 108), whereas IML/CL, ITL/ITarL, and IFL/IML exhibit the strongest reverse pattern (Fig. 107).

There is considerable evidence, however, to suggest character divergence between *A. pugnax* and *A. occultus*. Records indicate that *A. occultus* is found only in the Willamette River Valley region, where it is sympatric with *A. pugnax* (Map 2). Both species have been collected from



Figures 101–108. Geographic variation in *Antrodiaetus pugnax* males. (All measurements in mm. For scatter diagrams large black dots represent sample *H*, x's sample *G*, and circles samples *A–F*.) 101. Scatter diagram of IMD and IML. 102. Histogram of EGS number compared with that of *Antrodiaetus occultus*. (One unit of vertical scale represents one specimen.) 103. Scatter diagram of IFL and ITL. (Small black dots represent *A. occultus* males.) 104. Map of population sample localities. 105. Scatter diagram of IFL and IML. 106. Histogram of tibia I retrolateral-ventral macrosetae number . (One unit of vertical scale represents one tibia.) 107. Mod. Dice-Leraas diagram of IML/CL variation compared with that of *A. occultus* and *Antrodiaetus pacificus*. 108. Mod. Dice-Leraas diagram of IFL/ITarL variation compared with that of *A. occultus* and *A. pacificus*.

Eugene and Corvallis, Oregon. Unfortunately, the habitat of *A. occultus* is unknown. Of 43 quantitative characters examined, the sympatric population sample of *A. pugnax* is markedly more distinct from *A. occultus* than are the allopatric *A. pugnax* population samples—the pattern that could be the result of character displacement—in 20 of these characters, whereas only five characters show the opposite pattern. IML/CL, IFL/ITL, CW/CL, and IFL/ITarL are the best examples of the former pattern (Figs. 103, 107, 108); ITL/IML yields the most strongly expressed reverse pattern.

Noteworthy variation, usually with a geographic pattern similar to the dominant one shown by quantitative characters, are shown by a number of not strictly quantitatively defined characters. *Males:* Three specimens from *B* and *C* have only a tiny area devoid of setae on the upper ectal surface of the chelicerae, while the rest in the species sample have larger setaless areas, the largest being from the westernmost localities. There is considerable variation (but without a clear geographic pattern) in the shape of the i.c.s. tip and in the distance that it extends beyond the o.c.s. tip (Figs. 207, 209, 211). The o.c.s. tip is also quite variable in shape and averages wider and shorter in sample *H* (Figs. 208, 210, 212). The basal portion of the palpus is larger relative to the length of the conductor portion in most southwestern specimens (Figs. 207, 209). While specimens from the eastern part of the species range have either only two or three noncontinuous, heavily sclerotized patches on their abdominal dorsum, western specimens have three usually continuous patches. *Females:* Most specimens from *B* have the upper ectal surface of their chelicerae evenly covered with setae, the rest of the eastern specimens have here a small to medium size setaless area, and in western specimens this area is large. The seminal receptacle stalks are usually proportionately much longer and the stalk bases less expanded in eastern than in western specimens (Figs. 292–294). Occasionally a part of the anterior edge of the bursa copulatrix floor is very heavily sclerotized (Fig. 294).

Distribution. Northern Oregon, southern Washington, into northwestern Idaho (Map 2).

Records. IDAHO. *Latah Co.:* Troy [*A*], 16 Aug. 1908, ♂. OREGON. *Benton Co.:* Corvallis [*G*], 18 Aug. 1949, ♂; 3♀. — McDonald Forest [*G*], 3/4 mi. E of saddle, 10 Aug. 1962, ♂. *Columbia Co.:* St. Helens [*F*], 2 Aug. 1934, ♂; 6 Aug. 1936, ♂. *Lane Co.:* Eugene [*H*], Sept. 1941, 11♂. *Umatilla Co.:* Pendleton [C], ♂. *Union Co.:* Fly Creek Valley, S of Starkey, ♀. WASHINGTON. *Columbia Co.:* Lewis and Clark Trail St. Pk., 1000 ft, 4♀. *Grant Co.:* Larson Air Force Base [*D*], 10 Oct. 1958, ♂. *Pierce Co.:* Fort Lewis, 2♀. *Thurston Co.:* Olympia [*E*], winter 1939, ♂; 26 Aug. 1959, ♂; ♂, 2♀. *Walla Walla Co.:* W edge of Walla Walla [*B*], 930 ft, 8–9 July 1967, 2(♂), 11♀. — Walla Walla [*B*], 10 Sept. 1927, ♂; Oct. 1926, ♂. *Yakima Co.:* Tieton, ♀.

Antrodiaetus montanus (Chamberlin and Ivie)

Figures 140, 150, 162, 171, 180, 213–217, 253–255, 295–298. Map 2.

Brachybothrium hageni: Chamberlin and Ivie (not Chamberlin, 1917), 1933, Bull. Univ. Utah, 23(4): 4.

Brachybothrium montanum Chamberlin and Ivie, 1935, Bull. Univ. Utah, 26(4): 4, pl. 5, fig. 31. Holotype male and allotype female from 8 miles S of Lynn, Raft River Mountains, Box Elder Co., Utah, 6 Sept. 1932; in the American Museum of Natural History; examined. –Roewer, 1942, Katalog der Araneae, I: 190. –Bonnet, 1955, Bibliographia Araneorum, 2: 907.

Antrodiaetus montanus: Chamberlin and Ivie, 1945, Ann. Ent. Soc. America, 38(4): 549, pl. 1, figs. 1–2.

Antrodiaetus hageni: Bonnet (in part), 1955, Bibliographia Araneorum, 2: 335.

Description. See Tables 12–15, which contain measurements, meristic data, and diagnostic ratios for a sample of the species and for the holotype.

Male. Carapace: Setation usually rather dense on lateral border, particularly posteriorly. *Chelicerae:* Figure 150. Upper ectal surface covered with scattered setae. *Pedipalps:* Figures 180, 213–217. Tibia moderately swollen in lateral view; greatest diameter in lateral view at approximately 1/3 of distance from proximal to distal end. O.c.s. of palpus slightly widened distally; tip weakly pointed to blunt, usually not closely appressed to i.c.s. I.c.s. tip well sclerotized and curved (often strongly). *Leg I:* Figures 253–255. Rather large dense group of macrosetae (most are ensiform) on distal 1/2 to 2/3 of prolateral surface of tibia. Smaller group of more scattered macrosetae (1/3 or more are ensiform) centered more proximally at 1/2 to 2/3 of distance from proximal to distal end of tibia on ventral aspect of retrolateral surface. These groups clearly separated by ventral area lacking macrosetae. Prolateral portion of distal half of tibia swollen. Usually 1 (very rarely more) and sometimes no macrosetae ventrally at distal end of metatarsus. Metatarsus weakly sinuous in ventral view. *Abdomen:* 3 dorsal, heavily sclerotized, usually noncontinuous patches. Posterior patch usually smallest, sometimes reduced to bilateral pair of small patches. *Coloration:* Carapace pale gray-yellow to pale gray-orange. Sternum paler; labium darker yellow-gray or orange-gray. Chelicerae similar to carapace. Patella, tibia, and metatarsus of leg I often light to medium orange, darker than carapace; femur lighter. Pedipalps and other legs, sometimes also leg I, dorsally similar to carapace, ventrally lighter. Abdomen pale gray-yellow to light gray; dorsal sclerotized patches often slightly darker gray-yellow or gray-orange.

Female. Carapace: Setae sparsely scattered over much of pars thoracica, especially dense along lateral border. *Sternum:* Figure 140. Relatively broad. *Chelicerae:* Figures 162, 171. Microteeth positioned beside last 8 to last 5 macroteeth, sometimes extending beyond last macrotooth. Outermost microteeth usually very large. Entire upper ectal surface covered with scattered setae. *Abdomen:* Background setae on dorsum rather short, slender, and distributed densely. *Genitalia:* Figures 295–298. Seminal receptacles with well-sclerotized stalk and bowl; of moderate length and breadth. Stalk slightly expanded at its base and constricted above. Bowl well developed; its border with bulb sharply defined. Floor of bursa copulatrix rather well sclerotized. *Coloration:* Carapace pale to medium gray-yellow; pars cephalica sometimes slightly darker than pars thoracica. Sternum similar to pars thoracica; pedipalpal coxae and especially labium darker light gray-orange to light brown. Chelicerae light gray-orange to light orange-brown, darker than carapace. Pedipalps and legs dorsally similar to or slightly darker than carapace, ventrally lighter. Abdomen yellow-gray or gray; tergite usually darker gray-yellow or light brown.

Diagnosis. The presence of setae over the entire upper ectal surface of the chelicerae (Fig. 171) and the light coloration help separate both sexes of *A. montanus* from *A. pacificus*, *A. cerberus*, and some other *unicolor* group species and are especially important for female identifications. *Males.* The shapes and macrosetae distribution patterns of the tibia and metatarsus of leg I (Figs. 253–255; Table 12) are distinctive for this species. Because the femur, tibia, and tarsus of leg I are relatively longer in *A. montanus* than in other *unicolor* group species, ITL/CL, ITarL/CL, and other ratios involving these segment lengths (Table 13) are usually excellent characters for identification. ITL/IML (Table 13) is the character that most accurately separates *A. montanus* from the similar species, *A. pacificus*. *A. montanus* has a relatively long pedipalpal femur, making PFL/CL (Table 13) a useful ratio for separating this species from *A. cerberus* and a few other *unicolor* group species.

Females. The color and setation characters mentioned above are quite useful. Some raw measurements (particularly IVTL and IVML, Table 14) help separate *A. montanus,* with its large body size, from *A. pugnax* and *A. pacificus.* Individuals of this species usually have a higher CMT number (Table 14) and larger microteeth (Fig. 162) than those of other *unicolor* group species. The expanded seminal receptacle stalk bases (Figs. 295–298), apparently characteristic of this species, have not been found in any specimens of *A. hageni* or *A. cerberus.*

Variation. Males: No characters studied exhibit either discontinuous variation or marked geographic variation. Macroseta A on metatarsus I usually varies from large and ensiform to small and attenuate, but is occasionally reduced to a normal seta (Table 12). There is rather wide but continuous variation in the number of macrosetae (total and ensiform) and proportion of ensiform macrosetae in the tibia I macrosetae groups (Table 12; Figs. 253, 255). Specimens from Crater Lake and Fish Lake, Oregon, have the highest numbers of macrosetae in the prolateral group. Noteworthy variation is found in the thickness and rate of taper of the tip of the i.c.s. of the palpus. Figures 213 and 215 illustrate most of the variation range of this character. Figures 214–217 illustrate much of the variation range in o.c.s. tip shape and width. The size of the posterior (third) sclerotized patch on the abdominal dorsum varies greatly, from almost as large as the other patches to a pair of tiny, bilaterally arranged patches.

Females: Few characters exhibit marked variation. The considerable variation in the ratio of stalk diameter to bowl diameter of the seminal receptacles is illustrated in Figures 295–298. The smaller (perhaps younger) adult females often have relatively wider stalks and less well-defined bowls than larger females. In two of the larger specimens the seminal receptacle bowls are rather well sclerotized. Although most individuals have a high CMT number and cheliceral microteeth of large size (Fig. 162), one adult female (included in the species sample) from Crater Lake, Oregon, and a large immature female from Fish Lake, Oregon, are at the low end of the CMT number range (Table 14) and have relatively much smaller cheliceral microteeth than do the rest of the specimens.

Specimens of uncertain identity. There are a few geographically scattered adult female specimens and two larger samples of females, which, although they are similar to *A. montanus* in most characters (including most diagnostic characters), have not been included in the species sample because, in addition to being from localities where *A. hageni* and *A. pacificus* are sympatric with *A. montanus,* they also agree more closely with *A. hageni* or *A. pacificus* in some of the characters diagnostic for the *A. montanus* sample. Two adult females composing one such sample from Pendleton, Oregon, have smaller *A. hageni*-like cheliceral microteeth and seminal receptacle stalks shaped like those of *A. hageni,* and are clearly intermediate in other characters, including the normally diagnostic ratio SL/SW. The other such sample of three adult females, from Manzanita Lake (Shasta Co.), California, is similar to *A. pacificus* in CMT number and cheliceral microtooth size. If, as is suspected, such specimens prove to be *A. montanus* and not variants of the other species or hybrids, then the diagnostic usefulness for *A. montanus* of CMT number, cheliceral microteeth size and, to a lesser extent, of SL/SW will be reduced.

Distribution. Chiefly the Great Basin region from Utah and Nevada north to Washington (Map 2).

Records. IDAHO. *Ada Co.:* near Boise, Cottonwood Gulch, 2 Nov. 1919, ♂. *Bannock Co.:* 7 mi. S of Downey, 5200 ft, ♀. — 1 mi. E of Pocatello in Pocatello Creek

Valley, 3♀. *Bonneville Co.:* Idaho Falls, Aug. 1966, ♂. *Canyon Co.:* Notus, Oct. 1932, ♂. *Latah Co.:* Moscow, 4 Nov. 1964, ♂. *Power Co.:* American Falls, 28 Sept. 1962, ♂. NEVADA. *Elko Co.:* Elko, ♂, ♀. *Washoe Co.:* Reno, ♀. — Washoe Valley, 11 Oct. 1967, ♂. — Verdi, 9 Oct. 1967, ♂. OREGON. *Harney Co.:* Steens Mtns., Fish Lake, 7200 ft, 16 Aug. 1958, ♂, ♀. *Klamath Co.:* Crater L. Nat'l Pk., Annie Springs, 6000 ft, 6–7 Aug. 1959, 2♂; ♀. UTAH. 8 Oct. 1927, ♂. *Box Elder Co.:* Raft R. Mtns., 8 mi. S of Lynn, 6 Sept. 1932, ♂, ♀. *Salt Lake Co.:* Little Cottonwood Canyon, Aug. 1900, ♂. — vicinity of Salt Lake City, Oct. 1927–1931, 4♂. — Salt Lake City, 21 Aug. 1931, ♂; 1929, ♂; 2♀. — Salt Lake City at Fort Douglas, 22 Oct. 1932, ♂. — Mouth of City Creek Canyon near Salt Lake City, ♀. — Mill Creek Canyon, 2♀. *Summit Co.:* N Fork Provo R. at Cobble Rest, 23 Sept. 1932, 3♂. *Utah Co.:* W side Utah Lake, ♀. *Wasatch Co.:* Strawberry Reservoir, Oct. 1928, ♂. WYOMING. *Lincoln Co.:* Cokeville, Aug. 1931, ♂.

Antrodiaetus hageni (Chamberlin)

Figures 125, 133, 141, 151, 163, 172, 181, 218–219, 256–257, 299–300. Map 2.

Brachybothrium hageni Chamberlin, 1917, Bull. Mus. Comp. Zool., 61(3): 74, pl. 5, fig. 9. Holotype male from Loon Lake, Stevens Co., Washington, 25 July 1882; in the Museum of Comparative Zoology; examined. –Roewer, 1942, Katalog der Araneae, 1: 190.

Antrodiaetus hageni: Bonnet (in part), 1955, Bibliographia Araneorum, 2: 335. –Thorn, 1967, British Columbia Prov. Mus. Annual Report, p. 1. (*Antrodiaetes*).

Description. See Tables 12–15, which contain measurements, meristic data, and diagnostic ratios for a sample of the species and for the holotype.

Male. Carapace: Figure 125. Setae numerous over most of pars thoracica, particularly dense along lateral border. *Chelicerae:* Figure 151. Entire upper ectal surface covered with scattered setae. *Pedipalps:* Figures 181, 218, 219. Tibia moderately swollen in lateral view; greatest diameter in lateral view at approximately 1/3 of distance from proximal to distal end. Tip of o.c.s. of palpus pointed (profile knifelike) and closely appressed to i.c.s. I.c.s. somewhat widened; tip well sclerotized and only weakly curved. *Leg I:* Figures 256, 257. Large dense group of macrosetae (nearly all ensiform) on prolateral surface of middle 1/3 of tibia. Another smaller group of macrosetae (great majority ensiform) on ventral aspect of retrolateral surface of distal 1/2 of tibia. Usually a few macrosetae on ventral surface between these two groups. Tibia weakly bowed laterally so that prolateral surface convex. One to 3 macrosetae (rarely none) ventrally at distal end of metatarsus. Metatarsus with thick, strong, retrolaterally and ventrally produced elbow just proximal of midpoint. *Abdomen:* 3 dorsal, heavily sclerotized, noncontinuous patches, occasionally with a fourth area of tiny sclerotized spots at bases of 2 to 4 large, transversely arranged setae. Anterior patch largest; second patch next largest. *Coloration:* (The holotype probably darkened during the 35 years between its collection and its description by Chamberlin. The following description is based on less discolored specimens.) Carapace pale gray-yellow to pale gray-orange. Sternum paler gray-yellow; labium darker yellow-gray. Chelicerae light yellow to orange-gray, usually darker than carapace. Patella, tibia, and metatarsus of leg I orange to red-brown, femur lighter. Pedipalps and other legs dorsally similar to carapace, ventrally lighter. Abdomen pale yellow-gray to light gray; dorsal sclerotized patches usually slightly darker light gray-yellow or gray-orange.

Female. Carapace: Figure 133. Setae cover pars thoracica as in male; quite dense along lateral border. *Sternum:* Figure 141. *Chelicerae:* Figures 163, 172. Microteeth positioned beside last 8 to last 3 macroteeth, except sometimes not extending beyond penultimate macroteeth and sometimes extending beyond last macrotooth. Most microteeth rather large. Entire upper ectal surface covered with scattered setae. *Abdomen:* Dorsal background setae rather short, slender, and distributed densely. *Genitalia:* Figures 299, 300. Seminal receptacles with well-sclerotized stalk and bowl; of moderate length and breath. Stalk not expanded basally. Bowl well developed; its border with bulb sharply defined. Floor of bursa copulatrix rather well sclerotized. *Coloration:* Pars thoracica pale gray-yellow; pars cephalica slightly darker yellow. Sternum similar to pars cephalica; labium and pedipalpal coxae a darker light brown. Chelicerae light to medium brown, much darker than carapace. Pedipalps and legs dorsally similar to carapace, ventrally lighter. Abdomen yellow-gray; tergite gray-yellow.

Diagnosis. The light color of the carapace and abdomen, the presence of setae over the entire upper ectal surface of the chelicerae (Fig. 172), and the abundance of setae on the pars thoracica help to separate both sexes of *A. hageni* from *A. pacificus* and *A. cerberus*, and are especially important for female determinations. *Males.* The shapes and macrosetae distribution patterns of the tibia and metatarsus of leg I (Figs. 256, 257; Table 12) are distinctive for this species, and include the best characters for identification. Ratios expressing the relative lengths of leg I segments, particularly the proportionately short metatarsus, help separate *A. hageni* from some of the other *unicolor* group species (See ITL/IML, IML/CL, and ITL/CL; Table 13.). AMD/CL (Table 13) helps separate this species, with its relatively small AME's, from several others possessing large eyes. Because of its especially large pedipalp, PTL and PFL (Table 13) distinguish *A. hageni* from *A. yesoensis*, *A. pugnax*, and *A. cerberus*. The pointed knifelike profile of the o.c.s. tip is not found in several other *unicolor* group species.

Females. The color and setation characters mentioned above are diagnostically quite helpful. The following characters are the most useful in separating *A. hageni* from the similar species, *A. montanus:* 1) Seminal receptacle stalks not expanded basally (Figs. 299, 300). 2) Sternum usually narrower (Fig. 141; SL/SW, Table 14). 3) Usually fewer cheliceral microteeth (CMT, Table 14), and these average slightly smaller (Fig. 163). 4) ALE's usually larger and closer together (Fig. 133; ALS/ALD, Table 14).

Variation. Variation within the available species sample for each sex is not markedly large or discontinuous for nearly all characters studied. *Males:* Noteworthy variation is found (Table 12) in the metatarsus I macrosetae arrangement and in the total number of macrosetae in the prolateral group on tibia I; however, the percent of ensiform macrosetae in this latter group has a small range of variation. Although usually separated, the two tibia I macrosetae groups are essentially continuous on the specimen (Baker, Oregon) with the highest tibia I macrosetae number. Tibia I and particularly metatarsus I of most specimens are more slender than those of the holotype (Fig. 256). *Females:* Figures 299 and 300 are representative of the small amount of variation found in seminal receptacle shape and arrangement.

Distribution. South central British Columbia, eastern Washington, and eastern Oregon (Map 2).

Records. BRITISH COLUMBIA. Trail, 23 Oct. 1934, ♂. — E edge of Trail, 1500 ft, 13 July 1967 (♂), 2♀. — Summerland, 15 Aug. 1925, ♂. —Vernon, ♂. — Kamloops, ♀. — Kelowna, ♀. — Oliver, ♀. — E side Vaseux Lake, near Oliver, 1000 ft, ♀. OREGON. *Baker Co.:* Spring Creek, NW of Baker, 4000 ft, 16 Oct. 1955, ♂; 11–12 Sept. 1960, 2♂. — 1/2 mi. E of Baker, 3500 ft, 2♀. WASHINGTON. *Stevens Co.:* Loon Lake, 25 July 1882, ♂.

Antrodiaetus cerberus new species

Figures 126, 134, 164, 182, 220–221, 258–259, 301–302. Map 2.

Type specimens. Holotype male from Cedar Lake (N of Leadpoint), Stevens Co., Washington, May 1962 (W. Ivie); in the American Museum of Natural History. Three males and 5 females from type locality with same date designated as paratypes and deposited in AMNH and MCZ. The specific name is a noun in apposition after *Cerberus*, the dog of Greek mythology that guards the entrance to Hades.

Description. See Tables 12–15, which contain measurements, meristic data, and diagnostic ratios for a sample of the species and for the holotype.

Male. Carapace: Figure 126. Few setae on pars thoracica, most of these concentrated along lateral border. *Chelicerae:* Large area on upper ectal surface without setae. *Pedipalps:* Figures 182, 220, 221. Tibia moderately swollen in lateral view; greatest diameter in lateral view at between 1/3 to 1/2 of distance from proximal to distal end, but dorsal and ventral outlines in lateral view nearly parallel except near both ends. Tip of o.c.s. of palpus blunt and closely appressed to i.c.s. Tip of i.c.s. only moderately heavily sclerotized; side against o.c.s. very thin and translucent. *Leg I:* Figures 258, 259. Compact group of relatively elongate and slender macrosetae (over 80% are ensiform) centered at about 2/3 of distance from proximal to distal end of tibia on prolateral surface. Another smaller group of similarly slender macrosetae (over 80% are ensiform) scattered along retrolateral aspect of ventral surface of tibia; distalmost macroseta about 3/4 of distance from proximal to distal end of tibia. One to several slender macrosetae (most ensiform) on ventral surface between these two groups. Tibia swollen prolaterally and ventrally at macrosetae groups. Usually 2 (occasionally 1) macrosetae ventrally at distal end of metatarsus. Metatarsus rather sinuous in ventral view. *Abdomen:* 3 dorsal, heavily sclerotized, usually continuous patches; posterior patch smallest. *Coloration:* Carapace gray-yellow (tan). Sternum and pedipalpal coxae pale yellow; labium darker yellow-gray. Chelicerae similar to carapace. Pedipalps and legs dorsally similar to carapace, ventrally lighter. Abdomen pale yellow-gray dorsally; darker gray ventrally posterior of book lungs. Dorsal sclerotized patches gray-yellow, similar to carapace. Faint dark chevronlike markings on abdominal dorsum behind sclerotized patches.

Female. Carapace: Figure 134. Setae very sparsely scattered over pars thoracica, most along lateral border. *Chelicerae:* Figure 164. Microteeth positioned beside last 7 to last 4 macroteeth and often extend beyond last macrotooth. Largest microteeth moderately large. Most of upper ectal surface of chelicerae, except for patchy small to medium-sized bare area, covered with scattered setae. *Genitalia:* Figures 301, 302. Seminal receptacles with well-sclerotized stalk and bowl; of moderate length and breadth. Stalk not or very slightly expanded basally. Bowl well developed; its border with bulb well defined. Floor of bursa copulatrix quite weakly sclerotized. *Coloration:* Carapace gray-yellow (often a deep tan). Sternum similar or slightly lighter gray-yellow; labium and pedipalpal coxae a darker light brown. Chelicerae brown, markedly darker than carapace. Legs and pedipalps dorsally similar to carapace, ventrally lighter. Abdomen pale yellow-gray except for dark dorsal area which becomes chevronlike posteriorly; tergite similar to carapace.

Diagnosis. Males. The shapes and macrosetae distribution patterns of the tibia and metatarsus of leg I (Figs. 258, 259; Table 12) are distinctive for this species. AMD and ratios involving AMD (Fig. 126; Table 13) are helpful in separating *A. cerberus* from most other *unicolor* group species because of its small AME's. Because of the proportionately short tarsus

I and metatarsus I of this species, ITL/ITarL and other ratios incorporating ITarL and IML are excellent diagnostic characters (Fig. 259; Table 13). Clear separation from *unicolor* group species with strongly swollen pedipalpal tibia is obtained by using PTT and PTT/CL (Fig. 182; Table 13). The partly translucent i.c.s. tip (Fig. 220) is not found in any other sympatric *unicolor* group species. The absence of setae over a large part of the upper ectal surface of the chelicerae allows quick separation from *A. hageni* and *A. montanus*.

Females. As is true for the males, AMD, AMD/CL, and other ratios incorporating AMD are helpful in separating *A. cerberus* females, with their small AME's, from several other *unicolor* group species (Fig. 134; Table 14). *A. cerberus* has a proportionately short tarsus IV and metatarsus I, and a proportionately long tibia IV, metatarsus IV, and femur I, so that the following ratios are the best characters for separating *A. cerberus* from the following sympatric (or nearly sympatric) species: *A. pacificus*, IVML/IML; *A. hageni*, IFL/IVFL, IFL/IML; *A. montanus*, IFL/IML, IVML/IML; *A. pugnax*, IVTL/IVTarL, IVML/IVTarL. The very sparse setation of the pars thoracica, the small setaless area on the upper ectal surface of the chelicerae, and the darker pigmentation on the abdominal dorsum distinguish this species from *A. hageni;* the latter two characters help separate *A. cerberus* from *A. montanus*.

Variation. Within the small species sample, there is no marked variation in any characters studied. *Females.* Noteworthy variation occurs in the slenderness of the seminal receptacle stalks and in the ratio, stalk length/bowl length. Most of the range of this variation is illustrated by Figures 301 and 302.

Distribution. Known only from the type locality in northeastern Washington (Map 2).

Records. WASHINGTON. *Stevens Co.:* Cedar Lake, N of Leadpoint, May 1962, 4♂, 5♀. Another collection of 3 males made during "April to June" 1968 by H. Cusic at the same locality has been reported to me (W. Ivie, personal communication), but not examined.

Antrodiaetus yesoensis (Uyemura)

Figures 142, 165, 183, 222–223, 260–261, 303. Map 3.

Acattyma yesoensis Uyemura, 1942 Acta Arach., 7(1): 31, pls. 1–2. Holotype male from Yafugyu Tyo, Kitamiguni, Hokkaido, Japan, 15 June 1941; destroyed during World War II (Yaginuma, 1957). –Yaginuma, 1957, Acta Arach., 14(2): 52, pl. 3, fig. 1.

Antrodiaetus yesoensis: Yaginuma, 1960, Spiders of Japan in Colour, p. 20, fig. 13, pl. 1, fig. 3.

Description. See Tables 12–14, which contain measurements, meristic data, and diagnostic ratios for a sample of the species. Unfortunately this description is based on two males and only one female. The female specimen is possibly immature, but is nevertheless included since no females of this species have heretofore been described.

Male. Carapace: Setae sparse on pars thoracica. *Chelicerae:* Large setaless area on upper ectal surface. *Pedipalps:* Figures 183, 222, 223. Tibia strongly swollen in lateral view; greatest diameter in lateral view near midpoint. Tip of o.c.s. of palpus blunt and closely appressed to i.c.s. Tip of i.c.s. well sclerotized and weakly curved. *Leg I:* Figures 260, 261. Large dense group of macrosetae (great majority ensiform) centered at 1/2 to 2/3 of distance from proximal to distal end of tibia on prolateral surface. Small group of scattered macrosetae on retrolateral aspect of ventral surface of distal half of tibia. Macrosetae absent on ventral surface between these two groups. Tibia bowed laterally so that prolateral surface convex. No macrosetae on metatarsus. Metatarsus relatively short; in ventral view tapered toward distal end and sinuous. *Abdomen:* 3 broadly continuous, dorsal, heavily sclerotized patches. *Coloration:* Carapace light brown; border between pars cephalica and pars thoracica slightly darker. Sternum and pedipalpal coxae pale yellow-gray; labium a darker light brown. Chelicerae slightly lighter than carapace. Patella, tibia, and metatarsus of leg I very dark red-brown; femur lighter red-brown, but darker than carapace. Pedipalps and other legs dorsally similar to carapace, ventrally lighter. Posterior-dorsal surface of abdomen and dorsal sclerotized patches medium brown or gray-brown; rest light gray-yellow.

Female. Carapace: Setae sparse on pars thoracica, densest along lateral border. *Sternum:* Figure 142. *Chelicerae:* Figure 165. Microteeth relatively small; positioned beside last 5 macroteeth. Large setaless area on upper ectal surface. *Genitalia:* Figure 303. Seminal receptacles with only moderately sclerotized and somewhat elongate stalk and bowl; bowl weakly developed. Border of bowl with bulb not sharply defined. Bursa copulatrix very weakly sclerotized. *Coloration:* Carapace gray-yellow to light brown; pars thoracica slightly lighter than pars cephalica. Sternum similar to pars thoracica. Labium, pedipalpal coxae, and chelicerae almost medium brown, darker than carapace. Pedipalps and legs dorsally similar to carapace, ventrally lighter. Abdomen pale yellow-gray; tergite darker, similar to pars thoracica.

Diagnosis. Males. The shapes and the macrosetae distribution patterns of the tibia and metatarsus of leg I (Figs. 260, 261; Table 12) are in combination distinctive for this species. Because of the relatively short metatarsus and tarsus of leg I (Fig. 261), the ratios and measurements ITL/IML, IML, IML/ITarL, ITL/ITarL and ITarL (Table 13) are very helpful in separating this species from others in the *unicolor* group. The strongly swollen pedipalpal tibia and the relatively short pedipalpal femur (Fig. 183) are features also useful in identifying this species (PTT/PTL, PTL, and PFL/CL; Table 13). *Females.* On the basis of the single, possibly immature specimen available, the following character states best separate this species from others in the *unicolor* group: 1) Low CMT and IVMT numbers (Fig. 165, Table 14). 2) Some proportionately short leg segments resulting in some potentially useful leg segment ratios (Table 14). 3) Relatively long seminal receptacles with poorly developed bowls (Fig. 303). With a larger, definitely adult sample, it is likely that few of these characters will prove to be diagnostic.

Distribution. The Japanese island of Hokkaido (Map 3).

Records. JAPAN. *Hokkaido:* Abashiri, 12 Aug. 1955, ♂. — Asahigawa, 26 Aug. 1961, ♂. — ♀. In addition to the holotype male record (Yafugyu Tyo, Kitamiguni, Hokkaido, 15 June 1941), a few other *A. yesoensis* records, all from Hokkaido, are listed in the literature (Yaginuma, 1957 and 1960).

THE *LINCOLNIANUS* GROUP

Descriptive diagnosis. Male: AMD proportionately small to medium; AME's well separated (AMD/AMS, AMD/CL; Table 13). Setae scattered over much of labium; setaless area just posterior of labium relatively small. Pedipalpal tibia elongate (PTT/PTL, Table 13); greatest diameter in lateral view distal of midpoint. O.c.s. of palpus weakly to moderately heavily sclerotized; surface smooth to weakly file-like; relatively narrow apically. Relatively inconspicuous group of enlarged setae on prolateral surface of tibia I. *Female:* Carapace moderately to quite broad (CW/CL, Table 14). Labium setation as in male. Cheliceral microteeth proportionately large and numerous (CMT, Table 14). Tarsus IV claws (both prolateral and retrolateral) usually with only 0 to 2 teeth (IVCTR, Table 14). Leg IV segments proportionately short, particularly femur and metatarsus (IVML/CL, Table

14). Bursa copulatrix lacks median partition; lining very weakly sclerotized. Seminal receptacles small in proportion to body size, stalk short to moderately long, bowl poorly to well developed, and receptacles not closely paired.

Antrodiaetus lincolnianus (Worley)

Figures 119, 127, 135, 152, 166, 184, 224–225, 262–263, 304–305. Map 1.

Brachybothrium lincolnianum Worley, 1928, Ann. Ent. Soc. America, 21(4): 619, fig. 1. Holotype male and 3 male paratypes from Lincoln, Lancaster Co., Nebraska, March and April 1923. Holotype and 2 of 3 paratypes are in the Museum of Comparative Zoology; examined. –Roewer, 1942, Katalog der Araneae, 1: 190. –Bonnet, 1955, Bibliographia Araneorum, 2: 906.

Description. See Tables 12–15, which contain measurements, meristic data, and diagnostic ratios for a sample of the species and for the holotype.

Male. Carapace: Figure 127. Broad. *Chelicerae:* Figure 152. *Pedipalps:* Figures 184, 224, 225. Femur, patella, particularly tibia markedly elongate. Greatest diameter of tibia in lateral view at approximately 2/3 of distance from proximal to distal end. O.c.s. of palpus weakly sclerotized; surface nearly smooth; tip very thin, spatulate and erect. Tip of i.c.s. weakly sclerotized, short and straight; even with tip of o.c.s. in unflexed condition. Sperm reservoir looped very loosely. (Left palpus of holotype missing and tips of both o.c.s. and i.c.s. of right palpus are partially broken.) *Leg I:* Figures 262, 263. Distal 1/2 to 1/3 of prolateral surface of tibia with group of enlarged, decumbent, attenuate setae. Tibia slightly swollen near distal end. Metatarsus with 2 (rarely 1) usually attenuate macrosetae ventrally at distal end. Metatarsus nearly straight; slightly shortened and thickened. *Abdomen:* 3 continuous, dorsal, heavily sclerotized patches; second patch largest. *Coloration:* Carapace medium brown to darker red-brown. Sternum, labium, and pedipalpal coxae pale yellow-gray. Chelicerae medium brown. Pedipalps and legs dorsally similar to carapace, ventrally lighter; leg I darkest. Abdomen medium brown to dark gray; tergite lighter gray-yellow.

Female. Carapace: Figures 119, 135. Broad. *Chelicerae:* Figures 119, 166. Microteeth positioned beside last 6 macroteeth and sometimes extending beyond last macrotooth. *Genitalia:* Figures 304, 305. Seminal receptacles with very short, weakly sclerotized stalk and weakly developed bowl; border of bowl with bulb not sharply defined. *Coloration:* Pars cephalica light brown to medium brown; pars thoracica slightly paler. Sternum similar to pars thoracica; labium and pedipalpal coxae darker. Chelicerae medium to dark orange-brown or brown. Pedipalps and legs dorsally similar to carapace, ventrally lighter. Abdomen medium brown; tergite yellow-gray. (The observed specimens have been in alcohol over 18 years and may be significantly discolored.)

Diagnosis. Males. The very elongate slender pedipalpal tibia (Fig. 184) (PTT/PTL, Table 13), the palpus structure (Figs. 224, 225), and the small AME (AMD/AMS, AMD, AMD/CL, etc., Table 13) are distinctive for this species. The group of enlarged setae on the prolateral surface of tibia I consists of setae that are more decumbent and usually shorter (Fig. 262) than those of *A. stygius* and *A. apachecus*. Also, the darker abdominal coloration and frequent possession of metatarsal macroseta B help distinguish this species from *A. stygius* and *A. apachecus*. *Females.* (It must be kept in mind that the female samples for the *lincolnianus* group species are quite small; a future analysis of larger samples may show that some or all of the few characters now listed as diagnostic are not diagnostic.) *A. lincolnianus* has a larger CMT number and smaller IVMT number than *A. stygius* or *A. apachecus*. The stalk and bowl portion of *A. lincolnianus* seminal receptacles is more weakly sclerotized and smaller, and its border with the bulb less well defined (Figs. 304, 305) than that of the other *lincolnianus* group species. Also the carapace of *A. lincolnianus* (Fig. 119) is broader than that of *A. stygius* (CW/CL, Table 14).

Variation. Variation in both sexes within the available species sample is small for all characters studied.

Distribution. Eastern Kansas and eastern Nebraska (Map 1).

Records. KANSAS. *Jefferson Co.:* Kansas Univ. Nat. Hist. Reservation near Lawrence. 28 Feb. 1964, ♂. NEBRASKA. *Lancaster Co.:* Lincoln, 5–19 April 1923, 3♂; 18 Mar. 1926, ♂; 18 Mar. 1951, ♂; 2♀. Two unexamined literature records (Scheffer, 1906), almost certainly of misidentified *A. lincolnianus* specimens (Scheffer misidentified the specimens as *Brachybothrium robustum* Simon.), are worth adding tentatively. KANSAS. *Ottawa Co.:* Delphos. *Riley Co.:* Manhattan, 5 April, 2♂.

Antrodiaetus stygius new species

Figures 117–118, 128, 136, 143, 153, 167, 185, 226–228, 264–265, 306–307. Map 1.

Antrodiaetus lincolnianus: Peck (not Worley, 1928), 1966, American Midl. Nat., 76(1): 153.

Type specimens. Holotype male from Bennett Springs State Park, Dallas Co., Missouri, 4 September 1967 (F. A. Coyle), in the Museum of Comparative Zoology. Four males and 3 females from type locality with same date designated as paratypes and deposited in MCZ and AMNH. The specific name is a Latin adjective meaning "Stygian."

Description. See Tables 12–15, which contain measurements, meristic data, and diagnostic ratios for a sample of the species and for the holotype.

Male. Carapace: Figure 128. Somewhat narrowed. *Chelicerae:* Figure 153. Anterior-dorsal prominence weak. *Pedipalps:* Figures 185. 226–228. Tibia somewhat elongate; greatest diameter in lateral view at between 1/2 to 2/3 of distance from proximal to distal end. O.c.s. of palpus moderately strongly sclerotized; surface roughened distally but not filelike; tip thin, spatulate, and bent away from i.c.s. Tip of i.c.s. relatively well sclerotized, gradually tapering, and rather strongly curved; extends well beyond tip of o.c.s. in unflexed condition. Sperm reservoir looped tightly. *Leg I:* Figures 264, 265. Distal 2/3 of prolateral surface of tibia with group of scattered, enlarged, erect attenuate setae. Tibia not swollen distally. Metatarsus with or without 1 attenuate macroseta ventrally at distal end. Metatarsus rather slender and slightly sinuous in ventral view. *Abdomen:* 3 sometimes continuous, dorsal, heavily sclerotized patches; third patch smallest, sometimes faint or consisting of bilateral pair of small patches. *Coloration:* Pars cephalica light brown to medium brown; pars thoracica paler yellow-gray. Sternum and palpal coxae slightly lighter than pars thoracica. Labium and chelicerae slightly lighter than pars cephalica. Pedipalps and legs dorsally similar to adjacent part of carapace, ventrally like sternum. Abdominal dorsum pale yellow-gray; tergite darker yellow-gray.

Female. Carapace: Figures 117, 118, 136. Somewhat narrowed. *Sternum:* Figure 143. *Chelicerae:* Figures 117, 118, 167. Microteeth positioned beside last 7 to last 6 macroteeth, except sometimes not extending beyond penultimate macrotooth. *Genitalia:* Figures 306, 307. Seminal receptacles with well-sclerotized stalk and bowl; border of bowl with bulb well defined. *Coloration:* Pars cephalica medium brown; pars thoracica paler yellow-gray. Sternum similar to pars cephalica; labium and palpal coxae darker brown. Chelicerae dark brown. Pedipalps and legs dorsally similar to carapace, ventrally lighter. Abdomen pale yellow-gray; tergite darker yellow-gray.

Diagnosis. Males. The palpus structure (particularly the form of the o.c.s. tip) (Figs. 226–228) distinguishes this species from both *A. lincolnianus* and *A. apachecus.* Because of its relatively long tarsus I and metatarsus I (Fig. 265), this species can be readily separated from *A. lincolnianus* by ITL/IML and ITL/ITarL (Table 13); IFL/ITarL and ITL/ITarL (Table 13) help to separate it from *A. apachecus.* CW/CL aids separation of *A. stygius* from the broader carapaced *A. lincolnianus. Females.* IVML/CL and IML/CL (Table 14) help separate this species, with its proportionately short metatarsi, from *A. lincolnianus.*

Variation. Males. There is substantial variation in the shape and prominence of the anterior-dorsal protuberance of the chelicerae, but such variation is continuous and as extensive within the type locality sample as within the whole species sample. The chelicerae of most specimens are similar to Figure 153. The palpi of the Warrensburg, Missouri, and Imboden, Arkansas, specimens are less heavily sclerotized than those in the type locality sample. Most of the variation in the form of the o.c.s. tip falls within the range illustrated by Figures 227 and 228. *Females.* Figures 306 and 307 illustrate the range of seminal receptacle form in the three brooding females.

Distribution. Missouri and northern Arkansas (Map 1).

Records. ARKANSAS. *Lawrence Co.:* Imboden, 1935, 2♂. MISSOURI. *Dallas Co.:* Bennett Springs St. Pk., 4 Sept. 1967, 5(♂), 3♀. *Johnson Co:* Warrensburg, 1–10 Oct. 1962, ♂.

Antrodiaetus apachecus new species

Figures 154–156, 168, 186, 229–232, 266–267, 308–309. Map 4.

Type specimens. Holotype male from Wet Canyon (about 4 mi. SE of Mount Graham), Graham Mountains, Graham Co., Arizona, 14 September 1950 (W. J. Gertsch), in the American Museum of Natural History. Two males and 1 female from type locality with same date designated as paratypes and deposited in MCZ and AMNH. The specific name is derived from the name of the Apache Indian tribe.

Description. See Tables 12–15, which contain measurements, meristic data, and diagnostic ratios for a sample of the species and for the holotype.

Male. Chelicerae: Figures 154–156. *Pedipalps:* Figures 186, 229–232. Tibia somewhat elongate; greatest diameter in lateral view at between 5/8 to 2/3 of distance from proximal to distal end. O.c.s. of palpus moderately strongly sclerotized; surface roughened distally, sometimes weakly filelike; tip moderately thickened and erect. Tip of i.c.s. relatively well sclerotized, gradually tapering, and curved; extends far beyond tip of o.c.s. in unflexed condition. Sperm reservoir looped tightly. *Leg I:* Figures 266, 267. Distal 2/3 of prolateral surface of tibia with group of scattered, enlarged, suberect attenuate setae. Tibia not swollen distally. Metatarsus with 1 (rarely without) attenuate or ensiform macroseta positioned ventrally at distal end. Metatarsus very slightly sinuous in ventral view. *Abdomen:* 3 frequently continuous, dorsal, heavily sclerotized patches; third patch smallest and most weakly sclerotized, sometimes consisting of bilateral pair of small patches. *Coloration:* Pars cephalica light brown to medium brown; pars thoracica slightly lighter. Sternum pale gray-yellow; labium and palpal coxae slightly darker gray-yellow. Chelicerae similar to pars thoracica. Pedipalps and legs dorsally similar to carapace, ventrally lighter; leg I darkest. Abdomen gray-yellow or yellow-gray; tergites darker yellow-gray or brown.

Female. Chelicerae: Figure 168. Microteeth positioned beside last 8 to last 5 macroteeth and sometimes extend beyond last macrotooth. *Genitalia:* Figures 308, 309. Seminal receptacles with well-sclerotized stalk and bowl; border of bowl with bulb rather well defined. *Coloration:* Carapace yellow-gray to light brown; pars cephalica often slightly darker than pars thoracica. Sternum similar to pars thoracica; labium and palpal coxae darker. Chelicerae light brown to medium brown. Pedipalps and legs dorsally similar to carapace, ventrally lighter. Abdomen yellow-gray; tergite darker yellow-gray.

Diagnosis. Males. The palpus structure (particularly the form of the o.e.s. tip) (Figs. 229–232) distinguishes this species from both *A. lincolnianus* and *A. stygius.* The enlarged setae on the prolateral surface of tibia I are less erect in this species (Fig. 266) than in *A. stygius.* The normally large EGS number of this species (Table 13) may also help separate it from *A. stygius. Females.* The following ratios help distinguish this species, with its relatively long leg I and short leg IV segments, from the other *lincolnianus* group species (Table 14): IFL/IVFL and IVML/IML (from *A. stygius*); IVML/CL and IVTL/CL (from *A. lincolnianus*).

Variation. Males. Substantial variation occurs in the anterior-dorsal profile of the chelicerae, with most of the specimens similar to those in Figure 156. Much of the total range of this variation occurs within the Alpine, Arizona, sample (Figs. 154, 155). The slenderness of the pedipalpal tibia varies considerably. The PTT/PTL range for the three Graham Mountain, Arizona, specimens is 0.324–0.343. PTT/PTL values of three other specimens fall within this range. However, the other two known specimens (from near La Cueva, New Mexico, and Heber, Arizona) have PTT/PTL values of 0.308 and 0.297 respectively. Figures 230–232 illustrate most of the variation observed in the shape of the o.e.s. tip. There is noteworthy variation in the maximum size of the enlarged setae on the prolateral surface of tibia I; on several specimens these setae are only slightly larger than the background setae. *Females.* The bowl portion of the seminal receptacles is not as well developed in the Flagstaff, Arizona, specimen (Fig. 308) as in the Graham Mountain, Arizona, specimen (Fig. 309). There is considerable variation in AME diameter (Table 14).

Since *A. apacheus* is apparently limited to forest habitats which presently occur only at high elevations in the southwestern U. S., it consists of at least several populations each separated by extensive areas of lower unfavorable dry habitats. Consequently the gene flow between these populations is probably greatly reduced, certainly part of the explanation for the geographic variation indicated by the few specimens presently available.

Distribution. Mountains of Arizona and New Mexico (Map 4).

Records. ARIZONA. *Apache Co.:* ♀; 4 mi. N of Alpine, Alpine Divide Campgrd., 8500 ft, 18 July 1965, 2♂. *Cochise Co.:* Chiricahua Mtns., Rustlers Camp, 19 Aug. 1955, ♂. *Coconino Co.:* Flagstaff, ♀. *Graham Co.:* Graham Mtns., Wet Canyon, 14 Sept. 1950, 3♂, ♀. *Navajo Co.:* 6 mi. N of Heber, Overgaard Camp, 17 Sept. 1950, ♂. NEW MEXICO. *Sandoval Co.:* 2 mi. NW of La Cueva, Horseshoe Springs Campgrd., 7800 ft, 31 July 1961, ♂.

THE *RORETZI* GROUP

Antrodiaetus roretzi (L. Koch)

Figures 114–116, 129, 137, 144, 157, 169, 187, 233, 268–269, 310–312. Map 3.

Acattyma Roretzii L. Koch, 1878, Verh. zool.-bot. Ges. Wien, 27: 761, pl. 16, figs. 23–25. Two immature female syntypes from Japan; in the British Museum of Natural History; both examined. These are now designated lectotype and paralectotype and are so labeled. –Uyemura, 1942, Acta Arach., 7(1): 31, 35, 36, fig. p. 37.

Acattyma roretzii: Komatsu, 1942, Acta Arach., 7(2): 57. –Roewer, 1942, Katalog der Araneae, 1: 189. –Komatsu, 1961, Arach. Soc. E. Asia, p. 7, pl. 1, fig. 1.

Acattyma roretzi: Pocock, 1901, Proc. Zool. Soc. London, 1: 207, 211. –Bonnet, 1955, Bibliographia Araneorum, 2: 141.

Antrodiaetus roretzi: Yaginuma, 1960, Spiders of Japan in Colour, p. 19, fig. 14, pl. 1, fig. 2.

Description. See Tables 12–14, which contain measurements, meristic data, and diagnostic ratios for a sample of the species.

Male. Carapace: Figures 114, 129. Proportionately broad. Ocular tubercle projects strongly forward. Few setae on pars thoracica. *Sternum:* Similar to female sternum. *Chelicerae:* Figures 114, 157. Anterior-dorsal prominence broadly rounded. Upper ectal setation as in female. *Pedipalps:* Figures 187, 233. Tibia moderately swollen in lateral view; greatest diameter in lateral view just proximal of midpoint. O.c.s. of palpus heavily sclerotized, very broad, and curved in cross section to partially envelop i.c.s.; much of surface file-like, particularly at tip. I.c.s. extends slightly beyond tip of o.c.s. in unflexed condition; i.c.s. tip well sclerotized and straight. *Leg I:* Figures 268, 269. Group of long erect macrosetae (all attenuate) centered just proximal of midpoint of tibia on prolateral surface and prolateral aspect of ventral surface. Other macrosetae rare or absent on tibia. Tibia weakly bowed downward. No macrosetae on metatarsus. Metatarsus weakly sinuous in ventral view. *Abdomen:* 2 dorsal, heavily sclerotized, noncontinuous patches with transverse row of 2–4 tiny sclerotized spots behind second patch. Second patch much larger and thicker than first. *Coloration:* Carapace pale orange-brown to darker red-brown; pars cephalica darker than pars thoracica. Sternum and pedipalpal coxae like pars thoracica. Labium and chelicerae brown to dark red-brown; darker than pars cephalica. Patella and more distal segments of leg I similar to chelicerae; femur dorsally almost as dark, ventrally lighter. Pedipalps and other legs dorsally similar to adjacent part of carapace, ventrally lighter. Abdominal dorsum yellow-gray; tergite yellow-brown.

Female. Carapace: Figures 115, 116, 137. Proportionately broad. Few setae on pars thoracica. *Sternum:* Figure 144. Broad. Relatively large area just posterior to labium and all of labium (except anterior and lateral border) devoid of setae. *Chelicerae:* Figures 115, 116, 169. Microteeth positioned beside last 6 to last 4 macroteeth; occasionally extend beyond last macrotooth. Microteeth quite small. Large area on upper ectal surface devoid of setae. *Genitalia:* Figures 310–312. Seminal receptacles with rather weakly sclerotized stalk and bowl. Stalk long and relatively slender; not expanded at base. Bowl weakly developed; its border with bulb weakly defined. Receptacles clearly paired with each pair opening into widely separate parts of bursa copulatrix. Median partition divides bursa copulatrix into two lateral pockets. *Coloration:* Carapace and sternum orange-brown. Labium, pedipalpal coxae, and chelicerae darker brown. Pedipalps and legs dorsally similar to carapace, ventrally slightly lighter. Abdominal dorsum light gray-brown; tergite darker orange-brown.

Diagnosis. Males. The extremely wide palpal o.c.s. (Fig. 233) distinguishes this species from all other *Antrodiaetus* species. The shapes and macrosetae distribution patterns of the tibia and metatarsus of leg I are also distinctive (Table 12); no other *Antrodiaetus* species has such long erect macrosetae in the prolateral tibia I macrosetae group or has this group centered proximal of the midpoint (Fig. 268). The absence of other tibia I macrosetae separates *A. roretzi* from the *unicolor* group species. The rather large setaless area on the labium and adjacent part of the sternum and, to a lesser extent, the form of the carapace (Fig. 114) are distinctive. Because of *A. roretzi's* proportionately long metatarsus I (Fig. 269), ratios such as IML/CL, ITL/IML, and IML/ITarL (Table 13) will separate this species from most other *Antrodiaetus* species.

Females. The division of the bursa copulatrix into two lateral pouches by a median partition (Fig. 312) distinguishes *A. roretzi* from all other *Antrodiaetus* species. The combination of a long slender seminal receptacle stalk, a weakly developed bowl, and the closely paired nature of the seminal receptacles (Figs. 310, 311) is also distinctive. (Only some eastern *A. pacificus* females approach this condition.) The setaless area on the labium and adjacent part of the sternum is proportionately larger than on all other *Antrodiaetus* species. Low CMT number (Fig. 169, Table 14) distinguishes this species from most others. CW/CL (Table 14) separates this species, with its broad carapace and sternum (Figs. 115, 144), from most *unicolor* group species. The cheliceral microteeth are markedly smaller (Fig. 169) than those of the *lincolnianus* group species and there are more (3–4) leg IV claw teeth.

Distribution. Central portion of the Japanese island of Honshu (Map 3).

Records. JAPAN (Honshu Island). *Kanagawa Pref.:* Yokohama, 2 Dec. 1942, ♂. *Mie Pref. Nagano Pref. Saitama Pref.:* 3 May, 1957, ♂. *Tochigi Pref.:* 2♀. There are literature records for this species from Tokyo Pref. and Gifu Pref. (S side of Mt. Kinkazan) as well as literature records of some of the prefectures listed above (Komatsu, 1942 and 1961; Ohe, 1966; Uyemura, 1936; Yaginuma, 1960 and 1962; Yamamoto, 1942).

Aliatypus Smith, 1908

Aliatypus Smith, 1908, Ann. Ent. Soc. America, 1(4): 231. Type species by monotypy *Atypoides californicus* Banks, 1896, Jour. New York Ent. Soc., 4(4): 88. –Bonnet, 1955, Bibliographia Araneorum, 2(1): 225.

Descriptive diagnosis. Carapace: Figures 319, 320. Thoracic groove either an irregular pit (may be transverse or weakly longitudinal), reduced to a shallow depression, or absent. Usually a large seta medially on ocular prominence just anterior to AME's. *Sternum:* Figure 321. Labium usually proportionately small and strongly inclined from plane of sternum. *Chelicerae:* Figures 322, 323. Female with row of 6 to 9 macroteeth on prolateral side of closed fang; another row of 3–6 macroteeth on retrolateral side. Microteeth scattered between these rows. Female rastellum very strong. Male without anterior-dorsal prominence. *Pedipalps:* Figures 324, 325. Male patella very elongate, nearly as long as tibia; tibia elongate and swollen. O.c.s. and i.c.s. of palpus relatively weakly to moderately sclerotized. One edge of o.c.s. folded for most of its length to enclose embolus. I.c.s. extends to but not beyond o.c.s. tip; intimately combined distally with o.c.s. to envelop embolus. *Legs:* Figures 326, 327. One to 4 (rarely more than 1) trichobothria dorsally on female metatarsus IV. Zero to 2 (usually 0) teeth on each of prolateral and retrolateral claws of female tarsus IV. Male tibia I and metatarsus I with macrosetae scattered ventrally over most of length of both segments. *Spinnerets:* Figure 328. Three pairs (AL, PM, PL); all functional; AL's 2-segmented (segmentation may be vestigial) with at least several spigots clustered at tip of distal segment. *Genitalia:* Figures 329, 330. Bursa copulatrix very weakly sclerotized and often bilobed anteriorly. Seminal receptacles paired; uniformly unor very weakly sclerotized; stalks very narrow, sinuous. *Behavior:* Burrow entrance a trapdoor.

Remarks. This genus, which contains a single described species, *Aliatypus californicus* (see Smith, 1908; Gertsch, 1949), and several undescribed species, has not been found outside of southern California. Its populations appear to be widely scattered from the San Francisco Bay region and the central Sierra Nevada Mountains south to near the Mexican border. A revision of *Aliatypus* is in preparation.

TABLE 12. MACROSETATION OF TIBIA AND METARSUS OF MALE LEG I OF *ANTRODIAETUS* SPECIES. See Fig. 70 for identification of metatarsal macrosetae. The number of legs (out of the total given with a particular pattern) also with a macroseta E (= *) or F (= √) are given in parentheses. Range and median given for tibia macrosetae groups.

			Metatarsal macrosetae pattern frequency distribution								
	N	N legs	Absent	A	AB	ABC	ABCD	ABD	AC	ACD	AD
*unicolor**	110	195	15	145(1)	1				26(1)	6(3)	1(1)
robustus	14	28		5	20	2			1		
*pacificus**	106	106	103						3(3)		
occultus	21	21	21								
pugnax√	24	24		6	13(5)	2(2)	2(2)	1(1)			
montanus	26	26	4	21						1	
hageni	8	15	1	6	6			2			
cerberus	4	8		1	7						
yesoensis	2	4	4								
lincolnianus	6	12		1	11						
stygius	8	16	6	10							
apachecus	8	16	4	12							
roretzi	2	3	3								

			Tibia macrosetae groups					
			Number of macrosetae in prolateral group			Number of macrosetae in retrolat.-vent. group		
	N	N legs	Total	Ensiform	% ensi.	Total	Ensiform	% ensi.
unicolor	110	195	5–49 21	4–36 14	33–100	3–8 5	0–8 3	0–100
robustus	14	23	11–35 16	0–1 0	0–8	5–10 6	0–1 0	0–17
pacificus	106	106	15–55 38	0–7 0	0–27	3–17 9	0–8 1	0–100
occultus	21	21	19–38 29	7–23 14	37–74	2–9 5	0–3 1	0–60
pugnax	24	24	10–21 15	9–17 12	67–100	2–9 6	2–7 5	50–100
montanus	26	26	14–44 28	9–36 21	48–93	6–23 14	2–13 7	33–86
hageni	8	8	15–56 37	15–56 37	93–100	11–16 14	11–16 14	87–100
cerberus	4	8	15–26 17	15–26 17	88–100	6–14 8	6–12 8	86–100
yesoensis	2	4	36–50 46	35–45 41	88–95	7	3–7 5	43–100
lincolnianus	6	6	0			0		
stygius	8	8	0			0		
apachecus	8	8	0			0		
roretzi	2	3	20–25 24	0	0	0		

Table 13. Measurements, meristic character, and diagnostic ratios for adult males of *Antrodiaetus* species. The most useful diagnostic characters are circled. Range, mean, and standard deviation given for measurement characters (in mm) and ratios. Range and mean given for EGS. (EGS could be tallied on only one *A. lincolnianus* specimen.)

	N	CL	CW	OQW	ALS	ALD	AMS
unicolor	104	4.0-6.6 5.47±.57	2.97-5.24 4.241±.479	0.82-1.34 1.104±.102	0.38-0.63 0.498±.053	0.23-0.41 0.330±.036	0.07-0.19 0.132±.027
robustus	11	5.4-6.6 6.03±.38	4.33-5.27 4.800±.318	1.07-1.35 1.192±.093	0.47-0.66 0.564±.059	0.28-0.40 0.350±.037	0.11-0.22 0.153±.033
pacificus	105	4.1-6.9 5.61±.61	3.20-5.50 4.498±.486	0.83-1.32 1.082±.101	0.40-0.68 0.515±.057	0.26-0.47 0.343±.043	0.08-0.24 0.140±.038
occultus	21	4.2-6.2 5.32±.50	3.50-5.01 4.310±.389	0.95-1.23 1.092±.088	0.43-0.60 0.510±.042	0.27-0.37 0.333±.036	0.11-0.18 0.146±.020
pugnax	24	4.2-5.6 4.90±.43	3.31-4.56 3.875±.397	0.78-1.06 0.947±.083	0.39-0.57 0.457±.050	0.24-0.36 0.310±.030	0.11-0.20 0.140±.029
montanus	23	5.0-7.0 5.82±.51	4.07-5.80 4.847±.436	0.95-1.17 1.064±.057	0.49-0.63 0.565±.037	0.24-0.33 0.290±.031	0.11-0.22 0.177±.029
hageni	8	5.5-6.3 5.88±.30	4.29-5.24 4.772±.343	0.88-1.15 1.002±.093	0.40-0.57 0.497±.054	0.28-0.34 0.311±.022	0.14-0.18 0.160±.012
cerberus	4	5.2-5.4 5.26	4.18-4.44 4.265	0.90-0.95 0.930	0.45-0.47 0.457	0.25-0.31 0.275	0.15-0.18 0.162
yesoensis	2	4.6-5.1 4.85	3.73-4.07 3.900	1.06 1.060	0.42-0.51 0.465	0.27-0.33 0.300	0.16-0.17 0.165
lincolnianus	6	4.6-5.7 5.06±.40	3.92-4.86 4.263±.342	0.82-1.01 0.905±.065	0.40-0.53 0.455±.043	0.21-0.25 0.230±.013	0.18-0.22 0.205±.016
stygius	8	4.0-5.0 4.64±.36	3.24-4.07 3.606±.268	0.79-0.96 0.886±.058	0.40-0.47 0.435±.024	0.23-0.29 0.259±.019	0.18-0.22 0.192±.014
apachecus	8	4.6-5.4 5.00±.37	3.73-4.67 4.054 .322	0.83-1.07 0.931±.086	0.42-0.56 0.476±.053	0.24-0.30 0.266±.021	0.14-0.26 0.195±.043
roretzi	2	5.1-5.3 5.19	4.18-4.52 4.350	1.01-1.03 1.020	0.48-0.53 0.505	0.29-0.30 0.295	0.13-0.14 0.135

	AMD	IFL	ITL	IML	ITarL	PTL	PTL
unicolor	0.11-0.20 0.158±.017	3.84-6.40 5.097±.466	2.56-4.22 3.438±.394	3.01-5.35 4.280±.556	1.80-2.78 2.314±.219	2.33-3.92 3.215 .384	2.14-3.50 2.878±.368
robustus	0.14-0.18 0.162±.013	5.05-6.06 5.537±.321	3.31-3.95 3.625±.221	3.99-4.93 4.539±.312	2.33-2.78 2.547±.159	3.27-3.92 3.665±.222	2.94-3.43 3.216±.162
pacificus	0.11-0.18 0.136±.024	3.84-6.25 5.109±.586	2.48-4.22 3.248±.407	3.16-5.80 4.540±.568	1.69-3.05 2.356±.300	2.78-4.52 3.709 .407	2.41-3.92 3.164 .333
occultus	0.13-0.19 0.158±.018	3.99-5.73 4.801±.436	2.63-3.69 3.133±.278	3.09-4.22 3.671±.331	1.88-2.41 2.153 .178	2.78-3.88 3.297±.265	2.45-3.39 2.882±.250
pugnax	0.11-0.14 0.120±.008	3.77-5.31 4.584±.421	2.56-3.54 3.113±.281	2.86-4.07 3.561±.347	1.69-2.75 2.235 .247	2.60-3.77 3.065±.331	2.33-3.20 2.798±.240
montanus	0.11-0.16 0.133±.012	5.31-6.82 5.998±.464	3.65-4.75 4.140±.315	4.18-5.57 4.732±.396	2.56-3.46 2.912±.228	3.54-4.67 3.999±.294	3.05-4.03 3.452±.262
hageni	0.11-0.12 0.119±.004	5.20-5.65 5.484±.179	3.58-3.95 3.779±.156	3.92-4.44 4.221±.172	2.37-2.78 2.616±.159	3.61-4.07 3.837±.139	3.27-3.54 3.377±.107
cerberus	0.09 0.090	4.82-5.27 5.010	3.24-3.61 3.360	3.46-3.92 3.605	1.96-2.18 2.032	3.09-3.24 3.135	2.56-2.75 2.607
yesoensis	0.11 0.110	4.26-4.56 4.410	3.01-3.20 3.105	3.16-3.24 3.200	1.92-1.96 1.940	2.71-3.01 2.860	2.48-2.56 2.520
lincolnianus	0.05-0.07 0.063±.008	4.37-5.69 4.948±.431	3.09-4.07 3.522 .327	3.09-4.07 3.465±.334	1.80-2.07 1.925±.089	3.77-4.75 4.234±.165	3.39-4.26 3.774±.123
stygius	0.09-0.12 0.102±.010	4.10-5.31 4.660±.391	2.78-3.58 3.157±.246	2.97-3.95 3.520±.303	1.80-2.41 2.107±.202	3.31-3.95 3.585±.215	2.86-3.31 3.050±.163
apachecus	0.09-0.11 0.102±.009	4.41-5.84 4.915±.478	3.09-3.92 3.342 .285	3.16-4.33 3.561±.446	1.80-2.48 2.039 .239	3.43-4.44 3.680±.331	2.82-3.61 3.025±.250
roretzi	0.13-0.14 0.135	5.08-5.12 5.100	3.20-3.27 3.235	4.22-4.37 4.295	2.11 2.110	3.61 3.610	2.78 2.780

Table 13 (continued).

	PTT	EGS	AMD/CL	AMD/AMS	ITL/CL	IML/CL	IFL/IML
unicolor	0.98-1.58 1.291±.112	12-51 25.7	0.022-0.035 0.029± .003	0.67-2.42 1.251±.309	0.54-0.69 0.628±.028	0.67-0.88 0.780±.043	1.14-1.30 1.193±.041
robustus	1.25-1.52 1.388±.081	40-64 52.9	0.024-0.032 0.027± .002	0.73-1.54 1.100±.228	0.57-0.65 0.601±.022	0.72-0.83 0.753±.035	1.16-1.26 1.221±.031
pacificus	1.01-1.56 1.273±.112	17-56 33.8	0.018-0.030 0.024± .004	0.50-2.00 1.016±.316	0.51-0.70 0.578±.035	0.73-0.91 0.808±.042	1.03-1.22 1.128±.044
occultus	1.16-1.51 1.349±.103	10-40 22.5	0.026-0.033 0.030± .002	0.81-1.50 1.095±.162	0.57-0.62 0.589±.018	0.64-0.76 0.691±.027	1.25-1.38 1.308±.037
pugnax	1.03-1.32 1.165±.085	17-44 31.1	0.021-0.029 0.025± .002	0.60-1.18 0.883±.156	0.57-0.68 0.635±.027	0.64-0.81 0.727±.048	1.16-1.42 1.290±.083
montanus	1.20-1.45 1.308±.083	31-62 45.5	0.020-0.026 0.023± .002	0.59-1.09 0.770±.120	0.67-0.77 0.712±.019	0.77-0.87 0.814±.024	1.19-1.34 1.268±.036
hageni	1.23-1.41 1.326±.063	29-59 42.0	0.019-0.022 0.020± .001	0.67-0.80 0.745±.042	0.64-0.66 0.642±.013	0.70-0.74 0.718±.021	1.26-1.32 1.300±.020
cerberus	1.01-1.09 1.040	32-46 41.0	0.016-0.017 0.017	0.50-0.60 0.556	0.61-0.69 0.638	0.65-0.72 0.683	1.34-1.42 1.391
yesoensis	1.12-1.20 1.160	30-39 34.5	0.023 0.023	0.65-0.69 0.667	0.62-0.66 0.640	0.63-0.69 0.661	1.35-1.41 1.378
lincolnianus	0.81-1.01 0.897±.038	63	0.010-0.015 0.013± .002	0.27-0.37 0.309±.038	0.67-0.71 0.695±.018	0.67-0.71 0.683±.020	1.38-1.48 1.429±.036
stygius	0.90-1.05 0.982±.058	25-55 35.5	0.019-0.025 0.022± .002	0.45-0.63 0.533±.052	0.64-0.72 0.680±.027	0.71-0.79 0.758±.028	1.29-1.38 1.325±.029
apachecus	0.94-1.07 0.980±.048	32-69 50.8	0.016-0.024 0.021± .003	0.36-0.78 0.553±.149	0.63-0.72 0.668±.030	0.66-0.80 0.710±.042	1.27-1.49 1.385±.071
roretzi	1.09 1.090	22-39 30.5	0.024-0.026 0.026	1.00 1.000	0.62-0.63 0.623	0.82-0.83 0.827	1.17-1.20 1.188

	IFL/ITarL	ITL/IML	ITL/ITarL	IML/ITarL	PFL/CL	PTT/CL	PTT/PTL
unicolor	1.96-2.43 2.200±.114	0.74-0.85 0.805±.027	1.35-1.62 1.484±.068	1.60-2.06 1.845±.111	0.53-0.63 0.586±.022	0.20-0.27 0.237±.014	0.38-0.54 0.452±.038
robustus	2.11-2.33 2.176±.088	0.77-0.83 0.799±.019	1.36-1.53 1.424±.052	1.71-1.87 1.782±.050	0.58-0.65 0.608±.022	0.21-0.24 0.230±.008	0.40-0.47 0.432±.021
pacificus	1.84-2.46 2.174±.119	0.65-0.81 0.717±.041	1.26-1.53 1.381±.069	1.74-2.12 1.929±.106	0.61-0.71 0.661±.022	0.20-0.25 0.227±.014	0.33-0.48 0.404±.026
occultus	2.07-2.42 2.231±.115	0.81-0.90 0.854±.024	1.38-1.55 1.456±.063	1.60-1.84 1.706±.059	0.59-0.65 0.620±.019	0.23-0.27 0.254±.010	0.45-0.49 0.468±.016
pugnax	1.86-2.24 2.059±.116	0.82-0.91 0.875±.029	1.31-1.60 1.397±.053	1.48-1.74 1.597±.064	0.57-0.72 0.625±.036	0.22-0.25 0.238±.008	0.37-0.44 0.417±.013
montanus	1.98-2.20 2.061±.061	0.83-0.91 0.875±.018	1.36-1.50 1.422±.032	1.56-1.76 1.625±.046	0.63-0.73 0.688±.020	0.20-0.25 0.226±.013	0.35-0.40 0.380±.014
hageni	2.02-2.20 2.100±.071	0.88-0.90 0.895±.013	1.39-1.51 1.446±.043	1.56-1.70 1.616±.045	0.63-0.68 0.653±.021	0.21-0.23 0.225±.007	0.37-0.41 0.393±.011
cerberus	2.42-2.50 2.466	0.92-0.93 0.932	1.65-1.66 1.653	1.76-1.80 1.773	0.58-0.60 0.595	0.19-0.20 0.197	0.39-0.41 0.399
yesoensis	2.22-2.32 2.273	0.95-0.99 0.970	1.57-1.63 1.600	1.64-1.65 1.649	0.58-0.59 0.589	0.23-0.24 0.239	0.45-0.47 0.460
lincolnianus	2.43-2.75 2.567±.107	1.00-1.04 1.017±.018	1.71-1.96 1.826±.087	1.71-1.96 1.797±.094	0.81-0.87 0.837±.021	0.17-0.18 0.178±.005	0.23-0.24 0.238±.003
stygius	2.12-2.28 2.214±.061	0.87-0.94 0.898±.022	1.42-1.54 1.501±.042	1.60-1.75 1.672±.052	0.71-0.85 0.774±.041	0.20-0.22 0.212±.007	0.31-0.34 0.322±.011
apachecus	2.29-2.54 2.416±.074	0.89-0.99 0.943±.044	1.52-1.72 1.646±.007	1.64-1.86 1.746±.066	0.66-0.82 0.737±.053	0.18-0.21 0.196±.011	0.29-0.34 0.325±.015
roretzi	2.39-2.43 2.417	0.75-0.76 0.753	1.51-1.55 1.533	2.00-2.07 2.036	0.68-0.71 0.695	0.20-0.22 0.210	0.39 0.392

Table 14. Measurements, meristic characters, and diagnostic ratios for adult females of *Antrodiaetus* species. The most useful diagnostic characters are circled. Range, mean, and standard deviation given for measurement characters (in mm) and ratios. Range, mean, and mode given for meristic characters. Number of females containing large maturing eggs or with brood is given in parentheses after N. For the last 7 species the CT and CMT statistics include counts of both right and left chelicerae.

	N	CL	CW	OQW	ALS	ALD	AMS	AMD
unicolor	225(158)	5.4-10.7 7.38±.95	3.88-8.06 5.434±.758	1.08-2.02 1.447±.181	0.45-0.93 0.666±.083	0.27-0.57 0.381±.054	0.11-0.34 0.198±.036	0.11-0.22 0.159±.020
robustus	13(5)	6.2-9.3 7.26±.99	4.71-7.23 5.577±.810	1.33-1.83 1.506±.180	0.63-0.95 0.780±.097	0.29-0.45 0.374±.063	0.18-0.31 0.228±.035	0.14-0.20 0.160±.020
pacificus	56(24)	5.4-8.1 6.74±.59	4.07-6.37 5.160±.464	1.06-1.69 1.321±.114	0.47-0.77 0.621±.071	0.26-0.47 0.355±.043	0.12-0.29 0.184±.034	0.11-0.18 0.131±.018
pugnax	24(13)	4.2-5.9 5.02±.51	3.20-4.71 3.848±.413	0.87-1.29 1.057±.121	0.38-0.61 0.494±.070	0.23-0.36 0.309±.031	0.11-0.21 0.146±.029	0.09-0.14 0.112±.012
montanus	12(5)	6.9-9.2 8.14 .65	5.50-7.87 6.589±.703	1.34-1.83 1.532±.137	0.67-1.02 0.827±.091	0.33-0.45 0.387±.042	0.19-0.40 0.295±.055	0.12-0.18 0.157±.017
hageni	7(2)	6.5-8.3 7.54±.63	5.01-6.59 5.783±.586	1.20-1.58 1.386±.126	0.54-0.73 0.659±.065	0.34-0.47 0.396±.041	0.19-0.25 0.214±.026	0.12-0.16 0.140±.017
cerberus	4(2)	6.6-7.5 6.99	5.16-5.84 5.472	1.39-1.41 1.400	0.64-0.71 0.677	0.33-0.36 0.340	0.19-0.22 0.202	0.11-0.12 0.117
yesoensis	1(0)	5.5	4.41	1.12	0.57	0.31	0.20	0.11
lincolnianus	2(1)	6.7-6.9 6.84	5.35-5.73 5.540	1.32-1.34 1.330	0.61-0.66 0.635	0.29-0.33 0.310	0.24-0.25 0.245	0.09-0.11 0.100
stygius	3(3)	5.9-6.9 6.34	4.59-5.20 4.847	1.23-1.45 1.303	0.56-0.68 0.630	0.24-0.38 0.320	0.19-0.25 0.220	0.11-0.12 0.117
apachecus	3(0)	5.9-6.8 6.37	4.86-5.27 5.097	1.20-1.41 1.287	0.45-0.68 0.590	0.32-0.37 0.343	0.14-0.25 0.210	0.11-0.12 0.117
roretzi	2(0)	6.6-6.9 6.77	5.50-5.80 5.650	1.29-1.30 1.295	0.72-0.77 0.745	0.31-0.32 0.315	0.21 0.210	0.14-0.15 0.145

	SL	SW	IFL	ITL	IML	ITarL	IVFL	IVTL
unicolor	2.94-6.03 4.084±.587	2.45-5.08 3.444±.501	3.84-7.69 5.238±.672	2.29-4.71 3.191±.414	2.11-5.08 3.236±.423	1.13-2.26 1.629±.193	3.61-7.65 5.085±.643	2.10-4.37 2.970±.362
robustus	3.27-5.08 3.980±.582	3.01-4.44 3.532±.481	4.29-6.37 5.065±.664	2.52-3.84 2.969±.427	2.45-3.77 2.934 .433	1.28-1.88 1.512 .179	4.18-6.14 4.875 .629	2.33-3.50 2.763±.361
pacificus	3.01-4.90 3.903 .395	2.60-3.99 3.165±.298	4.07-6.22 5.094±.469	2.41-3.69 3.104±.301	2.48-3.88 3.150±.304	1.28-1.96 1.604 .160	3.69-5.76 4.609±.392	2.07-3.16 2.612 .216
pugnax	2.37-3.54 2.878±.312	2.07-2.97 2.461±.261	2.97-4.37 3.625 .406	1.77-2.63 2.199 .254	1.73-2.56 2.144±.262	0.90-1.28 1.084±.116	2.86-4.22 3.470±.366	1.62-2.48 2.030 .199
montanus	3.84-5.57 4.727±.470	3.39-5.05 4.190±.487	5.20-7.31 6.143±.636	3.16-4.52 3.804±.401	3.24-4.71 3.938±.443	1.54-2.07 1.759 .154	5.12-7.01 5.933 .564	3.05-4.07 3.486±.301
hageni	3.92-5.05 4.479 .393	3.20-3.84 3.551 .215	4.82-6.22 5.614±.447	2.97-3.84 3.439±.308	3.05-3.92 3.461 .290	1.47-1.84 1.677±.125	4.75-6.18 5.537±.474	2.82-3.61 3.229±.293
cerberus	3.92-4.29 4.085	3.24-3.61 3.425	5.12-5.73 5.367	3.01-3.39 3.190	2.94-3.27 3.105	1.50-1.65 1.577	4.86-5.35 5.077	2.90-3.16 3.012
yesoensis	3.24	2.71	3.99	2.37	2.33	1.13	3.88	2.18
lincolnianus	3.84-4.07 3.955	3.20-3.54 3.370	4.82-5.05 4.935	2.86-3.09 2.975	2.78-2.90 2.840	1.31-1.35 1.330	4.63-4.67 4.650	2.63-2.71 2.670
stygius	3.39-3.84 3.563	3.09-3.46 3.213	4.07-4.71 4.307	2.45-2.86 2.597	2.22-2.63 2.370	1.09-1.28 1.153	3.88-4.52 4.117	2.18-2.48 2.307
apachecus	3.61-4.10 3.813	3.24-3.39 3.300	4.22-4.97 4.683	2.60-3.05 2.873	2.45-2.86 2.687	1.28-1.47 1.343	3.88-4.41 4.193	2.26-2.41 2.360
roretzi	3.84-4.07 3.955	3.46-3.61 3.535	5.08-5.42 5.250	2.94-3.16 3.050	2.97-3.16 3.065	1.43-1.54 1.485	4.82-5.08 4.950	2.48-2.71 2.595

Table 14 (continued).

	IVML	IVTarL	CT	CMT	IVCTR	PTSP	PTSR	IMS	IVMT
unicolor	3.00-6.33 4.385±.527	1.28-2.03 1.664±.163	8-15 11.4(11)	6-23 12.0(12)	1-6 3.5(3)	5-10 6.9(7)	2-7 3.8(4)	9-15 11.6(11)	9-20 14.2(15)
robustus	3.35-4.86 3.942±.470	1.31-1.73 1.505±.125	11-14 12.1(11)	11-18 13.9(13)	2-5 3.6(3)	4-7 5.9(6)	3-4 3.5(3)	9-14 10.6(10)	10-17 12.9(13)
pacificus	3.05-4.82 3.918±.348	1.28-1.80 1.531±.114	9-14 10.9(11)	9-24 16.8(19)	1-6 4.0(4)	5-12 8.2(8)	3-5 3.9(4)	9-15 12.3(13)	9-21 15.1(14)
pugnax	2.56-3.69 3.018±.290	1.01-1.43 1.220±.109	9-14 11.3(11)	8-17 12.1(12)	4-6 4.2(4)	4-8 5.9(5)	2-5 3.2(3)	9-13 11.1(11)	8-15 12.2(12)
montanus	4.52-5.99 5.201±.456	1.65-2.11 1.789 .135	10-17 12.4(12)	16-29 21.9(23)	3-5 3.9(4)	6-9 7.5(7)	2-4 3.4(4)	12-16 12.9(13)	14-19 16.5(17)
hageni	3.99-5.24 4.810±.376	1.47-1.84 1.710±.139	11-12 12.0(12)	13-18 15.1(15)	2-5 4.0(4)	5-11 7.4(6)	3-7 4.3(3)	13-15 13.7(13)	11-17 15.0(15)
cerberus	4.26-4.71 4.510	1.47-1.58 1.512	11-13 12.0	12-19 15.7	4-5 4.5	6-8 6.7	3 3.0	11-13 11.7	12-18 15.0
yesoensis	3.16	1.24	11	7	4	8	4	10	9
lincolnianus	3.84-3.92 3.880	1.47-1.50 1.485	12-13 12.5	23-27 25.0	0-1 0.5	4-8 6.0	3-4 3.5	13 13.0	5-7 6.0
stygius	3.05-3.65 3.263	1.20-1.35 1.250	12-14 13.0	14-19 17.0	0-2 1.3	4-7 5.3	2-4 3.0	11-13 12.0	8-12 10.0
apachecus	3.09-3.46 3.327	1.35-1.39 1.363	12-13 12.3	10-16 13.0	0-2 1.0	4-6 5.0	3-4 3.3	11-12 11.3	10-11 10.3
roretzi	3.80-4.03 3.915	1.43-1.50 1.465	11 11.0	6 6.0	4 4.0	11-12 11.5	7 7.0	15 15.0	15 15.0

	CW/CL	AMD/CL	ALS/ALD	SL/SW	IFL/CL	IML/CL	IVMCR
unicolor	0.69-0.79 0.735±.020	0.016-0.025 0.022 .002	1.04-2.55 1.776±.296	1.13-1.27 1.187±.036	0.63-0.76 0.710±.023	0.35-0.48 0.439±.023	5-10 7.7(8)
robustus	0.73-0.79 0.767 .015	0.021-0.024 0.022± .001	1.61-2.75 2.124 .330	1.08-1.16 1.126 .021	0.68-0.72 0.698±.014	0.38-0.42 0.404 .012	6-9 7.3(7)
pacificus	0.71-0.79 0.766 .021	0.015-0.025 0.020± .003	1.37-2.65 1.768 .240	1.13-1.35 1.234 .052	0.71-0.80 0.756 .024	0.42-0.51 0.467±.020	6-9 7.1(7)
pugnax	0.72-0.80 0.765 .023	0.018-0.026 0.022± .002	1.26-2.04 1.607±.232	1.10-1.24 1.169±.031	0.68-0.77 0.721±0.28	0.39-0.48 0.426 .021	5-9 7.5(7)
montanus	0.77-0.85 0.808±.024	0.016-0.023 0.019 .002	1.67-2.63 2.157±.302	1.06-1.18 1.130±.033	0.70-0.79 0.754±.027	0.44-0.52 0.483 .022	5-9 7.3(7)
hageni	0.72-0.79 0.766±.031	0.017-0.020 0.019± .001	1.55-1.90 1.669±.130	1.21-1.37 1.260±.056	0.73-0.77 0.745±.017	0.43-0.48 0.459 .018	[illegible] [illegible](7)
cerberus	0.77-0.80 0.782	0.016-0.017 0.017	1.77-2.15 1.997	1.15-1.22 1.193	0.76-0.79 0.768	0.43-0.46 0.444	7-9 8.[illegible]
yesoensis	0.79	0.020	1.83	1.19	0.71	0.41	5
lincolnianus	0.79-0.82 0.809	0.013-0.016 0.015	1.85-2.27 2.062	1.15-1.20 1.175	0.71-0.73 0.721	0.41-0.42 0.415	8-9 8.5
stygius	0.76-0.77 0.764	0.017-0.020 0.018	1.64-2.70 2.048	1.09-1.12 1.109	0.66-0.69 0.679	0.35-0.38 0.373	6-9 8.[illegible]
apachecus	0.78-0.82 0.801	0.016-0.020 0.018	1.22-2.00 1.739	1.14-1.21 1.155	0.71-0.76 0.735	0.40-0.44 0.422	5-9 7.[illegible]
roretzi	0.83-0.84 0.834	0.021-0.022 0.021	2.25-2.48 2.367	1.10-1.13 1.119	0.76-0.78 0.775	0.45-0.46 0.453	6-7 6.5

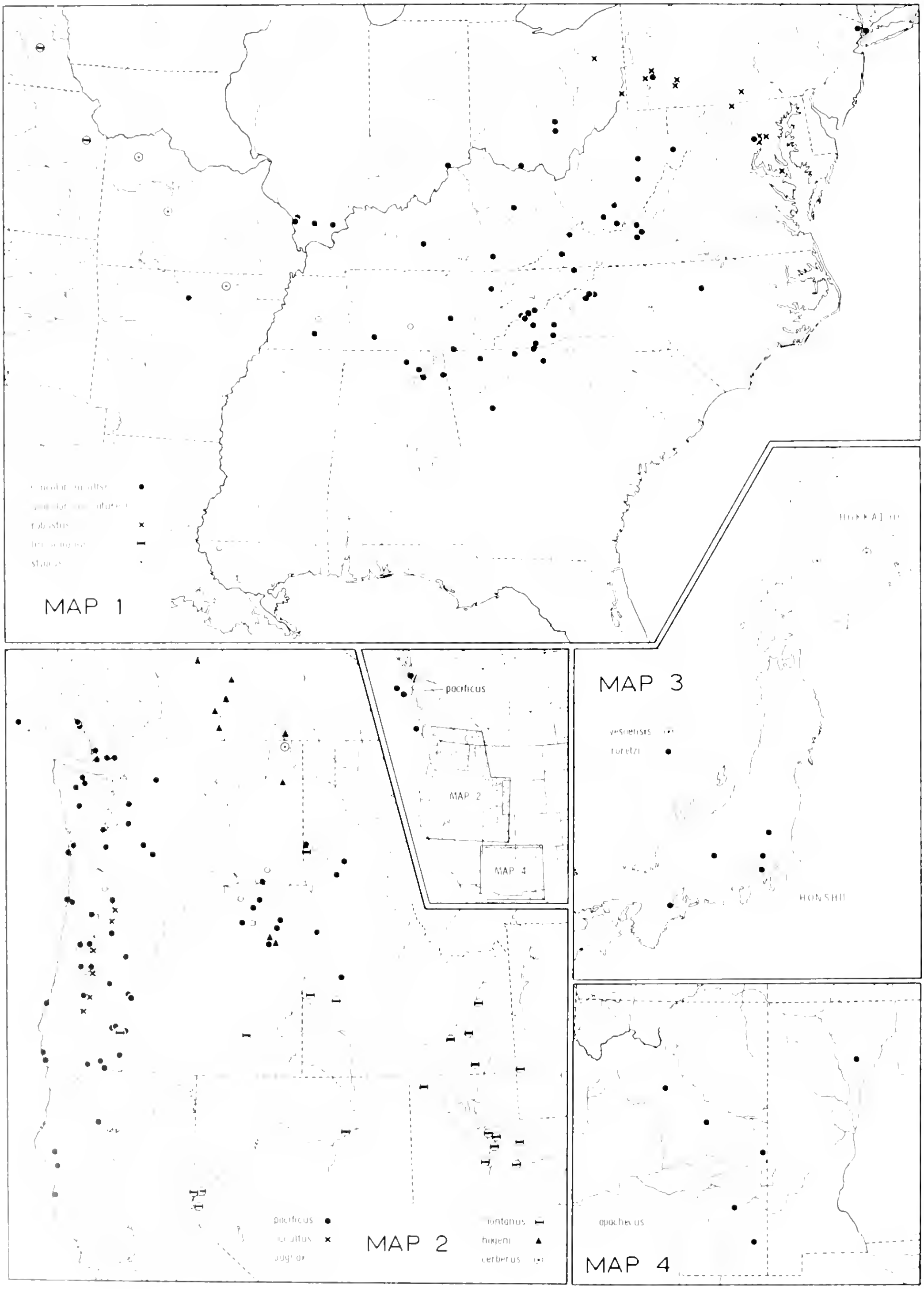
Table 14 (concluded).

	IVTL/CL	IVML/CL	IFL/IML	IFL/IVFL	IVTL/IVTarL	IVML/IVTarL	IVML/IML
unicolor	0.34-0.46 0.403 ± .022	0.49-0.68 0.596 .040	1.48-1.81 1.620 ± .059	0.98-1.11 1.030 .026	1.58-1.92 1.783 .093	2.33-3.06 2.632 .142	1.16-1.57 1.358 ± .063
robustus	0.37-0.39 0.381 ± .008	0.52-0.57 0.554 ± .015	1.65-1.78 1.730 .034	1.01-1.05 1.039 ± .011	1.77-2.02 1.830 .104	2.47-2.81 2.613 ± .107	1.28-1.41 1.349 .040
pacificus	0.35-0.41 0.388 ± .015	0.51-0.65 0.582 .032	1.50-1.69 1.618 .050	1.04-1.17 1.107 .036	1.60-1.85 1.706 .072	2.38-2.79 2.558 .119	1.09-1.38 1.247 ± .066
pugnax	0.37-0.43 0.404 .017	0.56-0.66 0.601 .026	1.60-1.74 1.693 .037	1.00-1.10 1.044 .021	1.52-1.74 1.663 .054	2.26-2.70 2.474 .101	1.31-1.50 1.413 .059
montana	0.40-0.48 0.429 .021	0.60-0.65 0.639 .016	1.48-1.61 1.562 .041	1.00-1.07 1.035 .018	1.58-2.16 1.953 .156	2.40-3.18 2.912 .224	1.24-1.39 1.324 .046
hageni	0.41-0.43 0.428 .088	0.61-0.67 0.638 .015	1.58-1.68 1.623 .032	1.00-1.03 1.014 .011	1.81-2.08 1.889 .104	2.59-2.92 2.814 .070	1.31-1.46 1.391 .060
cerberus	0.42-0.44 0.431	0.62-0.67 0.645	1.70-1.75 1.728	1.04-1.07 1.057	1.93-2.10 1.992	2.84-3.15 2.983	1.44-1.47 1.453
yesoensis	0.39	0.56	1.71	1.02	1.75	2.54	1.35
lincolnianus	0.38-0.39 0.390	0.56 0.567	1.73-1.74 1.738	1.04-1.08 1.061	1.75-1.84 1.798	2.56-2.66 2.613	1.35-1.38 1.367
stygius	0.35-0.38 0.364	0.48-0.53 0.514	1.79-1.86 1.819	1.04-1.05 1.046	1.81-1.88 1.846	2.54-2.70 2.607	1.36-1.38 1.376
apacheus	0.35-0.40 0.371	0.50-0.54 0.521	1.70-1.80 1.743	1.09-1.13 1.116	1.67-1.79 1.731	2.29-2.54 2.440	1.21-1.26 1.239
roretzi	0.37-0.39 0.383	0.57-0.58 0.578	1.71 1.713	1.05-1.07 1.060	1.73-1.81 1.770	2.66-2.68 2.672	1.27 1.277

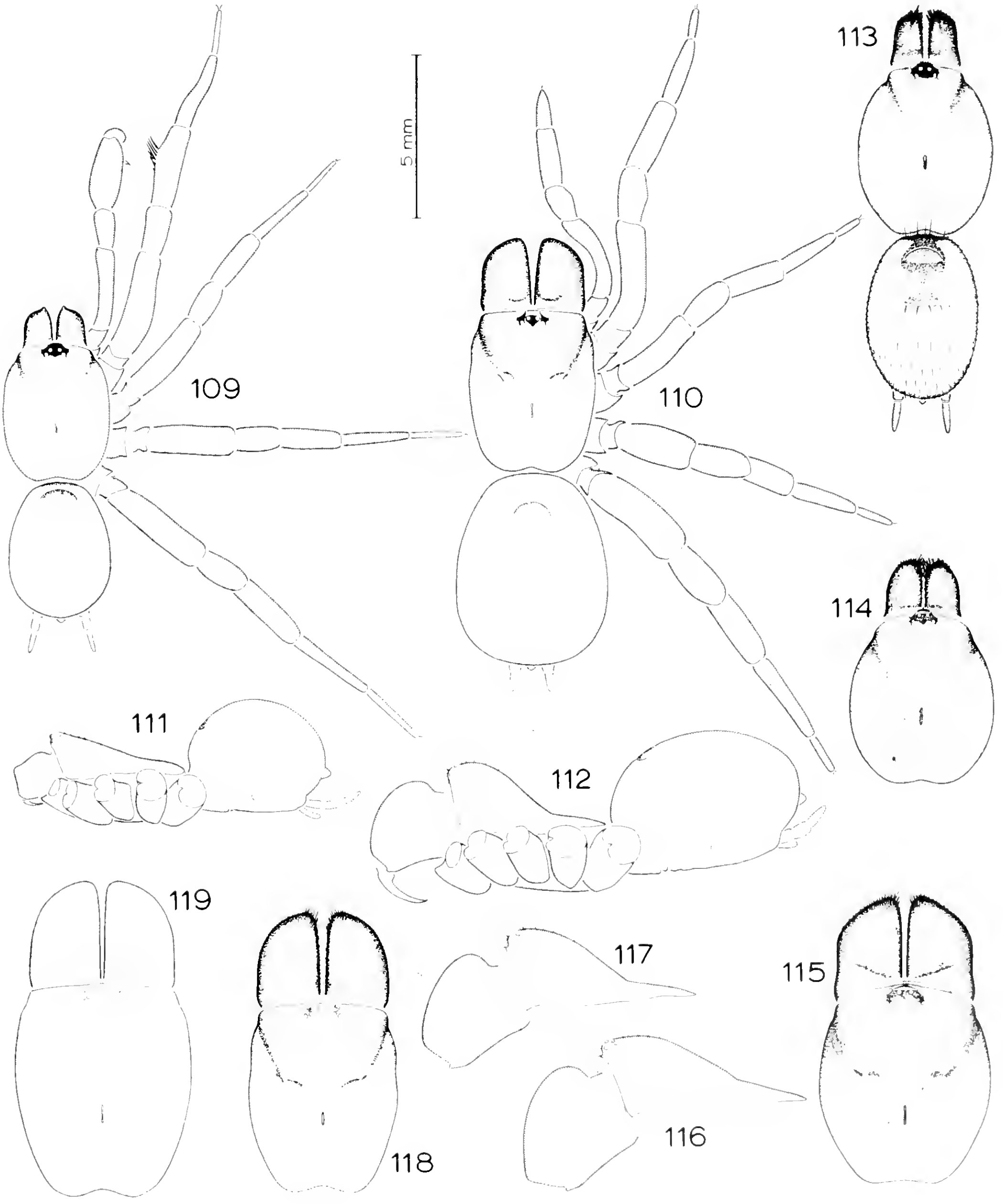
TABLE 15. MEASUREMENTS (IN MM) AND MERISTIC CHARACTER VALUES FOR HOLOTYPE AND LECTOTYPE SPECIMENS OF *ANTRODIAETUS* SPECIES.

Leg IV segments distal of femur missing on *A. robustus* lectotype. Pedipalp segments flattened out of shape on *A. lincolnianus* holotype. * MM is metarsus I macrosetae pattern; TP is number of macrosetae (total, ensiform) on prolateral surface of tibia I; and TRV is number of macrosetae (total, ensiform) on retrolateral aspect of ventral surface of tibia I.

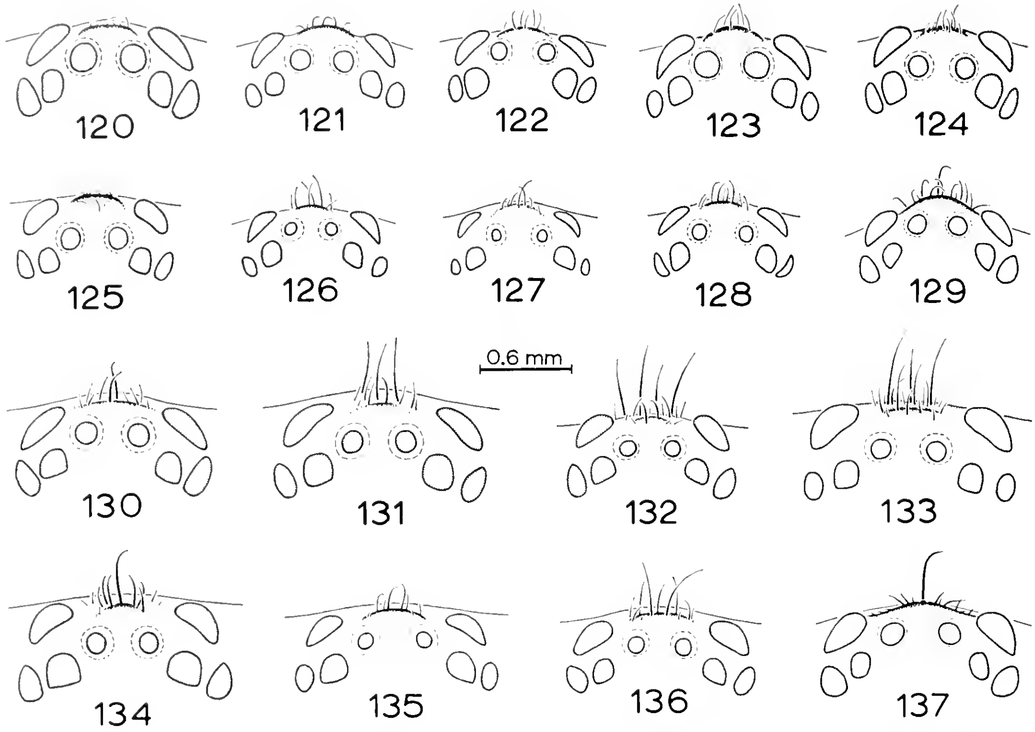
	robustus	*pacificus*	*occultus*	*montanus*	*hageni*	*cerberus*	*lincolnianus*	*stygius*	*apachecus*
CL	6.95	5.34	5.57	5.27	6.17	5.19	5.12	4.66	4.66
CW	5.48	4.33	4.56	4.48	5.16	4.22	4.22	3.54	3.73
OQW	1.44	1.03	1.12	1.03	1.08	0.93	0.90	0.91	0.86
ALS	0.75	0.51	0.51	0.57	0.57	0.47	0.44	0.45	0.43
ALD	0.35	0.31	0.35	0.29	0.33	0.25	0.23	0.25	0.25
AMS	0.21	0.14	0.14	0.18	0.18	0.16	0.22	0.20	0.17
AMD	0.17	0.14	0.16	0.14	0.12	0.09	0.07	0.11	0.09
SL	3.78								
SW	3.44								
IFL	4.88	4.71	4.97	5.46	5.61	5.05	4.90	4.63	4.41
ITL	2.80	3.01	3.31	3.77	3.95	3.35	3.58	3.20	3.09
IML	2.83	4.22	3.84	4.29	4.37	3.58	3.54	3.50	3.16
ITarL	1.40	1.96	2.33	2.63	2.71	2.03	1.92	2.18	1.80
IVFL	4.69								
PFL		3.54	3.39	3.65	3.92	3.12		3.61	3.54
PTL		2.94	3.01	3.12	3.54	2.56		3.09	2.94
PTT		1.23	1.38	1.20	1.40	1.01		0.98	0.96
EGS		36	25		59	46		31	69
CT	12								
CMT	12								
PTSP	6								
PTSR	3								
IMS	10								
*MM		none	none	A	AB	AB	AB	A	A
*TP		38,0	35,16	35,27	44,44	17,16			
*TRV		6,0	4,2	18,13	12,12	6,6			

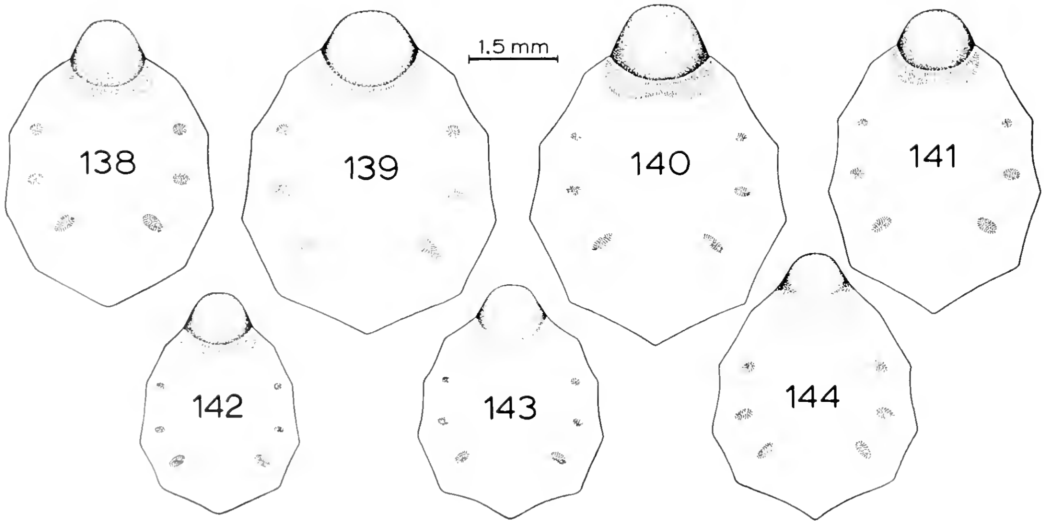


Maps 1–4. Distribution of *Antrodiaetus* species.

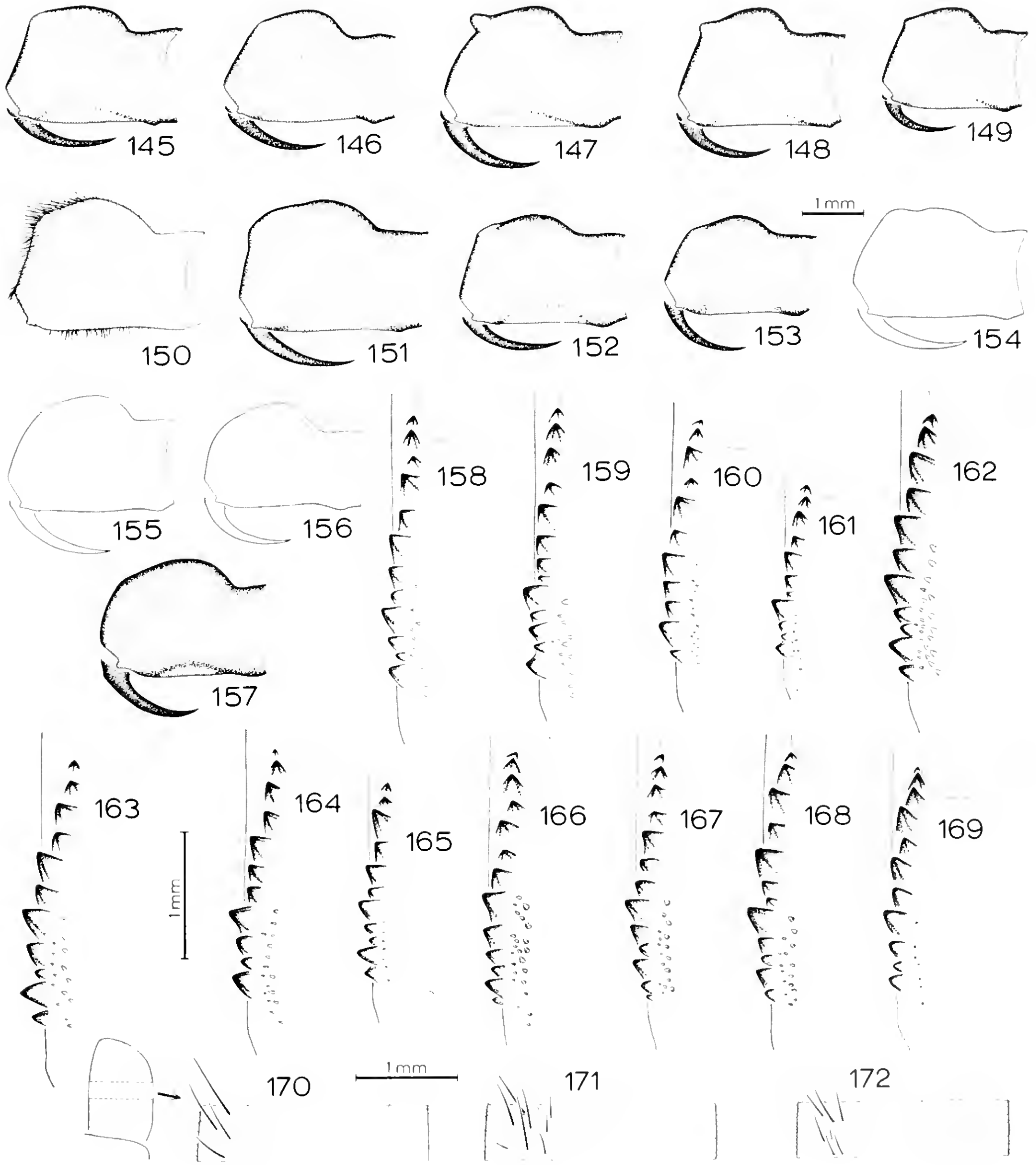


Figures 109–119. Whole body and carapace views of *Antrodiaetus*. (Dorsal and lateral views.) 109–112. *A. pugnax*, *B.* 109. Male. 110. Female. 111. Male. 112. Female. 113. *A. unicolor* male, *I.* 114–116. *A. roretzi*. 114. Male. 115–116. Female. 117–118. *A. stygius* paratype female. 119. *A. lincolnianus* female; Lincoln, Nebr.

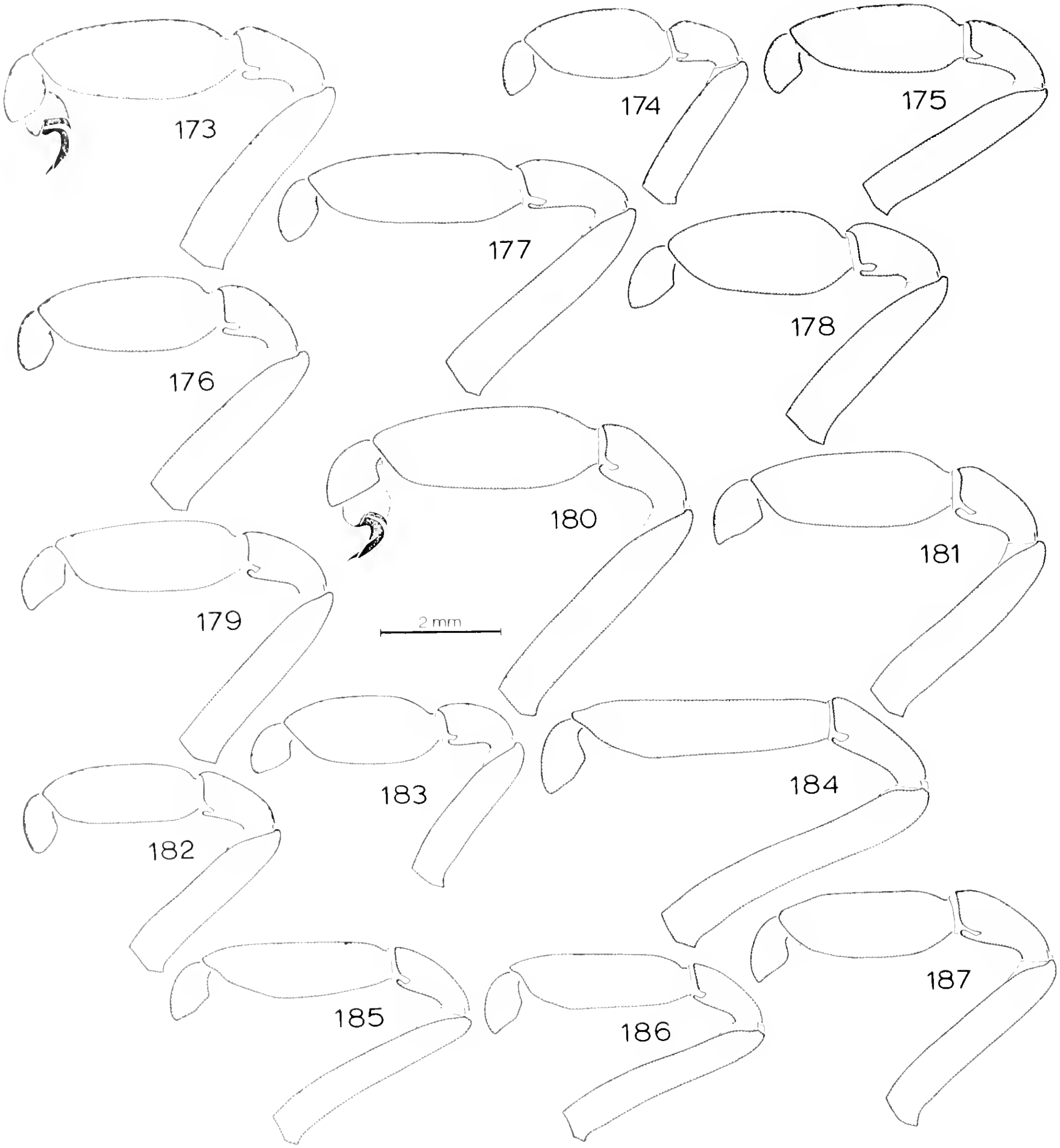




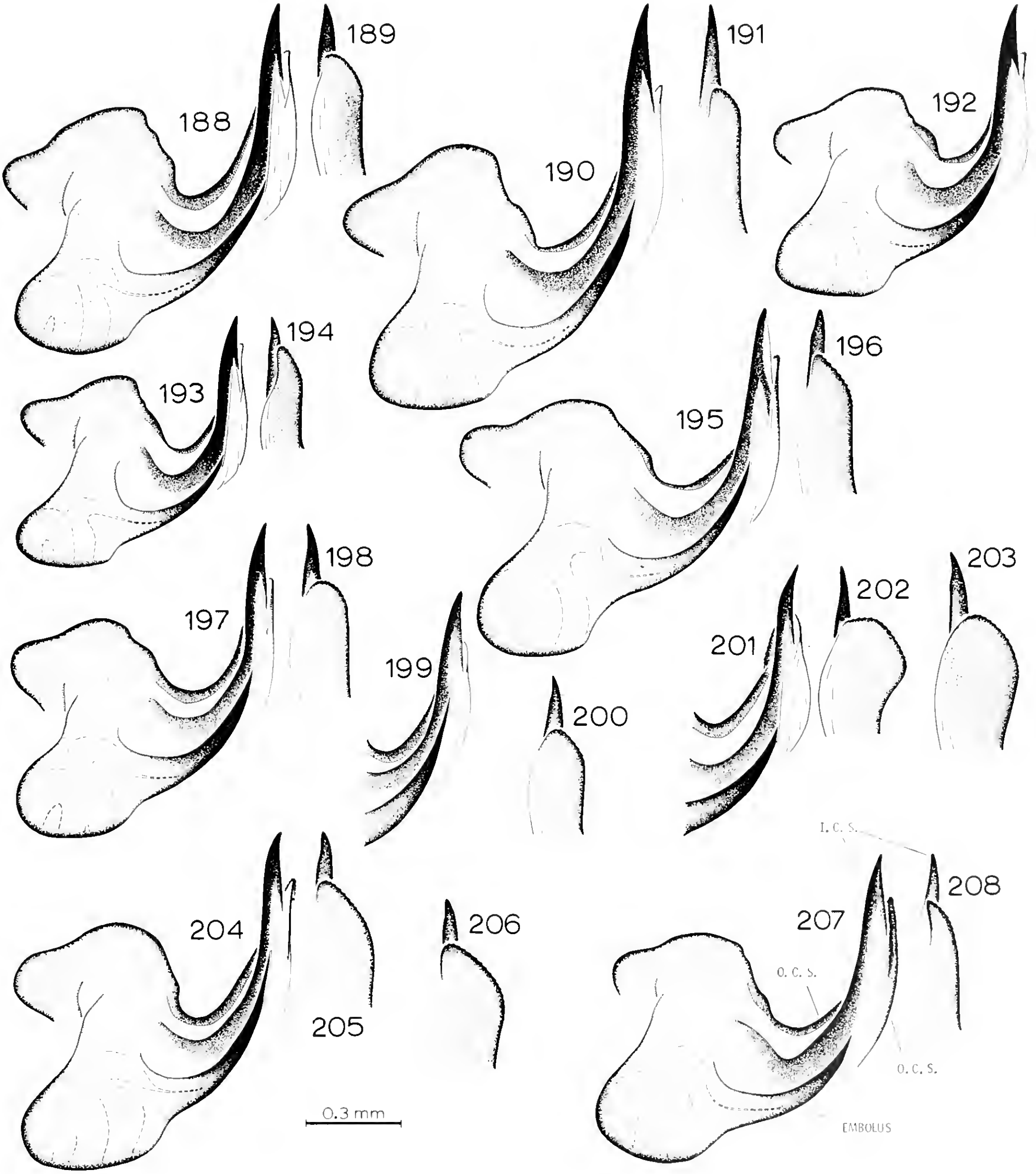
Figures 120–137. *Antrodiaetus* eyes. (Dorsal view with lateral border of carapace horizontal.) 120–129. Males. 120. *A. unicolor*, P. 121–122. *A. pacificus*. 121. Holotype. 122. *R*. 123. *A. occultus*, paratype. 124. *A. pugnax*, A (*Brachybothrium shoshoneum* Chamb., holotype). 125. *A. hageni*; near Baker, Ore. 126. *A. cerberus*, holotype. 127. *A. lincolnianus*, holotype. 128. *A. stygius*, holotype. 129. *A. roretzi*, Saitama Pref. 130–137. Females. 130. *A. unicolor*, *P*. 131. *A. pacificus*, *L*. 132. *A. pugnax*, B. 133. *A. hageni*; Trail, B. C. 134. *A. cerberus*, paratype. 135. *A. lincolnianus*; Lincoln, Nebr. 136. *A. stygius*, paratype. 137. *A. roretzi*. Figures 138–144. Sternum and labium of *Antrodiaetus* females. 138. *A. unicolor*, Q. 139. *A. robustus*; Canton, Ohio. 140. *A. montanus*; Salt L. City, Utah. 141. *A. hageni*; Kelowna, B. C. 142. *A. yesoensis*. 143. *A. stygius*, paratype. 144. *A. roretzi*, Tochigi Pref.



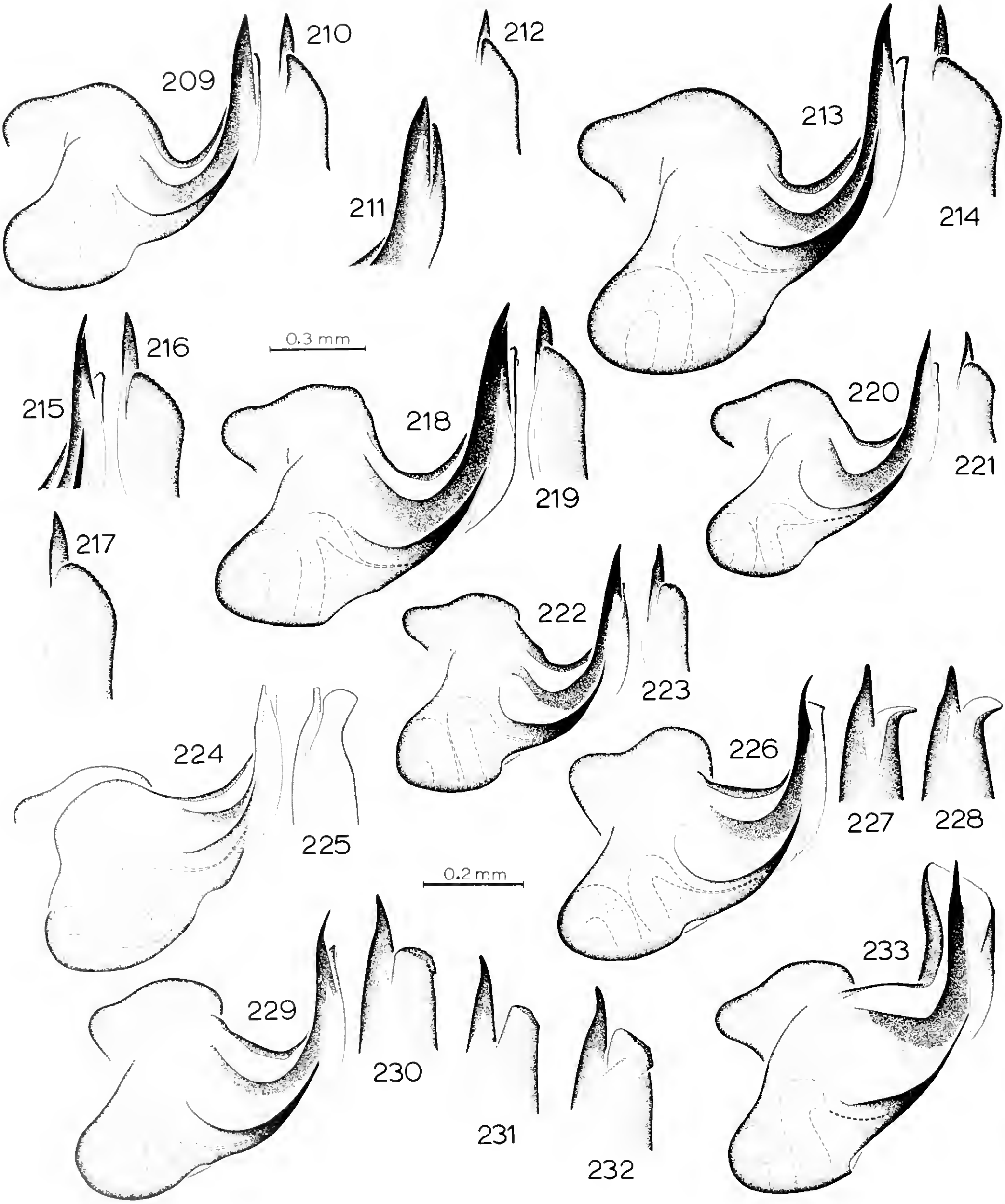
Figures 145–157. Chelicerae of *Antrodiaetus* males. (Retrolateral view of left chelicera.) 145–146. *A. unicolor*. 145. *F*. 146. *B*. 147–149. *A. pacificus*. 147. *B*. 148. *F*. 149. *D*. 150. *A. montanus*; Idaho Falls, Ida. 151. *A. hageni*; Baker, Ore. 152. *A. lincolnianus*, paratype. 153. *A. stygius*, holotype. 154–156. *A. apachecus*. 154–155. Near Alpine, Ariz. 156. Paratype. 157. *A. roretzi*, Yokohama. Figures 158–169. Cheliceral teeth of *Antrodiaetus* females. (Ventral view of left chelicera.) 158. *A. unicolor*, *J*. 159. *A. robustus*; Hagerstown, Md. 160. *A. pacificus*, *L*. 161. *A. pugnax*, *B*. 162. *A. montanus*; Downey, Ida. 163. *A. hageni*; Kelowna, B. C. 164. *A. cerberus*, paratype. 165. *A. yesoensis*. 166. *A. lincolnianus*; Lincoln, Nebr. 167. *A. stygius*, paratype. 168. *A. apachecus*; Flagstaff, Ariz. 169. *A. roretzi*; Tochigi Pref. Figures 170–172. Setation of upper ectal surface of *Antrodiaetus* female chelicerae. (Dorsal view.) 170. *A. pacificus*, *L*. 171. *A. montanus*; Downey, Ida. 172. *A. hageni*; Trail, B. C.



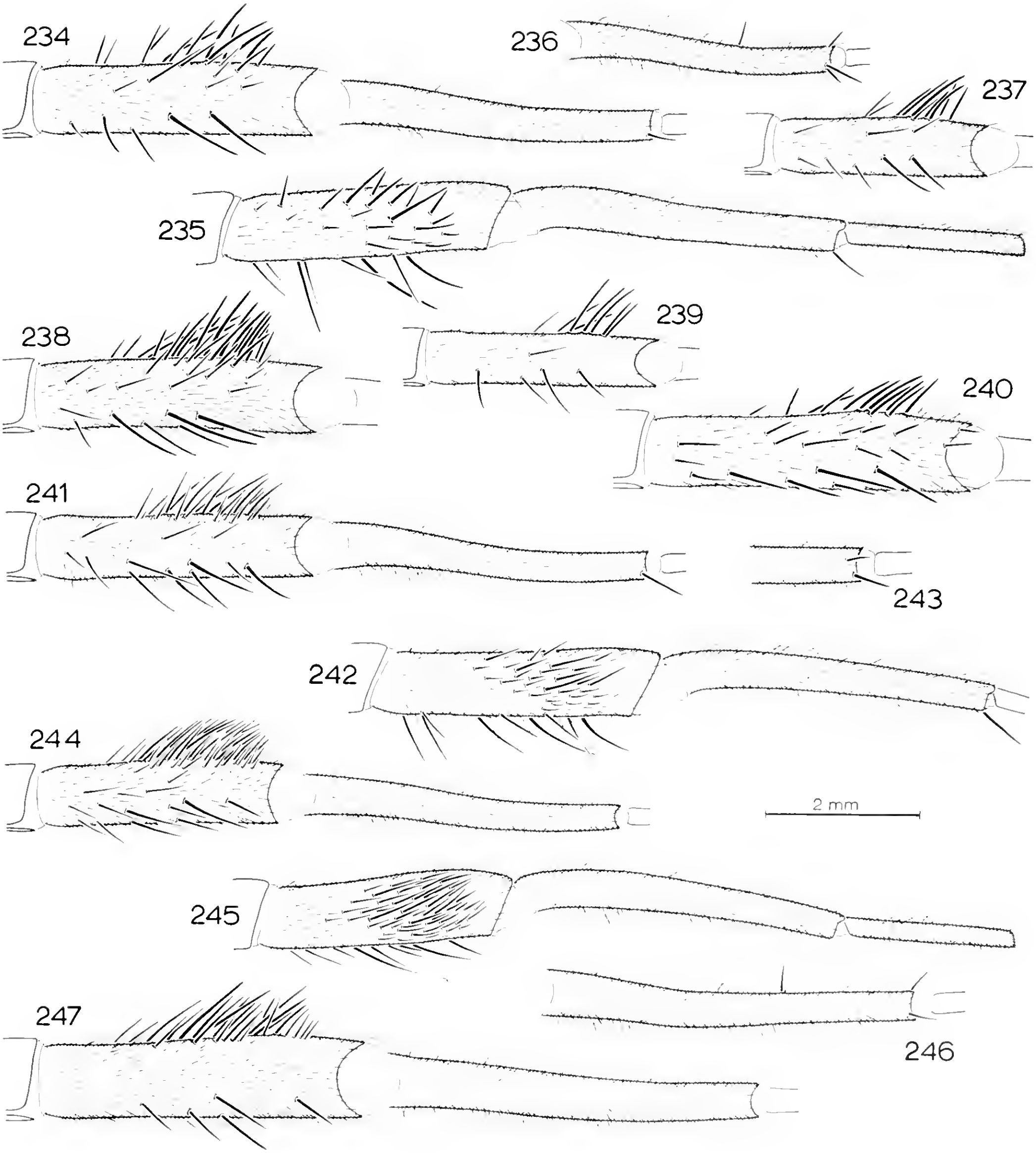
Figures 173–187. *Antradiaetus* male pedipalps. (Retrolateral view of left pedipalp.) 173–174. *A. unicolor*. 173. Q. 174. IJ. 175–177. *A. pacificus*. 175. D. 176. B. 177. J. 178. *A. occultus*, paratype. 179. *A. pugnax*, A (*Brachybothrium shoshoneum* Chamb. holotype). 180. *A. montanus*; Idaho Falls, Ida. 181. *A. hageni*; Summerland, B. C. 182. *A. cerberus*, holotype. 183. *A. yesoensis*. 184. *A. lincolnianus*; Lawrence, Kan. 185. *A. stygius*, holotype. 186. *A. apachecus*, holotype. 187. *A. roretzi*, Saitama Pref.



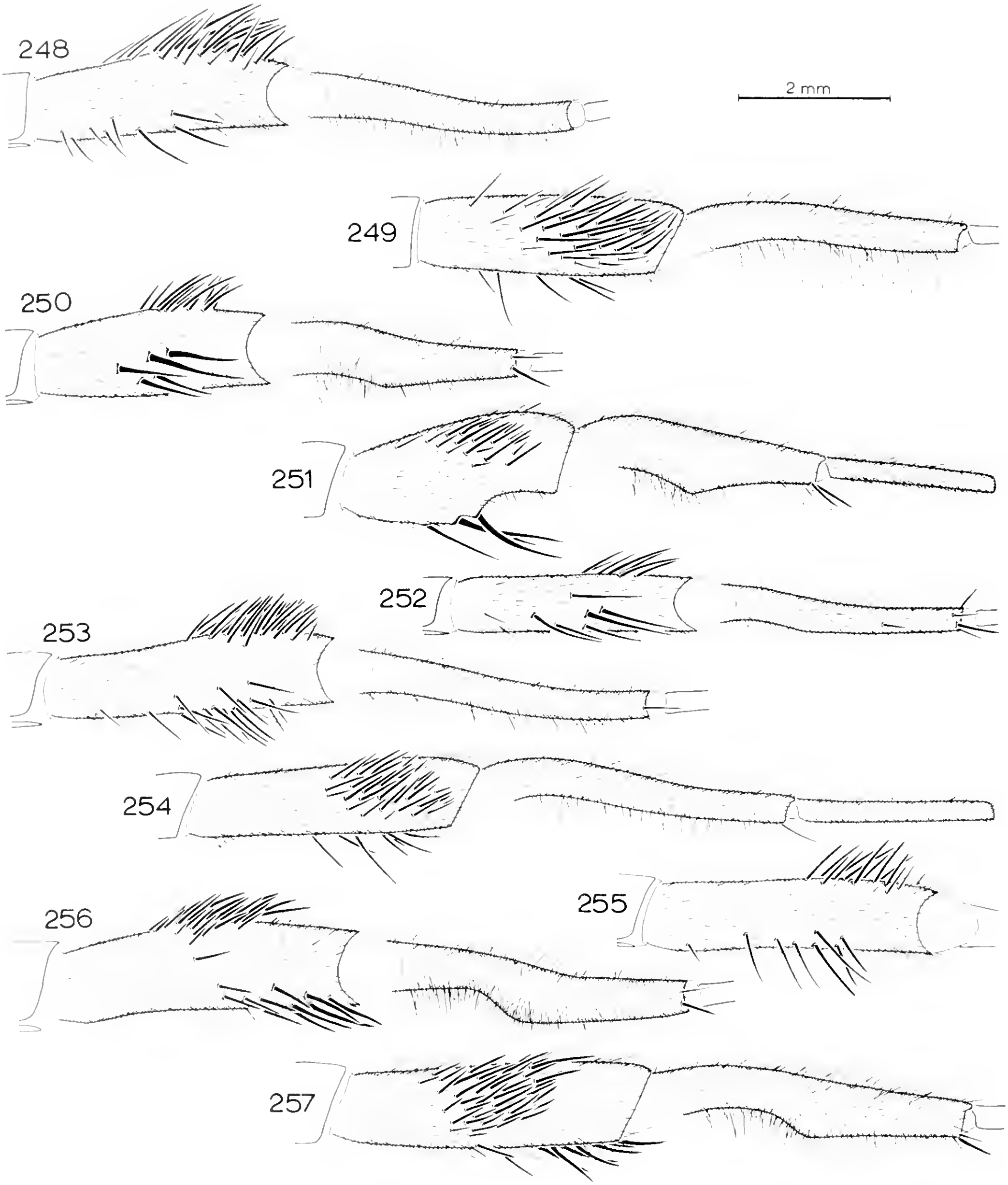
Figures 188–208. *Antrodiaetus* palpi. (Prolateral view of entire left palpus and view of tip after palpus rotated 90° on longitudinal axis of distal half of i.c.s. Occasionally prolateral view does not include bulb portion of palpus.) 188–194. *A. unicolor.* 188–189. Q. 190–191. *B.* 192. *N.* 193–194. *A.* 195–196. *A. robustus*; near Washington, D. C. (*Brachybothrium shoemakeri* Petrunk., lectotype). 197–203. *A. pacificus.* 197–198. *D.* 199. Holotype. 200. Ketchikan, Alaska. 201–202. *S.* 203. *W.* 204–206. *A. occultus.* 204–205. Holotype. 206. Yoncalla, Ore. 207–208. *A. pugnax, A* (*Brachybothrium shoshoneum* Chamb. holotype).



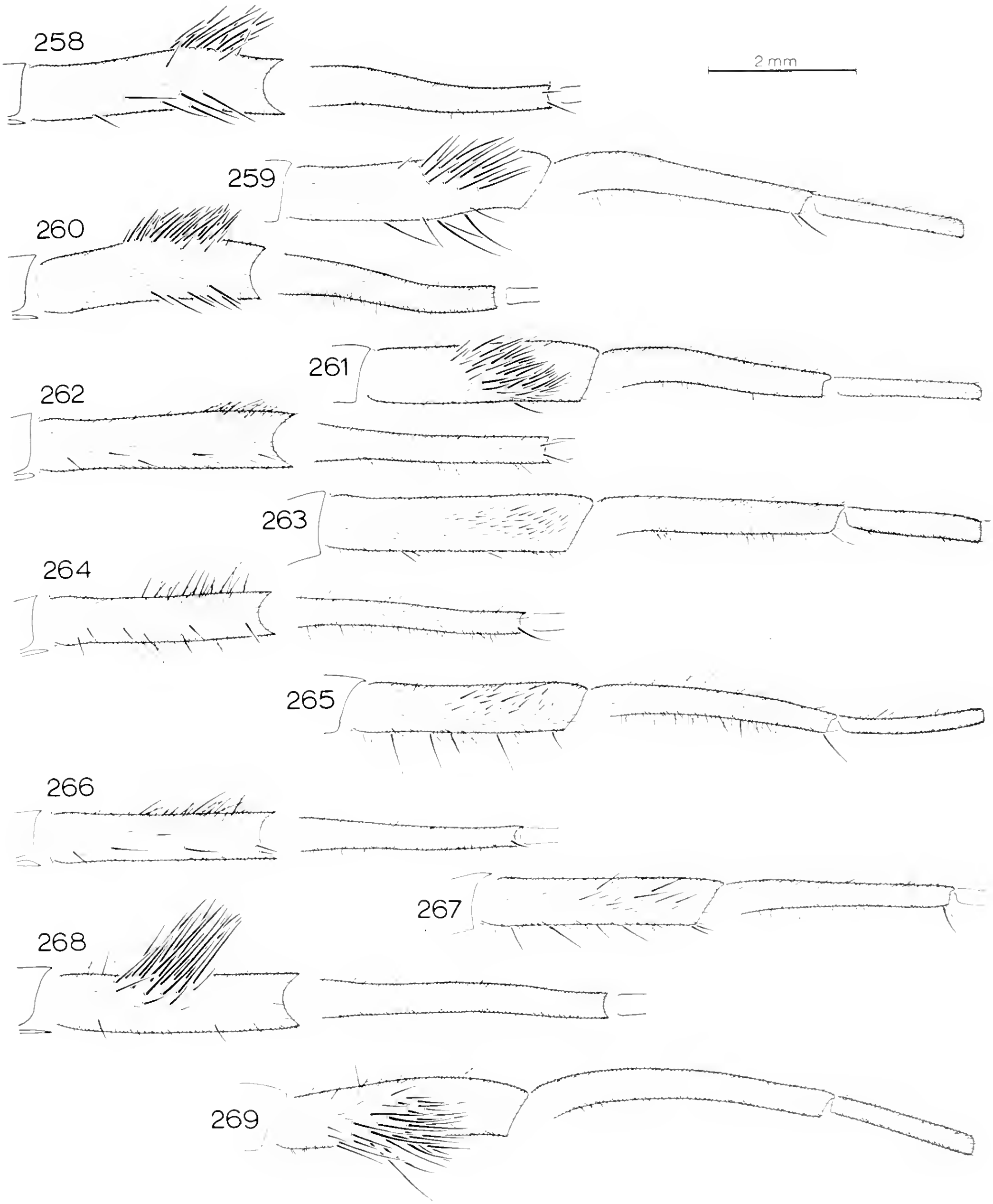
Figures 209–233. *Antrodiaetus* palpi. (Same views as previous plate. Figs. 225, 227–228, and 230–232 enlarged; match 0.2 mm scale.) 209–212. *A. pugnax*. 209–210. *H*. 211. *C*. 212. *E*. 213–217. *A. montanus*. 213–214. Paratype; Notus, Ida. 215–216. Fish Lake, Ore. 217. Washoe Valley, Nev. 218–219. *A. hageni*, holotype. 220–221. *A. cerberus*, holotype. 222–223. *A. yesaensis*. 224–225. *A. lincolnianus*, paratype. 226–228. *A. stygius*. 226–227. Holotype. 228. Paratype. 229–232. *A. apachecus*. 229–230. Paratype. 231. Near La Cueva, N. Mex. 232. Near Alpine, Ariz. 233. *A. roretzi*, Saitama Pref.



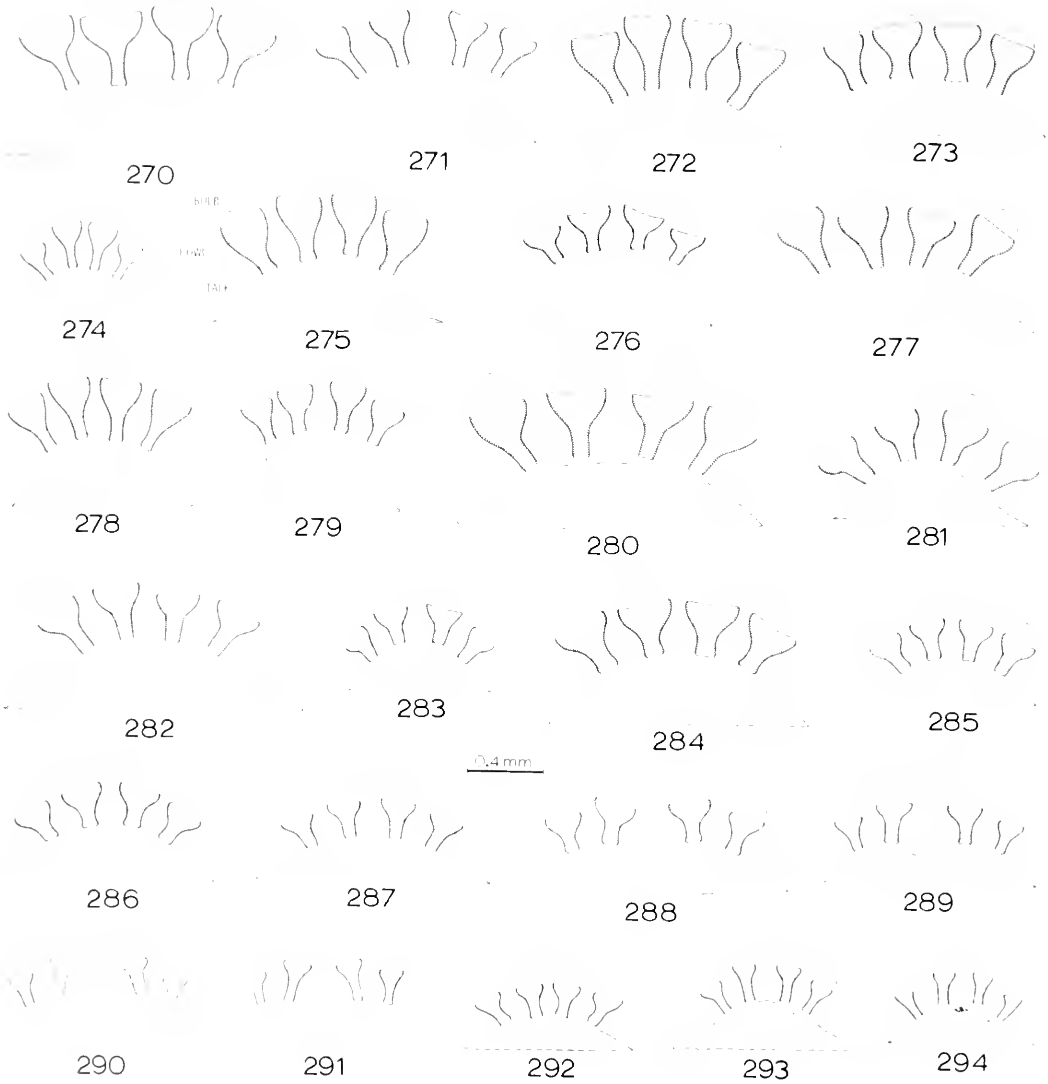
Figures 234–247. Tibia, metatarsus, and tarsus of leg I of *Antrodiaetus* males. (Ventral and prolateral views of left leg.) 234–240. *A. unicolor*. 234–235. *P*. 236. *F*. 237. *A*. 238. *I*. 239. *N*. 240. *Q*. 241–243. *A. robustus*. 241–242. Near Rector, Pa. 243. Distal end of metatarsus (ventral view), near Rector. 244–247. *A. pacificus*. 244–245. *D*. 246. *T*. 247. *W*.



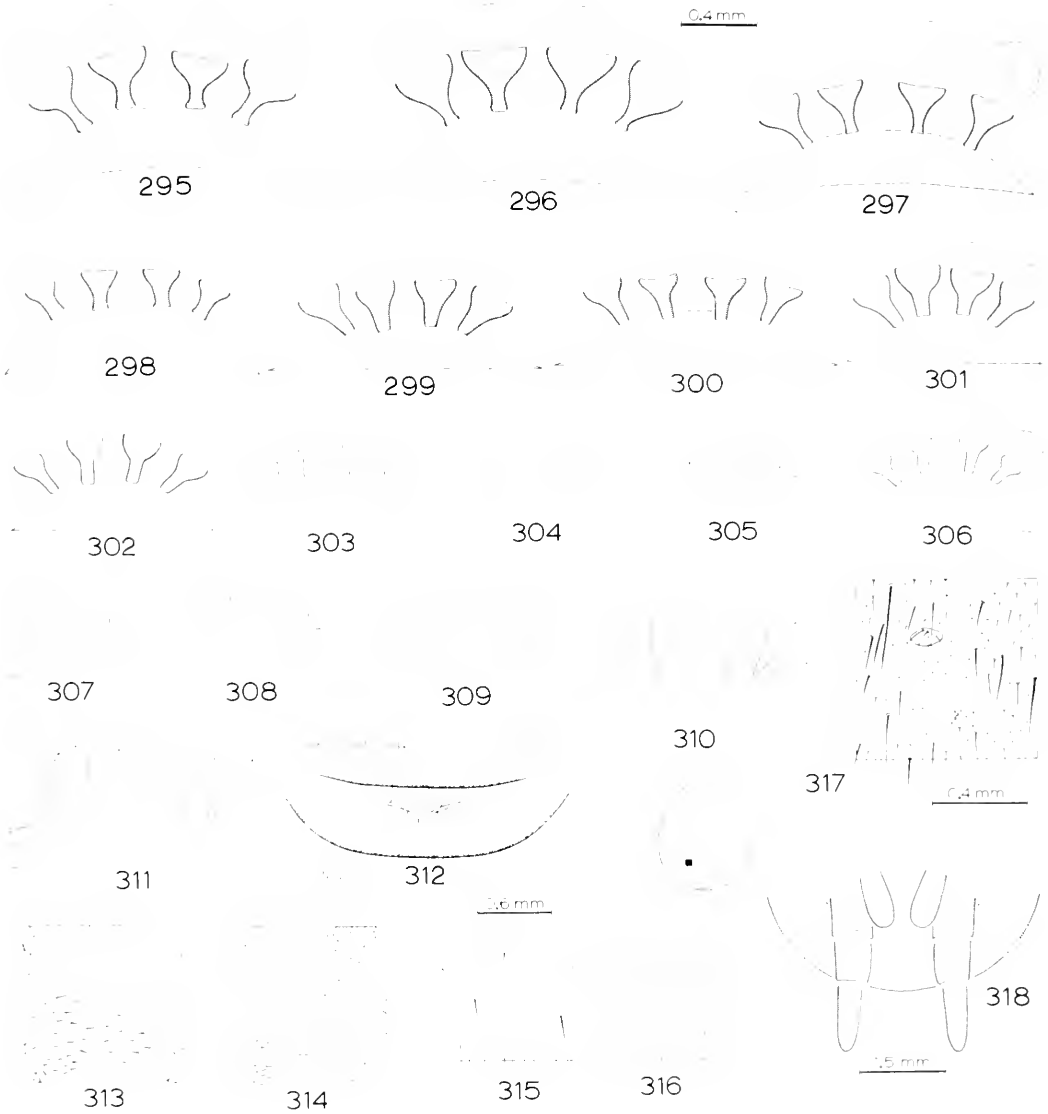
Figures 248–257. Tibia, metatarsus, and tarsus of leg I of *Antrodiaetus* males. (Ventral and prolateral views of left leg.) 248–249. *A. acultus*, holotype. 250–252. *A. pugnax*. 250–251. *A* (*Brachybothrium shoshoneum* Chamb. holotype). 252. *H.* 253–255. *A. montanus*. 253–254. Holotype. 255. Paratype; Strawberry Reservoir, Ida. 256–257. *A. hageni*, holotype.



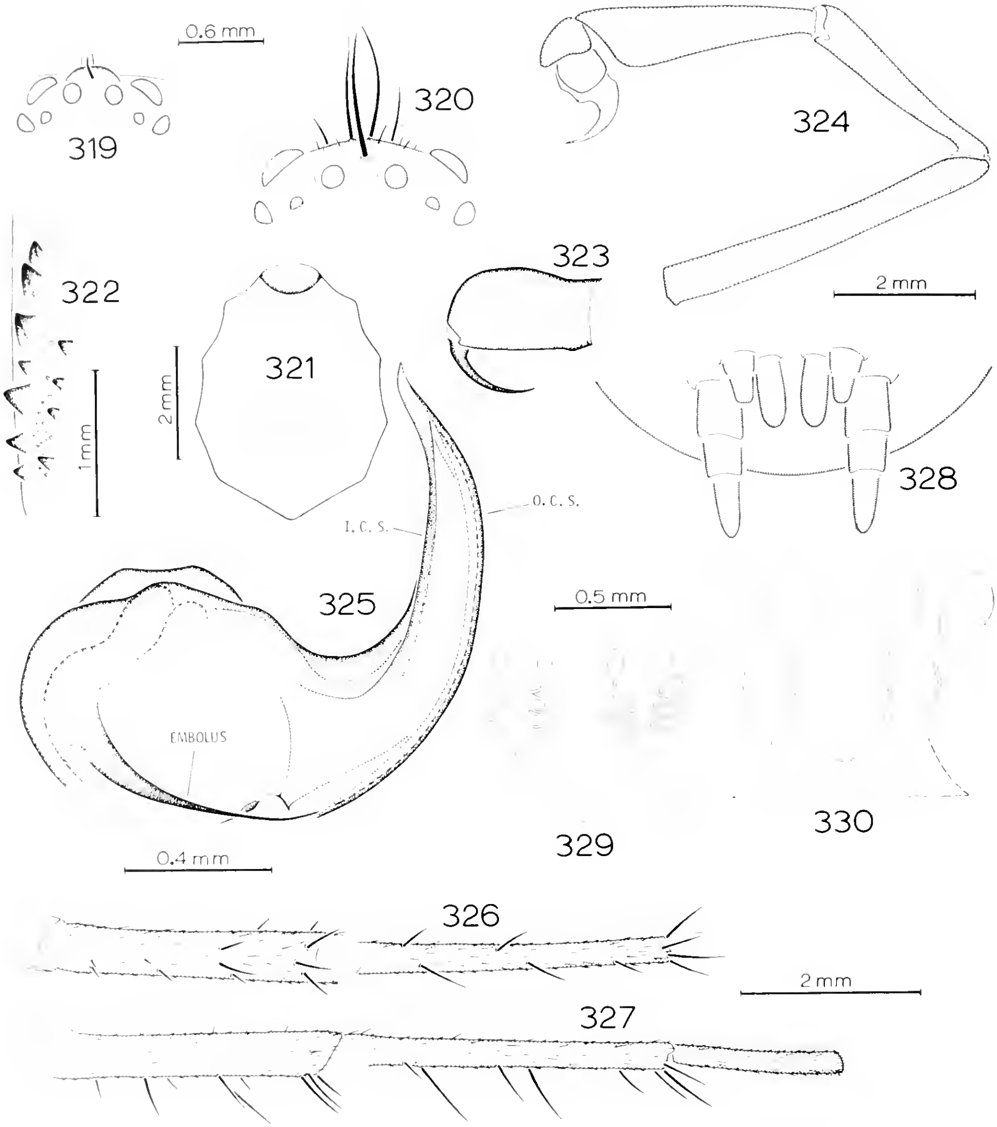
Figures 258–269. Tibia, metatarsus, and tarsus of leg I of *Antrodiaetus* males. (Ventral and prolateral views of left leg.) 258–259. *A. cerberus*, holotype. 260–261. *A. yesoensis*. 262–263. *A. lincolnianus*, paratype. 264–265. *A. stygius*, paratype. 266–267. *A. apachecus*, holotype. 268–269. *A. roretzi*; Yokohama.



Figures 270–294. *Antrodiaetus* seminal receptacles. (Dorsal view. Floor of bursa copulatrix outlined by broken line.) 270–279. *A. unicolor.* 270. *J.* 271. *C.* 272. *K.* 273. *I.* 274–275. *Q.* 276. *B.* 277. *K.* 278. *F.* 279. *O.* 280–283. *A. robustus.* 280. Baldwin, Pa. 281. Hagerstown, Md. 282. Canton, Oh. 283. Caledonia St. Pk., Pa. 284–291. *A. pacificus.* 284. Brookings, Ore. 285. *I.* 286. *M.* 287. Queen Charlotte Islands, B. C. 288–290. *S.* 291. *Y* (Kamiah). 292–294. *A. pugnax.* 292. Fort Lewis, Wash. 293. *B.* 294. Lewis and Clark St. Pk., Wash.



Figures 295–311. *Antrodiaetus* seminal receptacles. (Dorsal view. Floor of bursa copulatrix outlined by broken line.) 295–298. *A. montanus*. 295. Reno, Nev. 296. Pocotello, Ida. 297. Salt L. City, Utah. 298. Downey, Ida. 299–300. *A. hageni*. 299. Kelowna, B. C. 300. Kamlaops, B. C. 301–302. *A. cerberus*, paratypes. 303. *A. yesoensis* (likely immature). 304–305. *A. lincolnianus*; Lincoln, Nebr. 306–307. *A. stygius*; paratypes. 308–309. *A. apachecus*. 308. Flagstaff, Ariz. 309. Paratype. 310–311. *A. roretzi*. 311. Tochigi Pref. Figure 312. *A. roretzi*. Posterior ventral view of exterior surface of female genitalia. Figures 313–318. External morphology of female *Antrodiaetus* abdomen. 313–314. Setation medially and dorsally just posterior of pedicel. 313. *A. unicolor*, P. 314. *A. robustus*; Boldwin, Po. 315–316. Dorsal abdominal background setation (1 mm post. of tergite). 315. *A. unicolor*, P. 316. *A. robustus*; Baldwin, Pa. 317. *A. robustus*, AL spinneret vestige. 318. *A. unicolor* spinnerets, O. 0.6 mm scale for 312–316.



Figures 319–330. *Aliatypus* morphology. (Same views as for *Antradiaetus*.) 319–329. *Aliatypus* no. 2; Chatsworth, Calif. 319. Male eyes. 320. Female eyes. 321. Female sternum. 322. Female cheliceral teeth. 323. Male chelicera. 324. Male pedipalp. 325. Palpus. 326–327. Distal segments of male leg I. 328. Female spinnerets. 329. Seminal receptacles. 330. *Aliatypus* sp.; Shaver Lake (Fresno Co.), Calif. Seminal receptacles. 319–320: 0.6 mm scale. 321: 2 mm scale. 322: 1 mm scale. 323, 324, 328: 2 mm scale. 325: 0.4 mm scale. 326–327: 2 mm scale. 329–330: 0.5 mm scale.

EVOLUTION

Phylogeny

Atypoidea. Simon (1892) first emphasized the close relationship of the Antrodiaetidae, the Mecicobothriidae, and the Atypidae, but later (1903), impressed by the resemblance of the first two families to the ctenizids and diplurids, he separated these from the atypids and grouped them with the rest of the mygalomorph spiders. Smith (1908) studied *Atypoides* and *Aliatypus* and sided with Simon's earlier opinion. However, until the 1940's, many authors accepted Simon's second classification uncritically. Chamberlin and Ivie (1945) pointed out that the similarities of the antrodiaetids to the ctenizids and of the mecicobothriids to the diplurids were the result of convergence. Gertsch (1949, 1967) agreed, and grouped the Antrodiaetidae, Mecicobothriidae, and Atypidae together with the Liphistiidae to form the superfamily Atypoidea and to emphasize their close relationship and their distinctness from other mygalomorph taxa.

Evidence strongly indicates that the antrodiaetids, mecicobothriids, and atypids do form a distinct and monophyletic group. The homogeneity of genital structure within this group and the distinctness of the genitalia from those of nonatypoid taxa is perhaps the strongest indication of this monophyly; the genitalia are relatively complex structures probably not strongly affected by niche-oriented convergence. The always well-developed o.c.s. (Fig. 207) and the frequently present i.c.s. are absent from all nonatypoid palpi, and the Atypoidea possess four seminal receptacles (or a condition derived from this) rather than the usual two (or a derived condition) of other mygalomorphs. Other characters providing similar evidence are listed by Chamberlin and Ivie (1945). It is certain that the Antrodiaetidae are phylogenetically quite distinct from the ctenizids and that the similarity of their niches, together with a large number of functionally related (niche adapted) morphological and behavioral similarities, is simply the result of convergent, or at least parallel, evolution.

The unique ancestral characters (vestiges of abdominal segmentation) shared by the antrodiaetids, mecicobothriids, and atypids indicate a long evolutionary history for this group. Each of these families is distinct and contains few species—these are truly evolutionary relicts. The family Atypidae is highly specialized morphologically and behaviorally in accord with the unique tube-web niche which it has entered. The mecicobothriids apparently occupy a distinct sheet-web niche and are morphologically more similar to the antrodiaetids (not necessarily more closely related) than to the atypids.

Antrodiaetidae. The evidence summarized in Table 11 shows that *Aliatypus* arose from an ancestral stock distinct from that of *Antrodiaetus* and *Atypoides*, and also that *Aliatypus* may be as closely or more closely related to the Mecicobothriidae. Smith (1908) arrived at a somewhat similar conclusion. The first two characters (Table 11), which are heavily weighted for reasons given earlier, indicate that *Aliatypus* is more closely related to the mecicobothriids. Characters 3 to 5 probably compose a complex of characters functionally related to mating behavior and therefore are individually less heavily weighted. These provide only weak evidence that *Aliatypus* may be more closely related to the mecicobothriids. Some, perhaps even all, of the last nine characters are functionally correlated with the niche requirements of these taxa and therefore may be misleading. Although the trapdoor niche of *Aliatypus* is much more similar to (but still different from) the niche of *Antrodiaetus* and *Atypoides* than to the nonburrowing sheet-web niche of the mecicobothriids, the genital character evidence and the other distinct character states indicate that this is the result of either parallel or convergent evolution. A complete study of the

Table 11. Comparison of *Aliatypus* with related taxa. Thickness of arrows is roughly proportional to weight of character and degree of similarity of character states. *Hexura picea* (♂, ♀) and *Megahexura fulva* (♀) are the only mecicobothriids examined.

CHARACTER	*Antrodiaetus* & *Atypoides*		*Aliatypus*		Mecicobothriidae
1. Palpus form	distinct		similar to *Hexura*	↔	similar to *Aliatypus*
2. Seminal receptacle form	stalk moderately to well sclerotized, rarely sinuous, usually with bowl		stalk unsclerotized, very narrow, sinuous, without bowl	↔	stalk rather weakly sclerotized, narrow, sometimes sinuous, without bowl
3. Male chelicera	apophysis or anterior-dorsal prominence		unmodified	↔	unmodified
4. Male leg I modified	usually		no		yes
5. Male pedipalp patella	not elongate		elongate		not elongate
6. Burrow entrance structure	collar	↔	trapdoor		no burrow (sheet web)
7. Female rastellum	yes	↔	yes		no
8. Pars cephalica	strongly elevated	↔	strongly elevated		weakly elevated
9. Thoracic groove	longitudinal		pit, depression, or absent		longitudinal
10. No. of macroteeth rows per chelicera	1		2		1
11. Metatarsus IV trichobothria number	many		1 (rarely 1-4)		many
12. Large median seta just ant. to AME's	no		yes		no
13. AL spinnerets	absent or non-segmented and degenerating		2-segmented and functional	↔	functional and 1- or 2-segmented
14. Length of labium and inclination to plane of sternum	relatively long, weakly inclined		moderately short, strongly inclined	↔	short, strongly inclined

mecicobothriids and consideration of additional characters are required to clarify the relationships of *Aliatypus*.

Antrodiaetus and *Atypoides* together form a distinct monophyletic group. They are similar to each other in most of the Table 11 characters as well as many others, and are distinct from other related taxa in numerous characters. They differ from one another in two characters: the presence of AL spinnerets and of the male cheliceral apophysis. The former structures are clearly degenerating in *Atypoides* and could possibly have been independently lost more than once. The cheliceral apophysis is not degenerating in *Atypoides*. However, all *Antrodiaetus* males possess an anterior-dorsal cheliceral prominence which, because of its identical location, is more likely homologous to the cheliceral apophysis than independently evolved. That this prominence is probably either of low functional importance or a nonfunctional vestige is perhaps weakly indicated by the high intrapopulation variability of its form in at least some *Antrodiaetus* species. I shall tentatively assume the presence of a functional cheliceral apophysis in the ancestral *Antrodiaetus*-*Atypoides* stock.

Antrodiaetus consists largely of two distinct but similar species groups each clearly monophyletic and together forming a monophyletic group distinct from *Atypoides*. The *unicolor* group, consisting of nine closely related species, has evolved strongly modified male first legs. The *lincolnianus* group consists of three species, two of which (*A. stygius* and *A. apachecus*) are clearly cognate species. It is probable that this group has undergone a partial reduction in male leg I mating modifications and a functionally related elongation of the male pedipalp, a change convergent to the condition in *Aliatypus*.

Antrodiaetus roretzi, provisionally placed in this genus, is clearly distinct from these two species groups in several characters, the most important being the male palpus structure, female genital structure, and sternum form. It is distinct from *Atypoides* in the latter two characters. It also lacks a cheliceral apophysis and AL spinnerets, but these are probably rather easily lost structures of low reliability. The o.c.s. of the important male palpus is strikingly similar to that of *Atypoides*, but the i.c.s. base has one arm heavily sclerotized as in the other *Antrodiaetus* species, not as in *Atypoides*. The palpus is somewhat distinct in other difficult-to-describe features from all species in both genera. *A. roretzi* is apparently a relict combining some features of both genera; probably its ancestors branched off from or near the *Antrodiaetus-Atypoides* ancestral stock.

Atypoides is a small, rather heterogeneous taxon of three morphologically and behaviorally quite distinct species, each apparently an evolutionary relict. *A. gertschi* is particularly divergent in some characters—seminal receptacle form, male leg I macrosetation, o.c.s. length, male pedipalp shape, and burrow entrance structure. The first three characters bear noteworthy resemblance to *Aliatypus*.

Figure 69 summarizes what I believe to be one of the most probable interpretations of *Antrodiaetus* and *Atypoides* phylogeny, given the present evidence. It is a working hypothesis hopefully of some predictive value.

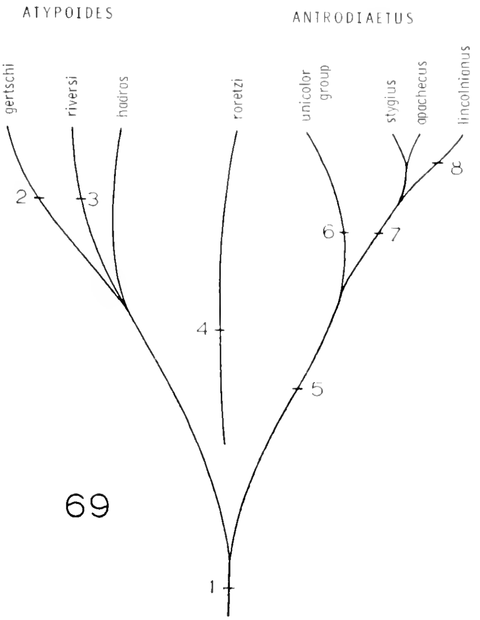


Figure 69. Diagrammatic representation of probable phylogeny of *Antrodiaetus* and *Atypoides*. Some of the more important and likely evolutionary events are indicated. Vertical axis roughly indicates time. Horizontal axis roughly indicates degree of difference. Point of origin of *A. roretzi* ancestral stock is unclear.

Some probable evolutionary events: 1. Character states of the ancestral stock: Male with cheliceral apophysis; male pedipalp not elongate; o.c.s. and i.c.s. strongly sclerotized; o.c.s. broad; male leg I unmodified or not strongly modified; seminal receptacles moderately well sclerotized; AL spinnerets unsegmented; burrow entrance a collapsible collar; bottom end of burrow enlarged. 2. Seminal receptacle sclerotization reduced; AL spinneret size reduced. 3. Collar becomes elongate and rigid; bottom end of burrow narrowed. 4. Male cheliceral apophysis lost; male leg I becomes more strongly modified; AL spinnerets lost. 5. Male cheliceral apophysis lost; o.c.s. narrows; male leg I increasingly modified (?); AL spinnerets lost. 6. Male leg I becomes strongly modified. 7. AME diameter reduced; male pedipalp elongate; o.c.s. and i.c.s. sclerotization somewhat reduced; male leg I modifications reduced; reduction of IVCT number. 8. AME diameter further reduced; male pedipalp further elongated; o.c.s. and i.c.s. sclerotization further reduced; seminal receptacle sclerotization reduced.

General zoogeographic considerations. The present day geographic distribution of *Antrodiaetus* and *Atypoides* (Map A) is markedly disjunct, with the greatest species diversity in far western North America. The disjunct east Asian, western North American, and eastern North American pattern and the present intimate association of these genera with the modern forest derivatives of the Arcto-Tertiary Geoflora, indicate that *Antrodiaetus* and *Atypoides* have evolved along with this well-documented (Axelrod, 1960) plant assemblage. The much greater present diversity of the Antrodiaetidae in North America indicates that this continent is probably the geographic origin of the family and of its genera. This was also Pocock's (1903) interpretation. Although the present day mecicobothriid distribution seems to support this idea, the Atypidae, with both its genera occurring in the Tropics and subtropics of the Old World (*Atypus* is also found in the Palearctic and Nearctic regions), could have originated there. This and the presence of the evolutionary relict, *Antrodiaetus roretzi*, in warm temperate Japan weakly hint that extinction could be camouflaging an Asian origin of the *Antrodiaetus-Atypoides* ancestral stock.

Dispersal Ability and Barriers

Although many araneomorph spiders balloon, it is generally believed that few mygalomorph species do. I am aware of only three observations of possible *pre*-ballooning behavior in mygalomorph spiderlings: Main (1957b) and Baerg (1928) on two ctenizid species, and Enock (1885) on the atypid, *Atypus affinis*. None of these observers actually saw ballooning.

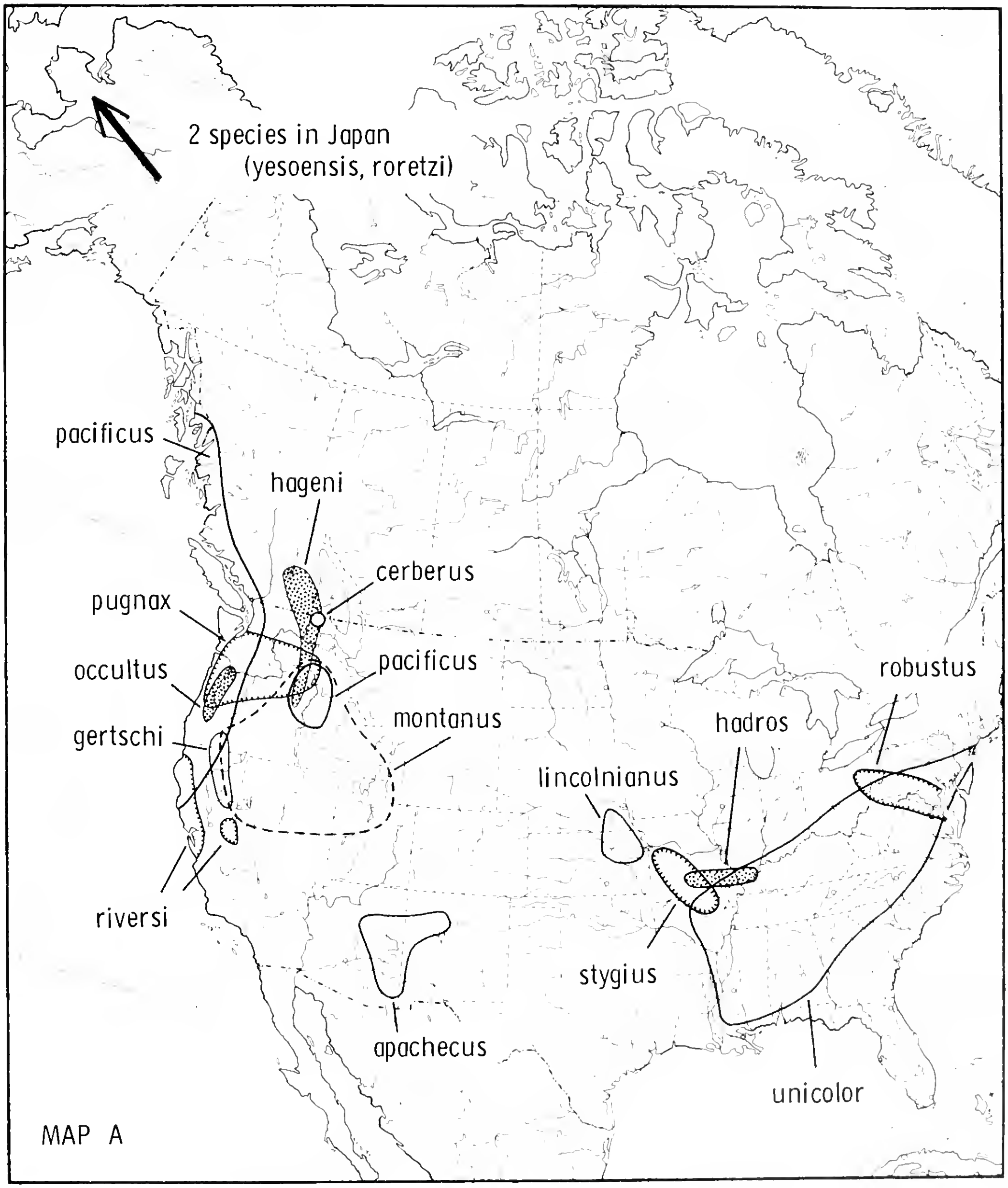
Antrodiaetus and *Atypoides* spiderlings have not been observed during dispersal away from the parental burrow, but some indirect evidence indicates that if they balloon at all, only short distances can be covered. Second instar spiderlings (the dispersal stage) desiccate quickly when not maintained in high humidity. Antrodiaetid species have considerably smaller geographic ranges than do many araneomorphs that are known to balloon. Several species exhibit marked geographic variation within relatively very small areas. Few to many offspring burrows are commonly clustered close to the parental burrow, indicating that at least some spiderling dispersal is short range.

Active dispersal of older immatures and adult females is probably prompted only by burrow microhabitat deterioration and is certainly short range. Passive rafting down streams, rivers, and perhaps across large bodies of water are likely, for burrows commonly occur within dense root systems at the bases of trees, in partly decaying logs, and near water. The colonization of the British Columbia coast and its islands by *Antrodiaetus pacificus* since the retreat of the Wisconsin ice might be largely the result of such rafting. The nocturnally wandering adult males can move rapidly (and probably far) over the ground surface. Such wandering cannot alone found new populations, but is certainly important in maintaining gene flow and probably also in fertilizing founder females in nearby localities.

Low humidity habitats (with soil humidity the immediate limiting factor) are apparently the outstanding barriers to dispersal and thus to gene flow in *Antrodiaetus* and *Atypoides* species. Geographic gaps and genetic variation discontinuities within a species population predominantly coincide with habitats drier than those occupied by the species in question. None of the likely means of antrodiaetid dispersal could bridge more than a narrow dry habitat barrier.

Geographic Variation

All relatively well-sampled species of *Antrodiaetus* and *Atypoides* exhibit geographic variation in numerous characters. Five of these species (*Antrodiaetus unicolor, Antrodiaetus pacificus*, *Antrodiaetus pugnax*, *Atypoides riversi*, and *Atypoides gertschi*) exhibit strong and sometimes discontinuous geographic variation in at least several characters. The reader is referred to the Taxonomy section and to Coyle



Map A. Approximate known distribution ranges of *Antrodiaetus* and *Atypoides* species.

(1968), where a description and discussion of the geographic variation in each of these species follows each species description. Different characters frequently show similar patterns of geographic variation in each of these species, i.e., they vary concordantly. Therefore divergent populations are often defined by several characters. In some cases—particularly in *A. unicolor, A. pugnax,* and *A. gertschi*—geographically and genetically intermediate populations are known and more will probably be discovered. The clearest cases of incipient speciation (perhaps speciation is complete?) are found in *A. pacificus* and particularly *A. riversi*, where the geographic barriers to gene flow also appear most formidable. Interestingly, the predominant pattern of geographic variation in *A. pugnax* may be largely the result of character displacement, i.e., the selection pressure resulting from competition or mating errors with *Antrodiaetus occultus* in the area of sympatry may have accelerated the genetic divergence of (probably) poorly connected *A. pugnax* gene pools.

The date of disjunction (and thus the rate of phenotypic divergence) can be roughly estimated for only a few divergent populations. It is nearly certain that Pleistocene climatic fluctuations isolated the present divergent populations of *A. unicolor*, *A. pacificus*, and *A. riversi*. These disjunctions probably occurred as recently as the end of the last glacial maximum (see below); perhaps these divergent gene pools have been evolving as separate entities for as little as 15,000 years.

In each of the above five species there is greater geographic variation per unit area than in many well-studied araneomorph species. Presumably, two important factors contributing to this situation are the somewhat narrow habitat requirements and particularly the poor, long range dispersal ability of antrodiaetids. The former factor favors population fragmentation and the latter a slow rate of gene exchange among such fragments. There is some indication that burrowing mygalomorph spiders may in general exhibit much geographic variation per unit area for perhaps these same reasons (see for example Main, 1957a; Loksa, 1964; Forster and Wilton, 1968).

SPECIATION: PROBABLE HISTORICAL EVENTS

Unicolor group of Antrodiaetus. Probably the last connection between eastern and western North American populations of this species group was severed in the late Tertiary during the formation of the broad semi-arid grassland of central North America. (Map A should serve as a reference throughout this section.) It is likely that one species disjoined in this manner was morphologically and ecologically similar to, and a direct ancester of, both *A. pacificus* and *A. unicolor* (and perhaps *A. robustus*) and that therefore relatively little phenotypic divergence has occurred between these species over the last 10 to 25 million years. More recent east-west contact, such as during the cool, moist, glacial maxima of the Pleistocene, appears less likely. Present evidence indicates the absence of any widespread Pleistocene forest on the Great Plains, and that probably even narrow forest corridors allowing east-west dispersal of humid forest animals were nonexistent (Dillon, 1956; Frey, 1965; Wade, 1966). However, some controversy exists regarding this last conclusion (Blair, 1965).

The last Bering land bridge favorable for *Antrodiaetus* dispersal existed no more recently than Miocene or perhaps Pliocene times. Pleistocene Bering bridges were unforested (Simpson, 1947; Flint, 1957; Péwé, Hopkins, and Giddings, 1965), but favorable Arcto-Tertiary forest extended across the bridge during its frequent and lengthy exposures from Eocene into at least Miocene times (Simpson, 1947, Axelrod, 1960). *A. yesoensis* is probably descendant from a population that extended west from North America when the bridge was last favorable ecologically. An east to west dispersal is inferred because all other *unicolor* group species are presently North American. Thus the evidence for disjunction time of all three geographic fragments of the *unicolor* group indicates that this species group had originated by early Pliocene. The presence of the evolutionary relict, *A. roretzi*, in Japan indicates another connection over perhaps an earlier Tertiary bridge.

The relatively great diversity of *unicolor* group species in the Pacific Northwest, the marked geographic variation in certain of them, and the strong habitat differences among some of them are perhaps largely attributable to the remarkable past physiographic, climatic, and thus ecological fluctuation in this region (Detling, 1968), and to the great diversity of these factors at any one time. Such fluctuation should favor speciation by causing expansions. shifts, contractions, and disjunctions of populations. Habitat diversity and fluctuation have perhaps accelerated the genetic divergence of disjunct gene pools and favored shifts into different habitat niches. It is unclear whether most of this speciation occurred during the Pleistocene or late Tertiary.

A possible case of incipient speciation exists in *A. pacificus,* which consists of a widespread coastal population and a possibly disjunct interior montane population. At least the Oregon-Washington portion of this interior population has undergone much genetic divergence since the reduction of gene exchange with the coastal population. The barrier to gene flow between these two forest populations is the broad arm of dry Juniper-sagebrush woodland plant formation (Detling, 1968) extending northward from the Great Basin through central Oregon and Washington into southern British Columbia. Gene flow reduction and resulting genetic divergence probably began with the climatic drying and warming just after (about 15,000 years ago) the last Wisconsin glacial advance. During this maximum, a boreal forest favorable for *A. pacificus* extended at least along the ice front from the Washington coast to the mountains of northern Idaho and possibly even extended across the Oregon plateau to connect directly the coastal and northeast Oregon populations (Heusser, 1960; Detling, 1968). If the interior population is now reproductively isolated, then disjunction and speciation could also have occurred earlier in the Pleistocene under similar conditions. It is noteworthy that this distribution pattern and probably the historical causes are very similar to those of the salamanders *Plethodon vandykei* (Highton, 1962; Wade, 1966) and *Taricha granulosa* (Riemer, 1958).

Antrodiaetus unicolor is a widespread species consisting of a dense, roughly continuous central population and numerous geographically semi-isolated (some perhaps isolated) peripheral populations. Presumably the eastern, southern, and western peripheral populations were continuous with the central population during the cooler, more humid Pleistocene glacial maxima when the favorable cool humid forest habitat expanded outward over the lowland areas. Some of these peripheral populations have since undergone considerable genetic divergence as a result of the increasing discontinuity of favorable habitat peripherally and the resulting reduction of gene influx from the central population.

Lincolnianus group of Antrodiaetus. The morphologically very similar *A. stygius* and *A. apachecus* are almost certainly sister species. Perhaps the parent population split into eastern and western fragments during the formation of the grassland in the late Tertiary, the same event postulated to have last disjoined the *unicolor* group. However, the small amount of phenotypic divergence of these two species suggests a more recent disjunction during a Pleistocene interglacial. Blair (1958, 1965) has suggested this for two southwestern montane relict species of lungless salamanders, but there is considerable evidence against an east-west Pleistocene forest corridor (Frey, 1965; Wade, 1966). Pollen analysis evidence for an extensive Parkland-yellow pine association extending eastward from Arizona well into Texas at the Wisconsin maximum (Martin and Mehringer, 1965) adds some support for a possible Pleistocene connection.

Antrodiaetus apachecus is presently fragmented by intervening arid habitats into a number of disjunct montane populations that have been sampled too poorly to indicate how much they have diverged from one another genetically. These were probably last continuous near the end of the Wisconsin glacial maximum roughly 17,000 years ago when all known present populations were apparently connected by habitats no dryer than Ponderosa (yellow) pine forest (Martin and Mehringer, 1965).

Atypoides. Disjunction of *Atypoides* into eastern and western North American segments occurred at least as long ago as the formation of the late Tertiary grassland. *A. riversi* reveals a pattern of incipient speciation (Perhaps speciation is complete?) with two probably disjunct and genetically quite divergent populations on both sides of the dry Central Valley of California. These were last connected by gene flow across the valley floor (or perhaps to the north of the valley) during one of the cooler, moister Pleistocene glacial maxima, perhaps during the recent (Wisconsin) one. Similar histories have been postulated for cognate populations of salamanders with similar distributions (Stebbins, 1949; Riemer, 1958).

Reproductive Isolating Mechanisms

I should emphasize that although the study of geographic variation and the foregoing discussion may help in understanding geographic isolate formation in these spiders as well as the rate of phenotypic divergence of such isolates, nothing can be inferred about the time required for the evolution of reproductive isolating mechanisms, the crucial part of speciation.

More data is needed on the relative importance of different reproductive isolating mechanisms in antrodiaetid species. Field observations suggest that ecological isolating mechanisms are important in some sympatric *unicolor* group species in the Pacific Northwest. Temporal (seasonal) isolation exists between *A. lincolnianus* and *A. stygius* and is suggested for other species. The importance of ethological isolating mechanisms may be suggested by the species specific morphology of the male first leg of *Antrodiaetus* species. The close similarity of the male palpus and of the female genitalia of all *unicolor* group species indicates that perhaps mechanical isolating mechanisms are unimportant in these species.

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A Monograph of the Genera *Calidviana*, *Ustronia*, *Troschelviana*, and *Semitrochatella* (Mollusca: Archaeogastropoda: Helicinidae) in Cuba

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A MONOGRAPH OF THE GENERA *CALIDVIANA*, *USTRONIA*, *TROSCHELVIANA*, AND *SEMITROCHATELLA* (MOLLUSCA: ARCHAEOGASTROPODA: HELICINIDAE) IN CUBA

WILLIAM J. CLENCH AND MORRIS K. JACOBSON

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ABSTRACT

This is the fourth in a series of papers on the representatives of the land prosobranch family Helicinidae in Cuba. The numerous taxa in Cuba previously assigned to the genus *Eutrochatella* were investigated. The conclusion was reached that *Eutrochatella s. s.* does not occur in Cuba. The Cuban forms which were previously placed in *Eutrochatella* are now assigned to five genera and two subgenera, using names which had previously been applied as subgenera or sections of *Eutrochatella*. No new superspecific taxa are introduced. All taxa hitherto proposed on the specific and subspecific levels were investigated: 29 species are recognized and one subspecies is described as new. Some conclusions regarding the phylogeny of the tribe Vianini, to which all the forms discussed belong, are advanced. It is assumed that the tribe originated in Central America, reached Pinar del Río via Yucatán and from there spread to other parts of Cuba.

INTRODUCTION

The family Helicinidae has been divided into four to six subfamilies (Thiele, 1929; Wenz, 1938; Keen, 1960), the most important of which are the Helicininae and the Proserpininae. The latter is composed of three tribes, the Proserpinini, the Stoastomatini, and the Vianini (Thompson, 1968: 51). The genera *Ustronia*, *Troschelviana*, *Calidviana*, and *Semitrochatella*, treated in the present study, as well as *Viana* and *Priotrochatella* treated previously (Clench & Jacobson, 1969; 1970a) belong to the tribe Vianini of the Proserpininae.

The Vianini are found in Jamaica, Cuba, Hispaniola, Puerto Rico, and the Bahamas. Only one genus, *Pyrgodomus*, occurs on the mainland in Central America. Hence this neotropical tribe must be considered West Indian.

The species contained in the Vianini can generally be recognized by their shells. While most helicinids are denticulate or depressed helicoid in shape, the Vianini are generally turbinate or low to elevated conic. In addition, all have a sharply raised, nipplelike or mucronate protoconch. Even when the shell is depressed, as in the genus *Priotrochatella* from the Isle of Pines, the elevated protoconch places it in the Vianini. This type of shell, together with a distinctive large lateral tooth complex of the radula (Baker, 1922), characterizes the group.

In some species of *Helicina s. s.* in Cuba (*lembayana* Poey, *subdepressa* Poey) as well as *neritella* Lamarck from Jamaica, the type of the genus, the spire is also somewhat raised, but a close examination reveals that the protoconch is almost planiform, with low sides that slope sharply. In the Vianini the protoconch is far more elevated, generally with the sides almost perpendicular to the base. Moreover, the more or less high conic form, common in the Vianini, is not seen in the Helicininae. The shells of the Vianini are also generally without a periostracum, but in life are frequently incrusted with a lighter or heavier layer of presumed inorganic material, which in some specimens shows signs of pseudosculpture such as keels and axial or spiral cords. Aguayo (1932: 32) supposed this layer to be the feces of the animal, but we have been unable to find anything in the literature regarding the chemical composition of this layer or its manner of deposition.

HISTORY

Blainville (1824: 235) first separated the group which we now call Vianini from the genus *Helicina*. He proposed the name *Ampullina* (non Bowdich, 1822) mentioning only *Helicina striata* Blainville (non De France, 1821). In 1825 he figured his *H. striata* showing a strongly mucronate spire but with a peculiar operculum which is unknown in the Helicinidae. Hence his type for the preoccupied *Ampullina* must be considered a nomen dubium (Clench & Jacobson, 1968: 9). Swainson (1840: 337) proposed *Trochatella* as a genus for *Heli-*

cina pulchella Gray (1825) apparently in recognition of the Vianini-like shell. This taxon was generally accepted, and several new species were described as *Trochatella* by Pfeiffer and Arango. Fischer (1885: 796), seeing that the name had been preoccupied by *Trochatella* Lesson, 1831, substituted the name *Eutrochatella.* Wagner (1907–1908) accepted *Eutrochatella* and divided the genus into several subgenera and numerous "Formenkreise," making use of shell and opercular characteristics for his new taxa. His work is unfortunately marred by numerous errors and disregard for earlier work and is illustrated with artificial looking figures which are frequently impossible to relate to natural forms.

An important paper in the study of the Helicinidae was published by H. B. Baker (1922). He worked principally with the radula, depending upon Wagner for the shell characteristics associated with this criterion. In the present work we lean heavily upon Baker's discussions (1922, 1926, 1928, 1956) but treat several of his subgenera as genera and his "sections" as subgenera. The category "section" has been eliminated from the taxonomic hierarchy (International Code Zoological Nomenclature, Art. 42d) but the distinctions noted by Baker deserve supraspecific recognition.

The last important contribution on the supraspecific level was the erection of the genus *Semitrochatella* by Aguayo & Jaume (1958) to accommodate species having a Vianini-like shell but several Helicininae-like radular characteristics (see below).

Baker (1922: 31) separated the Helicinidae into two subfamilies, the Helicininae and the Vianinae, based upon characters of the radula. In 1928 (p. 46) he reduced the family Stoastomidae C. B. Adams, 1849 to Stoastominae as an additional subfamily of the Helicinidae. In 1956 (p. 28) he included both the Stoastomatinae (which he emended from Stoastominae in accordance with Art. 11 (e) of the Code) and Vianinae as tribes in the subfamily Proserpininae Thiele, 1929. Keen (1960: 287) did not follow Baker, for she regarded the Stoastomatinae as a full subfamily and expanded the limits to include, in addition to the genera placed there by Baker, all the groups for which Baker had originally created the Vianinae.

Thompson (1968: 50–51) summarized the findings of Baker and others and elaborated Baker's (1956) stenographically presented ideas. He agreed with Baker's division of the Proserpininae into three tribes and, following Recommendation 29 (a) of the Code, called the tribes Stoastomatini, Vianini, and Proserpinini. This is a satisfactory arrangement, because it recognizes the essential similarity of the radula in the three groups and still acknowledges their strong conchological differences.

In addition to the Neotropical Vianini genera mentioned above, the Old World helicinid genera *Calybium* Morelet and *Geophorus* Fischer are also referred to this tribe. This arrangement is essentially the same as in Wenz (1938).

RADULA

In the following discussion we, as did Thompson (1968), follow the terminology of Baker (1922: 30).

The lateral tooth, also called the capituliform complex, is actually composed of two units, a larger comb-lateral and a smaller accessory plate. In the Proserpininae the comb-lateral plate generally assumes the shape of a mushroom or a crude letter T (Fig. 1). Hence Baker termed it the T-lateral. The accessory plate, which "meshes" with the larger T-lateral, is reduced in size and roughly triangular or occasionally rhomboid in outline. In the Helicininae the comb-lateral is irregularly elongate-rhomboid in shape. The base, which in Proserpininae forms the stem of the "mushroom" or the central bar of the "T," is situated terminally. The

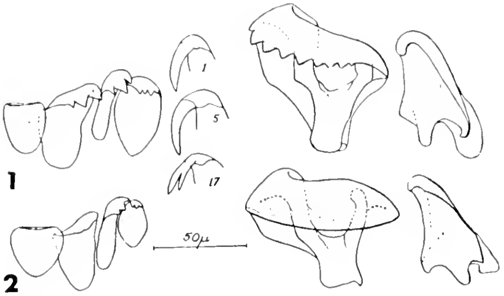

Figure 1. Radula of *Troschelviana* (*Troschelviana*) *erythraea* showing the central, marginal, and T-lateral teeth. 2. Radula of *Troschelviana* (*Microviana*) *rupestris*, showing central teeth and lateral T-complex (after Baker).

accessory plate, which is comparatively larger than in Proserpininae, is anvil-shaped.

The Vianini radula is characterized by having the typical T-lateral tooth of the Proserpininae. The cusps on the paired central teeth as well as on the lateral are, in general, reduced or absent. Thompson (1968: 50) wrote: "In the primitive taxa [of the Helicinidae] all of the paired central, lateral and marginal teeth have well developel acuminate cusps . . . . The major evolutionary trend in the family is modification and specialization of the capituliform complex and simplification of the central teeth." This view differs from the one expressed by Clench & Jacobson (1970: 62). We felt that since the "smooth" radula appears in both the old and new world tropics, this type must be the more ancient.

Baker (1922) separated the species of *Eutrochatella s. s.* from those of *Troschelviana* on the following radular characteristics: in *Eutrochatella* the single R-central rhachidian tooth is ovoid to circular in shape; in *Troschelviana* it is triangular ovoid to broadly elliptical. The T-lateral tooth of *Eutrochatella*, as well as the three paired centrals, are without cusps, or very occasionally with a single one, whereas in *Troschelviana* the T-lateral has five to ten cusps, and the centrals three to four each. Finally the radula of *Eutrochatella* has 62 to 90 marginals and 135 to 191 teeth per row; *Troschelviana* has 44 to 64 marginals and 99 to 103 total teeth per row.

DISTRIBUTION

In our arrangement of the Cuban Vianini we have made use of the cusped or uncusped nature of the radular teeth as well as certain shell characteristics. On this basis we concluded that the genus *Eutrochatella s. s.* with an uncusped T-lateral and a strongly sculptured shell does not occur in Cuba. *Calidviana* has the roughly sculptured shell typical of *Eutrochatella* but cusped central and lateral teeth like those of *Troschelviana. Ustronia,* on the other hand, has a *Eutrochatella*-like radula, but the relatively unsculptured shell is like *Troschelviana.* In this respect it is similar to *Viana* (Clench & Jacobson, 1968). We have already explained the characteristics of *Semitrochatella* (p. 405).

The tribe Vianini, which probably originated in neighboring Central America, underwent its greatest radiation in Cuba and Jamaica. In southeast Asia *Calybium* is like *Eutrochatella* in possessing uncusped radular teeth and a strongly sculptured shell surface. The shell of *Geophorus* is smooth like *Troschelviana*; its radula has not been examined. Both genera differ from the Neotropical Vianini in having a strongly depressed shell, the apex, however, being mucronate as in most Vianini.

In the western part of Cuba, the Vianini display an interesting morphological sequence. *Priotrochatella* is the only group in the area of Cuba with *Eutrochatella*-like uncusped central and T-lateral teeth and highly sculptured shells, and probably represents an introduction from Jamaica (Clench & Jacobson, 1970). The genus *Ustronia* has a smooth or uncusped radula and a smooth shell. The cusps in *Troschelviana s. l.* vary: in the subgenus *Cubaviana* the T-lateral has "a few scallops and points near the outer edge of the margin," and in

TABLE 1.

DISTRIBUTION OF THE SPECIES OF *CALIDVIANA*, *USTRONIA*, *TROSCHELVIANA*, AND *SEMITROCHATELLA*.

	I	P	H	M	L	C	O[1]
Troschelviana (Cubaviana) scopulorum	×						
T. (C.) rubromarginata		×					
T. (C.) pyramidalis		×					
Troschelviana (T.) chrysochasma		×					
T. (T.) jugulata		×					
T. (T.) erythraea		×					
T. (T.) mestrei		×					
Semitrochatella elongata		×					
S. fuscula		×					
S. alboviridis		×					
S. babei		×	×	×			
S. conica		×	×	×	×		
Ustronia acuminata acuminata		×					
U. acuminata columellaris		×					
U. sloanii aedilii				×			
U. sloanii sloanii		×	×	×			
Troschelviana (Microviana) callosa	×						
T. (M.) rupestris		×	×	×			
T. (M.) hians					×		
T. (M.) petitiana					×		
T. (M.) pfeifferiana najazaensis						×	
T. (M.) continua							×
T. (M.) granulum							×
T. (M.) holguinensis							×
T. (M.) methfesseli							×
T. (M.) tumidula							×
T. (M.) pfeifferiana pfeifferiana							×
T. (M.) spinopoma							×
Calidviana littoricola							×

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[1] I—Isle of Pines; P—Pinar del Río; H—Havana; M—Matanzas; L—Las Villas; C—Camagüey; O—Oriente.

the subgenus *Troschelviana s. s.* this plate "bears a number of well-marked cusps on its inner edge." (Baker, 1922: 60). The shells of *Cubaviana* and *Microviana* have spiral as well as axial sculpture, whereas the shell of *Troschelviana* shows only the usually fine incremental lines and occasionally very weak axial lirations. The largely Bahamian genus *Calidviana* has the cusped radula of *Troschelviana* but the strongly sculptured shell of *Eutrochatella*. Its limited presence in a narrow territory along the northeastern coast of Oriente Province strongly suggests that it is an introduction from the nearby Bahamas.

The six genera and subgenera discussed in this study are more strongly represented in the western than in the eastern part of the island. Four are found in Pinar del Río, three in both Havana and Matanzas, two in Las Villas and only one in Camagüey and Oriente. In the latter there appear to be two, but one of these, *Calidviana*, as we have noted, probably did not develop in Cuba. Only *Troschelviana s. s.* is limited to a single province, Pinar del Río. *Ustronia* is found in Pinar del Río, Havana, and Matanzas; *Cubaviana* appears in Pinar del Río, and the Isle of Pines. The subgenus *Microviana* alone reaches the easternmost provinces of Camagüey and Oriente (Table 1).

Of the 30 specific and subspecific taxa we recognize, none is found in all of the six provinces. The most widely distributed species, *Semitrochatella conica* (Pfeiffer), is found in the four westernmost provinces (Pl. 7). Interesting examples of radiation are seen in the subgenera *Troschelviana s. s.* and *Cubaviana*, where, of the nine species listed, six are limited to Pinar del Río. Two others occur in the neighboring Isle of Pines. On the other hand, the subgenus *Microviana* is almost exclusively eastern, seven of the ten taxa being found only in Oriente (Table 1).

The single member of the tribe Vianini in Camagüey is *Troschelviana* (*Microviana*) *pfeifferiana najazaensis* new subspecies. This situation is probably a reflection of the fact that Camagüey remains the most poorly collected of all the Cuban provinces. Havana and neighboring Matanzas have four and five taxa respectively, all either in the genera *Ustronia*, *Semitrochatella*, or *Microviana*. Neither province has any representatives of *Troschelviana s. s.* or *Cubaviana*, the latter and *Microviana*, however, appearing in the Isle of Pines. Las Villas has three species, one each in *Cubaviana*, *Microviana*, and *Semitrochatella*.

The distribution of the species and subspecies of Vianini confirms the picture presented by the supraspecific taxa. The first representatives of the tribe probably appeared in Pinar del Río, where we find today 14 of the 30 valid taxa. From here they spread sparsely to the neighboring provinces. *Microviana*, which probably derived from *Semitrochatella*, alone reached the two easternmost provinces, Camagüey and Oriente.

In Oriente, however, a surprisingly rich radiation took place. Seven of the twelve species of *Microviana* are found nowhere else. Since these organisms are all small, wind dispersal (Darlington, 1957: 17–20) can be regarded as a possible agent, and those individuals or ova of the strictly calciphilous species, which were deposited in limestone areas, survived. Isolation in a generally volcanic terrain resulted in speciation.

Previously (Clench & Jacobson, 1971) we concluded that the genus *Emoda* of the Helicinidae was probably derived from *Alcadia*, a genus endemic to northern and eastern South America and the Greater Antilles. Since Oriente is closest to the other West Indies, we assumed that *Emoda* first appeared there in Cuba. Furthermore, as expected, this is where the largest number of *Emoda* species is found.

The Vianini, however, differ, for this tribe probably originated in Central America where the genus *Pyrgodomus* Crosse & Fischer, its possible progentior, still occurs. The rich radiation of this group in the westernmost part of Cuba suggests that it first reached Pinar del Río, the point nearest to Yucatán. The only subgenus eventually to reach Oriente is *Microviana*.

NOMENCLATURE

The isolated populations of some species of gastropods in Cuba have developed rather striking variations. As a result many taxa were proposed on differences in color and size (or other minor features). The simplest way the taxonomic and diagnostic validity of these criteria could be evaluated was by studying the representative distributions of the various populations on the island. Marking the provenience of populations on a large map of Cuba quickly revealed either a clear geographic separation of easily separable forms or disclosed a random distribution associated with a single variable group, many of whose features had not yet become fixed. In their study of the *Cerion* of Bimini, Mayr and Rosen (1956: 1) stated, ". . . . variability is either due to true introgression (gene exchange between species) or due to gene flow among well-differentiated allopatric populations of the same species." In the case of the *Ustronia acuminata* complex and especially *Troschelviana chrysochasma*, as well as others, we feel that the second situation generally applies. We also agree with these authors (1956: 15) that ". . . the application of specific and subspecific names to population samples has perhaps hindered more than facilitated an understanding of variations and evolution." Fortunately, in the present case a large proportion of such names remained in manuscript and hence presented no problem.

The complete absence of all paleontological data argues strongly that most of these forms, if not all, are of rather recent origin. It was shown by Mead (1961: 8) in the case of *Achatina fulica*, that in a matter of no more than 25 years, colonies isolated on the islands of the Pacific developed easily recognizable geographic forms which, were it not for our knowledge of the recency of such separation, could be taken for valid subspecies. The junior author (1966: 5) found a similar effect in the various colonies of *Cepea nemoralis* (Linnaeus) in Rockaway, New York. It is not at all unlikely that a similar condition, even if of somewhat longer duration, obtained in some of the land prosobranchs of Cuba.

ENEMIES

Harry (1950: 26) reported the presence of a round, drilled, countersunk hole in 10 to 25 per cent of the chondropomid land shells which he collected in Yucatán, Mexico. Several specimens of *Troschelviana rupestris, T. erythraea, T. holguinensis, T. hians,* and *Semitrochatella conica* show a similar hole near the aperture (Pl. 5, fig. 1) considerably smaller than the ones noted by Harry. As in the case of the operculates from Yucatán, the operculum of the prey frequently remained in place, thus leading one to the supposition that the unknown predator is able to consume the soft parts through this hole. Harry quoted Martens (1903) who reported that the larva of a beetle, *Drilus*, produced a similar hole in the Old World inoperculates *Helix* and *Bulimulus*. Possibly the predator in Cuba will prove to be a related organism.

TYPES

Our difficulties in locating some type material were described in our monograph on *Emoda* (1971). We encountered the same difficulties in the present case. The phrase "Type destroyed" in the text indicates that the type specimen had been deposited in the Natural History Museum of Stettin (Szczecin) where it was lost during World War II. "Type, MP?" means that the type is presumably in the Museo Poey of the University of Havana. All specimens referred to in this study are in the collection of the MCZ unless otherwise specified.

ABBREVIATIONS

BM(NH)	British Museum (Natural History), London
IZW	Instytut Zoologiczny Warszawa, Poland
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts
MP	Museo Poey, Havana, Cuba
USNM	United States National Museum, Washington, D. C.

MAPS

On most maps which we have consulted, the entire mountain complex in Pinar del Río bears the name Sierra de los Organos. In some later maps this name is confined to the western ranges, and the eastern portion is called Sierra del Rosario. Since topographic maps do not show a distinct break in the mountain range in Pinar del Río, we have chosen to keep the name Sierra de los Organos for the entire range and to consider other ranges, e.g., Rangel, Guacamaya, Rosario, etc., as referring to localized portions of the single greater mass.

A series of small mogotes are found at kilometer 14 on the road from Pinar del Río City to Viñales. These have no special name and are generally referred to as simply kilometer 14.

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SYSTEMATICS

PROSOBRANCHIA

Family Helicinidae Latreille, 1825
Subfamily Proserpininae Gray, 1847
Tribe Vianini H. B. Baker, 1922

Key to the Cuban Genera and Subgenera of the Tribe Vianini, Subfamily Proserpininae

1. Lateral tooth comb-shaped, basal column almost terminal, outer marginals with 5 cusps, shell generally high, trochoid .... genus *Semitrochatella*
1. Lateral tooth T- or anvil-shaped, basal column medial, outermost marginals with 2 or 3 cusps, shell shape varied 2
2. T-lateral and paired central plates not denticulate 3
2. T-lateral and or paired central plates denticulate 4
3. Shell strongly sculptured .... genus *Eutrochatella* (not in Cuba)
3. Shell smooth or with weak spiral cords, relatively thin, generally large .... genus *Ustronia*
4. Shell globose, strongly sculptured .... genus *Calidviana*
4. Shell trochoid or depressed conic, generally smooth 5
5. T-lateral and paired central plates strongly denticulate, shell elevated conic .... genus *Troschelviana*
5. T-lateral with few or no cusps, paired centrals denticulate 6
6. Shell size moderate, high trochoid .... subgenus *Cubaviana*
6. Shell very small, depressed conic .... subgenus *Microviana*

Genus *Calidviana* H. B. Baker

Callida Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 113 (type-species, *Helicina callida* [*sic*]; *calida* Weinland 1862, monotypic, *non* Agassiz 1846 [Lepidoptera]).

Calidviana H. B. Baker 1954, Nautilus, 67: 139, new name for *Callida* Wagner 1908.

Bakerviana Aguayo & Jaume 1957, Mem. Soc. Cubana Hist. Nat., 23: 118 (type-species, *Eutrochatella littoricola maisiana* Aguayo & Jaume 1957, original designation).

Description. Shell small, subglobose, solid, with strong spiral ridges. Umbilical callus thick and pronouncedly raised above the basal surface. Central and T-lateral teeth denticulate with strong cusps, marginals variously cusped, not very numerous.

Remarks. Though well represented in the Bahamas, this genus has only a single species in Cuba. The radula with its cusped central and T-lateral teeth associate the group with *Troschelviana* rather than with *Eutrochatella*. The cusped marginals are also found in *Ustronia chrysostoma* (=*sloanii* Orbigny) although *Calidviana* has a smaller number of such teeth, about 33 in *Calidviana* as compared to about 40 in *Eutrochatella*. This difference is not enough to exclude *Calidviana* from the genus *Troschelviana*. However, the lower outline of the shell and the strong sculpture indicate relationship with *Eutrochatella s. s.* Hence *Calidviana* might stand as a full genus, characterized by a *Eutrochatella*-like shell and a *Troschelviana*-like radula.

Calidviana littoricola (Pfeiffer)
Plate 4, figure 13

Helicina littoricola (Gundlach MS) Pfeiffer 1861, Malak. Blät., 7: 25 (type-locality, bei Baracoa an der Meeresküste an Steinen; lectotype, here selected, MCZ 86610, Baracoa, ex. Gundlach; paralectotypes, same data, MCZ 273211).

Helicina littoricola Gundlach. Pfeiffer 1865, Monographia Pneumonopomorum Viventium, Suppl. 2, p. 219; Arango 1879, Contribución Fauna Malacológica Cubana, p. 45.

Helicina littoricola Gundlach. Sowerby 1866, Thes. Conchyl., London, 3: 283, pl. 269, figs. 121–122.

Eutrochatella (*Eutrochatella*) *littoricola* Pfeiffer. Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 114, pl. 21, figs. 22–23.

Eutrochatella (*Bakerviana*) *littoricola maisiana* Aguayo & Jaume 1957, Mem. Soc. Cubana Hist. Nat., 23: 118, pl. 1, fig. 5 (type-locality, Maisí, Baracoa, Provincia de Oriente, Cuba; holotype, MP 17399).

Description. Shell about 4 mm in height, subglobose, solid, lusterless, base little rounded. Color grayish white or very pale flesh colored, apex lighter, aperture yellow. Whorls 5¼, gently rounded, body whorl with a very obtuse keel, barely descending at aperture. Spire unevenly domelike, apex sharply raised. Aperture oblique, widely semilunate, yellow or orange within. Parietal wall with a strongly raised, somewhat glossy parietal callus, rounded at exterior margin, about the same extent as the aperture, joining the dorsal and basal lip margins. Palatal lip double, the inner lip being an extension of the margin of the parietal callus, raised sharply at the umbilical region where it is reflected to form a pseudo-chink. Columella weakly sigmoid, rounded at the insertion with the basal lip. Sculpture of diagonal, irregular growth lines crossed by much stronger, even, rounded, raised spiral cords, wider than their intervals, becoming obsolete near the umbilical region. Protoconch 1½ whorls, white, microscopically pitted, sharply raised above the succeeding whorls. Periostracum wanting. Operculum calcareous, whitish, with a low, rather wide external columellar ridge; outer margins with a narrow, low ridge.

Height mm	Width mm		
4.1	4.3	Baracoa,	lectotype
4.2	4.0	"	paralectotype
3.5	4.0	"	"
3.5	4.3	El Bagá,	Baracoa
4.5	4.3	"	"

Remarks. This is an easily recognized form. The subglobose shape and the strongly sculptured surface are found in no other Cuban members of the Vianini. Nevertheless, it possesses the sharply raised apex which is characteristic of the tribe.

The genus has had its greatest development in the various islands of the Bahamas. *C. littoricola* is closely allied to *calida* (Weinland, 1862) from the Crooked Island group and Great Inagua, Bahamas, but the latter species has a much larger shell and has pronouncedly weaker spiral sculpture. The fact that in Cuba the range of *littoricola* is confined to a strip on the north coast near Baracoa argues strongly for its having had its origins in the nearby Bahamas.

In the colonies of this species, there are some variations in size and in comparative dimensions, some shells being smaller than others and greater in width than in height, others being larger and greater in height than in width. This may prove to be a secondary sexual characteristic.

Aguayo & Jaume (1957: 118) gave the subspecific name *maisiana* to a population at Maisí with an orange instead of yellow aperture. They stated that the nominate form comes from Cayojuín (Cayo Juin) and other areas north of Baracoa, whereas *maisiana* comes from the region to the south. However, a series of *littoricola* in MCZ (127457, Bermúdez collection) comes from El Bagá, well to the south of Baracoa (Pl. 8). Hence zoogeographical reasons do not warrant the separation of the two forms which differ only in the color of the aperture. Moreover a large series of *C. calida* (Weinland) (MCZ 189022) from Great Inagua Island in the Bahamas, a possible ancestor of *littoricola*, shows a mixture of specimens with yellow and orange apertures. We must conclude that the color of the aperture is insufficient to establish taxonomic distinctions.

Specimens examined. ORIENTE. Baracoa; El Bagá.

KEY TO THE SPECIES OF *USTRONIA*

1. Shell, c.15 × 18 mm in size, rather thin shelled 2
1. Shell, c.12 × 13 mm in size, more solid 3
2. Shell without columellar blotch .... *a. acuminata*
2. Shell with columellar blotch ...... *a. columellaris*
3. Shell up to 12 mm in height .... *s. sloanii*
3. Shell less than 10 mm in height .... *s. aedilii*

Ustronia Wagner

Ustronia Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab., (2)1: sect. 18, pt. 2, p. 116 (type-species, *Helicina sloanii* Orbigny 1842, by subsequent designation, H. B. Baker 1922, Proc. Acad. Nat. Sci. Philadelphia, 74: 62; not *H. sloanei* Wagner *et auct.*).

Description. Shell moderately large, low to elevated turbinate, relatively thin, smooth, lip simple, moderately expanded, shallowly excavated in umbilical region; parietal callus narrow, often brightly colored. Axial and spiral sculpture present. Central and T-lateral radular teeth without cusps, as in *Eutrochatella*, but with a smaller number of unicuspid marginals.

Remarks. This group has the radula of *Eutrochatella* (see Troschel, 1857: 79, pl. 5, fig. 6) and the smooth shell of *Troschelviana*. In this way it occupies an analogous position to *Calidviana*, which has a *Troschelviana*-like radula and a *Eutrochatella*-like shell. In this genus we include the larger, rather thin-shelled species of western Cuba. The radula of *T. chrysostoma* Pfeiffer (=*sloanii* Orbigny) as pictured by Troschel (1857: 78, pl. 5, fig. 4) shows the uncusped smooth teeth of *Eutrochatella* *s. s.* Thus, we employ *Ustronia* Wagner as it was limited by Baker (1922).

Aguayo (1962: 9) tried to show that Baker's designation of *sloanii* Orbigny as the type of *Ustronia* was invalid, because, among other things, Baker was not justified in assuming that *sloanei* Wagner *et auct.* was indeed the same as *sloanii* Orbigny and that what was taken to be *sloanii* was actually a different species, *gouldiana* Pfeiffer. But Aguayo's discussion is irrelevant since there is no doubt that Baker clearly indicated his designation to refer to *sloanii* Orbigny 1842, the original and earliest form of the name. The spelling *sloanei* was a later emendation by Pfeiffer (1855). Moreover, there is little doubt that *gouldiana* Pfeiffer is a junior synonym of *sloanii*, a fact admitted by Pfeiffer himself (1855: 95). Later (1856: 138) Pfeiffer maintained the distinction of his species, but he did so on such relative bases as stronger sculpture, less elevated spire, and more depressed aperture. Our examination of large numbers of specimens from Pinar del Río, Matanzas, and Havana do not bear this out. Arango (1879: 42) also synonymized the two, but Crosse (1890: 307), having seen no specimens of either, felt that the published figures "nous semblent différer entre elles." A careful comparison of the published description of both taxa and an examination of specimens from near the type-locality of *sloanii* with large numbers of so-called *gouldiana* in the collection of the MCZ show that a valid differentiation is impossible.

The three taxa of *Ustronia* extend from Guane in Pinar del Río to Ceiba Mocha in Matanzas, with the strongest representation in the intervening Havana Province (Pls. 6, 7). In the west, from Guane to Viñales, we find *acuminata acuminata*, larger shells without the columellar stain. From San Andrés to San Diego de los Baños is found a somewhat smoother shell with an orange or yellow spot on the columella. From Sierra Anafe in Pinar del Río near the boundary of Havana, to Ceiba

Mocha in Matanzas is *sloanii*, a smaller shell without a columellar spot. There is also a colony of *sloanii* at Mariel, the northeastern corner of Pinar del Río Province near Havana.

Ustronia sloanii sloanii (Orbigny)
Plate 1, figures 9–12

Helicina sloanii Orbigny 1842, Mollusques, *in* Sagra, Histoire Physique, Politique, et Naturelle de l'Ile de Cuba, 1: 248, pl. 20, figs. 4–6 (type-locality, "l'intérieur de l'île au Cerro de Cuzco" [Pinar del Río]; type not in BM(NH), location unknown; not *H. sloanei* Potiez & Michaud 1836, Galerie des Mollusques, Paris, p. 299, [nude name]; nor *sloanei* Wagner *et auct.*).

Helicina sloanei Orbigny. Pfeiffer 1855, Malak. Blät., 2: 95 [error for *H. sloanii* Orbigny].

Trochatella chrysostoma Shuttleworth, *in* Pfeiffer 1850, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 1, p. 66, pl. 10, figs. 3–4 (type-locality, Cuba; type destroyed).

Trochatella gouldiana Pfeiffer 1850, Zeitschr. Malak., 7: 191 ("type-locality in insula Cuba"; type destroyed); Pfeiffer 1852, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 1, p. 67, pl. 10, figs. 5–6. Not to be confused with *Helicina gouldiana* Forbes 1851.

Eutrochatella (*Eutrochatella*) *chrysostoma* Pfeiffer. Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 111, pl. 21, figs. 3–5.

Eutrochatella (*Ustronia*) *sloanei* Orbigny. Wagner 1908, *op. cit.*, p. 118, pl. 23, fig. 16.

Eutrochatella (*Ustronia*) *gouldiana maris* Aguayo & Jaume 1953, Mem. Soc. Cubana Hist. Nat., 21: 270, pl. 31, fig. 5 (type-locality, Loma "Cantera Blanca," c. 2 km S of Playa, de Baracoa, Bauta, Havana; holotype, MP 13253).

Eutrochatella (*Ustronia*) *gouldiana camoensis* Aguayo & Jaume 1953, *ibid.*, p. 270, pl. 31, fig. 6 (type-locality, Loma de Camoa, Portugalete, San José de las Lajas, Habana; holotype, MP 17305).

Description. Shell about 13 mm in diameter, broadly conic to depressed trochoid, relatively thin, generally sublustrous. Color various, grayish white, pale to light yellow, or faintly rufous, apex occasionally darker, lip and columella generally white. Whorls about 7, flat or moderately rounded, strongly carinate in juveniles, body whorl gradually descending at aperture, with an obtuse or moderately sharp carina, suture well impressed. Spire moderately high to low conic, sides flat or gently inflated, apex sharply raised. Aperture oblique, widely semilunate, evenly rounded at outer edge. Parietal wall flat or weakly inflated, with a thin, lustrous parietal wash that does not extend beyond the aperture. Palatal lip simple, barely flaring centrally, straight at dorsal and basal insertions, slightly thickened within. Columella barely convex above, almost perpendicular below, slightly thickened near the base, set off from the umbilical area by a white lamella and a barely raised, triangular protuberance. Sculpture of moderately strong, diagonal, irregular growth lines crossed by weak or strong, closely set spiral cords, generally weaker or obsolescent on the body whorl and base. Protoconch 1½ whorls, rounded, closely punctate, sharply raised. Periostracum wanting; shell frequently incrusted with a thin inorganic layer. Operculum brownish, thin, glassy, almost transparent in palatal region, with a strongly raised, milk-white, bent lamella at the columellar margin; inner layer extending beyond the margins of the glassy outer layer, not separated by a marginal sulcus.

Height mm	Width mm	
12.2	13.1	Sierra Anafe, Pinar del Río
9.2	9.7	San Antonio de los Baños, Habana
10.3	12.4	Camoa, Habana
10.1	10.7	El Grillo, Madruga, Matanzas
11.2	11.9	El Palenque, Matanzas
10.0	10.1	Ceiba Mocha, Matanzas

Remarks. This species differs from *U. acuminata* in being smaller, more fragile, and more depressed. The spiral sculpture is frequently quite strong and in such a case it is stronger than in any populations of *acuminata.* The columella rarely bears a colored stain. In this last way *sloanii* differs additionally from the neighboring *acuminata columellaris.* Only at Punta Sabanilla at the eastern limit of the range of the species, can occasional individuals with a small orange stain near the parietal insertion of the columella be found. The operculum of *sloanii* is thinner, more transparent, and differently colored than the operculum of *acuminata*.

The strength of the spiral sculpture varies sharply. At Punta Sabanilla near the city of Matanzas, the spiral sculpture is quite strong, visible to the naked eye. At Sierra Anafe it is strong on the earlier whorls and very weak to obsolescent on the body whorl and the base. At Camoa the shells vary from being moderately to quite strongly sculptured. It is obvious that the spiral sculpture in this species is a variable characteristic of no diagnostic value in separating taxa.

Wagner (1908) discussed *chrysostoma* Pfeiffer and *sloanei* [*sic*] Orbigny, putting them into different subgenera. He overlooked *gouldiana* Pfeiffer, even as a synonym and Fulton (1915) did not notice this lapse. Arango (1879) synonymized *gouldiana* with *sloanei* [*sic*], giving several localities for its occurrence. However, for *chrysostoma* he gave only "isla de Cuba," apparently copying from Pfeiffer and indicating that he had collected no specimens himself. The *Ustronia* with the golden mouth is found at Sabanilla, near the city of Matanzas, and this is here selected as the type-locality. However, the golden mouth is not found in all specimens from Sabanilla and, besides, some individuals from the Sierra Anafe show indications of possessing that color in the aperture. Hence this feature cannot serve as a diagnostic distinction. This tinge of golden color is found also in the populations of *Emoda sagraiana* (Orbigny) at the Ensenada de los Burros near Luis Lazo in Pinar del Río. It is probably an unstable color form which cannot survive interbreeding.

The type-locality of *U. sloanii* is the Cerro de Cuzco, Candelaria, Pinar del Río. The series from Mariel is also from Pinar del Río, and hence these two localities represent the western limit of the species.

Specimens examined. PINAR DEL RÍO. Mesa de Mariel. HAVANA. Tapaste; Loma La Jaula, Tapaste. *Madruga:* Zanabria; La Chareta; Mogote La Curva; Pipian; Sitio Perdido; Paredones Entronque, Sierra El Grillo; El Inglés, Sierra El Grillo; eastern end of Sierra El Grillo; between Madruga and Aguacate. *Guayabal:* Peña Blanca, and Esperón (both Sierra de Anafe); Nazareno, Caimito de Guayabal. *Güines:* Gabina; Cuevas de Cotillas; Jamaica; Somorrostro near Jamaica. *Camoa:* Lomas de Camoa; Mendoza, Jaruco; Escalera de Jaruco; Central Merceditas, Milena del Sur; La Portada, Managua; El Altivo, Aguacate; San Antonio de los Baños; Finca Alianza, Cotorro. MATANZAS. El Palenque; Ramona, El Palenque; Paredones de Punta de Sabanilla; near Matanzas; Ceiba Mocha; 5 mi. W of Ceiba Mocha; vicinity of Paradero de Ceiba Mocha; Mogote de Ceiba Mocha; Finca Mona, Canasí.

Ustronia sloanii aedilii Aguayo & A. Torre

Eutrochatella chrystostoma aedilii Aguayo & A. Torre 1954, Rev. Soc. Mal. 'Carlos de la Torre,' 9: 67, fig. p. 68 (type-locality, La Ensenadita, a medio kilómetro al oeste de la Boca de Bacunayagua, Matanzas; holotype, MP?).

Description. "This subspecies is distinguished from the typical race by having a considerably smaller shell. In addition, the apex is less pointed, the spire consisting of $5\frac{1}{2}$ to 6 whorls while the typical [form] has $6\frac{1}{2}$ to 7. The other shell characters (color, etc.) seem to be sufficiently similar in both races, although the spiral sculpture of this new subspecies consists of wider and more strongly marked lines than in the typical." (Translated.)

Length mm	Major diameter mm	Minor diameter mm	
7.3	8.4	7.2	holotype
8.3–6.6	9.4–7.5	8.0–6.4	paratypes

Remarks. We have not examined this subspecies. We keep it provisionally because of its unusually small size as well as the fact that it appears to be sufficiently isolated at the periphery of the range of the species to be granted subspecific rank. According to the authors, the species is relatively abundant in the type-locality, the only place where it has been found. It is named for its co-discoverer, Edilio Estopinán.

Ustronia acuminata acuminata (Poey)
Plate 1, figures 1, 2, 4, 5, 6, 8

Helicina acuminata ("Velásquez" MS) Poey 1851, Memorias Historia Natural Isla de Cuba, 1: 112, pl. 5, figs. 13, 15 (type-locality, here restricted, Viñales, Pinar del Río; type, MP?).

Helicina lutescens Newc[omb] MS, fide Poey, *op. cit.*, p. 113.

Helicina blandiana Gundlach 1856, Malak. Blät., 3: 40 (type-locality, saxa ripae fluvii San Diego de los Baños; lectotype, here selected, MCZ 87885 [Cuba] ex Gundlach).

Helicina blandiana Gundlach. Poey, Memorias Historia Natural Isla de Cuba, 2: 14, pl. 1, fig. 19.

Helicina remota Poey 1858, *op. cit.*, 2: 87, pl. 8, fig. 26 (type-locality, Guane, montem Cubae occidentalem; type, MP?).

Eutrochatella (*Ustronia*) *acuminata* "Velásquez" Poey. Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 116, pl. 23, figs. 7–8, 10–11.

Eutrochatella (*Ustronia*) *acuminata blandiana* Gundlach. Wagner 1908, *ibid.*, p. 117, pl. 23, fig. 12.

Eutrochatella (*Ustronia*) *remota* Poey. Wagner 1908, *ibid.*, p. 118, pl. 23, figs. 13–15.

Viana acuminata Poey. Webb 1948, Foreign Land Shells, Rochester, N. Y., p. 143, pl. 65, fig. 5.

Helicina remota exhuberans "Torre" Aguayo 1962, Caribbean Jour. Sci., 2: 10 [nude name].

Description. Shell about 15 mm high, 18 mm wide, depressed to high turbinate, moderately thin, generally dull. Color pale yellowish or reddish white, more vivid in aperture, lip generally white. Whorls 7 to 7½, slightly swollen, body whorl rounded to sharply carinate, frequently with a short, wide, shallow groove near the palatal lip, not descending at the aperture. Suture well impressed. Spire depressed to raised conic, sides generally somewhat convex, apex raised, nipplelike. Aperture oblique, broadly semilunate, evenly rounded palatally. Parietal wall flat or variously inflated with a thin, highly lustrous parietal wash which extends only slightly beyond the aperture. Palatal lip entire, weakly expanded centrally, straight at terminations; upper lip faintly distorted by the shallow groove on the body whorl, occasionally with a shallow notch near the insertion in the body whorl. Columella short, slightly convex above, almost perpendicular below, slightly swollen in the center, with low, slightly curved, rather wide lamella at the insertion of the basal lip. Axial sculpture of strong, irregular, diagonal growth lines crossed by very faint, more or less regular spiral cords, widely and irregularly spaced on body whorl. Protoconch 1½ whorls, rounded, white, sharply raised, minutely punctate. Periostracum wanting, but shells frequently encrusted with a layer of inorganic matter. Operculum ear-shaped, columellar margin strongly twisted, with a high, rounded, narrow lamella reaching almost to the top. Outer layer white, lustrous; inner layer thin, brownish, darker toward the margins, extending slightly beyond the outer calcareous layer; outer margins thin.

Height mm	Width mm	
14.7	16.0	Sierra del Infierno
14.9	17.8	La Chorrera, San Vicente
15.2	15.4	Hoyo de Gallardo, El Queque, Viñales
10.2	14.2	La Muralla, Guane
12.2	14.6	Los Portales, Guane
13.6	16.1	Sierra Paso Real, Guane
15.1	16.0	Mendoza, Guane
11.0	11.0	lectotype of *blandiana*, San Diego de los Baños

Remarks. Specimens of *U. acuminata* from Guane, the type-locality of the synonym *remota*, especially those from La Muralla, have a depressed, rather strongly keeled shell with a flattened base. Specimens of *U. acuminata* from San Vicente and Viñales have an elevated shell with a well-rounded body whorl. Between these two extremes every degree of intergrade is found. We can only conclude that *U. acuminata* is a variable species, whose populations do not possess variations having definite geographical separation or clear morphological distinctions. As in the case of *Emoda sagraiana* (Orbigny), *Ustronia sloanii* (Orbigny) and *Viana regina* (Morelet), these variations do not suggest that a cline is present. In addition to the shape of the shell, variations in color, which are scattered haphazardly throughout the range, are frequently found even within populations. *H. blandiana* seems to be merely a small form of *acuminata* such as is found in small, isolated mogotes.

In spite of these variations, the shell is not difficult to determine. Its generally large size, relatively thin texture, lack of strong sculpture, thin, narrowly expanded lip, and localization in the Sierra de los Organos geographic complex in Pinar del Río Province are diagnostic. It differs from *U. sloanii* (Orbigny) of Havana and Matanzas in its larger size, generally more elevated shape, thinner texture, in the weak rather than strong, even spiral sculpture on the upper whorls, and in the nature of the operculum.

In occasional specimens in different populations we find a small notch on the upper lip, somewhat like that found in male specimens of *Viana*. This might have a similar significance, but we do not have enough material at hand to determine this. It should be born in mind that we find the notch in so few specimens that it would be difficult to assume that it is found in all specimens of a single sex. It might prove to be nothing more than a deformation caused by roughness in the microhabitat.

This species ranges from Mendoza to Punta de la Sierra at Guane, but is not present in the large mountainous area reaching from the Sierra San Carlos at Luis Lazo, past the Sierra Cabezas and Sierra Gramales at Cabezas and the Sierra Quemado at Isabel María (Pl. 6). It appears again at the Sierra Viñales region and then extends, as the subspecies *columellaris,* in an unbroken range to the Sierra Rangel (Pl. 6). In this gap the species *Troschelviana jugulata* (Poey) replaces it. Probably here the two species entered into competition and in time *jugulata* replaced *acuminata.* In the area around Guane where the two species everlap, the case is not so clear. Three possibilities may here be recognized: 1) that the competition has not been of sufficiently long duration to have been decided in favor of one of the two species; 2) that the microhabitats they occupy differ ecologically and geographically so that in these places the two species do not enter into direct competition; and 3) that somehow *acuminata* was transferred from its range in Viñales and beyond to Guane while skipping the intervening areas.

Unfortunately not enough paleontological and ecological data are available, so that the answers must remain in the realm of speculation. See also below in *Troschelviana chrysochasma.*

Poey stated that this subspecies is found at San Diego and other places of the western mountain range, hence making San Diego de los Baños the type-locality. But we have found that San Diego de los Baños is well within the range of *acuminata columellaris.* Hence we are here selecting Viñales as the type locality of *acuminata* (Poey).

Specimens examined. PINAR DEL RÍO. *Guane:* Mendoza; La Pedrera, Mendoza; Sierra de Guane; Sierra Paso Real; Los Portales; La Muralla; Puerta de la Muralla. *Viñales:* El Queque; Hoyo de Juan Gallardo, El Queque; El Cuajaní; Valle de las Delicias; Mogote de Martín Miranda; El Cejanal; Mogote Dos Hermanos; Mogote de Lorenzo López; Hoyo de los Muertos Niños; Ensenada de Basilio Torres, Sierra del Infierno; Sitio del Infierno; Sierra Penitencia; Mogote de Guallarico, near Sierra Penitencia; Sierra de Viñales; Hoyo del Cimarrón, near Pan de Azucar. *San*

Vicente: La Guasasa, Puerta del Ancón; Hoyo de Fania, Palmarito; Baños de San Vicente; Ensenada de San Vicente; Sierra La Chorrera; Mogote Pequeño, Costanera de San Vicente. *Consolación del Norte:* Ensenada de los Borges, Canalete; Mogote Canelete; Abra de Bejarano.

Ustronia acuminata columellaris (Gundlach)
Plate 1, figures 3, 7

Helicina columellaris Gundlach 1856, Malak. Blät., 3: 39 (type-locality, scopulos, Rangel; type, MP?).

Helicina columellaris Gundlach. Poey 1858, Memorias Historia Natural Isla de Cuba, 2: 14, pl. 1. fig. 16.

Helicina columellaris Gundlach. Pfeiffer 1856, Novitates Conchologicae, 1: 84, pl. 23, figs. 11–13.

Helicina columellaris Gundlach. Sowerby 1866, Thes. Conchyl., 3: 284, pl. 270, figs. 148–151.

Eutrochatella (*Ustronia*) *acuminata columellaris* Gundlach. Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 117, pl. 23, fig. 9.

Description. The shells of this subspecies resemble those of the nominate form in size and shape, but differ in being generally somewhat higher, rounded or less sharply carinate at the periphery, and in having a yellow or orange-yellow stain at the columella.

Height mm	Width mm	
15.0	13.0	Rangel (type-locality)
16.0	15.8	Mogote Grande, San Andrés
19.1	18.5	Sierra La Güira
16.3	16.2	Sierra Galalón
15.4	14.4	Sierra Limones
13.0	12.2	Kilometer 14

Remarks. This subspecies is readily distinguished by the yellow or orange-yellow stain at the columella. This stain varies in size and intensity, but it is invariably present. Normally this character alone would not be of sufficient diagnostic value, but in the present case there are geographic considerations that support subspecific separation. *Ustronia acuminata* with an unstained columella extends from Mendoza to the area of Consolación del Norte, just to the west of Sierra San Andrés. *U. columellaris* with the stained columella occurs from the Sierra San Andrés and extends to the limit of the Sierra de los Organos at Rangel. It is also found as isolated populations at Kilometer 14 and El Guamá in the south.

The present subspecies differs also in being generally larger, glossier, and less strongly keeled. However, some variation occurs in the latter feature, from a well-rounded periphery in the population at Sierra La Güira and Rangel to a subcarinate form at Sierra San Andrés and Sierra Guacamaya.

The population at Sierra Guacamaya shows a wide, reddish, subsutural band, weakly defined at its outer margin. The shells are moderately high with the keel subcarinate. Nearby, at the Sitio de la Sierra in San Andrés, another population with a similar subsutural band is found. Here the keel of the shells is much weaker and the shells are somewhat higher. In spite of the strikingly different color pattern, we do not feel that a special name is necessary, since we regard it as a color variation that is probably not stable in the case of interbreeding.

Specimens examined. PINAR DEL RÍO. Mogote Lamas near the Entronque de Herredura; Bermejales; Hoyo de la Sierra, San Andrés; Falda de Pico Chico, San Andrés; Sitio de La Sierra, San Andrés; Mogote Grande, SW of Pico Chico, San Andrés; Ensenada de la Ayúa, San Andrés; Galalón; Cueva de Abano, Galalón; Colena de la Piedra, Galalón; Abra del Caiguanabo; Mogote de Caiguanabo; Mogote de los Portales, San Diego de los Baños; Mogote el Indio, San Diego de los Baños; Sierra La Güira; Sierra Guacamaya; El Toro, Sierra Limones; Sierra Rangel; Pedrera, Kilometer 14, Viñales; El Guamá, Viñales.

KEY TO THE SPECIES OF *TROSCHELVIANA* S. S.

1. Shell small, usually less than 6 mm in height, thin shelled, colors subdued 2
1. Shell larger, generally 9 to 11 mm in height, more solid, colors frequently vivid 3
2. Shell with acute, white basal carina .... *mestrei*
2. Shell with obtuse or rounded carina .... *erythraea*
3. Shell acutely conic, solid, columellar blotch wanting .... *chrysochasma*
3. Shell broadly conic, less solid, with red, yellow or orange columellar blotch .... *jugulata*

Genus *Troschelviana* H. B. Baker

Troschelviana H. B. Baker 1922, Proc. Acad. Nat. Sci. Philadelphia, 74: 59 (type-species, *Helicina erythraea* "Wright" Sowerby 1866, original designation, as subgenus of *Eutrochatella*).

Description. Shell small to moderate in size, sharply elevated, quite smooth, sculptured generally only with faint axial growth lines. Color generally pale, either yellow, greenish or orange, occasionally with more vivid color at the aperture. Paired central radular teeth and T-lateral armed with rather high cusps, three on the central, about nine on the T-lateral. Periostracum generally wanting; shells frequently encrusted with layer of inorganic matter. Operculum auriform, composed of an outer calcareous layer of varied strength, color, and sculpture, and a thin inner chitinous layer, generally light brown or buff; columellar margin with a variously high, rounded lamella.

Remarks. The radula of *T. chrysochasma* (Poey) was described and figured by Troschel (1857: 79, pl. 5, fig. 6), and that of *T. erythraea* by H. B. Baker (1922: 59, pl. 6, fig. 27). These figures clearly show the contrast between the smooth radular plates of *Eutrochatella s. s.* and the cusped plates of *Troschelviana* and the subgenus *Cubaviana* (Fig. 1). We include in subgenus *Troschelviana* the species with small, smooth, rather sharply elevated shells.

Subgenus *Troschelviana s. s.*

Description. Shell very small to moderate in size, strong, smooth, elevated conic, with axial sculpture of fine growth lines. Spiral sculpture wanting.

Remarks. This subgenus is confined to Pinar del Río Province. We include in it the species with a smooth shell, without spiral sculpture, and with a high, almost turreted shape. The white, undulate axial lineolations within the shell substance, which Pilsbry (1933: 131) calls characteristic of the Helicinidae, are generally visible here under moderate magnification. However, in some specimens of *T. chrysochasma* Poey, they are less easily seen or even completely absent.

Troschelviana (*Troschelviana*) *erythraea* (Sowerby)

Plate 4, figure 3

Helicina rubella 'Wright,' *in* Pfeiffer 1864, Malak. Blät., 11: 107 (type-locality, Cayos de San Felipe); Pfeiffer 1865, Monographia Pneumonopomorum Viventium, Suppl. 2, p. 237 (lectotype, here selected, MCZ 73779, Cayos de San Vicente, ex Wright; not *Helicina rubella* J. Green 1833).

Helicina erythraea "Wright" Sowerby 1866, Thes. Conchyl., 3: 284, pl. 278, figs. 461–463 (no locality; type, BM(NH) 1969101).

Helicina rubella Wright. Arango 1879, Contribución Fauna Malacológica Cubana, p. 55.

Eutrochatella (*Ustronia*) *rubella* "Wright" Pfeiffer. Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 126, pl. 24, figs. 24–25.

Eutrochatella (*Ustronia*) *rubella citrinocallossa* Wagner 1908, *ibid.*, p. 126, pl. 24, figs. 26–27 (Vignales auf Cuba; type, IZW 8561).

Helicina chryrochasma [*sic*] var. *calloflava* Wagner 1908, *ibid.*, p. 127 (as synonym of *citrinocallossa*).

Eutrochatella (*Troschelviana*) *erythraea* ("Wright" Sowerby). H. B. Baker 1922, Proc. Acad. Nat. Sci. Philadelphia, 74: 59, pl. 6, fig. 27 [radula].

Description. Shell about 6 mm in height, elevated conic, sublustrous, moderately thin, apex acute. Color pale reddish brown, occasionally greenish yellow, base lighter, lip white. Whorls 7½, rather flat, body whorl obtusely carinate or rounded, base moderately inflated, suture weakly impressed. Aperture oblique, widely semilunate, bright orange-yellow, outer margin evenly rounded. Parietal wall with a triangular, slightly swollen callus at the columella. Palatal lip thin, slightly thickened within, mildly flaring but not reflected, white or lighter than the rest of the shell. Columella short, evenly rounded at insertion into the basal lip. Sculpture of very fine, frequently somewhat wavy, diagonal growth lines; spiral sculpture wanting. Protoconch 1½ whorls, same color as rest of shell, microscopically pitted, raised above succeeding whorls. Periostracum wanting, but shells are frequently encrusted except at parietal region. Operculum thin, glassy, pale yellow, outer margin darker.

Height mm	Width mm	
6.0	4.1	Cayos de San Vicente, Viñales, lectotype
5.3	4.2	Cayos de San Felipe
5.8	4.8	"
5.7	4.9	"
6.1	5.5	Cayos de San Diego
6.2	5.2	"

Remarks. The shells of this species differ from those of *alboviridis* in their larger size, their predominantly brown or yellow color, and in the absence of darker apical and basal areas. They have a narrower shape and a more acute carina than *mestrei* in addition to being colored differently.

The species probably has a wider distribution than the records available to us would indicate (Pl. 8). As in the case of many small shells in Cuba, they tend to be overlooked by collectors.

Specimens examined. PINAR DEL RÍO. *Viñales:* Cayos de San Vicente; Cayos de San Felipe; El Queque. *Consolación del Norte:* Canalete.

Troschelviana (Troschelviana) chrysochasma (Poey)

Plate 3, figures 10, 11, 12, 13, 16, 17

Helicina chrysochasma Poey 1853, Memorias Historia Natural Isla de Cuba, 1: pl. 25, figs. 17–19 [figure only]; Poey 1858, *ibid.*, 2: 26 [description], (type-locality, Rangel; type, MP?).

Trochatella chrysochasma Poey. Troschel 1857, Gebiss der Schnecken, 1: 79, pl. 5, fig. 6 [radula].

Helicina jucunda Gundlach. Pfeiffer 1863, Malak. Blät., 10: 197 (type-locality, in parte occidentali insulae Cubae; lectotype, here selected, MCZ 86604, ex Gundlach).

Helicina chrysochasma Poey. Sowerby 1866, Thes. Conchyl., 3: 285, pl. 270, fig. 160–162.

Eutrochatella (Ustronia) chrysochasma Poey. Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 127, pl. 25, figs. 8–9.

Eutrochatella (Ustronia) chrysochasma hernandezi Wright. Wagner 1908, *ibid.*, p. 128, pl. 25, figs. 3–4 (type-locality, Vignales auf Cuba; type, IZW 8567).

Eutrochatella (Troschelviana) chrysochasma (Poey). H. B. Baker 1922, Proc. Acad. Nat. Sci. Philadelphia, 74: 59.

Eutrochatella chrysochasma mendozana Pilsbry 1928, Nautilus, 41: 79 (type-locality, Caves near Mendoza, Pinar del Río, Cuba; holotype, ANSP 141897; paratypes, MCZ 12487).

Eutrochatella (Troschelviana) jaumei Clench & Aguayo 1957, *in* Aguayo & Jaume, Mem. Soc. Cubana Hist. Nat., 23: 120, pl. 1, fig. 8 (type-locality, Mogote de la Finca "La Esperanza," San Andrés, Consolación del Norte, Provincia de Pinar del Río; holotype, MP 13262). Contrary to the statements of the authors, there are no paratypes in MCZ.

Description. Shell elevated, narrow, conic, reaching about 11 mm in height, but varying to about 7 mm, shining, strong; color generally confined to aperture, parietal wall, and occasionally the spire, varies from bright orange to pale yellowish and white; rest of shell bluish or yellowish white, occasionally flesh colored. Whorls 7 to 8, flat; body whorl gently rounded or with a variously sharp carina, not descending at aperture. Suture well impressed. Spire high conic, occasionally colored like aperture. Apex acute. Aperture oblique, widely semilunate, generally bright orange, lemon-yellow or pale yellow within, rarely white. Parietal wall smooth with a rather narrow, weakly raised parietal callus colored like the parietal wall, irregularly rounded at outer edge. Palatal lip weakly expanded except at both terminations, with a rounded groove separating the peritreme from the body whorl; a rounded thickening at point of basal insertion, colored like the parietal wall. Columella short, deeply concave. Sculpture consisting only of very fine diagonal, irregular incremental lines. Narrow, white undulate lineolations in the shell substance are also visible. Protoconch 1½ whorls, raised, rounded, minutely pitted, white or generally of the same color as the aperture, occasionally somewhat lighter. Periostracum wanting. Operculum thin, weakly concave, orange, yellow or white, with a raised, rounded parietal margin; outer margin with a shallow marginal sulcus.

Height mm	Width mm	
8.9	5.7	Paso Real, Guane
6.8	4.7	Constanera de San Vicente, Viñales
7.9	5.9	Laguna de Piedras, Viñales
10.5	7.7	El Abra, Viñales
6.9	4.7	Las Delicias, Viñales
10.2	6.6	Mogote de la Mina Constancia, Viñales
10.8	6.7	Sierra del Infierno, Viñales
8.8	6.4	Sierra del Infierno (peak), Viñales
9.3	6.8	Rangel, Consolación del Norte
8.6	6.1	Rangel, Consolación del Norte
8.9	5.4	La Güira, San Diego de los Baños
9.8	6.5	Galalón, Consolación del Norte
6.5	5.0	Mendoza, Guane (*mendozana* Pilsbry)
6.0	4.6	Viñales, (*hernandezi* Wagner)
9.2	9.2	*jucunda* Gundlach

Remarks. As evidenced by the measurements, this is a highly polymorphic species; it would be easy to apply subspecific or varietal names to several of the populations. The late Dr. de la Torre did so in manuscript, and lots bearing unpublished names are in many museums and private collections. However, after mapping the various populations carefully, we find that here, as in the case of other species in the same region, we have a single variable group which, living in isolated limestone habitats of varying size and of varying ecological conditions, has developed populations of different color, shell size, and shape. Viewed on a range-wide scale, these populations do not easily permit taxonomic separation.

The limits of variation are interesting. In size the shells vary from 10.7 × 7.7 mm in Sierra La Cumbre near the eastern end of the range of *chrysochasma* to 6.9 × 4.7 mm at Las Delicias, near the center of the range. At Rangel, the type-locality, the shells range from 9.3 × 6.8 to 8.6 × 6.1 mm, a difference which might involve secondary sexual characteristics. It must not be thought that the size variations follow any distinct geographical pattern. Populations of comparatively large shells (Sierra del Abra, 10.5 × 7.7 mm) live not far from populations of considerably smaller individuals (Las Delicias, 6.9 × 4.7 mm). Similarly, the population of Mina Constancia (10.2 × 6.6 mm) is near the Laguna de Piedras (7.9 × 5.9 mm), yet the difference in shell size is striking. Populations of large shells (San Diego de los Baños, 10.1 × 5.8 mm; Sierra Infierno, 10.8 × 6.7 mm; Galalón, 9.8 × 6.5 mm) alternate with populations of small shells (Costanera de San Vicente, 6.8 × 4.7 mm; Cuajaní, 7.4 × 4.8 mm). Populations of intermediate size (La Jagua, 8.6 × 6.5; Sierra Paso Real, 9.4 × 6.1; La Güira de San Diego, 8.9 × 5.4) are scattered from one end of the range to the other. Even in single localities with different microhabitats, populations may differ in size: shells from the lower reaches of Sierra Infierno are 10.8 × 6.7, but shells from near the peak (cima) are 8.8 × 6.4.

The color, generally confined to the aperture and the earlier post-nuclear whorls, shows similar considerable but apparently random variations. The color varies from a rather bright orange, through yellowish and pale orange, to bright and finally very faint yellow and white. Shells with bright orange color are found at Galalón and La Cumbre in the region of San Andrés near the eastern limits of the range, as well as in Constancia, Capón, and Puertecitas near Viñales, the center. Yellowish orange is found at Paso Real in the west, Sierra Quemado, near the center, and at San Diego de los Baños in the east; yellow is found at Mendoza and La Muralla in the west, Cuajaní in the center, and Rangel in the east.

The color of the apex is also variable. In several populations (Cejanal, Sierra del Infierno, Sierra La Cumbre, Puertecitas, El Queque) it is white; in other localities it varies, as does the color of the aperture. Frequently the apical color, though generally paler, more or less resembles the color of the aperture in the same specimen. In some areas, however, it varies as in Sierra de la Cumbre, where the apex is white but the aperture brightly colored.

In spite of all this, the shells of the species as a whole are not hard to recognize. The strong shell, the glossy texture, the high, acutely conic shape, the rounded carinate periphery, the presence, generally, of color surrounding the aperture, sometimes appearing also at the apex, and the localization of the species in the Sierra de los Organos and adjacent hills always betray the true identity.

Pfeiffer separated *jucunda* from *chrysochasma* on the basis of a rounded body whorl ("ohne eine Spur von Winkel."). An examination of a large number of series shows this to be a variable characteristic, intergrading from moderately carinate to smoothly rounded forms. Hence taxonomic separation is not feasible.

Shells which lack the columellar coloration were called *jaumei* by Clench & Aguayo. The columellar spot of color is highly variable in shade and in intensity. Specimens without any sign of this color fit into the range of variation. It is significant that such shells vary in no other respect. Moreover, in addition to the "type-locality" (San Andrés), shells with a white parietal or columellar area are found also at Costanera de San Vicente, a good distance away. It is clear that this is a population characteristic which appears at random and apparently has no taxonomic significance.

The names *hernandezi* Wagner 1908 and *mendozana* Pilsbry 1928 were given to races of small shells from Viñales and Mendoza respectively. We have series of shells of similar size from Las Delicias and Costanera in Viñales, and Los Portales and La Muralla in Guane. These series not only have a wax yellow color at the aperture but also vary, as do typical *chrysochasma*. The small size is rather constant, about 6 mm in height, but the population at La Muralla is larger, about 8 mm and hence serves as the transition to the normal size of *chrysochasma*. Because of the scattered occurrence of these small forms, we assume that here we are dealing with dwarfed forms affected by some factor in their environment. We found similarly dwarfed forms of *Viana regina* (Morelet) in small, isolated mogotes in the same region (Clench & Jacobson, 1968: 11).

Troschelviana chrysochasma ranges from Mendoza near Guane in the west to the region of San Diego de los Baños in the east. It is most strongly distributed throughout the region of Viñales, which might be considered the center of its range (Pl. 6). There are fewer records as both limits of its range are reached. The complete lack of any records from the area around Luis Lazo is surprising, since the species is represented both to the west (Guane) and east (Viñales) of this region. Here it is replaced by *C. jugulata* Poey (Pl. 6). (See under *acuminata.*) We have a single small series of shells from Sierra Quemado near Isabel María immediately to the northeast of Luis Lazo, but none nearer.

This species is one of the numerous groups of Cuban helicinids that are strictly confined to the calcareous hills of the Sierra de los Organos. However, we have been unable to find any field notes that would give us more data on its ecological preferences.

Specimens examined. PINAR DEL RÍO PROVINCE. *Guane:* Sierra Paso Real; Cueva del Catre, Sierra Paso Real; Pedrera de Mendoza; La Cantera, Mendoza; *Isabel María:* Sierra Quemado. *San Vicente:* Sierra La Chorrera; Ensenada de la Catuna, La Chorrera; Ensenada Miranda; Hoyo de la Fania; Costanera de San Vicente; Punta de la Costanera de San Vincente; Central Mogote, El Cao, Mogote de Mongo Cruz, Mogote Grande de los Cabrera (all Laguna de Piedras). *Viñales:* Ancón; mogote near Ancón; El Abra; Sierra de Galeras, El Abra; La Guasasa; Mogote Capón; Mogote del Refugio; Bermejales; Mogote de la Mina Constancia; Mogote Coco Solo; Mogote de la Dinamita; Mogote de los López; Mogote del Marmol; Mogote de Lorenzo López; Mogote de José María García; Mogote Palmarito; Mogote Santoro, Cuajaní; Mogote Abascar, Cuajaní; Pedregal de Vega Larga; Sierra Cejanal; Sierra Serrucho; Sierra del Infierno; Hoyo de los Cimarrones, Sierra del Infierno; Sierra Cejanal; Puertecitas; Cueva del Agua; Las Delicias; Hato Morales; Hoyo del Majá; Hoyo de Jaruco. *Consolación del Norte:* Mogote de Vegas Nuevas; Hoyo Corto de San Antonio, La Jagua; Mogote de Pastor Rivera; Cueva del Abono, Galalón, San Andrés. Guajaibón (*jucunda* Pfeiffer). *Rangel:* El Retiro; Paredones del Río Taco Taco. *San Diego de los Baños:* Sierra de la Cumbre; Mogote Colorado; La Catalina (*jucunda* Pfeiffer); Mogote near Finca de Cortino; Mogote Herrera; La Güira.

Troschelviana (Troschelviana) jugulata (Poey)

Plate 2, figures 1–2

Helicina jugulata Poey 1858, Memorias Historia Natural Isla de Cuba, 2: 34, pl. 4, figs. 3–4 (type-locality, Guane; lectotype, here selected, MCZ 73780, Anthony Collection ex Poey; paralectotype, same data, MCZ 262651).

Helicina jugulata Poey. Pfeiffer 1858, Monographia Pneumonopomorum Viventium, Suppl. 1, p. 196.

Helicina jugulata Poey. Sowerby 1866, Thes. Conchyl., 3: 284, pl. 270, figs. 154–156.

Helicina jugulata Poey. Pfeiffer 1862, Novitates Conchologicae, 2: 203, pl. 53, figs. 16–19.

Helicina jugulata Poey. Arango 1879, Contribución Fauna Malacológica Cubana, p. 51.

Eutrochatella (Ustronia) jugulata Poey. Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 127, pl. 25, figs. 1–2.

Eutrochatella (Troschelviana) jugulata (Poey). H. B. Baker 1922, Proc. Acad. Nat. Sci. Philadelphia, 74: 59.

Helicina jujulata Poey. Paetel 1889, Catalog der Conchylien-Sammlung, Berlin, 4th ed., pt. 2, p. 496, error for *jugulata*.

Helicina jujularis Poey. *Op. cit.*, p. 496, error for *jugulata*, nude name.

Description. Shell reaching about 15 mm in height, elevated conic, moderately strong, shining. Color of upper whorls light reddish brown merging gradually into rufous-tinged bluish white, orange, or yellow in the lower whorls with a paler subsutural band on the last whorl; parietal region with a gleaming, dark reddish brown spot. Whorls 8, barely convex, body whorl inflated, not descending at aperture, with an obtuse keel in earlier portion; keel sharp in juvenile specimens. Suture moderately impressed. Spire steep, elevated conic, apex acute, raised. Aperture capacious, width equal to height, pale yellow within, outer edge evenly rounded. Parietal wall smooth with a gleaming, barely raised, dark reddish brown callus, entering shortly into the aperture, unevenly rounded at outer margin. Palatal lip thin, flaring centrally, narrow and barely flaring above, reflected only briefly at insertion into columella where it forms a small, elongate, low tubercle. Columella unevenly convex, more so below, with a subacute angle at insertion into basal lip. Sculpture faint, composed of fine diagonal growth lines. The wavy lineolations in the shell substance are rather wide, easily visible. Protoconch 1½ whorls, glassy, lighter than the early postnuclear whorls, sharply raised. Periostracum wanting, but shells occasionally encrusted with nonorganic matter, parietal area usually clean. Operculum same color as parietal callus; columella margin with a narrow, rounded ridge; palatal margin weakly twisted, thin.

Height mm	Width mm	
16.0	11.5	[Guane] (lectotype)
14.5	12.2	" (paralectotype)
12.5	10.5	Sierra de Guane
14.5	13.0	Sumidero
12.0	9.5	La Muralla
11.5	9.0	Sierra San Carlos, Luis Lazo
13.0	10.5	Los Portales

Remarks. The lectotype has a light colored spire but the faint rufous-tinged bluish white color of the later whorls is very distinct. The shell color throughout the range of the species is variable, some specimens having pale orange shells while other populations or individual specimens have a strong yellow tinge.

The shells of this species are easily identified by their widely conical shape, medium-large size, rather thin texture, flaring lip and the brilliant parietal blotch. The species is limited to the western portions of the Sierra de los Organos complex, from Mendoza to Cabezas. In the area between Luis Lazo and Sierra Quemado it has displaced both *Ustronia acuminata* (Poey) and *Troschelviana chrysochasma* (Poey) (Pl. 6).

Specimens examined. Pinar del Río. *Guane:* Sierra de Guane; W of Sierra de Guane; Cueva del Agua, Cueva del Catre, (both Sierra de Guane); Sierra Paso Real; Pedrera de Mendoza; Los Portales; Cueva Oscura; Punta de la Sierra; La Muralla. *Luis Lazo:* Sierra de San Carlos; Sabanas Llanas, Sierra de San Carlos; Ensenada del Sijú, Sierra de San Carlos; La Estrechura; El Potrero (=Valle de San Carlos); Las Vírgenes, El Potrero; Farallon del Resolladero, El Potrero; Mogote Los Arenales, Sumidero; Pica Pica, Sumidero. *Cabezas:* Mogote del Valle; Kilometer 68 on road to Pinar del Río; Ensenada de los Burros.

Troschelviana (*Troschelviana*) *mestrei* (Arango)

Plate 4, figure 16

Helicina mestrei Arango 1879, Contribución Fauna Malacológica Cubana, p. 133 (type-locality, Bebedero in Pinar del Río partis occidentalis; type, MP?).

Helicina mestrei Arango. Crosse 1890, Jour. de Conchyl., 38: 313, pl. 6, figs. 6, 6a, 6b.

Eutrochatella (*Ustronia*) *mestrei* Arango. Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 129, pl. 25, figs. 10–11.

Eutrochatella (*Troschelviana*) *mestrei* (Arango). H. B. Baker 1922, Proc. Acad. Nat. Sci. Philadelphia, 74: 60.

Description. Shell about 6 mm in height, high conic, moderately shining, subcarinate basally, rather thin. Color yellowish green, apex yellowish, lip white, with a white band at base of body whorl. Whorls 6½, rather flat, body whorl carinate, not descending at aperture; base weakly inflated, shallowly concave in umbilical region. Suture weakly impressed. Spire rather narrowly conic, acute. Aperture oblique, widely semilunate, greenish yellow within, lip white. Parietal wall shining, parietal callus glassy, slightly raised, irregularly rounded at outer margin. Lip weakly flaring but not reflected, widest at center, narrowing at both terminations, with a rounded, low tubercle at basal insertion. Columella short, deeply concave, weakly sigmoid above. Sculpture of the last three whorls of diagonal, very weak, wavy axial lines which become weakly sigmoid on the body whorl. Protoconch 1½ whorls, yellowish, somewhat darker than the rest of the shell, regularly minutely punctate. Periostracum wanting, but occasional specimens have a pseudoperiostracum of amorphous inorganic matter. Operculum as in genus, thin, corneous, somewhat darker in color than the rest of the shell.

Height mm	Width mm	
5.8	4.5	Mogote El Arabo
6.3	4.8	Mogote Cerro de Cabras
6.0	5.0	"

Remarks. This species is apparently confined to a few localities south of the Sierra Viñales complex of mountain ranges (Pl. 8). However, its small size may have caused it to be overlooked, and more intensive collecting may prove that it has a larger range.

Arango (1879: 134) compared it to *Helicina chrysochasma*, but *mestrei* is smaller, and lacks the color spot at the umbilical region. The axial lineolations appear also in *T. alboviridis* (Pfeiffer), but the shells of this species are considerably smaller and less sharply carinate than *mestrei* and have a dark instead of white basal band.

We have been unable to locate Mogote El Arabo on any map; it probably is a small mogote not far from Pinar del Río City, near Bebedero, the type-locality of the species.

Although we were unable to examine any type-material, there is little doubt about the identity of this species, largely because of the excellent illustrations in Crosse (1890).

Specimens examined. PINAR DEL RÍO. Mogote El Arabo; Mogote del Cerro de Cabras; La Güira de Laguneda.

KEY TO THE SPECIES OF SUBGENUS *CUBAVIANA*

1. Shell with a variously acute basal carina, base flattened .... *pyramidalis*
1. Shell with rounded basal carina, base somewhat inflated 2
2. Shell with yellow or orange aperture and/or columellar blotch; in Pinar del Río .... *rubromarginata*
2. Shell with aperture same color as the rest of shell; in Isle of Pines .... *scopulorum*

Subgenus Cubaviana H. B. Baker

Cubaviana H. B. Baker 1922, Proc. Acad. Nat. Sci. Philadelphia, 74: 60 (type-species, *Helicina politula* Poey 1852, [=*H. pyramidalis* Sowerby 1842], original designation).

Description. Shell broadly conic, moderately elevated, smooth, with faint growth lines and relatively weak spiral lines. Radula cusped as in *Troschelviana s. s.*, but more weakly, the cusps of the T-lateral fewer and noticeably weaker.

Remarks. This section was set up by Baker to include the smooth *Eutrochatella*-like species of Cuba with lower shells and with less strongly cusped radular teeth. Spiral sculpture, though still weak, is more noticeable than in *Troschelviana s. s.* The shells generally are somewhat larger than those of *Troschelviana s. s.*

Troschelviana (*Cubaviana*) *pyramidalis* (Sowerby)

Plate 2, figures 7, 11

Helicina conica Orbigny 1842, Mollusques, *in* Sagra, Histoire Physique, Politique, et Naturelle de l'Ile de Cuba, Paris, 1: 249, pl. 20, figs. 7–9 (not fig. 10); [not Pfeiffer 1839] (type-locality, l'intérieur de l'île de Cuba; type, BM(NH) 1854.10.4.170).

Helicina pyramidalis Sowerby 1842, Thes. Conchyl., 1: 9, pl. 3, fig. 104; 1866, *op. cit.*, 3: 284, pl. 270, fig. 157.

Helicina straminea Morelet 1851, Testacea Novissima Insulae Cubanae et Americae Centralis, 2: 18 (type-locality, montes insulae Cubanae Guajaibon dictos; 3 syntypes, BM(NH) 1893.2.4.1615–17).

Helicina politula Poey 1852, Memorias Historia Natural Isla de Cuba. 1: 113, pl. 5, figs. 4–6 (type-locality, la cordillera frente a Santa Cruz, en tierra de D. Francisco Adolfo Sauvalle; type, MP?).

Helicina exacuta Poey 1852, *op. cit.*, 1: 114, pl. 5, figs. 7–9 (type-locality, en las lomas de Cayajabos: type, MP?).

Eutrochatella (*Ustronia*) *pyramidalis percarinata* Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab. (2) 1: sect. 18, pt. 2, p. 121, pl. 23, fig. 25 (type-locality, Rangel auf Cuba; type, IZW 8540).

Description. Shell 6 to 8 mm in height, broadly turbinate, moderately solid to rather thin, periphery sharply carinate, occasionally extremely so, base flat to moderately inflated, shell sublustrous. Color bluish white or yellowish, occasionally very faintly rufous-tinged, base greenish or greenish yellow, lustrous, frequently translucent, carina with a white band below, margined by a somewhat wider, glassy, olivaceous line; colored spot on columella wanting. Suture well impressed, occasionally subchanneled. Spire broadly conic, sides straight or faintly convex, apex sharpely raised, nipplelike. Aperture oblique, subrhomboid, outer angle acutely rounded, sometimes yellow internally. Parietal wall flat or moderately inflated, shallowly excavated in umbilical region, with a thin, gleaming parietal wash that extends shortly beyond the aperture, and with a low, curved, rounded lamella at the columellar insertion of the basal lip. Palatal lip weakly flaring, except at the extremities, set off from the body whorl by a shallow, rounded groove that runs along the base of the peritreme. Columella short, shallowly concave below, rounded convex above. Sculpture of diagonal growth lines, crossed by variously strong, regularly spaced spiral cords which are generally weaker or obsolescent on the body whorl and the base. Protoconch $1\frac{1}{2}$ whorls, white, rounded, microscopically punctate, sharply raised. Periostracum wanting, but occasional specimens are encrusted with a thin layer of inorganic matter. Operculum as in genus, strongly punctate on the surface, outer layer glassy white, subtransparent in center; concentric growth lines unevenly spaced; columellar margin weakly twisted, armed with a raised, rounded lamella with a punctate surface; inner layer thin, light brown, barely darker at margins, extending beyond the edge of the calcareous layer.

Height mm	Width mm	
6.5	6.8	Rangel
6.0	7.1	Rancho Lucas, Guajaibón
6.2	7.3	Callajabos (Cayajabos)
6.8	7.2	Callajabos (Cayajabos)
7.6	7.6	Rangel
6.3	6.2	Santa Cruz de los Pinos, type-locality
6.2	6.0	El Retiro, Rangel

Remarks. The specimens we have examined indicate that the range of this species reaches from the region of Cayajabos near the Sierra del Rosaria and Bahía Honda westward to the Pan de Guajaibón and Rangel. In these latter two localities the range apparently overlaps that of *Troschelviana rubromarginata* (Pl. 6).

The shells of this species are easily recognized by the variously sharp peripheral carina, marked by a white band which below is margined by a subequal, olivaceous, generally subtranslucent line. The carina varies slightly in strength and in the prominence of the two color bands, but these are always prominent enough to identify the species.

Some populations of *rubromarginata* in the vicinity of Viñales (Kilometer 14 and El Cuajaní) have shells that are also carinate, but the keel is always less acute and is not marked by the two bands as in *pyramidalis.*

In addition to the presence of the keel, the present species differs from the neighboring *rubromarginata* in its lower and wider shape, its generally smaller size, its flatter whorls and in the consistent absence of the colored columellar spot.

There is little doubt in our minds that all the names listed in the synonymy refer to the same species. When attempting to distinguish their species—in the few cases where the attempt was made—the various authors refer to such characters as shell color, the strength of the carina as well as size, shape, and sculpture, all of which we find to be variable in this group.

Poey's *exacuta* is very sharply keeled, but it is not difficult to find specimens in which the keels are weaker and clearly intergrade with the weaker keel of typical *pyramidalis*. Poey (1852: 114) admitted that his form "tal vez no es más que una variedad de la *H. straminea* Morelet," distinguished by its smaller size (6 mm instead of 8) and the greenish rather than yellow color, both variable characteristics. Poey's *politula* has longitudinal striations confined to the upper whorls, a flattened base, a deep suture, all as in *pyramidalis*. It differs, according to Poey, in the swelling (hinchazón) of the last three whorls "which makes it appear more globulose when viewed from above" (translated). This characteristic seems to be associated with specimens which have a less sharply keeled carina and is of no diagnostic value. From the material available for this study, we are not able to judge whether the geographically separated populations are consistent in their variations or are composed of forms which show differing characteristics.

Specimens examined. PINAR DEL RÍO. El Taco; Las Animas; El Retiro (all Rangel); Guajaibón; Rancho Lucas, Guajaibón; El Mamey, Sierra del Rosario, Cayajabos; Quiñones, Bahía Honda; Santa Cruz de los Pinos; Ingenio Quiñones, Sierra de Guacamaya.

Troschelviana (Cubaviana) rubromarginata (Gundlach)

Plate 2, figures 3, 4, 5, 6, 10

Helicina rubromarginata Gundlach *in* Poey, 1858, Memorias Historia Natural Isla de Cuba, 2: 15, pl. 1, figs. 17–18 (as *Cylindrella* [*sic*]; type-locality, in monte Guajaibón insulae Cubae; lectotype, here selected, MCZ 90024, Guajaibón ex T. Bland Collection; paralectotypes, MCZ 273215, same.)

Helicina (*Helicina*) *nodae* Arango 1862, Jour. de Conchyl., 10: 409 (not *Helicina nodae* Sowerby 1866; type-locality, rupes prope Guane Cubae occidentalis; lectotype, here selected, MCZ 73781, Guane, ex Arango).

Helicina wrighti Pfeiffer 1863, Malak. Blät., 10: 195 (type-locality, Vignales in westlichen Theil von Cuba; lectotype, here selected, MCZ 73865, ex Wright, J. G. Anthony Collection).

Helicina festa Gundlach *in* Sowerby 1866, Thes. Conchyl., 3: 284, pl. 270, figs. 152–153.

Helicina rubromarginata Gundlach, Pfeiffer 1858, Monographia Pneumonopomorum Viventium, suppl. 1, p. 213; Arango 1879, Contribución Fauna Malacológica Cubana, p. 56.

Eutrochatella (*Ustronia*) *straminea rubromarginata* (Gundlach) Poey. Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 122, pl. 23, figs. 22–23.

Eutrochatella (*Ustronia*) *wrighti xanthacme* Wagner 1908, *ibid.*, p. 119, pl. 24 (not 25), figs. 10–11 (type-locality, Guajaibón in Cuba; type, IZW, 8542).

Eutrochatella (*Troschelviana*) (sect. *Cubaviana*) *straminea rubromarginata* ("Gundlach" Poey). H. B. Baker 1922, Proc. Acad. Nat. Sci. Philadelphia, 74: 60.

Description. Shell reaching about 8 to 10 mm in height, raised turbinate, rather solid, sublustrous, generally obtusely carinate. Color generally white, occasionally with a faint bluish, yellowish or flesh-colored tinge and with a yellow or orange-yellow irregular spot in the columellar region. Whorls about 7, gently inflated, body whorl with a rounded carina, not descending at the aperture; the three earlier whorls strongly shouldered. Suture well impressed, channeled in the earlier whorls. Spire broadly conical, sides somewhat swollen, lending a bulbous appearance to the lower portion of the shell. Aperture oblique, roundly triangular, the palatal angle widely rounded, with a pale yellow or yellow-orange spot in the columellar region. Parietal wall moderately inflated, generally marked by the faint spiral cords as well as the axial growth lines, with a raised, lustrous, generally yellow or yellow-orange callus which is widest in the umbilical region. Palatal lip thin, entire, weakly flaring except at extremities, generally white, in occasional populations colored like the callus, shortly angled at columellar insertion. Columella almost perpendicular below, slightly swollen near base, obtusely angled at insertion of basal lip. Sculpture of oblique, diagonal growth lines, crossed by spiral cords which are strongest on early postnuclear whorls, becoming weaker, occasionally obsolescent on body whorl and base. Protoconch 1½ whorls, white, rounded, microscopically punctate, sharply raised. Periostracum wanting; shells occasionally encrusted with a thin, amorphous layer of inorganic matter. Operculum as in genus, subopaque, outer layer lustrous, minutely punctate. Internal chitinous layer thin, pale brown, darker marginally. Parietal margin twisted, with a low, rounded lamella, highest near dorsal end. Outer margin thin, slightly twisted.

Height mm	Width mm	
8.1	7.2	Guane, lectotype of *nodae*
7.6	6.8	La Furnia, Sierra La Güira
8.8	8.1	Sierra Galalón
9.0	7.4	Mogote Capón
10.7	9.6	Cayos de San Felipe
10.4	9.4	Viñales, lectotype of *wrighti*
8.0	7.2	Guajaibón, lectotype of *rubromarginata*
6.8	6.9	Guajaibón, paralectotype of *rubromarginata*

Remarks. This species ranges from Mendoza in the west to San Diego de los Baños in the east, but it appears to be absent from the large intervening area about Luis Lazo, Isabel María, and Cabezas (Pl. 6). In this way it almost duplicates the range of *Ustronia acuminata* and *Troschelviana chrysochasma* (q. v.). At the Pan de Guajaibón its range overlaps that of *T. pyramidalis* Sowerby.

The shells can be recognized by the rather high conic shape, the generally rounded periphery, the spiral cords occasionally covering the entire shell, and the colored spot in the columellar region. The shells of *Ustronia acuminata* (Poey) and its subspecies *columellaris* (Gundlach) are larger, generally less solid and less glossy, more depressed and wider in shape, and have less or no spiral sculpture. In addition most specimens of *rubromarginata* have a shallow, rounded groove along the outer palatal edge of the peritreme so that the flare of the lip appears to be stronger than in *acuminata.*

The shells vary in size, but this feature seems to be controlled by ecological forces on whose nature we can only speculate, since populations of larger shells alternate indiscriminately with populations of small shells. Populations having shells with the yellow or orange-yellow columellar color and a colorless outer lip have been called *nodae.* We have specimens of such populations from Sierra La Güira, Pan de Guajaibón, San Diego de los Baños, and Mendoza. They are interspersed among populations of more typical *rubromarginata.* Moreover, in at least one population of *pyramidalis* (Sierra Guacamaya), some individuals show the *nodae* lip, whereas others do not. Thus it seems that this taxon refers to an unstable color variety that probably cannot survive interbreeding.

The color of the animals of several of the taxa discussed here were transmitted by Gundlach to Pfeiffer, who published them in 1856. Some variations were noted, but we have no way of knowing to what extent intra-population variations exist. It is known that in some marine prosobranchs (*Littorina, Thais*) as well as in some pulmonates (*Cepea*), the color of the animals of the same species and of a single population varies. Such variation is generally regarded to be of little taxonomic value.

Wagner (1908) and H. B. Baker (1922) considered the present taxon as a subspecies. We have decided to treat it as a full species. The differences between it and *pyramidalis* in size, shape, and color —especially the columellar color spot—are considerable. More important is the fact that there is an apparent overlap of forms at the Pan de Guajaibón. By definition subspecies must be allopatric, and we feel that this principle should be applied here.

Specimens examined. PINAR DEL RÍO. *Guane:* Mendoza. *Viñales:* El Queque; Ensenada del Valle, El Queque; Hoyo de la Cidra, El Queque; cliff before Mogote Largo; Mogote Trujillo; E of Mogote Mamí; Mogote Vigil; Mogote de Justo; Kilometer 14; Cayos de San Felipe; Mogote Mina Constancia; Ensenada Miranda, Palamarito; La Guasasa; Mogote Capón; Conguita; Mogote de Coco Solo; Paso de Dolores; El Cuajaní. *Consolación del Norte:* Farallón de las Avispas; Arroyo Cueva del Chino (both Galalón); slopes of Pico Chico; Pico Chico; Canalete; Pico Grande; Pasada de la Ayúa (all San Andrés); Caiguanabo; Abra de Caiguanabo; Hoyo de San Antonio; Los Camarones, San Antonio; La Jagua; Mogote S of Galalón; La Furnia, Sierra La Güira; Pan de Guajaibón; Pinalito, W of Galalón. *San Diego de los Baños:* Mogote de La Tumba; Ensenada del Corojal (both Puerto Escondido); Mogotico Herrera; Mogote de los Portales; Mogote Cuatro Caminos; Sierra de la Cumbre.

Troschelviana (*Cubaviana*) *scopulorum* (Morelet)

Plate 3, figures 14–15

Helicina scopulorum Morelet 1849, Testacea Novissima Insulae Cubanae et Americae Centralis, 1: 20 (type-locality, insulam Pinorum; type, BM(NH) 1893. 2.4.1612.14).

Helicina scopulorum Morelet. Pfeiffer 1853, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 1, p. 72, pl. 10, figs. 21–23; Arango 1879, Contribución Fauna Malacológica Cubana, p. 54; Sowerby 1866, Thes. Conchyl., 3. 284, pl. 270, fig. 147.

Helicina luteopunctata Poey 1852, Memorias Historia Natural Isla de Cuba, 1: 115, pl. 5, figs. 10–12 (no locality; type, MP?).

Helicina luteoapicata Poey 1852, *op. cit.*, 1: 394 [emended name for *luteopunctata*].

Eutrochatella (*Ustronia*) *scopulorum* Morelet Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 120, pl. 24, figs. 16–18, 22–23.

Eutrochatella (*Troschelviana*) *scopulorum* (Morelet) sect. *Cubaviana*, H. B. Baker 1922, Proc. Acad. Nat. Sci. Philadelphia, 74: 60.

Description. Shell reaching about 7 mm in height, elevated trochoid, subcarinate when mature, strongly carinate when juvenile, moderately strong, sublustrous. Color wax-white, occasionally tinged with pale yellow or pale red, apex occasionally darker, lip white. Whorls $7\frac{1}{4}$, almost flat, earlier postnuclear whorls strongly shouldered, body whorl obtusely carinate, somewhat inflated basally, not descending at aperture. Suture well marked, especially so at early postnuclear whorls. Spire broadly conic, sides weakly convex, apex sharply raised. Aperture oblique, roundly triangular, palatal angle widely rounded, widest below the periphery, yellow or reddish within, white near palatal lip. Parietal wall weakly inflated, with a rather strong, white, triangular callus which is strongly reflected in the umbonal region, forming a pseudo-chink there. Palatal lip entire, weakly flaring and barely reflected basally, straight at columellar insertion. Columella concave, almost perpendicular below, gently curved at insertion with basal lip, separated from the parietal callus by a subacute, low lamella. Axial sculpture of diagonal, irregular growth lines crossed by weaker spiral ridges which become weaker and obsolescent on the body whorl. The wavy axial lineolations within the shell substance are readily visible. Protoconch $1\frac{1}{2}$ whorls, white, rounded, minutely punctate, sharply raised. Periostracum wanting but shells occasionally encrusted with a thin, irregular layer of inorganic matter. Operculum thin, outer layer whitish, glassy, smooth, subtranslucent, columellar edge slightly twisted with an opaque-glassy, raised, punctate ridge near the columellar margin, highest near the base; inner layer thin, pale brownish, reaching beyond the margin of the outer layer.

Height mm	Width mm	
7.5	7.5	Sierra de Casas
7.9	7.8	Sierra Colombo
7.4	6.8	Sierra de Caballos
7.7	7.5	Sierra de Bibijagua
6.6	6.3	Sierra de San Juan de la Mar

Remarks. This species is confined to the Isle of Pines where apparently it occurs in large numbers. We have seen specimens from the two large sierras, Casas and Caballos, as well as such smaller ones as Colombo, Bibijagua, and San Juan de la Mar. The specimens from the last locality are smaller. Most specimens in the series we examined were taken dead.

The shell differs from *conica* (Orbigny) in being lower and more widely conic, in having a lip that does not flare as widely or as flatly, and in showing a pseudo-chink as the result of the basal reflection of the parietal callus margin. In addition the axial sculpture is stronger and more regular. It differs from *rubromarginata* in being somewhat wider, less glossy, and more strongly sculptured, in the stronger and larger parietal callus, and in the lack of the colored columellar blotch.

Specimens examined. ISLE OF PINES. Sierra de Casas; Sierra Columbo (Columbus); Sierra de Caballos; Sierra de Bibijagua; Sierra de San Juan de la Mar.

KEY TO THE SPECIES OF SUBGENUS *MICROVIANA*

1. Shell relatively large, generally more than 5 mm in width, occasionally reaching 8 to 11 mm 3
1. Shell smaller, less than 5 mm in width 2
2. Shell 3 to 4.5 mm in width 4
2. Shell quite small, less than 3 mm in width .... *granulum*
3. Shell with simple lip .... *hians*
3. Shell with flatly expanded lip .... *petitiana*
4. Shell with upper whorls steplike 5
4. Shell with upper whorls rounded, not steplike 10
5. Operculum more or less smooth 6
5. Operculum with variously long spines on outer surface 9
6. Shell with strong lamella entering in upper angle of aperture .... *callosa*
6. Shell with aperture unarmed 7
7. Shell with noticeable spiral cords .... *rupestris*
7. Shell with spiral sculpture wanting 8
8. Shell glassy white or pale yellow .... *pf. pfeifferiana*
8. Shell flesh colored .... *pf. najazaensis*
9. Shell with upper angle of aperture entire .... *holguinensis*
9. Shell with notch in upper angle of aperture .... *spinopoma*
10. Spiral sculpture absent .... *methfesseli*
10. Some spiral sculpture present 11
11. Shell with deeply channeled suture .... *tumidula*
11. Shell with deep pit in umbilical region .... *continua*

Subgenus *Microviana* H. B. Baker

Microviana H. B. Baker 1928, Occas. Pap. Mus. Zool., Univ. of Michigan, no. 193, p. 46 (type-species, *Helicina rupestris* Pfeiffer 1839, original designation).

Torreviana Aguayo 1943, Rev. Soc. Malac. 'Carlos de la Torre,' 1: 69 (type-species, *Eutrochatella spinopoma* Aguayo 1943, original designation).

Description. Shell small (4 to 5 mm in height), depressed to low trochoid; spiral sculpture present or wanting. Basal callus a raised, wide or narrow, rounded lamella; umbilical depression present. T-lateral tooth without cusps, centrals cusped as in *Troschelviana s. l.*

Remarks. Baker (1922: 61) referred to the subgenus *Artecallosa* Wagner (1908: 132) for the shell characteristics of this subgenus. The diagnostic shell characteristics are the "basal callus . . . reduced to a lamellar-like, rather raised thickening ("Der Basalcallus zumeist auf eine leistenförmige, ziemlich erhobene Verdickung reduziert."). Spiral sculpture is always present. To these shell characteristics Baker (*loc. cit.*) adds radular features which he found in *E. rupestris,* the type-species of *Microviana.* These show that this group stands between the group having strongly cusped radular teeth (especially the paired centrals and the T-laterals) of *Troschelviana* and the smooth teeth of *Eutrochatella s. s.*

Artecallosa Wagner 1908, type *Helicina chryseis* Tristram 1861 (=*H. microdina* Morelet 1851) by subsequent designation of Baker 1922, is a synonym of *Pyrgodomus* Crosse & Fischer 1893, type *Helicina chryseis* Tristram 1861, monotypy. Baker (1922: 60) placed *Helicina rupestris* Pfeiffer 1839 in *Pyrgodomus.* In 1928 (p. 46) he established *Microviana,* type-species *Helicina rupestris* Pfeiffer 1839, by original designation, for the Cuban forms and wrote that *Pyrgodomus* apparently included only the type-species from the mainland, which lacks the unicuspid marginals of the Vianinae (=Vianini). It resembles the Vianini in its sexual apparatus.

The only difference between *Torreviana* Aguayo and *Microviana* H. B. Baker is the presence of spines or projecting papulae on the operculum. However, the strength of this type of opercular sculpture of helicinids varies; even in the case of the two species included in *Torreviana*, *holguinensis* has its opercular spines "menores y menos aguzados que en *E. spinipoma*" [sic] (*loc. cit.*). Moreover, Aguayo reported (1932: 31) that "The radula [of *holguinensis*] is quite similar to that of *E. rupestris*." *Troschelviana petitiana* Orbigny, in the adult stage, presents a very similar kind of operculum. This last species is not closely related to the species in *Torreviana*. In view of all this, it would be hard to maintain a division on the basis of this opercular characteristic alone.

Troschelviana (Microviana) rupestris (Pfeiffer)

Plate 4, figure 17

Helicina rupestris Pfeiffer 1839, Wiegmann's Arch. Naturgesch., 5th year, 1: 355 (type-locality, selected by A. Torre [1952: 18], El Fundador, Canímar, Matanzas; type destroyed).

Trochatella rupestris Pfeiffer 1850, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 1, p. 8, pl. 5, figs. 12–15.

Eutrochatella (Artecallosa) rupestris (Pfeiffer). Wagner 1908, *ibid.*, sect. 18, pt. 2, p. 134, pl. 22, figs. 13–14.

Helicina rupestris Pfeiffer. Sowerby 1842, Thes Conchyl., 1: 10, pl. 3, fig. 120.

Trochatella rupestris Pfeiffer. Sowerby 1866, *op cit.*, 3: 284 pl. 269, figs. 143–144.

Eutrochatella (Pyrgodomus) rupestris (Pfeiffer). H. B. Baker 1922, Proc. Acad. Nat. Sci. Philadelphia, 74: 61, pl. 6, fig. 28 [radula].

Description. Shell about 3 mm in diameter, width generally as great as or greater than height, depressed trochoid, imperforate, moderately thin, not shining. Color pale to lemon yellow, occasionally faintly rufous. Whorls 4½, flat, frequently raised, rounded steplike above the well-impressed suture. Body whorl with a rounded carina, slightly descending at aperture, base gently rounded. Aperture oblique, widely semilunate. Parietal callus reduced to a rounded lamella near the parietal lip. Palatal lip thin, entire, barely flaring near basal insertion. Umbilical area shallowly excavated. Columella concave, rounded. Sculpture of faint, irregular growth lines crossed by evenly spaced, low but much stronger spiral lines, more closely set on earlier whorls and at summit of body whorl. Protoconch 1½ whorls, sharply raised above succeeding whorls, minutely pitted, paler in color than the rest of the shell. Periostracum wanting but occasional specimens encrusted. Operculum concave, shining, translucent, outer surface with numerous irregularly placed pustules.

Height mm	Width mm	
2.5	3.1	El Fundador
2.8	3.4	Elena, El Palenque
3.0	3.2	San Miguel de los Baños
3.2	3.2	Jaruco
3.0	3.1	Mesa de Mariel

Remarks. This small species can be readily recognized by the depressed, trochoid shape, the steplike nature of the whorls, and the rather strong spiral sculpture. It inhabits the western third of the island from Guane, Pinar del Río Province, to Canímar, Matanzas (Pl. 7). The discontinuous records are doubtlessly due to the failure to see and collect such small individuals.

Specimens examined. PINAR DEL RÍO. Guane. HAVANA. Finca Almeida Pipian, Madruga; Managua; Sitio Perdido, Jaruco; Lomas de Camoa; La Portada; Mesa de Mariel; Peña Blanca, Sierra Anafe. MATANZAS. El Fundador, Canímar; Elena, El Palenque; Ramona, El Palenque; El Palenque; Cueva El Negro, San Miguel de los Baños.

Troschelviana (Microviana) hians (Poey)
Plate 3, figures 1–9

Helicina hians Poey 1852, Memorias Historia Natural Isla de Cuba, 1: 113, pl. 5, figs. 1–3 (type-locality, las altas montañas de Trinidad [Las Villas, Cuba] Lavalée leg.; type, MP?).

Trochatella petrosa (Gundlach MS) Pfeiffer 1857, Malak. Blät., 4: 111 (type-locality, an Steinen und Felsen von San Juan Letran; type, MP ?); 1858, Monographia Pneumonopomorum Viventium, suppl. 1: 174.

Trochatella rubicunda (Gundlach MS) Pfeiffer 1857, Malak. Blät., 4: 111 (type-locality, Magua [Trinidad, Las Villas]; lectotype, here selected, MCZ 73880, ex Anthony, Gundlach leg.; not Pease 1868).

Trochatella capillacea Pfeiffer 1857, Malak. Blät., 4: 111 (type-locality, San Juan de Letrán [Las Villas]; lectotype, here selected, MCZ 47525, ex Anthony, cotype *fide* Torre); 1858, Monographia Pneumonopomorum Viventium, suppl. 1: 176.

Eutrochatella (Microviana) petrosa pilsbryi Aguayo & Jaume 1957, Mem. Soc. Cubana Hist. Nat., 23: 119, pl. 1, fig. 4 (type-locality, San José, Hornos de Cal, Sancti Spiritus, Provincia de Las Villas, Cuba; holotype, MP 13258).

Trochatella rubicunda Gundlach. Sowerby 1866, Thes. Conchyl., 3: 284, pl. 269: figs. 141–142.

Trochatella capillacea Gundlach. Sowerby 1866, *op. cit.*, p. 284, pl. 269, fig. 138.

Trochatella petrosa Gundlach. Sowerby 1866, *op. cit.*, p. 283, pl. 269, figs. 136–137.

Trochatella rubicunda Gundlach. Arango 1879, Contribución Fauna Malacológica Cubana, p. 43.

Eutrochatella (Artecallosa) rubicunda Pfeiffer. Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 133, pl. 22, figs. 8–9.

Eutrochatella (Artecallosa) petrosa Pfeiffer. Wagner 1908, *ibid.*, p. 134, pl. 22, figs. 10–12.

Eutrochatella (Microviana) alcaldei Aguayo & Jaume 1958, Mem. Soc. Cubana Hist. Nat., 24: 95, pl. 1, fig. 1 (type-locality, Monte del Pico, Gavilán, Provincia de las Villas, Cuba; holotype, MP 17431).

Eutrochatella (Microviana) petrosa boqueronensis Aguayo & Jaume 1958, *ibid.*, 24: 96, pl. 1, fig. 2 (type-locality, Boquerón de Jatibonico between Las Villas and Camagüey, Cuba; holotype, MP 17422).

Eutrochatella (Microviana) purioensis Aguayo & Jaume 1958, *ibid.*, 24: 97, pl. 1, fig. 4 (type-locality, El Purio, Calabazar de Sagua, Provincia de las Villas, Cuba; holotype, MP 17420).

Eutrochatella (Microviana) clenchi Aguayo & Jaume 1958, *ibid.*, 24: 98, pl. 1, fig. 3 (type-locality, Guabairo, Soledad, Cienfuegos, Provincia de las Villas; holotype, MP 17429).

Eutrochatella (Microviana) subangulata Aguayo & Jaume, 1958, *ibid.*, 24: 99, pl. 1, fig. 5 (type-locality, Loma Ternero, entre San Juan de los Yeras y Seibabo, Manicaragua, Provincia de las Villas, Cuba. Carlos de la Torre leg.; holotype, MP 17425).

Eutrochatella (Microviana) subangulata cienfuegosensis Aguayo & Jaume, 1958, *ibid.*, 24: 100 (type-locality, Limones, Soledad, Cienfuegos, Provincia de las Villas, Cuba; holotype, MP 17427).

Description. Shell varying from 4 to 8 mm in width, broadly depressed trochoid, moderately thin, variously bluntly carinate. Color varied, grayish yellow, yellowish green or pale to dark rufous, spire occasionally darker in color. Whorls 5½ to 6, quite flat, shortly carinate above the impressed and somewhat inserted suture, body whorl with a variously blunt carina peripherally, rounded truncate or recurved at the insertion into the aperture where it descends gradually under the keel. Spire broadly turbinate, apex raised. Aperture widely triangular, almost straight above, rounded below. Parietal wall with a rather narrow, rounded callus, strongly punctate on the surface; parietal wash thin, shining, smaller in area than the aperture. Palatal lip whitish, simple, somewhat undulate above, thickened within, not flaring, with a narrow, blunt lamella at the point of basal insertion. Columella short, concave below, rounded convex above. Sculpture varied, smooth with only weak growth lines, or with growth lines crossed by variously strong spiral lirations, variously spaced. Protoconch 1½ whorls, rounded, raised, minutely and regularly punctate. Periostracum wanting, but shells frequently encrusted with a layer of inorganic material. Operculum as in genus, outer calcareous layer strongly and regularly pustulose, interior layer thin, light brownish, darker at the margins.

Height mm	Width mm	
4.3	4.4	San Juan de Letrán (lectotype of *capillacea*)
4.1	4.1	Magua, Trinidad (lectotype of *rubicunda*)
5.1	5.2	Cayo Lucas
4.2	5.0	"
7.5	8.1	Guabairo, Soledad
4.8	5.0	½ mi. E of Guabairo, Soledad
6.1	6.2	San Juan de los Perros, Camagüey
6.0	6.3	La Vigía, Mayajigua
6.0	5.5	Hornos de Cal, Sancti Spiritus
7.0	8.0	Boquerón de Jatibonico, Camagüey
5.8	5.8	Loma La Canterilla, San Juan de Los Yeras
5.2	6.0	La Viruela, Calabazar de Sagua
6.7	7.2	El Purio, Calabazar de Sagua
7.6	8.0	Palma de los Negros, Mayajigua
6.4	6.6	" "

Remarks. This is a polymorphic species which occupies the entire eastern half of Las Villas Province, running slightly beyond the borders into neighboring Camagüey Province (Pl. 7). This area is mountainous and of such a nature that the extreme isolation of populations such as is found, for example, in Pinar del Río Province, does not exist. Hence, the populations vary within themselves and frequently with other populations, the result perhaps of ecological forces that are not clear. Some apparent genotypic characters also occur, such as the sharpness of the peripheral keel and the presence or absence of spiral lirations. This last detail, in point of fact, seems to demonstrate the lack of isolation, since in at least one population (Boquerón de Jatibonico, Camagüey) both lirate and smooth individuals occur together with many intergrading. Where lirations do occur, they vary from quite weak to strong. The intervals between the lirations also vary, some individuals having the lirations much more closely spaced than others, and in some cases so closely spaced that the intervals equal the width of the lirations (MCZ 127629). Lirate and smooth populations live in close proximity and in general show an irregular geographic distribution. Aguayo (1962: 10–11) writes that shells which are strongly sculptured may show an ecological adaptation to a dry, sunny, rocky situation, whereas those in more shady areas presumably are smoother.

Size variations likewise do not show a distributional pattern and seem to be strongly affected by unknown ecological factors. Several populations of larger shells occur at Jatibonico toward the northeastern limit of the species range, but several series of shells from Soledad, near the southwestern limit contain individuals just as large in size. At Guabairo, for example, the population is quite large (7.5 × 8.1 mm) but nearby, one-half mile to the east, the more normal size (4.8 × 5.0 mm) prevails. Large shells are also found at Mayajigua (7.6 × 8.0 mm) far to the east, with many intervening populations of small shells.

Color presents similar variations. The shells vary from grayish white to pale and somewhat deeper yellow on the one hand and light to dark rufous on the other. In some individuals the lower whorls and the apex have a deeper color, the rest of the shell being paler. Sometimes the color is more or less uniform in a single population (Cayo Lucas, La Viruela, Lomas Castellanos), in other cases there is much variety with varying degrees of intergrading (Loma Esperanza).

Aguayo & Jaume (1957, 1958) proposed names for several of these populations. In addition, lots have been sent out widely under manuscript names. The name *E. subangulata* Aguayo & Jaume and its subspecies *cienfuegosensis* was applied to juvenile specimens which are sharply carinate and occasionally show a secondary more or less rounded carina near the base. Some of the populations so named apparently consist entirely of such juvenile forms and may well represent colonies of phenotypic paedomorphs.

The names *rubicunda* and *capillacea* were proposed by Pfeiffer for populations of small shells. It was early realized that both were synonymous, and, except for size, indistinguishable from the usual *hians*. Wagner (1908: 134) noted the resemblence of *rubicunda* to *petrosa*. He wrote, "Eutrochatella petrosa hat das Aussehen einer unausgewachsenen, aber grösser angelegten Eutrochatella rubicunda Pfeiffer und stellt nach meiner Ansicht eine Geschlechtsform derselben dar." It should be noted that whereas many populations show a marked uniformity of size, in others (Palma de los Negros) the difference is greater. In the description of *Trochatella petrosa*, one of Pfeiffer's distinctions was of color—"lutea"—where Poey wrote of *hians* "rosado en la última vuelta, amarillo un poco sucio en las otras, con el ápice de un canario pálido muy puro" (1851: 113). We have already seen that color is not a characteristic of specific value.

Aguayo and Jaume (1957: 119) gave the name *pilsbryi* to a population near Sancti Spiritus having shells with the operculum "hundido en el interior de la abertura, mientras en *E*[*utrochatella*] *petrosa petrosa* de Magua, Trinidad se encuentra a ras del borde." Now it happens that Magua, Trinidad, is the type-locality of *Trochatella rubicunda,* selected by Pfeiffer himself. The lectotype in the MCZ has the operculum very much "hundido en la abertura." It would appear that *hians* normally keeps its operculum near the rim of the aperture but in exceptional cases—the nature of which we can only guess—draws it in further. In this respect it does not resemble *Troschelviana holguinensis* Aguayo and *Semitrochatella elongata* (Orbigny) where the operculum, being bigger than the aperture, is not retractable. The other features which are to serve to distinguish *pilsbryi*, such as size, sculpture, and color, are variable, as we have seen. It is interesting to note that in the type-lot of *pilsbryi* itself, as reported by the authors, the color varies from generally yellow to a few rosy ("rosado") individuals.

Viewed from the inside of the aperture, the palatal lip of *T. hians* seems to be flaring. This effect is caused by the bevelled lip being somewhat thickened within and sloping more or less gradually toward the thinned edge. Viewed from the outer surface the shell rarely shows a barely perceptible sign of flaring.

It is surprising that the true nature of *hians* Poey 1852 has been overlooked for such a long time. Pfeiffer (1854: 101) redescribed the species in Latin and later (1858: 174–176) repeated the description and also proposed *petrosa, rubicunda,* and *capillacea.* For some reason he changed Poey's description of the palatal lip from "perístoma simple, cortante" (1852: 114) to "perist. expansum" (1854: 101; 1858: 175). This resulted in confusion so that Sowerby (1866: 296) was unable to identify *hians.* Reeve (1874) omitted it entirely, as did Wagner (1908). Nor was it noted by Fulton (1915) in his list of omissions from Wagner's monograph. Arango (1879: 44) and Crosse[1] (1890: 310) merely listed it together with *petrosa* and *rubicunda,* giving the identical locality cited by Poey, thus showing that the supposed *hians* as described by Pfeiffer had not been found again.

This situation may also have come about because Poey's figures are somewhat misleading: they show a thickened lip, definitely not "cortante" as Poey put it in his description, and the carina is more rounded than is common in *hians* (=*petrosa*). The figures, moreover, are quite generalized and can scarcely be distinguished from the figures of *politula, exacuta, luteopunctata,* and *acuminata* given on the same plate.

Aguayo & Jaume (1957: 119) were the first, as far as could be determined, who called attention to *hians* in recent times. They tried to distinguish it from their subspecies *petrosa pilsbryi* but did not compare *hians* with *petrosa petrosa.*

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[1] Crosse's great contribution lies in the magnificent figures of several Cuban species. Otherwise much of his paper is a translation of Arango (1878–80).

Although we have been unable to examine the type or to see any specimens labeled *hians*, we feel that there is no doubt about what Poey had in mind. The locality, the dimensions, the sculpture, the apex, the obtuse carina of the body whorl, the simple, sharp ("cortante") peristome, and the blunt, recurved truncation of the body whorl at the apertural insertion ("volteado") all point to what has been hitherto known as *petrosa* Pfeiffer.

Specimens examined. LAS VILLAS. *Soledad:* Guabairo; ½ mi. E of Guabairo; Dolores Potrero, ½ mi. E of RR to Guabairo; Vilche's Potrero, 2½ mi. E of Soledad; Vilches Caves; Finca La Caldera, opposite Vilche's Caves; La Portuguesa, Seboruco, 2 mi. NE of Soledad; Limones, Seboruco, 1 mi. SE of Soledad; Seboruco, near Guaos, 2 mi. N of Soledad; Galdó near Santa Teresa; ½ mi. W of La Vega; Santa Tecla, Corralillo [6½ km from Soledad]; Quesada, 3 mi. S of Soledad; Monte de la Veguita; Harvard House. *Vega Alta:* El Guajén; Loma Sola, El Guajén; La Sierra; Mogote Chicharrón, La Sierra; Potrero Penton, La Sierra; Mogote Solo, La Sierra; Loma Murcielagos; La Sinaloa; Rincón; El Hoyón; Mogote between Vega Alta and Piedras. *Sagua la Grande:* Las Delicias; La Rubia; Central Ramona; El Mamey; Cueva La Virgen, Corazón de Jesús; San Miguel; San Francisco. *Calabazar de Sagua:* Mogote Ortiz; Cueva Galona; Mogote El Infierno, Natalia; Loma Castellanos, Natalia; La Viruela; Las Jumaguas; El Purio. *San Juan de los Yeras:* Loma del Ternero; Loma La Canterilla; El Miradero, San Diego del Valle. *Trinidad:* Magua; La Vigía; Loma Palo Seco, Yaguanabo. *Remedios:* Bartolomé; Rojas; Buenavista; Las Dos Sierras, Buenavista; La Culebra, Buenavista; Guajabana; La Puntilla; near La Puntilla; El Palenque de Taguayabón; Finca Las Marías, Palenque de Taguayabón; Finca El Mamey. *Zulueta:* Cueva de Las Veinte; San Augustín; Mogote near San Augustín; Guanijibe; Loma Ramón Martínez; El Boquerón; Charco Majá. *Sancti Spiritus:* Pedrera de Acosta; San José; La Esperanza; Loma La Esperanza; Hornos de Cal; Finca Bermúdez, Tuinicú; Finca San Vicente, Iguará; Siguaney; Loma Grande; Loma Gabino Galvez. *Yaguajay:* Urbaza; Muguirre; Cañón del Yigre; Guainabo; Cambao; Vereda del Resbalillo, Cambao; Pie Valdez; Vereda Herrera. *Mayajigua:* Los Baños; Rosa Perdida; Palma de Los Negros. *Caibarién:* Cayo Salinas; Cayo Lucas; Cayo Caguanes; Punta Caguanes. *San Juan de Letrán:* Loma Colorado, Vueltas; between km 42 and 43, Sierra de Meneses. CAMAGÜEY. Sierra de los Perros; La Espinosa, Chambas; Florencia, near Chambas; Iguará, Jatibonico; Finca Santa Felicia, Iguará, Jatibonico; Sierra del Boquerón de Jatibonico; Loma Marín, Jatibonico.

Troschelviana (Microviana) petitiana (Orbigny)

Plate 2, figures 12–13

Helicina petitiana Orbigny 1842, Mollusques, *in* Sagra, Histoire Physique, Politique et Naturelle de l'Ile de Cuba, 1: 247, pl. 20, figs. 1–3 (type-locality, Jagua, île de Cuba; type not in BM(NH), location unknown).

Helicina petitiana Orbigny. Pfeiffer 1850, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 1, p. 43, pl. 7, figs. 30–32.

Trochatella petitiana Orbigny. Pfeiffer 1852, Monographia Pneumonopomorum Viventium, 1: 331.

Helicina dilatata Poey 1857, Memorias Historia Natural Isla de Cuba, 2: 26 (type-locality, Trinidad; type, MP ?).

Trochatella petitiana Orbigny. Sowerby 1866, Thes. Conchyl., 3: 283, pl. 269, figs. 132–133.

Trochatella petitiana Orbigny. Arango 1879, Contribución Fauna Malacológica Cubana, p. 43.

Eutrochatella (Artecallosa) petitiana d'Orbigny. Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 132, pl. 22, figs. 4–7.

Eutrochatella (Artecallosa) petitiana laticosta Wagner 1908, *op. cit.*, p. 133, pl. 22, fig. 12 (type-locality, die Insel Cuba; type, IZW 8572).

Description. Shell varying in width from about 6 to about 13 mm, widely depressed conic, moderately shining or dull, thin.

Color generally white to pale yellow, occasional specimens pale reddish, lip white. Whorls from $5\frac{1}{2}$ to $7\frac{1}{2}$, narrowly shelved, moderately rounded or more or less sharply carinate, the carina not reaching the area of the palatal lip; body whorl about equal to the spire in width, not descending, or else gently rising at the aperture. Suture well impressed. Spire depressed conic, apex sharply raised. Aperture subtriangular, outer angle widely rounded, yellow or reddish internally with a narrow white zone near the palatal lip. Parietal wall somewhat inflated, shallowly excavated in umbilical region; at the columella there is a low triangular callus, with a strongly punctate surface. Palatal lip widely flaring but not reflected, occasionally gently undulate, widest above, narrower below the periphery, fluted in larger specimens, almost alate at the upper and basal insertions. Columella oblique, scarcely concave below, moderately convex above, set off from the umbilical excavation and the punctate callus by a low, rounded lamella. Spiral sculpture of varying strength, generally somewhat weaker on the base. Axial sculpture of diagonal, irregular growth lines which sometimes lend a wavy appearance to the spiral lines where they cross. Protoconch $1\frac{1}{2}$ whorls, rounded, closely punctate, sharply raised. Periostracum wanting. Calcareous plate of the operculum of mature individuals thickly set with low, blunt, glassy papillae, smaller and more thickly set than in *holguinensis* Aguayo and *spinopoma* Aguayo. Inner chitinous layer thin, set off by a deep marginal sulcus from the outer layer, darker at palatal margin where it extends beyond the calcareous layer.

Height mm	Width mm	
7.2	8.0	San José, Las Villas
11.6	13.3	Buenos Aires near Soledad
7.0	7.9	Naranjo Dulce
6.3	6.9	Mina Carlota
10.2	11.9	Ciegos de Ponciano
8.5	10.0	El Jarico, Banao, Sancti Spiritus

Remarks. This species is limited to a broadly triangular area whose angles are formed by Cienfuegos, Trinidad, and Sancti Spiritus in the south central part of Las Villas Province (Pl. 7). In this rather limited area (40 × 36 × 70 mi.) the shells display an astonishing amount of variation, the most apparent of which is in size. The largest shells are found at Buenos Aires near Soledad, and Ciegos de Ponciano near Trinidad, the smallest at Naranjo Dulce and Mina Carlota. (See measurements above.) Medium sized shells occur at San José and Sancti Spiritus. It is difficult to discern any distributional pattern among the various populations. It seems that the smallest shells appear in the western part of the range about Cienfuegos and the larger ones in the center and the west. Nevertheless, shells of moderate size appear in Moscas, which is closer to Cienfuegos than Mina Carlota. The shells from the type-locality, presumably Jagua at the entrance to the Bay of Cienfuegos, are given as 10 × 11 mm by Orbigny, and 8 × $12\frac{1}{2}$ mm by Pfeiffer (1852), rather large shells, making the concept of cline difficult to accept.

The periphery varies from very rounded at Buenos Aires to quite sharply keeled at Naranjo Dulce with moderately carinate specimens occurring at Mina Carlota and Ciegos de Ponciano. The color is generally subdued, but at Ciegos de Ponciano the yellow is somewhat deeper, and rather handsome rufous specimens make their appearance. The strength of the spiral sculpture also shows some variation, being strong at San José and Ciegos de Ponciano, and weak at Buenos Aires.

The subspecies *laticosta* Wagner falls well into the range of variations of *petitiana*. The description given by Wagner seems to relate to shells from Ciegos de Ponciano.

The operculum is unique in possessing a surface of rather closely set, low papillae, similar to *holguinensis* Aguayo and *spinopoma* Aguayo. In the present species the papillae are lower and much more closely set. In submature specimens the papillae are lower and the surface seems to be merely pebbled; in very young individuals the operculum is smooth and glassy without a sign of surface sculpture. It is difficult to see how the animal can apply more sculpture to the outer surface of the operculum as it matures, but such seems to be the case.

Specimens examined. LAS VILLAS. *Cienfuegos:* San José; Aguada de Carreño, Las Moscas; Naranjo Dulce, La Sierra; Loma Dividente, Buenos Aires; Buenos Aires; Mina Carlota, Sierra de San Juan; Loma Chivo, Sierra de San Juan; Tetas de Doña Tomasa, Sierra de San Juan; Loma Puerca, Sierra de San Juan. *Trinidad:* Ciegos de Ponciano; Los Cinco, Sierra de Ponciano; Puriales Plantation; Fuentes Claras. *Sancti Spiritus:* El Jarico, Banao.

Troschelviana (Microviana) holguinensis (Aguayo)

Plate 4, figures 7, 12

Eutrochatella (Pyrgodomus) holguinensis Aguayo 1932, Occas. Pap. Boston Soc. Nat. Hist., 8: 31, pl. 3, figs. A, B (type-locality, Cerro Ramón Leyva, Sao Arriba, Holguín, Eastern Cuba [Oriente]; holotype, MCZ 86474; paratypes, MCZ 86475; also MCZ 86493, Las Cuevas).

Description. Shell about 3 mm in diameter, wider than high, depressed trochoid, thin, not shining, roundly carinate. Color pale brown or pale yellow. Whorls 5½, moderately inflated, raised, rounded steplike above the deeply inset suture, body whorl roundly carinate, descending slightly at aperture. Spire very broadly conic, apex raised. Aperture widely triangular, angles well rounded. Parietal wall shallowly excavated in umbilical area, parietal callus small, slightly raised, surface roughened by thickly set, low pustules. Palatal lip entire, not flaring, somewhat thickened at basal insertion. Columella short, shallowly concave. Axial sculpture of low, diagonal growth lines crossed by numerous, regularly spaced, slightly raised spiral cords, these cords more widely spaced on the later whorls. Protoconch 1½ whorls, glassy, minutely punctate. Periostracum wanting. Operculum widely triangular, larger than the aperture, not retractible into aperture; inner chitinous layer thin, pale brown, separated by a rather deep marginal sulcus from the outer calcareous layer; outer layer white, solid, strongly concave, the sloping sides with irregularly spaced, raised lamellae which become rather high, slanting, blunt papillae on the depressed inner surface.

Height mm	Width mm	
3.1	3.2	Cerro Ramón Leyva, holotype
3.0	3.3	Las Cuevas, paratype
3.0	3.1	Loma Pichín, El Yayal
2.9	3.0	Cerro Cariblanco

Remarks. The shells of this species strongly resemble *rupestris* Pfeiffer from the western end of the island in size, shape, color, and sculpture. They are readily separated, however, by the peculiar operculum. Aguayo (1932: 31) reports that the radulae are quite similar. Hence *holguinensis* may be regarded as the eastern homolog of *rupestris.* It is restricted to the area about Holguín in northwestern Oriente (Pl. 8), where Aguayo reports that it lives on limestone cliffs. The shells are frequently encrusted with a thick, irregular layer which Aguayo thinks is of fecal origin.

Specimens examined. ORIENTE. *Holguín:* Cerro Ramón Leyva, Sao Arriba; Cerro de la Cañada de Jagüeyes; Cerro Corralito, 17 km NE of Holguín; Las Cuevas; Loma Tino Pupo, 6 km N of Unas and 19 km NW of Holguín; Cerro Cariblanco, 16 km NE of Holguín; Loma Pichín, El Yayal. *Gibara:* Curva de la Campana.

Troschelviana (Microviana) methfesseli (Pfeiffer)

Plate 4, figures 4, 10

Trochatella methfesseli Pfeiffer 1862, Malak. Blät., 9: 8 (type-locality, Pflanzung Catalina, Sagua de Tanamo [Oriente]; lectotype[1], here selected, MCZ 273216, Monte Toro, Guantánamo, ex Dohrn; paralectotype, *ibid.*, MCZ 86494); 1865, Monographia Pneumonopomorum Viventium, suppl. 2: 212.

Trochatella methfesseli Pfeiffer. Arango 1879, Contribución Fauna Malacológica Cubana, p. 43.

Eutrochatella (*Ustronia*) *methfesseli* Pfeiffer. Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 125, pl. 24, figs. 8–9.

Eutrochatella (*Cubaviana*) *methfesseli* Pfeiffer. H. B. Baker 1922, Proc. Acad. Nat. Sci. Philadelphia, 74: 60.

Description. Shell, reaching 4 mm in diameter, wider than high, turbinate, rather thin, moderately glossy. Color pale yellow or pale brown. Whorls $5\frac{1}{2}$, rounded, body whorl not descending at aperture, rounded at periphery. Suture well impressed. Spire broadly conic, apex sharp. Aperture very oblique, widely semilunate; parietal wall rounded, shallowly excavated in umbilical region; callus a thin, narrow lamella. Outer lip entire, thickened at margin, not reflected or flaring, with a raised, triangular protuberance at basal insertion. Columella short, curved at insertion of basal lip. Sculpture of weak, diagonal growth lines only. Protoconch $1\frac{1}{2}$ whorls, microscopically pitted, well rounded, raised over first postnuclear whorl. Periostracum wanting, but shell is frequently encrusted. Operculum with columellar edge weakly twisted, thin, horn colored; calcareous layer translucent, moderately shining, roughened by closely set minute pustules; chitinous layer glassy, extending beyond margin of calcareous layer.

Height mm	Width mm	
3.2	3.8	Monte Toro, lectotype
2.8	3.3	La Silla, Gibara

Remarks. The shells of this species resemble the group of *rupestris* in size and shape. They differ in having a rounded periphery, inflated whorls which do not present a steplike appearance, and by the absence or obsolescence of spiral sculpture. Pfeiffer wrote that it looks like a "miniaturform der *Tr. gouldiana.*" The records indicate that *methfesseli* has a wide distribution over the eastern three-quarters of Oriente (Pl. 8). The paucity of records is probably due to the diminutive size of the shell and its habit of encrusting its shell, both features causing it to be overlooked by collectors.

Specimens examined. ORIENTE. Baracoa; Monte Toro, Guantánamo.

Troschelviana (*Microviana*) *tumidula* (Clench & Aguayo)

Plate 4, figure 14

Eutrochatella (*Microviana*) *tumidula* Clench & Aguayo 1957, *in* Aguayo & Jaume, Mem. Soc. Cubana. Hist. Nat., 23: 119, pl. 1, fig. 6 (type-locality, Cerro de los Portales, Camayén, Barrio de Bariay, Gibara, Provincia de Oriente, Cuba; holotype, MP 13260; paratypes, MP 13261; MCZ 212978).

Description. Shell about 4 mm in height, depressed trochoid, thin, sublustrous. Color pale lemon-yellow or pale reddish brown, darker near the spire, aperture yellow or rufous internally. Whorls $5\frac{1}{2}$, earlier postnuclear whorls roundly keeled, penultimate whorl shelved and slightly convex, body whorl inflated, periphery evenly rounded. Suture strongly impressed, subchanneled. Spire low, widely conic, apex well raised. Aperture oblique, semilunate, yellow or reddish within, with occasionally an uneven, yellowish orange band entering at the upper angle. Parietal wall somewhat inflated, microscopically and irregularly pebbled, with a low, marginally rounded, whitish, lamellate umbilical callus, thickest near the umbilical region. Palatal lip entire, simple, not expanded, roundly angled at point of columellar insertion. Columella evenly concave below, gently convex above, thickened, with a triangular protuberance where it merges with the

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[1] The specimens referred to here were identified as cotypes (Gundlach leg.) by Dr. C. de la Torre in June 1912.

parietal callus. Sculpture of fine, irregular, diagonal growth lines; faint spiral cords limited to the first postnuclear whorl. Protoconch 1½ whorls, rounded, microscopically pebbled, raised. Periostracum wanting. Operculum thin, brown, glassy; surface microscopically pebbled and with a low, rounded lamella on the columellar margin.

Height mm	Width mm	
4.1	4.0	Silla de Gibara, paratype
4.0	3.6	Cerro San Juan, Sao Arriba
3.8	3.8	Portales de Camayén, Holguín
3.0	3.4	Cerro Cariblanco

Remarks. This species occurs in a restricted area in the region of Holguín and Gibara in the northwestern part of Oriente (Pl. 8). The shells can be recognized by their shape, which is more depressed and more rounded peripherally than its congeners of equal size. In addition, as Clench & Aguayo noted, the shells are distinctive in possessing a deep, almost channeled suture.

The shells show little variation throughout the range. The populations at Cerro Cariblanco and Portales de Camayén are somewhat smaller. In most of the series we examined, we found a mixture of rufous and yellowish individuals.

Specimens examined. ORIENTE. Sao Arriba; Cerro San Juan, Sao Arriba; Portales de Camayén (all Holguín); Cerro Cariblanco, 16 km NE of Holguín; Silla de Gibara.

Troschelviana (Microviana) continua (Pfeiffer)

Plate 5, figure 4

Helicina continua (Gundlach MS) Pfeiffer 1858, Malak. Blät., 5: 49 (type-locality, Guisa [Bayamo, Oriente]; lectotype, here selected, USNM 489514, Gundlach leg., ex Gill).

Helicina continua Gundlach. Poey 1858, Memorias Historia Natural Isla de Cuba, 2: 6.

Trochatella continua Gundlach. Pfeiffer 1865, Monographia Pneumonopomorum Viventium, suppl. 2: 212.

Trochatella continua Gundlach. Arango 1879, Contribución Fauna Malacológica Cubana, p. 44.

Eutrochatella (Artecallosa) continua (Gundlach MSS) Poey. Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 136, pl. 22, figs. 21–24.

Description. Shell about 4 mm in diameter, depressed trochoid, moderately thin, translucent, faintly lustrous. Color pale greenish yellow, lip somewhat lighter. Whorls 5, somewhat inflated, body whorl rounded carinate, not descending at aperture, suture well impressed. Spire low conic, apex raised. Aperture rounded trapezoid, acutely angled at upper columellar angle, same color as shell internally. Parietal wall weakly convex, with a deep, circular, subperpendicularly-sided pit adjacent to the columella; parietal callus thin, not projecting beyond the aperture. Palatal lip simple, barely flaring, straight at terminations, subtruncate at dorsal insertion in the body whorl. Columella short, shallowly concave below, set off from the basal pit by a low lamella. Sculpture of fine, irregular, diagonal growth lines, crossed by very faint spiral cords which are a reflection of the periostracal sculpture. Protoconch 1½ whorls, rounded, moderately raised, closely and microscopically punctate. Periostracum thin, deciduous, marked by low, widely spaced spiral ridges; shell usually encrusted. Operculum irregularly trapezoid, weakly concave, outer layer translucent, microscopically and closely pebbled, growth lines barely perceptible; inner layer set off from outer layer by a shallow marginal sulcus, faintly brownish, darker at the margins.

Height mm	Width mm		
2.5	3.8	USNM 489514	Guisa, Cuba
3.0	3.8	USNM 489515	Cuba

Remarks. The shell of this species can be readily separated from its congeners of equal size by the depressed shape, the subtruncate insertion of the palatal lip in the aperture, and especially by the deep, umbilicuslike pit with its subperpendicular sides. In several other species the umbilical area is also more or less shallowly excavated, but the excavation is not as deep nor are the sides as straight. In addition *continua* differs from *pfeifferiana* Pfeiffer in being larger and having a more or less straight-sided spire, whereas in the latter species the outline is steplike. It is wider and more depressed than *methfesseli* Pfeiffer.

Pfeiffer and others gave only Guisa as the type-locality. Arango (1879) was the first to show that the Guisa in Oriente Province was meant. The species is known only from the type-locality (Pl. 8).

This species has been credited to Gundlach *in* Poey on the basis of the 1858 reference in the *Memorias*. But here the name alone appears, without description. Pfeiffer's paper appeared in April 1858, whereas volume 2, pages 1–96 of the *Memorias* did not appear until October of the same year.

The figure given by Sowerby (1866: pl. 272, fig. 48) is not of this species.

Troschelviana (Microviana) spinopoma (Aguayo)
Plate 4, figure 11

Eutrochatella (Torreviana) spinopoma Aguayo 1943, Rev. Soc. Malac. 'Carlos de la Torre,' 1: 70, pl. 10, figs. 5–6, text fig. p. 80 (type-locality, Pan de Samá, Limpio de la Cañada, Barrio de Cañadón, Banes [Oriente]; holotype, MP 2780).

Description. Shell about 3 mm in diameter, wider than high, thin, depressed turbinate, not shining. Color very pale yellow, edge of aperture white. Whorls 5½, moderately inflated, raised steplike above the deeply inset and moderately impressed suture; body whorl rounded peripherally, an acute, shallow notch at the posterior (upper) insertion with the aperture. Spire wide and depressed conic, apex sharply raised. Aperture widely semilunate, outer edge well rounded. Parietal wall well excavated in umbilical region, with a small, barely raised parietal callus, surface roughened by very fine, regularly spaced pustules. Palatal lip thin, entire, not flaring, slightly thickened at the widely rounded angle of the basal insertion. Columella short, shallowly concave. Axial sculpture of irregularly spaced, diagonal growth lines, crossed by more or less regularly spaced, slightly raised spiral cords. Protoconch 1½ whorls, glassy, rounded, minutely punctate. Periostracum wanting, but shell in life encrusted. Inner chitinous layer of the operculum very thin, pale brown, separated from the outer calcareous layer by a distinct marginal sulcus. Outer layer thin, translucent, greenish grey in color, deeply dished, outer margin with raised, regularly and closely spaced lamellae, which in the depressed center rise into high, slightly curved, sharp papillae; outer margin denticulated by the tips of the lamellae.

Height mm	Width mm	
2.4	2.9	Baracoa
3.0	3.2	"
2.3	3.2	"

Remarks. The shells of this species closely resemble *rupestris* Pfeiffer and *holguinensis* Aguayo in size and shape. They can be readily separated by the presence of the notch on the body whorl at the posterior apertural insertion, the rounded rather than carinate periphery, and the sculpture of the parietal callus which has the surface covered with finer and more regularly spaced pustules. The operculum differs from that of *holguinensis* in being thinner and in having higher, more slender and sharper papillae. The species has been reported from Banes and Baracoa, and probably will be found in areas between the two (Pl. 7).

Specimens examined. Oriente. Baracoa.

Troschelviana (Microviana) pfeifferiana pfeifferiana (Pfeiffer)

Plate 4, figure 9

Helicina pfeifferiana (Arango) Pfeiffer 1866, Malak. Blät., 13: 64 (type-locality, Yunque de Baracoa [Oriente]; lectotype, here selected, MCZ 73864, ex Arango; paralectotype, MCZ 273214 same data); 1876, Monographia Pneumonopomorum Viventium, suppl. 3: 251.

Trochatella pfeifferiana Arango 1879, Contribución Fauna Malacológica Cubana, p. 44.

Eutrochatella (Artecallosa) pfeifferiana Pfeiffer. Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 138, pl. 22, figs. 15–16.

Description. Shell about 3 mm in diameter, width and height almost equal, depressed turbinate, rather thin, in life generally encrusted. Color glassy white, occasionally with a lemon yellow tinge. Whorls 5½ to 6, subcarinate, earlier whorls raised steplike above the well-impressed suture. Spire low conic, sides strongly marked by the steplike character of the whorls. Aperture very oblique, widely semilunate, same color as shell. Parietal wall rounded, strongly excavated in umbilical region, with a very thin, narrow, strongly and regularly punctate parietal callus. Palatal lip thin, entire, slightly thickened within, not flaring. Columella rather short, almost straight above, strongly rounded at insertion with basal lip. Sculpture of weak irregular growth lines only; spiral sculpture wanting. Protoconch 1½ whorls, rounded, microscopically punctate, sharply raised. Periostracum, except for encrusted matter, wanting. Operculum translucent, outer calcareous layer dull, minutely and thickly punctate; inner chitinous layer thin, darker in color at the margins, concentric growth lines not clearly perceptible.

Height mm	Width mm	
3.0	2.6	Yunque de Baracoa, lectotype
2.3	2.6	paralectotype (juvenile)
2.5	2.5	Monte Libano

Remarks. This small species resembles the shells of *holguinensis* and *spinopoma* but differs in having a smooth, rather than a spinose, operculum. The roughened, minutely punctate parietal callus is also characteristic. Specimens vary slightly in color, but pale, almost white translucent shades predominate. It is confined to the eastern end of the island. The presence of a subspecies in the isolated Najaza Mountains of Camagüey suggests that the present species has a wider distribution than appears from the few records (Pl. 7).

Specimens examined. ORIENTE. Guaro, Monte Libano; Yunque de Baracoa.

Troschelviana (Microviana) pfeifferiana najazaensis new subspecies

Plate 4, figure 8

Description. This subspecies resembles the nominate species, but differs in having the steplike structure of the whorls more sharply angulate and in the rather dark flesh color, especially in the aperture. In addition, the axial sculpture is stronger and the spiral lines are weaker.

Height mm	Width mm	
3.1	3.0	holotype
3.0	3.0	paratype
2.7	2.6	"

Remarks. The shells are similar to *pfeifferiana pfeifferiana* in size, in shape, and in the roughened surface of the operculum and the parietal wall. In color a rufous or flesh colored tint prevails, whereas in the nominate form pale yellow and translucent white are predominant. It probably occurs only in the Najaza Mountains of Camagüey (Pl. 7), whereas the nominate form is limited to the area about Baracoa in the extreme east of Oriente. We have seen specimens only from the type locality. Holotype, MCZ 92091 (Bermúdez leg.), El Cacaotal, Najaza, Camagüey, Cuba; paratype, MCZ 127517, same data, MCZ 273217, same locality, Torre leg.

Troschelviana (*Microviana*) *granulum* (Pfeiffer)

Helicina granulum (Gundlach MS) Pfeiffer 1864, Malak. Blät., 11: 161 (type-locality, Monte Toro; type, MP ?); 1865, Monographia Pneumonopomorum Viventium, 2: 233.

Helicina granulum Gundlach. Arango 1879, Contribución Fauna Malacológica Cubana, p. 53.

Description. "Shell minute, depressed, rather thin, smooth, translucid, amber-colored; spire scarcely conoid-elevated; whorls nearly 4, rather convex, the last depressed rounded, subexcavated below, lightly callused; columella very short, vertical, aperture oblique, widely semi-ovate; peristome briefly expanded, with the basal margin inserting roundly into the columella. Operculum? Major diameter 2 2/3, altitude scarcely 1 mm," (translated).

Remarks. We have not seen this species, which does not appear to have been collected since. The description was based upon a single specimen which has never been figured. Sowerby (1866: 296) was unable to identify it, and it is not mentioned in the works of Reeve (1874) or Wagner (1908). The only smaller species of the Vianini from Monte Toro is *Troschelviana methfesseli* Pfeiffer, but *granulum* does not belong here because of much smaller size and depressed shape.

We put the species provisionally in *Microviana* because of its small size.

Troschelviana (*Microviana*) *callosa* (Poey) Plate 4, figure 15

Helicina callosa Poey 1854, Memorias Historia Natural Isla de Cuba, 1: 430, pl. 33, figs. 13–14 (type-locality, Isla de Pinos, Gundlach leg.; type, MP ?).

Trochatella callosa Poey. Pfeiffer 1856, Monographia Pneumonopomorum Viventium, suppl. 1: 176; Arango 1879, Contribución Fauna Malacológica Cubana, p. 44; Sowerby 1866, Thes. Conchyl., 3: 284, pl. 269, fig. 146.

Eutrochatella (*Artecallosa*) *callosa* Poey. Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 137, pl. 22, figs. 25–28.

Description. Shell reaching about 5 mm in height, slightly higher than wide, low conic, rather solid, sublustrous, sides strongly stepped. Color very pale brown, whitish at apex and near the aperture. Whorls 5½, obtusely carinate, earlier ones flat or weakly concave, rising steplike from the well-impressed suture, the last 2 slightly swollen; body whorl with a strong, rounded carina, descending briefly at the aperture underneath the peripheral carina. Spire widely conic, sides strongly stepped, apex sharply raised. Aperture oblique, rounded triangular, palatal angle widely rounded, a strong, white, rounded lamella entering at the upper parietal angle. Parietal wall with a heavy, subcircular, wide ridge setting off the umbilical area and extending into the aperture in the form of the lamella. Palatal lip simple, entire, not expanded, inserting with a rounded angle into the columella. Columella straight, subperpendicular, with short, rounded angles at upper and lower insertions. Sculpture of raised, widely and irregularly spaced spiral cords crossed by low, regularly and closely spaced oblique axial cords. Protoconch 1½ whorls, glassy, rounded, microscopically punctate, sharply raised. Periostracum wanting, shell frequently encrusted. Operculum subrhomboid, glassy, thin, deeply dished, columellar margin sigmoid, armed internally with a rather high, strongly pebbled columellar ridge, highest near the upper angle, and provided with a short, shallow, marginal sulcus; inner chitinous layer glassy, colorless, reaching beyond the margin of the outer layer. Nucleus laterally central, near the columellar margin.

Height mm	Width mm	
5.0	4.5	NW part of Sierra de Casas
4.75	4.5	near N end of Sierra de Casas
4.75	4.25	" "

Remarks. This species is limited to the sierras in the north central part of the Isle of Pines. The shells are unique in the family in possessing the strong, rounded lamella extending from the parietal callus and entering into the aperture. They have the steplike character of *T. rupestris*, but are larger and more solid. The operculum is provided with a rather deeply sigmoid columellar edge to accommodate the lamellar obstruction of the aperture. The color of the shells available for this study, where they were not completely faded, was pale brown, but Poey describes the color as "rosea" or "pallida rosea." We may assume that this rose color is present in life but fades to pale brown after death.

Specimens examined. ISLE OF PINES. Small mogote between Sierra de Caballos and Sierra Colombo; W side, third hill from N end of Sierra de Casas; NW part of Sierra de Casas, W side of first hill (all USNM).

KEY TO THE SPECIES OF *SEMITROCHATELLA*

1. Shell relatively large, reaching 7.5 or 10.5 mm in height 2
1. Shell relatively small, reaching 4 mm in height 3
2. Shell reaching 7.5 mm in height, surface with spiral sculpture .... *conica*
2. Shell reaching 10.5 mm in height, surface strongly malleated .... *elongata*
3. Shell white .... *alboviridis*
3. Shell light brown or buff 4
4. Spiral sculpture weak, protoconch lighter than rest of shell .... *babei*
4. Spiral sculpture strong, protoconch like burnished copper .... *fuscula*

Genus *Semitrochatella* Aguayo & Jaume

Semitrochatella Aguayo & Jaume, Mem. Soc. Cubana Hist. Nat., 1958, 24: 101 (type-species, original designation, *Helicina conica* Pfeiffer).

Description. "Shells conical, small, the sides almost straight and the suture impressed. The lip lightly reflected. Radula apparently of the subfamily Helicininae, that is to say, with the capituliform process in the form of a comb not like a T as in the subfamily Vianinae (Proserpininae). The A-lateral with 3–4 cusps; B-lateral with 2–3 cusps, C-lateral with 2–3 cusps, the pectiniform tooth with 6–8 cusps. The marginal teeth are almost never unicusped, usually with 2 to 5 deep cusps. In the type species there are no marginals with fewer than 4 cusps." (Translated.)

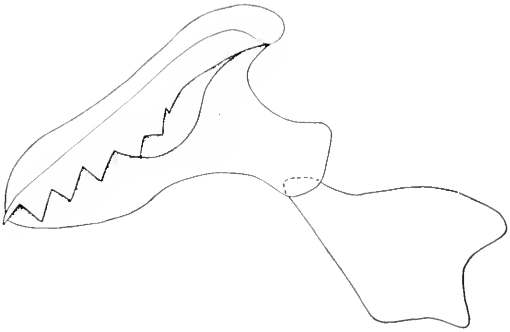

Figure 2. Lateral tooth complex of *Semitrochatella conica*.

The radula is narrower than most Vianini radula of similar length. The shape of the important comb-lateral is intermediate between that of Proserpininae, with the basal pillar more or less medially placed, and Helicininae where the basal column is terminally located (Fig. 2). The outer marginal teeth are armed with 5 cusps, and in this respect they more closely resemble the condition in Helicininae. The lateral accessory plate has the irregular rhomboid shape found in Proserpininae. There are 37 marginal teeth on each side, the innermost being unicuspid.

Remarks. We have examined the radula of some specimens of the type-species (MCZ 127676 from Píe Valdes, Yaguajay, Las Villas Bermúdez Collection). As Aguayo & Jaume stated (*loc. cit.*) their new genus seems to stand between the two subfamilies Helicininae and Vianinae (=Proserpininae). In shell characters it stands very near the latter, especially the tribe Vianini, but in the radula it has several features characteristic of the Helicininae. Nevertheless, we think that the genus had best be kept in the Proserpininae, tribe Vianini. The shape of the comb-lateral is very close to Stoastomatini, which is one of the tribes placed in the Proserpininae, and the shell shape, as stated, is that of another tribe of the Proserpininae, Vianini.

Semitrochatella conica (Pfeiffer)
Plate 5, figures 1–3

Helicina conica Pfeiffer 1839, Wiegmann's Arch. Naturgesch., 5th year, 1: 355 (Cuba; lectotype[1], here selected, MCZ 273210 [Trinidad], ex Dohrn; paralectotypes, same MCZ 273212).

Trochatella conica Pfeiffer. Sowerby 1847, Thes. Conchyl., 1: 9, pl. 3, fig. 101.

Helicina elegans Orbigny 1842, Mollusques, *in* Sagra, Histoire Physique, Politique et Naturelle de l'Ile de Cuba, Paris, 1: 250, pl. 20, figs. 13–15 (l'intérieur de l'Ile de Cuba; type not in BM(NH), location unknown).

Helicina elongata Pfeiffer 1852, Monographia Pneumonopomorum Viventium, p. 389 (type-locality, "Isla de Pinos" prope Cubam), not Orbigny 1842.

Trochatella conica Pfeiffer 1850, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 1, p. 7, pl. 5, figs. 9–11.

Eutrochatella (*Artecallosa*) *conica* Pfeiffer. Wagner 1908, *op. cit.*, sect. 18, pt. 2, p. 136, pl. 23, figs. 5–6.

Semitrochatella conica anafensis Aguayo & Jaume 1954, Mem. Soc. Cubana Hist. Nat., 24: 102 (type-locality, Peña Blanca, Sierra Anafe, Pinar del Río, Cuba; holotype, MP 17437).

Description. Shell about 8 mm in height, low conic, higher than wide, not shining, moderately thin. Color pale flesh or very pale yellow, lip and callus white, whorls about 6, moderately inflated; body whorl more than three times wider than penultimate whorl, rounded peripherally, descending near aperture; suture well impressed. Spire widely conic, apex well raised. Aperture widely semilunate. Callus on parietal wall smaller than aperture, white, opaque, raised, unevenly rounded at outer margin, surface strongly roughened. Lip white, thin, flaring but not reflected, widest in center, narrowest at terminations. Columella short, oblique, angled at insertion of basal lip. Sculpture of diagonal, closely set growth lines, crossed by raised, unevenly spaced spiral cords, weak on early whorls, strongest at base. Fine, wavy axial lineolations are visible within the shell substance. Protoconch $1\frac{1}{2}$ whorls, minutely pitted, sharply raised. Periostracum wanting, but live shells frequently covered by irregular layer of inorganic matter. Operculum strong, concave, calcareous layer opaque, faintly colored in center, white at outer edges, surface roughened like surface of parietal callus. Inner corneous layer pale buff, not reaching outer margin of calcareous layer. Nucleus lateral central near parietal margin, growth lines unevenly concentric.

Height mm	Width mm	
6.3	5.4	lectotype
6.1	5.1	Abra del Yumurí, Las Villas
7.8	6.4	Esperón, Sierra Anafe, Pinar del Río
7.5	7.5	Esperón, Sierra Anafe, Pinar del Río
6.0	5.1	Casa Azul, Cárdenas, Las Villas
5.8	5.7	Guanajay, Pinar del Río

Remarks. This species can be recognized by its low conical shape, by its comparatively large body whorl, by the roughened surface of the operculum and parietal callus and by the stronger or weaker spiral sculpture which covers practically the entire shell. It is quite uniform throughout its range, the various populations differing only slightly in color and size. It ranges from about the center of Pinar del Río at Sierra la Güira, through Havana and Matanzas, and reaches to the eastern part of Las Villas at Yaguajay (Pl. 7). It resembles *scopulorum* (Morelet) from the Isle of Pines but *scopulorum*, besides being lower and more widely conic in shape, has a less widely flaring palatal lip.

The name *anafensis* was given as a subspecies to the larger specimens from the Sierra de Anafe. However, populations of large and small shells are scattered throughout the range from Pinar del Río to

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[1] According to Dance (1966: 297), H. Dohrn acquired the L. Pfeiffer collection. The material from Dohrn in the MCZ may thus be assumed to have been examined by Pfeiffer and may serve as the basis for type-selections.

Las Villas. The size of the shells is probably determined by ecological conditions and needs no taxonomic recognition.

Specimens examined. Pinar del Río. La Furnia, Sierra La Güira; San Diego de los Baños; La Tumba, Candelaria; Las Animas; El Retiro (both Rangel); El Mamey, Callajabos (Cayajabos); Ceiba del Agua (both Guanajay); Artemisa; Monte Cristo, Limonar; El Toro, Sierra Limones; Peña Blanca; Esperón (both Sierra Anafe); Havana. Vereda El Padre; Finca El Inglés; extreme east of Sierra el Grillo (all Sierra El Grillo); E of Zanabria, Madruga; Caimita de Guayabal; Camoa. Matanzas. 5 km W of Ceiba Mocha; Abra del Yumurí. Las Villas. *Soledad:* La Portuguesa, Seboruco; Sierra de San Juan; Mina Carlota, Sierra de San Juan; Limones Seboruco, 1 mi. SE of Soledad; El Hacha; Murciélagos (both Vega Alta); Mogote between Vega Alta and Piedras; Trinidad; Morales, Jumagua, Sagua La Grande. *Zulueta:* Cueva la Veinte; Charco Majá; El Boquerón de Jatibonico. *Yaguajay:* Camaján; Pie Valdés; Canón del Yigre; Muguirre. *Cienfuegos:* Vega de Los Negros, Arimao.

Semitrochatella alboviridis (Pfeiffer)
Plate 4, figures 1–2

Helicina alboviridis (Wright MS) Pfeiffer 1864, Malak. Blät., 11: 108 (type-locality, Ysabel Maria und Vignales an Felswänden; lectotype, here selected, MCZ 73778, ex Tryon; paralectotype, MCZ 73777, J. G. Anthony Collection ex Gundlach); 1865, Monographia Pneumonopomorum Viventium, suppl. 2: 165.

Helicina alboviridis Wright. Arango 1879, Contribución Fauna Malacológica Cubana, p. 56.

Eutrochatella (*Ustronia*) *alboviridis* (Wright) Pfeiffer. Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 125, pl. 24, figs. 12–13.

Eutrochatella (*Troschelviana*) *alboviridis* ("Wright" Pfeiffer). H. B. Baker 1922, Proc. Acad. Nat. Sci. Philadelphia, 74: 59.

Description. Shell about 4 mm in diameter, elevated conic, shining, smooth, rather solid. Color white, dark olivaceous at spire, a band of similar color occasionally on the base below the carina and in the columellar area. Whorls 7, rounded, body whorl with an obtuse but distinct carina, base somewhat flattened. Early postnuclear whorls obtusely angled at suture. Suture well impressed. Spire narrow, elevated; apex sharp, white. Aperture widely semilunate, irregularly rounded at outer margin, less rounded above. Parietal wall somewhat inflated, with a narrow, glassy, minutely punctate callus near the columella. Outer lip oblique, sinuous, retracted sharply into body whorl at dorsal insertion. Columella short, very oblique, obtusely angled at insertion into basal lip. Sculpture of fine, diagonal growth lines. The narrow, undulate axial lineolations in the shell substance appear on the penultimate whorl where they run in a generally more diagonal direction than those on the body whorl. On the base these lines are finer and more broken, and radiate from the umbilical region as center. Protoconch 1½ whorls, milk white, rounded, microscopically pitted, raised above succeeding whorls. Periostracum wanting. Operculum glassy, concave, columellar edge with a strong, rounded, rather wide ridge, outer margin thin.

Height mm	Width mm	
3.6	3.4	Isabel María (lectotype)
4.2	3.4	" " (paralectotype)
4.3	3.6	Dos Hermanos
3.3	2.6	La Muralla

Remarks. This species is easily recognizable by its shining texture, white color, and darker apical and basal areas. Under moderate magnification the strong wavy axial ornamentation will immediately help identify the species. It differs from *mestrei* Arango in its smaller size, different color, and in having a rounded rather than acute periphery.

The darker areas prove to be translucent in dead, weathered specimens, and the subperipheral line is sometimes absent. In life this is a handsome species, especially striking being the rather wide, well-delimited olive line margining the base in most specimens. The line fades in dead collected shells. The only lots we have seen prove to consist of few specimens, indicating that it is either a scarce form or that it is not easily seen on the lichens where, according to Arango (1879), it lives.

We have specimens of this species from the type-locality, Dos Hermanos in Viñales, and La Muralla on the road to Guane (Pl. 8). This is an extensive distribution and the lack of intermediate occurrence—or even more extended limits of its range—is undoubtedly due to the small size of the shell which is easily overlooked by collectors bemused by larger, more spectacular species.

Specimens examined. PINAR DEL RÍO. Isabel María; Dos Hermanos, Viñales; Punta de La Muralla, Guane; Luis Lazo; Lagunillas, Consolación del Norte.

Semitrochatella babei (Arango)
Plate 4, figures 18–19

Helicina (*Trochatella*) *babei* Arango 1876, An. Real Acad. Cien. Méd., Fís. Nat. Habana, 12: 281 (type-locality, Sabana de Robles [Matanzas][1]; type, MP?).

Trochatella babei Arango 1879, Contribución Fauna Malacológica Cubana, p. 45.

Helicina cisnerosi Arango 1879, *op. cit.*, p. 134 (type-locality, Bebedero, Pinar del Río; lectotype, here selected, MCZ 73867, Cerro Cabras, Pinar del Río, Arango leg.; paralectotype, same data, MCZ 273218).

Helicina cisnerosi Arango. Crosse 1890, Jour. de Conchyl., 38: 313, pl. 6, figs. 7, 7a, 7b.

Description. Shell about 4 mm in height, rather broadly conic, moderately thin, subcarinate, translucent, moderately shining. Color light brown, frequently with a pale, well-defined line just above and bordering the carina, lip white. Whorls 6½, weakly inflated, body whorl roundly carinate at base. Suture strongly impressed. Spire broadly conic, apex raised. Aperture widely sublunate, light colored at outer margin. Parietal wall smooth, sublustrous, marked by rather distantly spaced microscopic pits. Parietal callus barely perceptible. Palatal lip entire, barely flaring, straight at summit, a rounded, triangular protuberance at basal insertion. Columella short, evenly concave. Axial sculpture of rather strong diagonal growth lines crossed by raised, stronger, subregularly placed spiral cords on the later whorls. There are also wide, low, whitish, wavy axial lines within the shell substance confined to the region of the carina and the base. These lines are so closely spaced on the carina that they give the impression of a white peripheral line. Protoconch 1½ whorls, rounded, weakly punctate, sharply raised, somewhat lighter in color than the rest of the shell. Periostracum wanting. Operculum concave, glassy in center, darker colored at outer margin.

Height mm	Width mm	
4.1	3.9	Cerro Cabras (lectotype)
4.2	3.6	Hoy del Guamá, Pinar del Río
4.0	3.5	Mendoza, Jaruco, Havana
4.0	3.3	Sabana de Robles, Matanzas

Remarks. This species resembles *alboviridis* in size, but differs in being brown rather than white, in lacking the subperipheral dark or pellucid band, and in the presence on the later whorls and the carina of spiral grooves. The peculiar wavy axial lineolations are confined to the lower portions of the body whorl instead of being distributed over most of the shell. It differs from *fuscula* in its smaller size and darker color, and in lacking the burnished color of the protoconch.

On the basis of the very general Latin descriptions, it is impossible to distinguish

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[1] Arango did not locate the type-locality in its province. In Matanzas (22° 57′N, 81° 53′W) there is a Sabana de Robles (also called Sabanas de Roble, Roble, Robles), not far from Canímar in Matanzas, and Jaruco and Camao in Havana where this species was subsequently taken. Hence we assume that Arango's type-locality is in Matanzas though localities with identical names appear in some of the other provinces of the republic.

babei from *cisnerosi*. The former seems not to have been figured, whereas *cisnerosi* was figured by Crosse (1890) from specimens supplied him by Arango.

There is some confusion regarding the reported dimensions of these two taxa. According to Arango, *babei* is greater in height than in width (4 × 3½ mm). Yet in contrasting this species with *rupestris*, which is wider than high (2.8 × 3.4 mm, for example), Arango makes no mention of this important difference in dimensions and outline. At the same time the dimensions which he gives for *cisnerosi* are for a shell greater in width than height (3 × 3½ mm), but the figures presented by Crosse show a shell definitely higher than wide. Furthermore, *cisnerosi* is compared to *fuscula*, a species having a shell that is higher than wide, with no mention made of this fact.

It is also important to note that Arango did not contrast his species *babei* with *cisnerosi*. On the basis of the material available to us, determined by Arango (*cisnerosi*) and P. Bermúdez (*babei*), we can detect no consistent difference. The species ranges from near the middle of Pinar del Río Province to the western end of Matanzas (Pl. 7). Specimens of *babei* from the east, at Sabana de Robles near Matanzas City, are indistinguishable from *cisnerosi* in the west at Cerro Cabras in Pinar del Río.

Specimens examined. PINAR DEL RÍO. Cerro Cabras; Hoyo del Guamá. HAVANA. Mendoza, Jaruco; Sitio Perdido, Jaruco; Pozo Bonilla, Sitio Perdido, Jaruco; Camoa. MATANZAS. Sabana de Robles; 1 km W of Río Canímar; Abra de Figueroa, Valle del Yumurí; Ramona, El Palenque, Ciudad Matanzas.

Semitrochatella elongata (Orbigny)
Plate 2, figures 8–9

Helicina elongata Orbigny 1842, Mollusques *in* Sagra, Histoire Physique, Politique et Naturelle de l'Ile de Cuba, 1: 251, pl. 20, figs. 16–18 (intérieur de l'île de Cuba; type BM(NH) 1854.10.4.172) [not Pfeiffer 1852].

Helicina elongata Orbigny. Pfeiffer 1858, Monographia Pneumonopomorum Viventium, suppl. 1, p. 200.

Helicina elongata Orbigny. Sowerby 1842, Thes. Conchyl., London, 1: 9, pl. 3, fig. 110.

Trochatella elongata Orbigny. Sowerby 1866, *op. cit.*, 3: 284, pl. 270, fig. 158.

Helicina elongata Orbigny. Arango 1879, Contribución Fauna Malacológica Cubana, p. 52.

Eutrochatella (*Artecallosa*) *elongata* Orbigny. Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 135, pl. 23, figs. 1–4.

Eutrochatella (*Troschelviana*) *elongata* (Orbigny) (sect. *Cubaviana*) H. B. Baker 1922, Proc. Acad. Nat. Sci. Philadelphia, 74: 60.

Description. Shell about 8 to 10 mm high, elevated conic, smooth, sublustrous, rather solid. Color wax white, occasionally with a yellowish or reddish tinge, darker in parietal region and inside the aperture, lip white. Whorls 6 to 7½, moderately rounded, earliest postnuclear whorls roundly shelved, body whorl obtusely carinate, not descending at aperture, base well rounded. Suture strong, especially so at earlier whorls. Spire elevated conic, sides straight but deeply marked by the strong suture. Aperture oblique, broadly triangular, palatal angle widely rounded, yellow or pale reddish brown internally. Parietal wall moderately swollen, with a raised callus which is thickest at the umbilical area, generally colored pale yellow or pale orange, outer margin barely rounded. Palatal lip white, strong, flatly flaring, reflected above, widest near the center, very narrow at basal insertion. Columella shallowly concave, assuming the shape of a thin lamella near the insertion of the basal lip. Sculpture of fine growth lines. The axial lineolations within the shell substance are readily visible. Shells generally strongly malleated in a large diversity of patterns or in no pattern. Protoconch 1½ whorls, white, rounded, minutely punctate, sharply raised. Periostracum wanting, shell frequently encrusted with a thin, uneven layer. Operculum lusterless, sharply dished, minutely but thickly pebbled, larger than the aperture, not retractable into the aperture; marginal sulcus at columellar edge only; palatal edge raised, white, opaque in mature shells, subtransparent in submature individuals so that the color of the thin, orange-brown inner layer shines through.

Height mm	Width mm	
9.0	7.5	Sierra La Güira
9.8	7.5	La Chorrera
8.5	7.3	"
10.2	6.9	"
8.9	7.7	Hoyo de Gallardo, El Queque
9.4	8.1	Puerta del Ancón

Remarks. The shells of this species are quite distinctive. They can be recognized by the high conic shape, the rounded base, the generally malleated surface which rarely has any sign of spiral sculpture, the lack of color at the umbilical area, the flat, wide, flaring lip, and the lusterless, nonretractive operculum. They differ additionally from *conica* Pfeiffer in being generally larger and more solid, and in the absence of spiral sculpture on the later whorls. They are higher and more solid than *pyramidalis* Sowerby and lack the colored columellar spot.

We have seen specimens from localities in Viñales to San Diego de los Baños and Pan de Guajaibón. The range of the species seems to be limited to the more easterly portions of the Sierra de los Orgãnos (Pl. 8, I). We are unable to confirm Arango's statement "casi toda la cordillera de los Organos" (1879: 52).

Pfeiffer (1852: 389) did not describe *elongata* Orbigny correctly, having confused it with *scopulorum*, and gave the Isle of Pines as the locality. In 1856 (pp. 148, 149) he corrected this error and in 1858 (p. 200) published a fitting description with the proper localities. It may be that the occasional reports of *elongata* occurring in the Sierra de las Casa on the Isle of Pines, e. g., Henderson (1916: 318); Poey[1] (1854: 426, 427) are based upon this error.

Specimens examined. PINAR DEL RÍO. *Viñales:* Sierra de Viñales; Hoyo de Gallardo, El Queque; Hoyo de la Cidra, El Queque; La Guasasa; Los Camerones, San Antonio; Sierra La Chorrera, San Vicente; Mogote Trujillo, Palmarito; Puerta del Ancón. *San Andrés:* Mogote de la Cidra, Caiguanabo; Sitio de la Sierra; Sierra La Güira; Sierra Chiquita, Guajaibón; Pan de Guajaibón; Mogote Colorado, San Diego de los Baños.

Semitrochatella fuscula (Pfeiffer)
Plate 4, figures 5–6

Helicina fuscula (Gundlach MS) Pfeiffer 1863, Malak. Blät., 10: 197 (type-locality, in parte occidentali insulae Cubae [Guajaibón]; lectotype, here selected, MCZ 90025, ex Gundlach, T. Bland Collection; paratypes, same data, MCZ 273231).

Helicina fuscula Gundlach. Sowerby 1866, Thes. Conchyl., 3: 284, pl. 278, figs. 465–466.

Helicina fuscula Gundlach. Arango 1879, Contribución Fauna Malacológica Cubana, p. 55.

Eutrochatella (*Ustronia*) *fuscula* (Gundlach) Pfeiffer. Wagner 1908, *in* Martini & Chemnitz, Conchyl.-Cab., (2) 1: sect. 18, pt. 2, p. 124, pl. 24, figs. 14–15.

Eutrochatella (*Cubaviana*) *fuscula* ("Gundlach" Pfeiffer) H. B. Baker 1922, Proc. Acad. Nat. Sci. Philadelphia, 74: 60.

Semitrochatella trochulina fuscula "Gundlach" Pfeiffer. Aguayo & Jaume, 1958, Mem. Soc. Cubana Hist. Nat., 24: 102.

Description. Shell about 4 mm in height, high conic, subglossy, rather thin. Color light brown to light buff, lip white, protoconch brown, burnished. Whorls 6, gently rounded, body whorl obtusely keeled, somewhat flattened at base. Suture well impressed. Spire rather steeply conic, apex sharp. Aperture oblique, widely semilunate, subevenly rounded at outer margin. Parietal callus short, narrow, triangular,

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[1] Poey cited Gundlach for this species and indicated that it was "exclusivamente pinense." Since he also listed *scopulorum* in the same way, we find it difficult to guess what shells Gundlach was referring to.

raised; parietal area around columella translucent, glassy. Palatal lip expanded, narrower at dorsal and basal insertion. Columella quite short, rounded. Umbilical area with a shallow depression. Surface lightly sculptured by irregular, diagonal growth lines, crossed by indistinct, raised spiral cords. The wavy, white, rather wide lineolations within the shell substance are close spaced, readily perceptible. Protoconch $1\frac{1}{2}$ whorls, color like burnished copper, sharply raised above early postnuclear whorls. Periostracum wanting. Operculum faintly tinged with brown at margins, microscopically pitted.

Height mm	Width mm	
4.0	3.7	Mogote Las Cuevitas, Viñales
4.8	3.4	El Descanso, Viñales
4.1	3.3	La Güira de Luis Lazo
4.3	3.9	"

Remarks. The shells of this species can be recognized by the small size; straight sided, conic shape; white, expanded lip; the triangular, raised parietal callus; and, the moderately obtuse keel which is white in occasional specimens. The whitish wavy axial lines are not as pronounced as in S. *alboviridis.* The protoconch in fresh specimens gleams like burnished copper when viewed under low magnification. This species is limited to the central part of Pinar del Río Province (Pl. 8). We have seen specimens from "La Güira" in Luis Lazo but did not find them to be "fere duplo maiorem" (=almost twice bigger) as Pfeiffer reported (1865: 239). Sowerby's figures show banded specimens, which we have not seen and which Pfeiffer did not include in his description. Perhaps Sowerby misinterpreted "laevissime striatula."

Specimens examined. PINAR DEL RÍO. El Descanso; Mogote Las Cuevitas (both Viñales); La Güira, Luis Lazo; Lagunillas de Consolación.

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Plate 1.

Fig. 1. *Ustronia acuminata acuminata* (Poey). MCZ 127441. Topotype, Sierra de Guane, Pinar del Río. × 2½. Fig. 2. *Ustronia acuminata acuminata* (Poey). MCZ 257881. Falda de Pico Chico, San Andrés, Pinar del Río. × 3. Fig. 3. *Ustronia acuminata columellaris* (Poey). MCZ 257853. Ensenada de la Ayúa, San Andrés, Pinar del Río. × 2½. Fig. 4. *Ustronia acuminata acuminata* (Poey). MCZ 127441. Topotype, Sierra de Guane, Pinar del Río. × 3. Fig. 5. *Ustronia acuminata acuminata* (Poey). MCZ 127441. El Cuajaní, Viñales, Pinar del Río. × 3. Fig. 6. *Helicina blandiana* Poey (= *Ustronia acuminata acuminata*). Lectotype, MCZ 87885. [Pinar del Río], Cuba. × 4. Fig. 7. *Ustronia acuminata columellaris* (Poey). MCZ 257853. Ensenada de la Ayúa, San Andrés, Pinar del Río. × 3. Fig. 8. *Ustronia acuminata acuminata* (Poey). MCZ 127439. El Cuajaní, Viñales, Pinar del Río. × 3½. Fig. 9. *Ustronia sloanii* (Orbigny). MCZ 127530. Lomas de Camoa, Habana. × 3. Figs. 10, 11. *Ustronia chrysostoma* (Pfeiffer) (= *sloanii* Orbigny). MCZ 257920. Punta de la Sabanilla, Matanzas. × 3. Fig. 12. *Ustronia sloanii* (Orbigny). MCZ 127530. Lomas de Camoa, Habana. × 3.

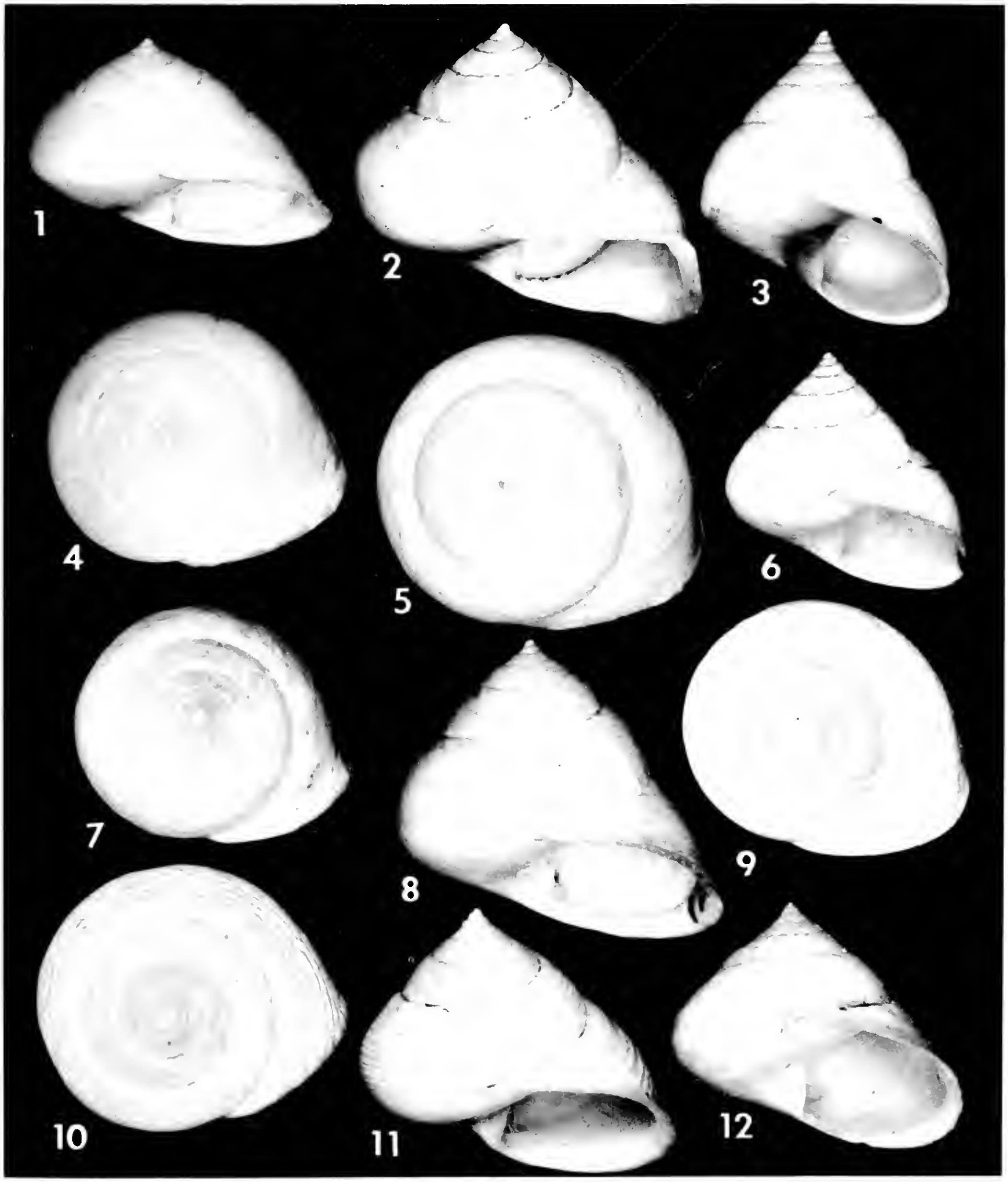
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Plate 2.

Fig. 1. *Helicina jugulata* Poey. Paralectotype, MCZ 262651. [Guane], Pinar del Río. × 3. Fig. 2. *Helicina jugulata* Poey. Lectotype, MCZ 73780. [Guane], Pinar del Río. × 3½. Fig. 3. *Helicina rubramarginata* Gundlach. Lectotype, MCZ 90024. [Guajaibón, Pinar del Río], Cuba. × 4½. Fig. 4. *Troschelviana rubromarginata* (Gundlach). MCZ 273247. Kilometer 14, Viñales, Pinar del Río. × 4. Fig. 5. *Helicina wrighti* Pfeiffer. (= *Troschelviana rubramarginata* (Gundlach)). Lectotype, MCZ 73865. [Viñales, Pinar del Río], Cuba. × 4½. Fig. 6. *Traschelviana rubromarginata* (Gundlach). MCZ 273247. Kilometer 14, Viñales, Pinar del Río. × 4. Fig. 7. *Traschelviana pyramidalis* (Sowerby). MCZ 127506. El Mamey, Cayajabos, Pinar del Ría. × 5. Figs. 8, 9. *Semitrochatella elongata* (Orbigny). MCZ 257804. Sierra La Güira, San Diego de los Baños, Pinar del Río. × 4½. Fig. 10. *Helicina nodae* Arango. (= *Troschelviana rubromarginata* (Gundlach)). Lectotype, MCZ 73781. [Guane, Pinar del Río]. Cuba. × 4. Fig. 11. *Traschelviana pyramidalis* (Sowerby). MCZ 127506. El Mamey, Cayajabos, Pinar del Río. × 5. Figs. 12, 13. *Troschelviana petitiana* (Orbigny). MCZ 108957. San José, Cienfuegos, Las Villas. × 5.


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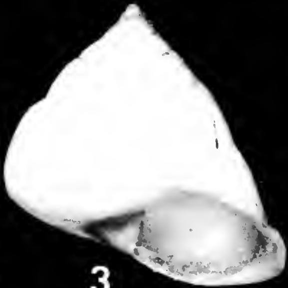
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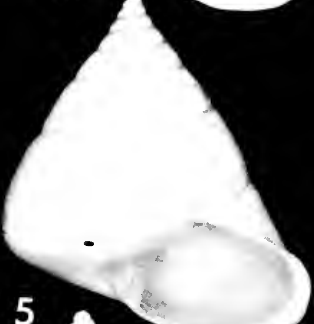
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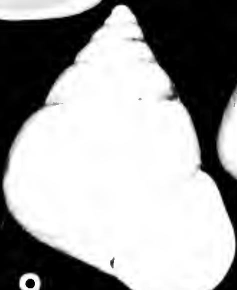
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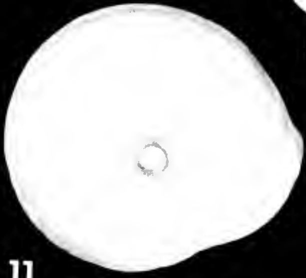
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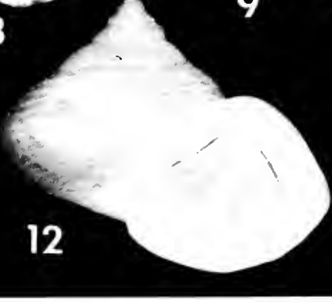
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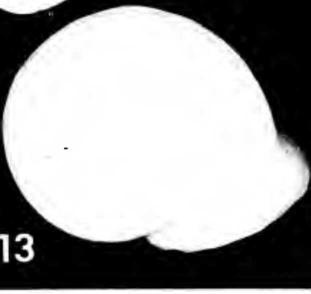
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Plate 3.

Fig. 1. *Troschelviana hians* (Poey). MCZ 127624. Paedomorph (?), El Capiro, Las Villas. × 8. Figs. 2, 3. *Troschelviana hians* (Poey). MCZ 59243. ½ mi. E of Guabairo, Soledad, Cienfuegos, Las Villas. × 0.5. Fig. 4. *Trochatella capillacea* Pfeiffer (= *Troschelviana hians*) Lectotype, MCZ 47525. [San Juan de Letrán, Las Villas], Cuba. × 10. Fig. 5. *Troschelviana hians* (Poey). MCZ 127616. Mogote el Infierno, Natalia, Calabazar de Sagua, Las Villas. × 10. Fig. 6. *Eutrochatella pilsbryi* Aguayo and Jaume. (= *Troschelviana hians*). Topotype, MCZ 127634. Hornos de Cal, Sancti Spiritus, Las Villas. × 5. Fig. 7. *Troschelviana hians* (Poey). MCZ 127616. Mogote El Infierno, Natalia, Calabazar de Sagua, Las Villas. × 5. Fig. 8. *Eutrochatella pilsbryi* Aguayo and Jaume (= *T. hians*). Topotype, MCZ 127634. Hornos de Cal, Sancti Spiritus, Las Villas. × 5. Fig. 9. *Helicina rubicunda* Pfeiffer (= *T. hians*). Lectotype, MCZ 73880. [Magua, Trinidad, Las Villas], Cuba. × 10. Fig. 10. *Eutrochatella chrysochasma hernandezi* Wagner. (= *T. chrysochasma*). Topotype, ex Anthony, MCZ 73796. [Viñales, Pinar del Río], Cuba. × 0.5. Fig. 11. *Eutrochatella jaumei* Clench and Aguayo (= *T. chrysochasma*) MCZ 127486. Mogote del Camino de la Mina a la Jagua, Pinar del Río. × 5. Fig. 12. *Trochatella jucunda* Gundlach (= *T. chrysochasma*). Lectotype, MCZ 86604. Guajaibón, Pinar del Río], Cuba. × 4. Fig. 13. *Troschelviana chrysochasma* (Poey). MCZ 127480. Sierra Paso Real, Guane, Pinar del Río. × 5. Figs. 14, 15. *Semitrochatella scopulorum* (Morelet). MCZ 127492. Sierra de Casas, Isle of Pines. × 0.5. Fig. 16. *Troschelviana chrysochasma* (Poey). MCZ 80854. El Retiro, Rangel, Pinar del Río. × 5. Fig. 17. *Troschelviana chrysochasma* (Poey). MCZ 127488. Puerta de la Muralla, Guane, Pinar del Río. × 5.

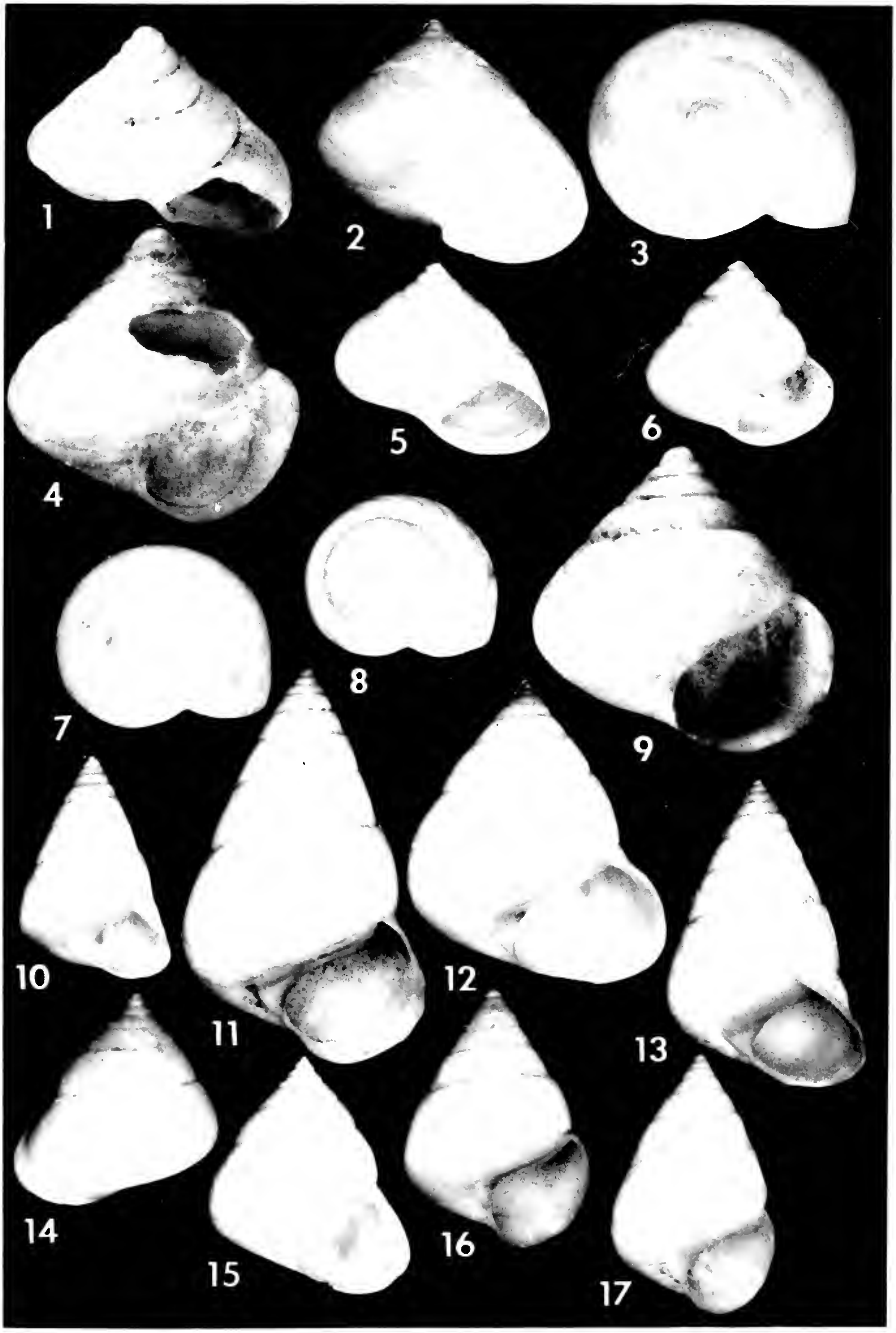
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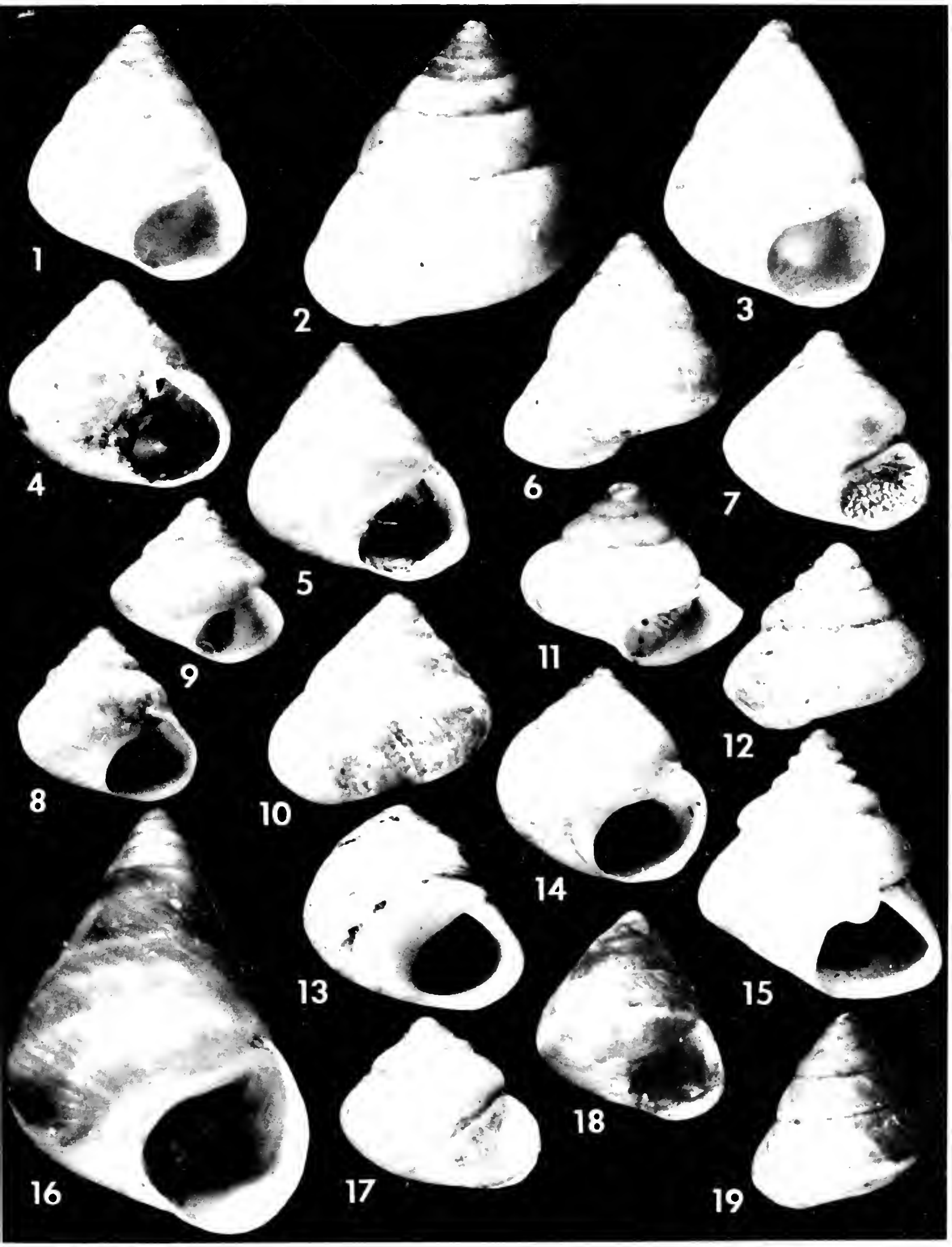
Plate 4.

Fig. 1. *Helicina alboviridis* Pfeiffer. Lectotype, MCZ 73778. Isabel María, Pinar del Río. × 10. Fig. 2. *Semitrochatella alboviridis* (Pfeiffer). MCZ 257859. Mogote Dos Hermanos, Viñales, Pinar del Río. × 10. Fig. 3. *Troschelviana erythraea* (Sowerby). MCZ 127512. Cayos de San Felipe, Viñales, Pinar del Río. × 10. Fig. 4. *Trochatella methfesseli* Pfeiffer. Lectotype, MCZ 273216. [Monte Toro, Guantánamo, Oriente], Cuba. × 8. Fig. 5. *Helicina fuscula* Pfeiffer. Lectotype, MCZ 90025. [Pinar del Río], Cuba. × 9. Fig. 6. *Semitrochatella fuscula* (Pfeiffer). MCZ 273253. Mogote Talavera, La Palma, Pinar del Río. × 9. Fig. 7. *Eutrochatella holguinensis* Aguayo. Paratype, MCZ 86493. Las Cuevas, Holguín, Oriente. × 10. Fig. 8. *Troschelviana pfeifferiana najazaensis* new species. Holotype, MCZ 273219. El Cacaotal, Najaza, Camagüey. Fig. 9. *Helicina pfeifferiana* Pfeiffer. Lectotype, MCZ 73864. Yunque de Baracoa, Oriente. × 9. Fig. 10. *Trochatella methfesseli* Pfeiffer. Paralectotype, MCZ 86494. [Monte Toro, Guantánamo, Oriente], Cuba. × 8. Fig. 11. *Troschelviana spinopoma* (Aguayo). MCZ 257916. Baracoa, Oriente. × 9½. Fig. 12. *Eutrochatella holguinensis* Aguayo. Paratype, MCZ 86493. Las Cuevas, Holguín, Oriente. × 10. Fig. 13. *Helicina littoricola* Pfeiffer. Lectotype, MCZ 86610. [Baracoa, Oriente], Cuba. × 8. Fig. 14. *Eutrochatella tumidula* Clench and Aguayo. Paratype, MCZ 52728. Silla de Gibara, Oriente. × 8. Fig. 15. *Troschelviana callosa* (Poey). USNM 429111. W side, 3rd hill from N end of Sierra de Casas, Isle of Pines. × 10½. Fig. 16. *Helicina mestrei* Arango. Cotype, MCZ 53782. Cerro de Cabras, Pinar del Río. × 10. Fig. 17. *Troschelviana rupestris* (Pfeiffer). Topotype, MCZ 73877. [Fundador, Matanzas], Cuba. × 9. Fig. 18. *Semitrochatella babei* (Arango). MCZ 273250. Hoyo del Guamá, Viñales, Pinar del Río. × 8. Fig. 19. *Helicina cisnerosi* Arango (= *babei* Arango). Lectotype, MCZ 73867. Cerro de Cabras, Pinar del Río. × 8.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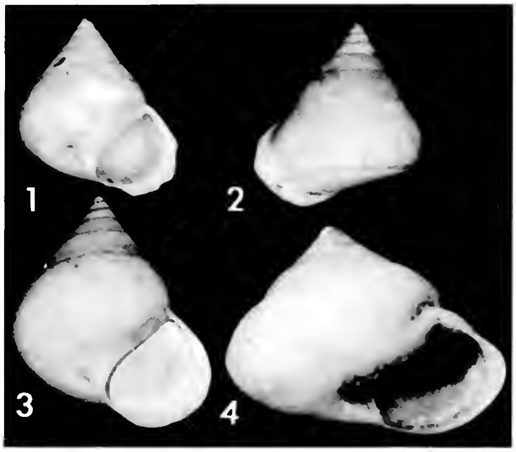
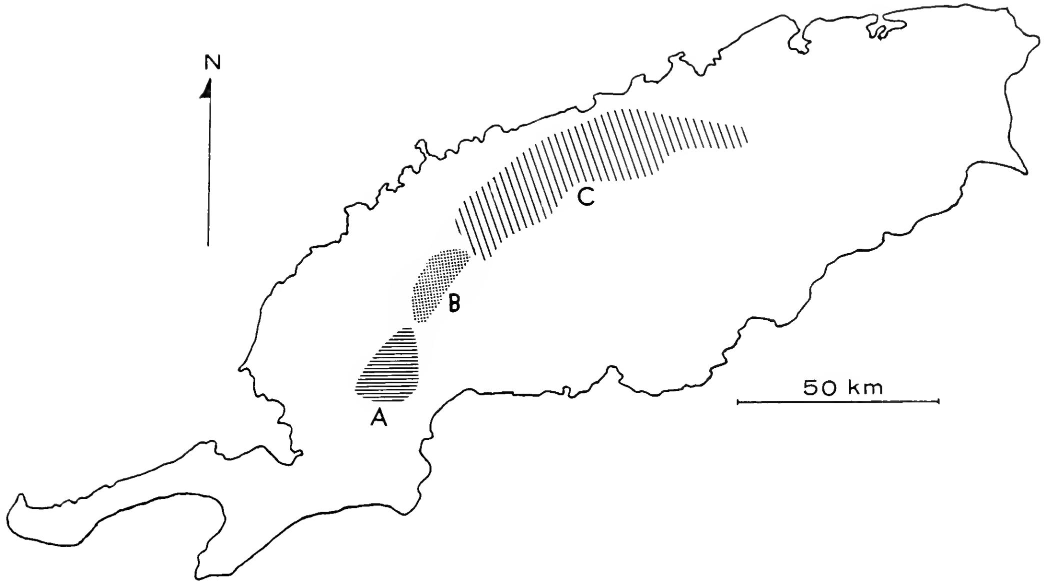


Plate 5.

Fig. 1. *Helicina conica* Pfeiffer. Lectotype, MCZ 273210. [Trinidad], Las Villas, Cuba. ×4. Figs. 2, 3. *Semitrochatella conica* (Pfeiffer). MCZ 127659. Peña Blanca, Sierra Anafe, Habana, Cuba. ×4½. Fig. 4. *Helicina continua* Pfeiffer. Lectotype, USNM 489514, Guisa, [Bayamo], Oriente, Cuba. ×10.



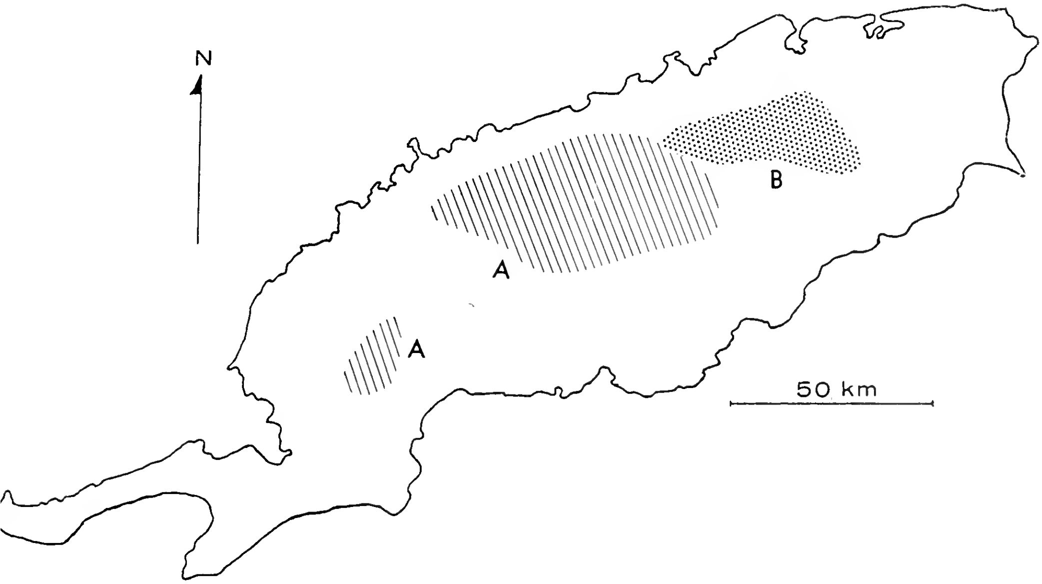


Plate 6. UPPER. Distribution of *Ustronia acuminata*, *Traschelviana jugulata*, and *T. chrysochasma* in Pinar del Rio: A, *acuminata*, *jugulata*, and *chrysachasma*; B, *jugulata*; C, *acuminata* and *chrysochasma*. LOWER. A, *Troschelviana* (*Cubaviana*) *rubromarginata* and B, *T.* (*C.*) *pyramidalis* in Pinar del Rio.

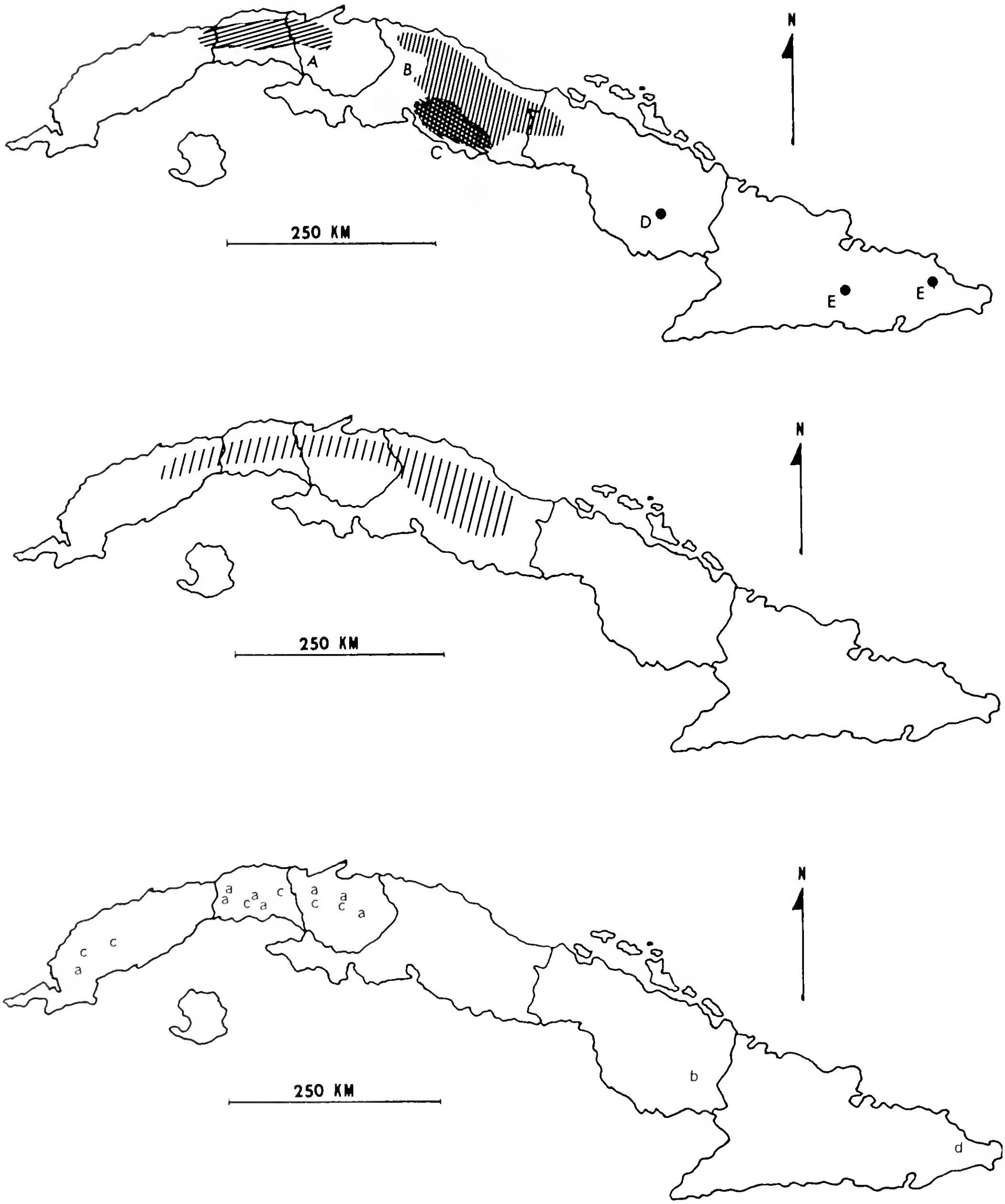


Plate 7. UPPER. Distribution of A, *Ustronia sloanii*; B, *Traschelviana (Cubaviana) hians*; C, *T. (C.) hians* and *T. (Microviana) petitiana*; D, *T. (M.) pfeifferiana najazaensis*; E, *T. (M.) pfeifferiana pfeifferiana*. MIDDLE. *Semitrochatella conica*. OWER. a, *Traschelviana (Microviana) rupestris*; b, *T. (M.) pfeifferiana najazaensis*; c, *Semitrochatella babei*; d, *Traschelana (Microviana) spinopoma*.

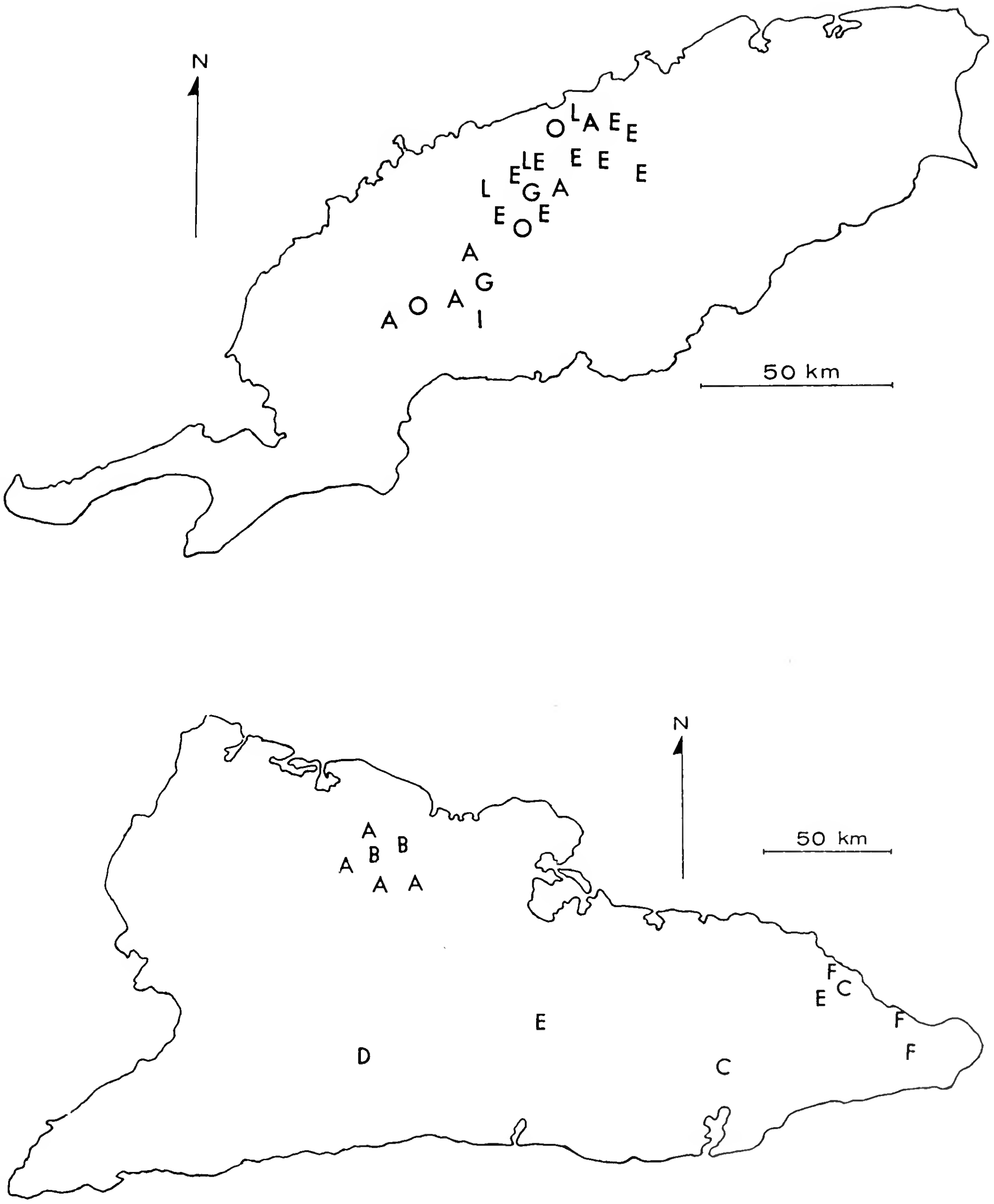


Plate 8. UPPER. Distribution of tribe Vianini in Pinar del Río: A, *Semitrochatella alboviridis;* E, *S. elongata;* L, *Traschelviana erythraea;* I, *T. mestrei;* G, *Semitrochatella fuscula;* O, *T. rubromarginata.* LOWER. Distribution of tribe Vianini in Oriente: A, *Traschelviana (Microviana) holguinensis;* B, *T. (M.) tumidula;* C, *T. (M.) methfesseli;* D, *T. (M.) continua;* E, *T. (M.) pfeifferiana;* F, *Calida littoricola.*

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Principal references in boldface type.

Bulletin OF THE
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The Orb Weaver Genus *Neoscona* in North America (Araneae: Araneidae)

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THE ORB WEAVER GENUS *NEOSCONA* IN NORTH AMERICA (ARANEAE: ARANEIDAE)

JONATHAN D. BERMAN* AND HERBERT W. LEVI

ABSTRACT

The number of North American *Neoscona* species has been reduced to ten. Characters of the male palpus, the epigynum, and the dorsal abdominal pattern have been found useful in species diagnosis. There are keys to the species, and the distributions have been mapped.

Although *Neoscona* species are among the most common spiders in North America and species are found throughout most parts of the world, no thorough study of the group has ever been made. The most important works dealing with the genus are those of F. O. P.-Cambridge (1904), who first recognized several North American species and included detailed descriptions of a number of others, and Archer (1941), who listed many of the North American species but did not give any indication of how he was able to separate them.

Because *Neoscona* includes common spiders, the problem of determining specimens frequently arises in ecological studies. In addition, members of the genus have sometimes been used as laboratory animals. For these reasons it is important that reliable characters for separating the species be found.

While it is easy to find differences between individual specimens of *Neoscona,* it is far more difficult to find similarities that reflect the common gene pool of species. In this investigation it was found that the most dependable character for separating females of the genus is the epigynum together with the color pattern. Details of the palpus are the best characters for distinguishing males; the macrosetae of the second tibia are not always reliable.

Ten species of North American *Neoscona* were segregated on the basis of these and other characters. Most specimens in collections can readily be placed in one of these species and between the species there are gaps in the characters used. Occasional specimens are difficult to determine, perhaps because poor preservation removed the color pattern, and because of abnormalities or, perhaps, hybridization.

Dr. J. A. L. Cooke made available the collections of both the American Museum of Natural History and Cornell University, Dr. C. D. Dondale, the collections of the Canadian National Museum. Other Canadian collections were supplied by D. J. Buckle. Dr. H. K. Wallace loaned large collections from Michigan and Florida with ecological data, and Dr. W. Shear provided specimens and other help. Dr. H. V. Weems sent specimens from the Florida State Museum. Dr. M. Grasshoff loaned

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* This study was started as a senior thesis for Harvard College by J. D. B. The object was to find characters that can be used in separating species of the genus. The characters carefully studied were coloration and pattern, size, epigynum, and spination of the second tibia of males. The palpi of the species separated by these criteria were later studied in detail by H. W. L. and nomenclatural problems resolved.

specimens from the Senckenbergischen Naturforschenden Gesellschaft. Dr. J. G. Sheals and Mr. D. J. Clark made it possible for H. W. L. to examine the many types at the British Museum (Natural History). Dr. J. Prószyński of the Polish Academy of Sciences made the Taczanowski collection available to us, Prof. M. Vachon and Mr. M. Hubert of the Muséum National d'Histoire Naturelle, Paris, loaned many specimens. Specimens from the University of Costa Rica were made available by Dr. D. C. Robinson and Mr. C. E. Valerio. Mr. D. Bixler and Dr. R. E. Leech loaned specimens from personal collections. Dr. H. T. Boschung of the University of Alabama, Museum of Natural History, made Archer specimens available. Laurie Gutman helped with the draft of the thesis first prepared by J. D. B., Lorna R. Levi edited the final manuscript. Dr. Peter van Helsdingen was most helpful in discussions about the unusual nomenclatural complications. This investigation was supported by Public Health Service Research Grant AI-01944, from the National Institute of Allergy and Infectious Diseases.

INTRODUCTION

Although observations were restricted primarily to spiders collected from North America (including Central America), the West Indies and Hawaii, some study of Old World *Neoscona* was undertaken in order to assess similarities and differences between Old and New World forms.

Selection of characters. The choice of characters to be studied was guided primarily by trial and error, as well as some knowledge of what characters are useful in the classification of other groups of spiders. Although the reasons for it are not well understood (Mayr, 1963), the structure of the genitalia of both sexes is often a highly specific character in spiders, as well as in a number of other arthropods. The initial observations were therefore made on the epigynum of the female and the palpus of the male. On the inspiration of Kaston (1948), who distinguished between male *Neoscona* from Connecticut on the basis of the macrosetae of the second tibia, comparisons of the arrangements and patterns of macrosetae on that leg segment were made.

During the course of the study, large and often striking variations in the dorsal coloration of the abdomen were noted, and so systematic observations on this character were made, as well as comparisons of ventral abdominal patterns. The specific carapace coloration of some spiders and the presence of a coniform spur on coxa IV of certain others were noted as incidental observations.

The measurements are not expected to be useful in separating species, but were taken to provide supplementary data on species separated by other means. Since the abdomen size is particularly variable, depending on how well-fed the spider was at the moment of collection, the carapace measurements are undoubtedly more useful in comparing species. Measurements of less than 10 mm are probably accurate to within 0.2 mm.

Epigynum. Differences in the structure of the epigynum proved to be the best basis for separating females. In *Neoscona* the epigynum may have one or two pairs of lateral bulges or none at all. These bulges may be positioned either flush with the ventral surface of the scape, somewhat dorsal to it, or with either the proximally or distally situated end of each bulge connecting with the ventral margin and the opposite end extending dorsal to it. In the latter two cases, in ventral view, part of each bulge projects beyond the margin and part can usually be seen beneath the surface of the scape, as the epigynum in *Neoscona* tends to be somewhat transparent. The number of pairs of bulges and their position, both proximal-distal and dorsal-ventral, on the scape appears to be highly specific. Occasionally the bulges were obscured, however, especially in specimens (presumably collected late in their lives) that had unusually heavily sclerotized epigyna. This tendency is particularly pronounced in *N. oaxacensis.*

The presence or absence of a contraction near the midpoint of the scape is apparently constant for a species and is sometimes useful (especially when absent, as most species have it). The contraction seems to be variable in *N. oaxacensis.*

It is possible that small epigynal differences such as occur between *N. arabesca* and the much larger *N. domiciliorum* may be more functions of the size of the spider than good specific differences, and therefore the epigynum of an unusually large *N. arabesca* might resemble that of a very small specimen of *N. domiciliorum.*

Palpus. The palpi in male *Neoscona* are apparently very similar in all species. Some differences were noted in the shape and position of the paracymbium and median apophysis and in the location of the terminal spine on the median apophysis, but these differences were not consistent and did not appear to be usefully specific. Not until near the end of the study were palpal characters found more usable than the macrosetae of the second tibia: the shape and attachment of the terminal apophysis, the shape of the embolus with its lamella, the shape of the conductor and the places where the unusual fused bulb is broken and the parts are slightly movable against each other.

Macrosetae of second tibia. The arrangement of macrosetae on the second tibia, sometimes in conjunction with other characters, provided a useful criterion for separating males. In *Neoscona* there may be one, two, or three rows of clasping macrosetae along the prolateral surface of this leg segment. Although the total number of macrosetae varies considerably within a species, their gross pattern, including the number of rows (maximum number of macrosetae abreast), appears to be quite fixed. In addition to the clasping macrosetae, the second tibia usually possesses one prominent ventral macroseta at the proximal end and two or three large dorsal spines. Some *Neoscona arabesca* and *N. nautica* can easily be recognized by striking and characteristic deviations from this pattern. Also, the tibia itself may be curved, with the prolateral surface concave, but this curvature is quite variable and not especially reliable in most cases.

Although Beatty (1970) reports that injuries during the course of development may produce sizeable variations in the leg macrosetae of *Ariadna,* it is not likely that such an occurrence would produce a sizeable change in the overall pattern in *Neoscona,* especially as the clasping macrosetae do not appear until the final molt. Another possible hazard in using the tibial macrosetae to separate the species is that the number of rows may vary with the size of the specimen. However, in southern specimens of *Neoscona arabesca,* which vary considerably in size (total length of the male: 3.9–9.2 mm) and were at first separated primarily by the presence of a large number of ventral tibial macrosetae, it was noted that the number of rows of clasping macrosetae remains fixed, although the number and size of the macrosetae increases somewhat with the increasing body size. As the macrosetae at the proximal end of prolateral surfaces are often longer and more variable than the stout, relatively uniform macrosetae of the distal half, in some species it is uncertain whether just the distal or all the prolateral setae should be referred to as clasping macrosetae. We have tried to make clear, in the descriptions of individual species, exactly which macrosetae are considered clasping in each case.

Dorsal abdominal pattern. When one gains familiarity with spiders of this group, it becomes possible to recognize most individuals of most species solely on the basis of the dorsal coloration of the abdomen (Plates 1, 2, 3). In some cases this coloration can be a reliable specific char-

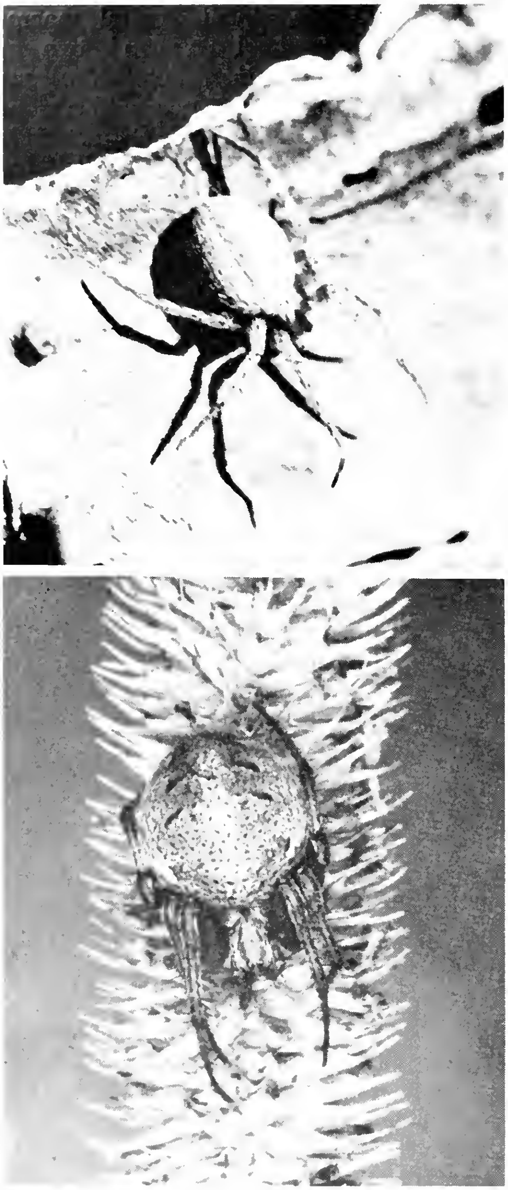


Plate 1. Top Fig. *Neoscona pratensis*, juvenile from Florida. Bottom Fig. *Neoscona arabesca*, female from Massachusetts.

Plate 2. *Neoscona domiciliorum*, female from Florida.

acter, while in others there is too much variation or the pattern may be faded too often to be of use. A major cause of variability in the dorsal pattern is the content of the abdomen, which may show through the cuticle. In species in which bright colors, presumably because of pigment in the cuticle, make up the pattern, observed differences are usually reliable. As males are generally lighter colored than females, they are usually more variable and more difficult to separate on the basis of this character.

A possible cause of error in separating *Neoscona* by coloration is variation resulting from uneven preservation. If the alcohol has been changed often, more pigment may be removed than if there are long delays between changes, and significant differences in the coloration of specimens may result.

Ventral abdominal pattern. Characteristically, the ventral pattern consists of an area of black bordered by white, roughly forming a square with the epigastric furrow as the anterior edge (Plate 3). The differences observed are too inconsistent for use in separating species. Furthermore, in adults the pattern is often faded and indistinct, although in juveniles it tends to be clear.

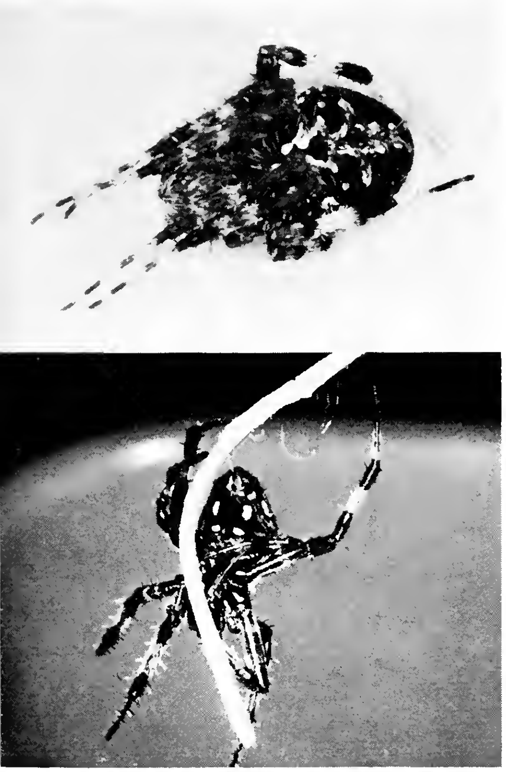


Plate 3. *Neoscona domiciliorum.* Top Fig. female from Washington, D. C. Bottom Fig. female from Florida.

Carapace. Distinct carapace coloration was observed in females of three species. In two (*Neoscona hentzii* and *N. nautica*) it is probably too variable to be of much use, but in *N. orizabensis* it is highly characteristic (Fig. 7) and will separate the female of that species.

The fourth coxa. Males of several species can easily be separated by the presence of a coniform spur on the posterior edge of the ventral surface of coxa IV (Fig. 9).

After lengthy testing, dependable characters have been found that provide clear gaps between the populations (Michener, 1970), and these populations are presumed to be the species.

Neoscona Simon

Neoscona Simon, 1864, Histoire Naturelle des Araignées, ed. 1: 261. Type species: *N. arabesca* Walckenaer, designated by F. O. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 466.

Chinestela Chamberlin, 1924, Proc. U. S. Natl. Mus. 63: 20. Type species by monotypy *C. gisti* Chamberlin, 1924, 63: 20, pl. 5, fig. 37, ♂. Male holotype without palpi from Soochow, China, in the U. S. National Museum, examined. One palpus marked holotype in the Museum of Comparative Zoology, examined (which has since been presented to the U. S. National Museum). The other palpus is presumably in the Univ. Utah collection.

Cubanella Franganillo, 1926, Cuba Contemporare, 41 (161): 14. Type species by monotypy *C. nidicola* Franganilla [=*Neoscona neotheis*].

Eriovixia Archer, 1951, Amer. Mus. Novitates, 1487: 34. Type species by original designation *Eriovixia rhinurus* (Pocock) [=*Araneus rhinurus*]. NEW SYNONYMY.

Neosconopsis Archer, 1951, Natur. Hist. Misc., Chicago Acad. Sci., 84: 3. New subgenus. Type species by monotypy and original designation *Neoscona adianta* (Walckenaer) [=*Araneus adiantus*]. NEW SYNONYMY.

Note. Chinestela gisti is very close to *Neoscona hentzii* in appearance. *Cubanella* was first synonymised by Franganillo himself. *Eriovixia* is considered a synonym because the female genitalia are like those of *Neoscona* species. The scape differs slightly in being flatter. Also the abdomen has a "tail." There is no reason to keep this name for a separate genus, unless the unknown male proves to have characters distinct from *Neoscona*. *Neosconopsis*, according to Archer, differs from *Neoscona* in that "the stalk on which the main piece of the median apophysis of the male palpus is situated is wide instead of pedunculate." As far as we could tell, the median apophysis attachment is like that of all other carefully examined species and Archer's observation is erroneous.

The name *Neoscona* is of feminine gender.

Description. In all species the anterior median eyes are largest or subequal to posterior medians; the secondary eyes are just slightly smaller. The posterior lateral eyes may be the smallest. The anterior median eyes are usually slightly more than their diameter apart, the posterior medians slightly less than their diameter. The height of the clypeus is slightly less than the diameter of an anterior median eye. The carapace has a longitudinal thoracic groove, which in males may be extended by a line stretched over most of the carapace. It is less distinct in females (Fig. 7), and is hidden in living specimens by setae (Plates 1–3). The first legs are longest, the second, second in length, the third shortest. All males have a hook on the distal rim of the venter on the first coxa and have macrosetae on the prolateral surface of the second tibia. The abdomen varies in shape: oval in *Neoscona arabesca*, elongate in *N. oaxacensis*, triangular in *N. nautica*, and with humps in *N. redempta*. In all, the venter of the abdomen is black bordered on the sides by white spots (Figs. 10–13).

Males are only slightly smaller than females.

Diagnosis. The longitudinal thoracic groove on the carapace separates all members from *Araneus*. Together with the fused epigynum and unique palpus (see below) the species are readily separated from related *Araneus*. All species have a black patch between epigastric furrow and spinnerets, bordered by one or two white spots on the sides.

Genitalia. Both male and female genitalia have structures fused, probably secondarily. The epigynum is a simple tongue, the scape completely fused to the base. The openings are underneath (dorsal surface), an indication that most of the structure may be derived from the base which in *Araneus* has the openings (Figs. 14–25).

The palpus is unique in several ways. It seems never to have been described before. The cymbium covers the face of the bulb (Figs. 1, 4), and has expanded in such a way that most structures are hidden by it (Y in Fig. 4). In *Araneus* the cymbium is a more or less narrow strip. The radix (R), stipes (I), and embolus (E) have fused almost immovably in *N. arabesca* (Fig. 5). In *N. oaxacensis* (Fig. 4) and in *N. nautica* (Fig. 116) a small hematodocha separates two sclerites, probably the stipes and radix. The hematodocha is reduced compared to that of *Araneus* species. The embolus (E) is more or less drawn out, tube-shaped to conical, to the side of which the embolus lamella (L) is attached. The embolus rests against the conductor (C) and is covered apically by the terminal apophysis (A). The terminal apophysis is a thin flap in most species; it is much reduced in *N. nautica* (Figs. 118, 119). The conductor is in all a thumb-shaped projecting structure, sclerotized, the side of its tip light in color and facing the embolus. The base of the conductor varies in shape. The greatest difference between species is in the shape of the embolus with its lamella, the terminal apophysis (seen in apical view), and also the conductor. Unfortunately, this embolus is completely surrounded by conductor, terminal apophysis, and also the cymbium. In *Neoscona neotheis* the stipes-radix joint is sclerotized, facilitating its recognition.

In this study the cymbium was removed

→

Figs. 1–6. The left palpus of *Neoscona*. 1–3, 5–6. *N. arabesca*. 4. *N. oaxacensis*. 1. Ventral view. 2. Lateral view. 3. Dorsolateral view. 4. Ventral view with cymbium cleared. 5. Expanded, bulb subventral view. 6. Expanded, bulb dorsal view.

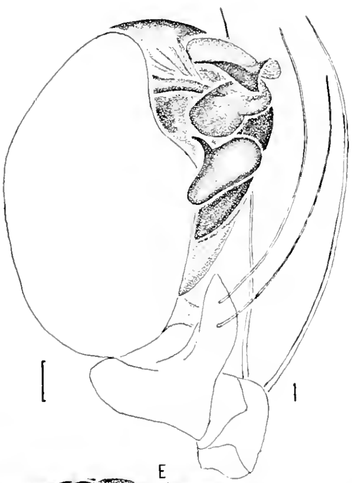
Fig. 7. *Neoscona orizabensis* F. P.-Cambridge, female carapace.

Fig. 8. *Neoscona arabesca* (Walckenaer), venter of male cephalothorax with legs beyond coxae removed.

Fig. 9. *Neoscona oaxacensis* (Keyserling), fourth male coxa and trochanter.

Figs. 10–13. Female abdomen, ventral view. 10. *N. arabesca*. 11. *N. oaxacensis*. 12. *N. neotheis*. 13. *N. nautica*. Scales. Palpi, 0.1 mm; others, 1 mm.

Abbreviations. A, terminal apophysis; C, conductor; DH, distal hematodocha; E, embolus; H, basal hematodocha; I, stipes; L, lamella of embolus; M, median apophysis; R, radix; T, tegulum; Y, cymbium.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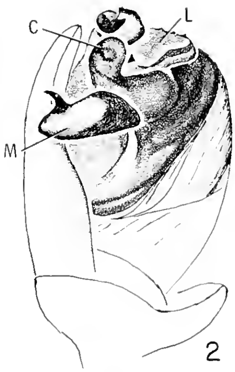

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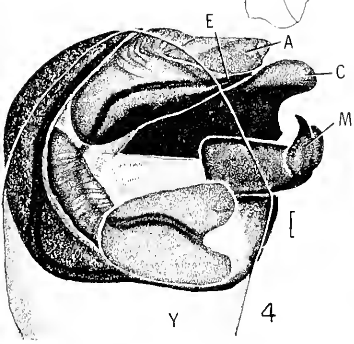

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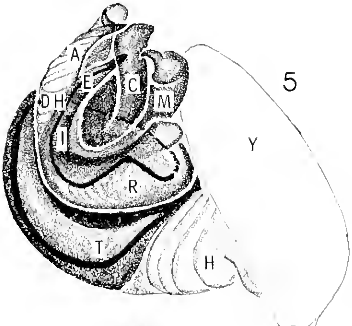

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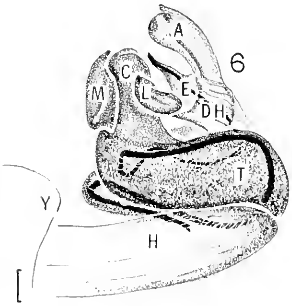

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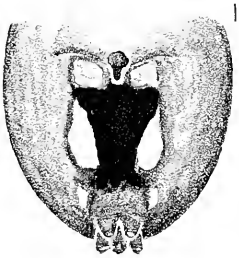

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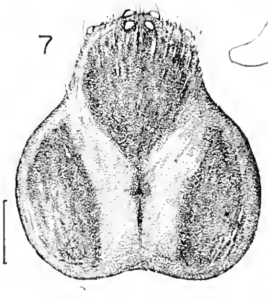

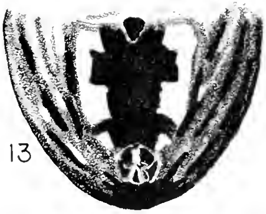
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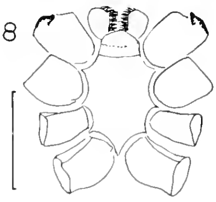

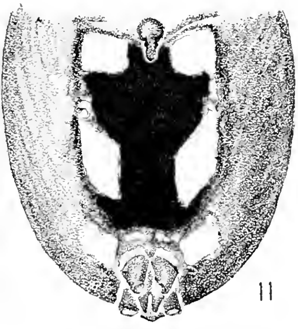
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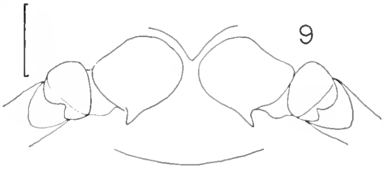
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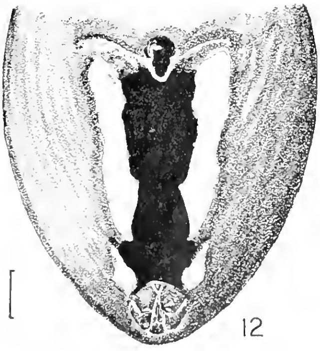
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from at least one specimen of each species to facilitate drawing. However, for routine examination this is not necessary.

The terminal apophysis is of characteristic shape and one can readily separate *Neoscona arabesca* from related species by looking at it (in apical view, ventral view of the spider with the palpus flexed). It was the decisive factor in synonymizing *N. minima* and *N. arabesca.* For the purpose of making the diagrammatic drawings (Figs. 26, 27), an outline drawing was first made, then the structure torn off. The terminal apophysis is opaque at its base, transparent at its distal margin. The individually variable transparent area may at first be confusing to those wanting to use the structure for determining species. The terminal apophysis does not have to be removed for making determinations. In *N. nautica* the terminal apophysis is minute.

The median apophysis, at first studied carefully, seems to be of little use in separating species. Its general appearance is as in *Araneus diadematus* relatives. The detailed shape of the conductor may be useful: Its large head and S-shaped appearance seem to separate *N. hentzii* from other species. The conductor is best studied in lateral view.

The palpal tibia has two setae, one of which may be longer than the other.

When naturally expanded, the bulb is propelled away from the enclosing cymbium. The various sclerites of the bulb hardly shift in position. Males in collections rarely have the palpi expanded.

Natural history. *Neoscona* species are among the most common and abundant orb weavers. *Neoscona arabesca* can be obtained in large numbers by sweeping meadows or fields in summer or late summer (in southern Canada and the northern states). I found the European *Neoscona adianta* (Walckenaer) just as common in southern Europe, collecting it in every meadow and field visited in southern Italy and Dalmatia.

In New England and Wisconsin there is only one generation a year (of both *Neoscona arabesca* and *Neoscona hentzii*), males maturing in late June and July, females in July and August. Collections of *N. oaxacensis* suggest that it also has only one generation a year, most adults having been collected between August and November.

In shape, the egg case varies from a flattened sphere to a lens-shape (of *N. arabesca* and *N. hentzii*), and is covered by some loose silk. Kaston (1948) described that of *N. arabesca* as being about 10 mm in diameter and containing 280 yellow eggs agglutinated in a mass measuring 9.0 × 5.4 × 3.6 mm. *Neoscona hentzii* egg cases (according to Kaston, 1948) are made of fluffy yellow threads in a rolled up leaf. One had a large diameter of 12 mm, another one, spherical, had a diameter of 5 mm. The first had 1000 eggs, the second 867. The eggs were oval, measuring 0.97 × 1.15 mm.

We assume that because of its great abundance, every spiderling having a web, *Neoscona* may be of importance in controlling insect numbers.

Web. The webs of *N. arabesca* and *N. hentzii* are vertical. Kaston (1948) describes the *Neoscona arabesca* web as having about 20 radii and being 15–45 cm in diameter. One with 18–20 radii is illustrated in Comstock (1940, figs. 530, 531). The hub is open, crossed by only one or two threads, unlike webs made by species of *Araneus*. There are relatively few threads toward the retreat. According to Comstock, *N. arabesca* rests in the center of the web with the tip of the abdomen pushed through the open space. All our observations (and apparently those of Kaston) agree that during daytime *N. arabesca* stays in a retreat to the side of the web, usually in a curled up leaf. The web of *N. oaxacensis* is illustrated in Plate 4.

Distribution. Species of *Neoscona* are found on all continents. Unfortunately, many have always been placed in *Araneus*. The common species found in Europe is *Neoscona adianta* (Walckenaer), the genitalia of which are much closer to those of North American species than to the cosmotropical *N. nautica*. *Neoscona nautica* may be native to the Pacific area, judging by the similar species in this area. Other European species belonging to *Neoscona* are *Epeira crucifera* Lucas, 1839 and *E. byzanthina* Pavesi, 1876, both of the Mediterranean region.

Species groups. *Neoscona nautica*, presumably introduced, is the most distinct species occurring in North America. It is the only species in which the male palpus has a minute curved terminal apophysis; the terminal apophysis of all other species is a flap. Also, the females of *N. nautica* have a short triangular epigynum, shorter than that of other species.

The three species *N. oaxacensis*, *N. neotheis* and *N. pratensis* are very similar. The pattern characteristic of each of the first two may be similar. The males of all three have a spur on the fourth coxa. Their distribution is allopatric: *N. oaxacensis* is found from California and Texas to South America, *N. neotheis* is West Indian, *N. pratensis* is found in the United States, outside the range of *N. oaxacensis*.

Of the remaining North American species, *Neoscona hentzii* (east of the Rocky Mountains to Arizona) is the largest and most distinct, having a scape with a spoon-shaped end following a constriction (Figs. 51–53). The male has an S-shaped, short conductor (Fig. 55). The genitalia of *N. arabesca* (from Canada to Central America), *N. domiciliorum* (eastern United States), *N. utahana* (south-central states) and *N. orizabensis* are much alike. However, *N. arabesca* is smaller than the species sympatric with it and all four have distinct dorsal abdominal patterns. Most illustrations were drawn to the same scale.

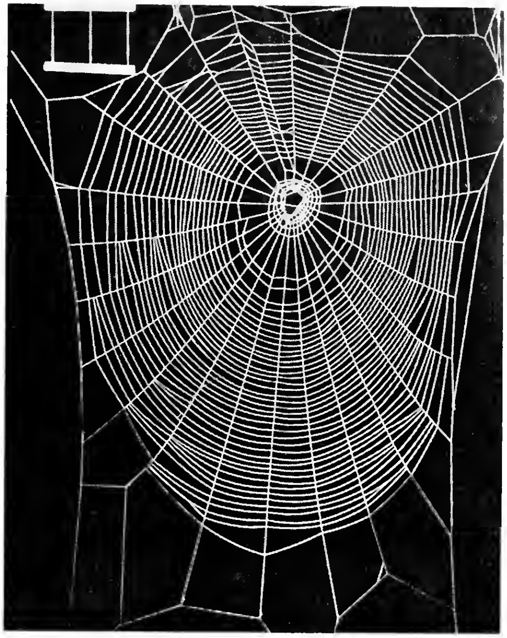


Plate 4. Web of *Neoscona oaxacensis* made in the laboratory. Space between two rods on top is 20 mm, photographed on high contrast film. (Courtesy Peter N. Witt)

Asiatic species were examined and many were found similar to the North American *Neoscona*, but they are believed distinct.

Misplaced species. *Neoscona granadensis* (Keyserling) = *Araneus granadensis* (Keyserling). The type of this species appears to be lost.

Key to *Neoscona* females

1a. Abdomen with distinct humps and a lateral wavy line (Fig. 124), Texas .... *redempta*
1b. Abdomen without humps and not having a wavy line on each side 2
2a. Epigynum with scape very broad and triangular (Figs. 111–115); dorsal abdominal pattern indistinct, dark olive to brown (Fig. 120) .... *nautica*
2b. Epigynum not as above 3
3a. Dorsal abdominal pattern of longitudinal bands as Fig. 100 or Fig. 110 4
3b. Dorsal abdominal pattern otherwise 5
4a. A median dark band bordered by a light line on each side (Fig. 110); epigynum without lateral bulges at midpoint (Fig. 101) .... *pratensis*

4b. A median white band bordered by two black, longitudinal bands (Fig. 100); scape with lateral bulges near midpoint (Fig. 91); West Indies ... *neotheis*
5a. Abdomen subtriangular with a dorsal folium sharply delimited on sides (Fig. 77); south-central states to northern Mexico ... *utahana*
5b. Abdomen oval or if subtriangular, marked otherwise ... 6
6a. Epigynum without lateral bulges (Figs. 14–25); abdomen suboval with dorsal posterior black marks at an angle (Figs. 34, 35); total length (north of Mexico) usually less than 8.2 mm, carapace less than 2.8 mm long ... *arabesca*
6b. Epigynum with more or less distinct lateral bulges (Figs. 43, 59, 78); abdomen triangular, if suboval marked otherwise; total length (north of Mexico) usually more than 8.5 mm, carapace more than 3.7 mm long ... 7
7a. Abdomen oval to elongate with median light band made up of spots (Figs. 88–90); epigynum with one pair of bulges (Figs. 78, 81–83); California, Utah, Texas to Peru ... *oaxacensis*
7b. Abdomen triangular or oval and marked otherwise; epigynum with one or two pairs of bulges ... 8
8a. Carapace chestnut brown with light brown longitudinal bands (Fig. 7), central Mexico ... *orizabensis*
8b. Carapace otherwise or, if similar, not found in central Mexico ... 9
9a. Epigynum with one pair of bulges (Fig. 43), abdomen contrastingly marked (Fig. 50), eastern U. S. ... *domiciliorum*
9b. Epigynum with two pairs of bulges, the proximal indistinct (Fig. 51), abdomen without contrasting markings (Fig. 58); east of Rocky Mountains, Arizona ... *hentzii*

Key to *Neoscona* males

1a. Coxa IV with a spur (Fig. 9) ... 2
1b. Coxa IV without a spur ... 4
2a. Abdomen with a median dark band bordered by a white line (Fig. 110); bulb of palpus not sclerotized near attachment of terminal apophysis (Figs. 106, 108), Canada, United States ... *pratensis*
2b. Abdomen colored otherwise, palpus sometimes having this sclerotization ... 3
3a. Abdomen with a median light band with straight margins bordered by black bands (Fig. 100); bulb of palpus sclerotized near attachment of terminal apophysis (Figs. 96, 98), West Indies ... *neotheis*
3b. Abdomen otherwise; bulb of palpus not sclerotized near attachment of terminal apophysis (Figs. 84, 86); California, Utah, Texas to Peru ... *oaxacensis*
4a. Terminal apophysis a minute curved structure (Figs. 118, 119) ... *nautica*
4b. Terminal apophysis a flat flap (Figs. 3, 4, 6) ... 15
5a. Abdomen with a dorsal folium distinctly set off on its sides (Fig. 77); south-central states ... *utahana*
5b. Abdomen without such a folium ... 16
6a. Terminal apophysis with sides more or less parallel and a wide notch on distal end (Figs. 26, 27) ... *arabesca*
6b. Terminal apophysis of different shape ... 7
7a. Central Mexico ... *orizabensis*
7b. Canada, U. S. and northern Mexico ... 8
8a. Conductor in lateral view S-shaped (Fig. 55) ... *hentzii*
8b. Conductor in lateral view, elongated, with tip and base only slightly curved (Fig. 47) ... *domiciliorum*

Neoscona arabesca (Walckenaer)

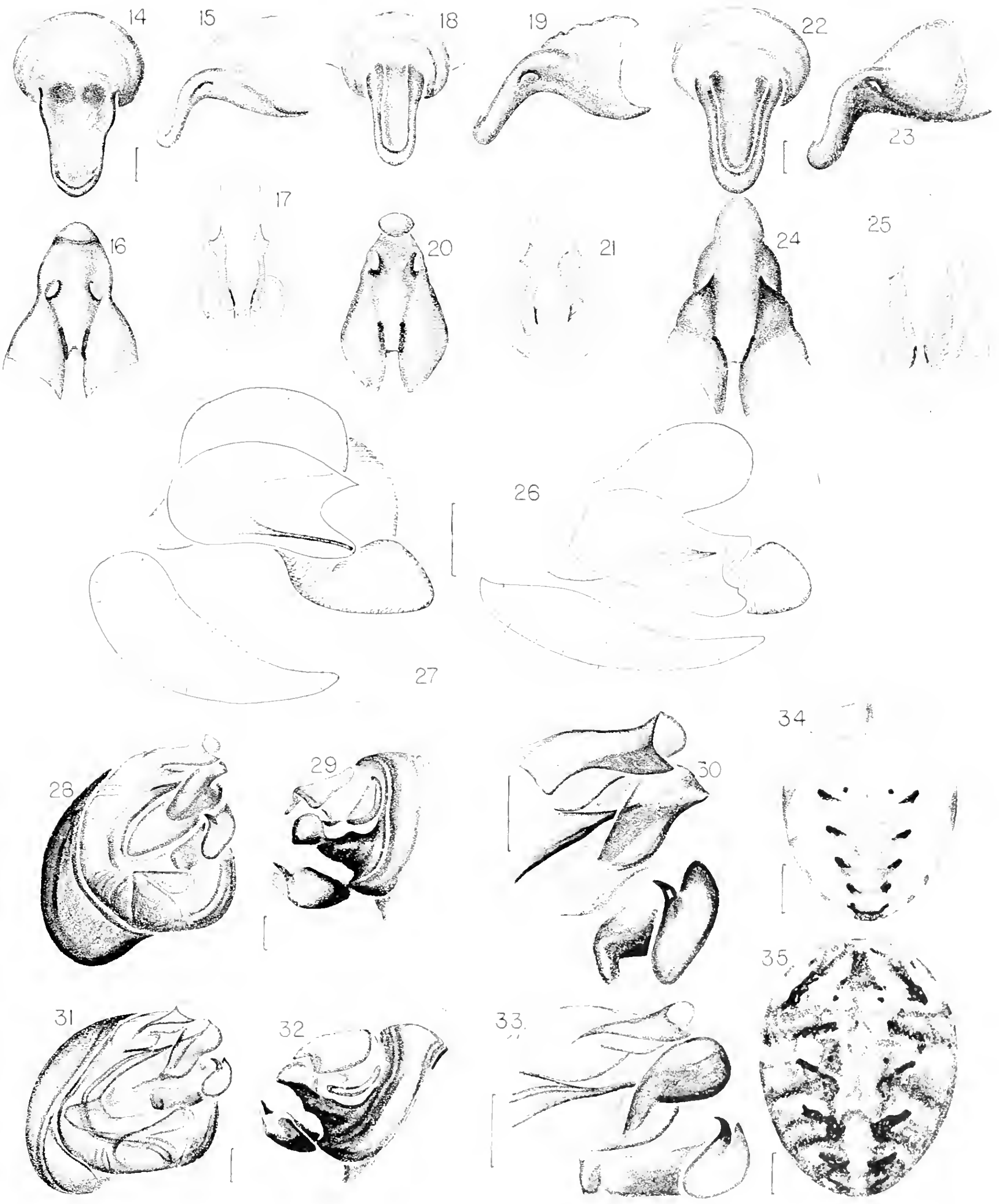
Plate 1, Figures 1–3, 5–6, 8, 10, 14–42, 125, 126, Map 1

Epeira arabesca Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2: 74. The types are Bosc, Araignée de Caroline illustration, p. 13, pl. 5, fig. 2, in the library of the Muséum National d'Histoire Naturelle, Paris, and Abbot manuscript illustrations, figs. 331, 446 from Georgia in the British Museum, Natural History. Copies in the Museum of Comparative Zoology examined. McCook, 1893, American Spiders, 3: 148, pl. 1, fig. 8, pl. 2, figs. 6, 7, ♀, ♂.

Epeira trivittata Keyserling, 1863, Sitzungsber. Naturf. Ges., Isis, Dresden, p. 95, pl. 5, figs. 6–9, ♀. Female type from North America in the C. L. Koch collection probably in Berlin. Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 311, pl. 33, fig. 16, pl. 36, figs. 2, 3, 5, 8, ♀, ♂. Keyserling, 1892, Spinnen Amerikas, 4: 172, pl. 8, fig. 127, ♀. Emerton, 1902, Common Spiders, p. 166, figs. 393–395, ♀, ♂.

?*Epeira singularis* Banks, 1898, Proc. California Acad. Sci., (3), 1(7): 252, pl. 15, fig. 4, ♀. Female holotype from Pescadero [? Baja California], was in the California Academy of Sciences and was destroyed. NEW SYNONYMY.

Neoscona arabesca, — F. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 472, pl. 44, figs. 13, 14, ♀, ♂. Comstock, 1912, Spider Book, p. 497, figs. 527–531, ♀. Comstock, 1940, Spider Book, rev. ed., p. 510, figs. 527–531, ♀. Kaston, 1948, Bull. Connecticut Geol. Natur.



Neoscona arabesca (Walckenaer). Figs. 14–25. Epigynum. 14, 18, 22. Ventral. 15, 19, 23. Lateral. 16, 20, 24. Posteriodorsal. 17, 21, 25. Posteriodorsal, cleared. 14–17. (Michigan). 18–21. (Michigan). 22–25. (Florida). Figs. 26–33. Left palpus. 26, 27. Apical view. 26. (Ontario). 27. (California). 28, 31. Ventral, cymbium removed. 29, 32. Lateral. 30, 31. Ventral view of palpal structures. 28–30. (Wisconsin). 31–33. (Texas). Figs. 34, 35. Dorsal view of female abdomen. 34. (Michigan). 35. (Texas).

Scales. 0.1 mm, for abdomens 1 mm.

Hist. Surv., 70: 245, figs. 750, 771–773, ♀, ♂. Bonnet, 1958, Bibliographia Araneorum, 2: 3055.

Neoscona minima F. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 471, pl. 44, figs. 11, 12, ♀, ♂. Male, female syntypes from numerous Central American and Mexican localities, only female and males from Teapa, Mexico, examined in British Museum, Natural History. Gertsch and Mulaik, 1936, American Mus. Novitates, 863: 20, fig. 30, ♂. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 245, figs. 751, 776, ♀, ♂. Bonnet, 1958, Bibliographia Araneorum, 2: 3058, NEW SYNONYMY.

Neoscona naiba Chamberlin and Gertsch, 1929, J. Entomol. Zool., 21: 104, figs. 46–48, ♀. Female holotype from St. George, Utah, in the University of Utah collection, lost. NEW SYNONYMY.

Note. The measurements given, and the dorsal abdominal markings described for *Neoscona naiba* suggest that the name is a synonym of *N. arabesca*.

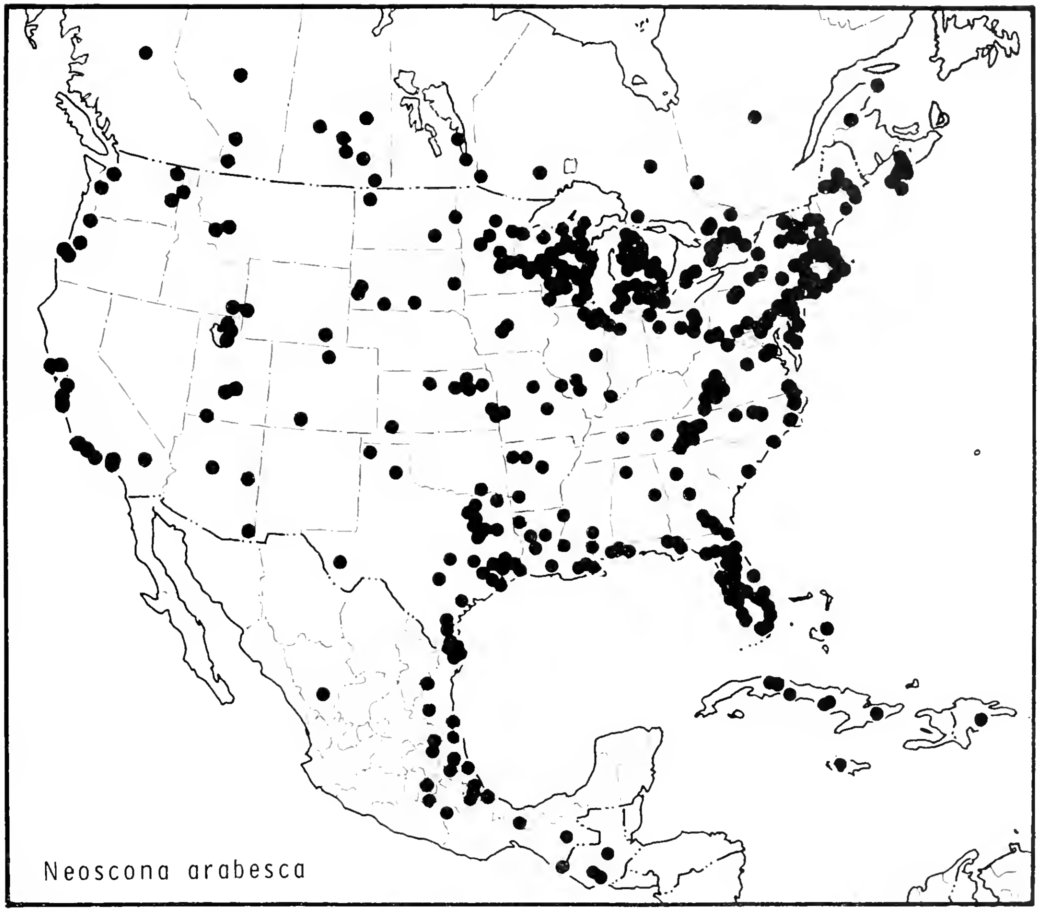
Female. Total length 5.2–12.3 mm. Carapace 1.9–4.6 mm long, 1.7–4.4 mm wide. A female from Wisconsin, 6.8 mm total length. Carapace 2.5 mm long, 2.3 mm wide. First femur, 2.9 mm; patella and tibia, 3.5 mm; metatarsus, 2.1 mm; tarsus, 0.8 mm. Second patella and tibia, 2.9 mm; third, 1.8 mm; fourth, 2.9 mm. A female from southern Texas, 8.0 mm total length. Carapace 2.9 mm long, 2.8 mm wide. First femur, 3.6 mm; patella and tibia, 4.4 mm; metatarsus, 3.3 mm; tarsus, 0.9 mm. Second patella and tibia, 3.6 mm; third, 2.2 mm; fourth, 3.5 mm.

Male. Total length 4.2–9.2 mm. Carapace 2.1–4.5 mm long, 1.8–4.0 mm wide. A male from Wisconsin, 5.4 mm total length. Carapace 2.6 mm long, 2.3 mm wide. First femur, 3.2 mm; patella and tibia, 4.0 mm; metatarsus, 2.8 mm; tarsus, 1.0 mm. Second patella and tibia, 3.0 mm; third, 2.0 mm; fourth 3.2 mm. A male from southern Texas, 5.4 mm total length. Carapace 2.7 mm long, 2.2 mm wide. First femur, 3.6 mm; patella and tibia, 4.0 mm; metatarsus, 3.1 mm; tarsus, 1.0 mm. Second patella and tibia, 3.0 mm; third, 1.9 mm; fourth, 3.0 mm.

Variation. Total length of female specimens from Canada and the northern tier of states, 5.2–7.7 mm, carapace 1.9–3.1 mm long, 1.7–2.5 mm wide; from southern United States and West Indies the three figures are: 5.6–8.2, 2.0–2.8, 1.8–2.5 mm; from Mexico: 5.8–12.3, 2.5–4.6, 2.1–4.4 mm. Males from the same northern area: 4.2–5.9, 2.1–3.0, 1.8–2.7 mm; from southern United States and West Indies: 3.9–5.2, 2.0–2.6, 1.8–2.4 mm; from Mexico: 4.6–9.2, 2.4–4.5, 2.1–4.0 mm.

Canadian specimens, those from the northern states, and the region south along the eastern seacoast are smallest and lightest and have a more variable epigynum, at times even lacking a border around the scape (Fig. 14). Males in this area generally have a more or less curved second tibia. Mexican specimens are most variable in size. Both the male embolus and the connecting ducts of the female are of variable length.

Diagnosis. The epigynum of the female has a short scape with no lateral lobes or bulges. The contraction near the midpoint is more abrupt and more pronounced in southern specimens (Fig. 36). In northern specimens the second tibia of the male is usually curved, with the prolateral surface concave. A single row of clasping macrosetae along the distal half connects with a proximal row of more variable (often larger) macrosetae (Figs. 125, 126). In southern specimens the second tibia of the male is nearly straight, with a single row of clasping macrosetae running its entire length; the macrosetae tend to get longer toward the distal end. The conspicuous presence of a large number of macrosetae on the ventral surface of tibia II is characteristic. The terminal apophysis has its sides almost parallel and has a deep notch distally (Figs. 26, 27), unlike that of other species of *Neoscona*. Since the distal part is partly transparent, it has to be carefully examined. Most specimens can readily be



Map 1. Distribution of *Neoscona arabesca* (Walckenaer).

assigned to this species by the small size, and oval abdomen with series of pairs of black dorsal marks. The dorsal marks may also be present in poorly preserved or bleached specimens of *N. domiciliorum* and *N. hentzii*.

Natural history. The vertical web is found in shrubs, meadows, and in sunny, preferably moist situations. Specimens are frequently collected by sweeping. This is one of the most common orb weavers. Collecting labels read: apple foliage (Nova Scotia), grassland, swamp grasses, beating juniper, sweeping meadow, tamarack.

Distribution. Southern Canada to Central America, West Indies. Probably most abundant in the northern part of its range (Map 1).

Neoscona domiciliorum (Hentz)

Plates 2, 3, Figures 43–150, 127, Map 2

?*Epeira benjamina* Var. A., Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2: 42. Type is Abbot's Georgian Spiders, fig. 126, manuscript in British Museum, Natural History. Copy in the Museum of Comparative Zoology examined. *Nomen dubium.*

Epeira domiciliorum Hentz, 1847. J. Boston Natur. Hist. Soc., 5: 469, pl. 30, fig. 7, ♀. Type from Alabama destroyed. A female neotype from Tuscaloosa, Tuscaloosa County, Alabama, 1938–1939, here designated (one specimen from

Archer's five neotypes), and deposited in the American Museum of Natural History.

Epeira benjamina, — McCook, 1893, American Spiders, 3: 147 (in part), pl. 1, fig. 7 (Not pl. 2, figs. 4, 5).

Neoscona domiciliorum, — Archer, 1941, Papers Alabama Mus. Natur. Hist., 14: 48, pl. 4, fig. 2, ♀. Chamberlin and Ivie, 1944, Bull. Univ. Utah, Biol. Ser., 8(5): 108, fig. 65.

Names. To avoid switching of names and to straighten out present confusion (see discussion under *N. hentzii*), a neotype has been designated for *Epeira domiciliorum.* Without the neotype, the name *Epeira domiciliorum* would be a doubtful name. Archer (1941) interpreted Hentz's description to be this species, designated a neotype and deposited it in the Archer collection of the Alabama Museum of Natural History. Five specimens marked neotype by Archer were found in Alabama. One of these was taken out, relabelled neotype, and the specimens deposited in the American Museum of Natural History where other Archer specimens are kept. Hentz's comment on the epigynum's being like that of *Araneus diadematus* might indicate he had specimens with the longer scape, the commoner species, here called *N. hentzii.* According to Archer, the name *domiciliorum* also better fits *N. hentzii*, found in darker places in Alabama. However, many if not most *N. hentzii* of Florida and Alabama lack a pattern and Hentz does show a dorsal design in the illustration of *E. domiciliorum.*

Female. Total length 7.2–16.2 mm. Carapace 3.7–6.1 mm long, 2.2–5.1 mm wide. A female from Florida, 10.5 mm total length. Carapace 4.3 mm long, 4.1 mm wide. First femur, 5.6 mm; patella and tibia, 7.0 mm; metatarsus, 5.0 mm; tarsus, 1.6 mm. Second patella and tibia, 6.4 mm; third, 3.6 mm; fourth, 6.1 mm.

Male. Total length 8.0–9.0 mm. Carapace 4.8–5.0 mm long, 3.9–4.6 mm wide. A male from Florida, 8.9 mm total length. Carapace 4.8 mm long, 4.0 mm wide. First femur, 5.5 mm; patella and tibia, 7.2 mm; metatarsus, 4.3 mm; tarsus, 1.5 mm. Second patella and tibia, 5.6 mm; third, 3.4 mm; fourth, 5.5 mm.

Variation. Southern specimens are larger than northern ones. The northernmost females do not seem to be as contrastingly colored as the southern ones.

Diagnosis. Females can be separated by the characteristic pattern and bright white or yellow color of the anterior dorsal surface of the abdomen (Fig. 50) and by the almost transverse bars on each side of the posterior. The scape of the epigynum is short, rounded at the tip with a lateral expansion near the base dorsally infolded to form a pair of lateral bulges, and is positioned slightly dorsal to the ventral surface (sometimes not very distinct) (Figs. 43, 44). The males may not be brightly colored. The second tibia of the male is nearly straight and has three rows of clasping spines (Fig. 127). It can probably be distinguished from the male of *N. pratensis* only by the latter's characteristic abdominal pattern and the spur on the fourth coxa. The conductor is, in lateral view, longer and more elongated (Fig. 47) than the conductor of *N. hentzii.* The terminal apophysis may have a lobe as in *N. hentzii*, but usually this lobe is absent (Fig. 49). Specimens do not overlap in size with sympatric specimens of *N. arabesca.* Bleached, poorly preserved specimens may have dark spots like those of *N. arabesca.*

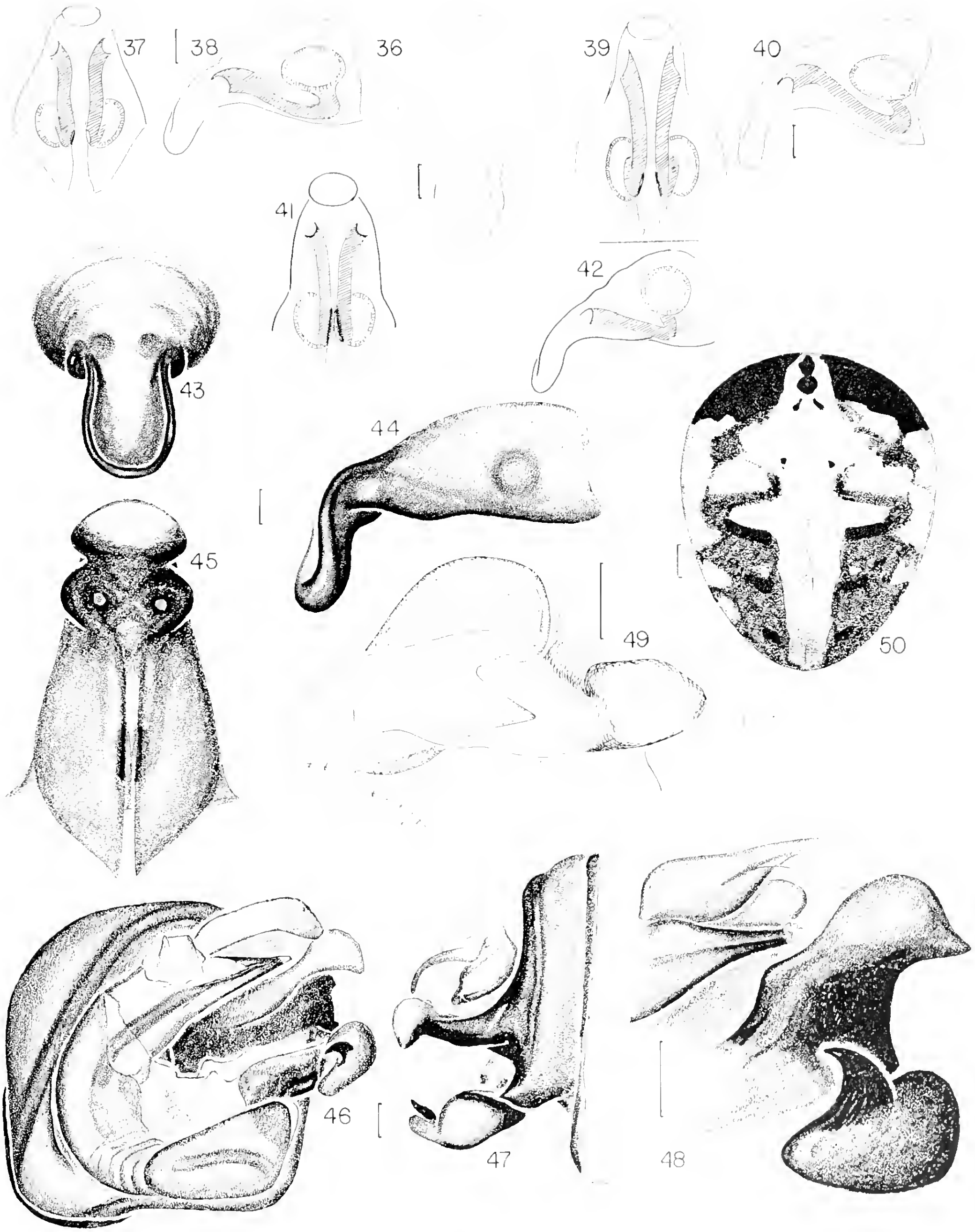
Natural history. Specimens have been collected from woods in Torreya State Park, Florida; a dry area with oaks and palms and little ground vegetation, Florida; prairie and disturbed area, Florida. A record from Texas indicates flood plain as a collecting site.

Distribution. Eastern Massachusetts and Indiana to Florida and Texas (Map 2).

Neoscona hentzii (Keyserling)

Figures 51–58, 128, Map 3

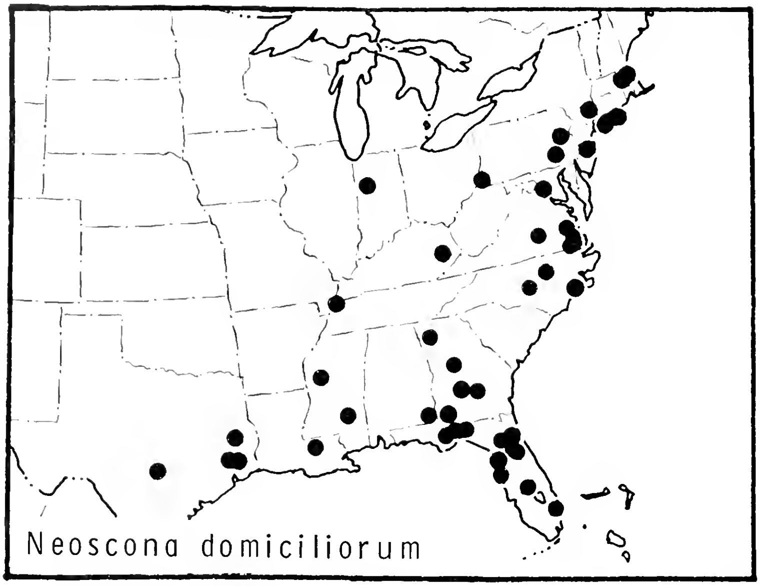
?*Epeira benjamina* Var. B, Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2: 43.



Neoscona arabesca (Walckenaer). Figs. 36–42. Epigynum. 36. Syntype of *N. minima* (Tabasco). 37, 39, 41. Posteriodorsal, cleared. 38, 40, 42. Lateral, cleared. 37, 38. (Texas). 39, 40. (Oregon). 41, 42. (New Hampshire).

Neoscona domiciliarum (Hentz). Figs. 43–45. Epigynum. 43. Ventral. 44. Lateral. 45. Posteriodorsal. Figs. 46–49. Left palpus. 46. Ventral, cymbium removed. 47. Lateral. 48. Ventral view of palpal structures. 49. Apical view. Fig. 50. Female abdomen.

Scales. 0.1 mm, for abdomen 1 mm.



Map 2. Distribution of *Neoscona domiciliorum* (Hentz).

Type is Abbot's manuscript-drawing fig. 351 from Georgia, manuscript in British Museum, Natural History. Copy in the Museum of Comparative Zoology examined. Not Var. A. *Nomen dubium.*

?*Epeira rubicunda* Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2: 43. Provisional name for variety B of *E. benjamina. Nomen dubium.*

?*Epeira mutabilis* Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2: 73. Type is Abbot's manuscript-drawing fig. 351 from Georgia, manuscript in British Museum, Natural History. Copy in the Museum of Comparative Zoology examined. An objective synonym of *E. rubicunda. Nomen dubium.*

Epeira hentzii Keyserling, 1863, Sitzungsber. Naturf. Ges., Isis, Dresden, p. 97, pl. 5, fig. 10, 11, ♀. Female lectotype here designated from Baltimore, Maryland, in the L. Koch collection of the British Museum, Natural History, examined. Also one female paralectotype.

Epeira domiciliorum, — McCook, 1881, Proc. Acad. Natur. Sci. Philadelphia, p. 173, fig. 13 (web). Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 312, pl. 33, fig. 17, pl. 36, figs. 1, 4, ♀, ♂. (Not *Epeira domiciliorum* Hentz.)

Epeira benjamina, — Marx, 1890, Proc. U. S. Natl. Mus. 12: 543. Keyserling, 1892, Spinnen Amerikas, 4: 134, pl. 7, fig. 100, ♀. McCook, 1893, American Spiders, 3: 147, pl. 2, figs. 4, 5 (not pl. 1, fig. 7). Not *Epeira benjamina* Var. A, Walckenaer.

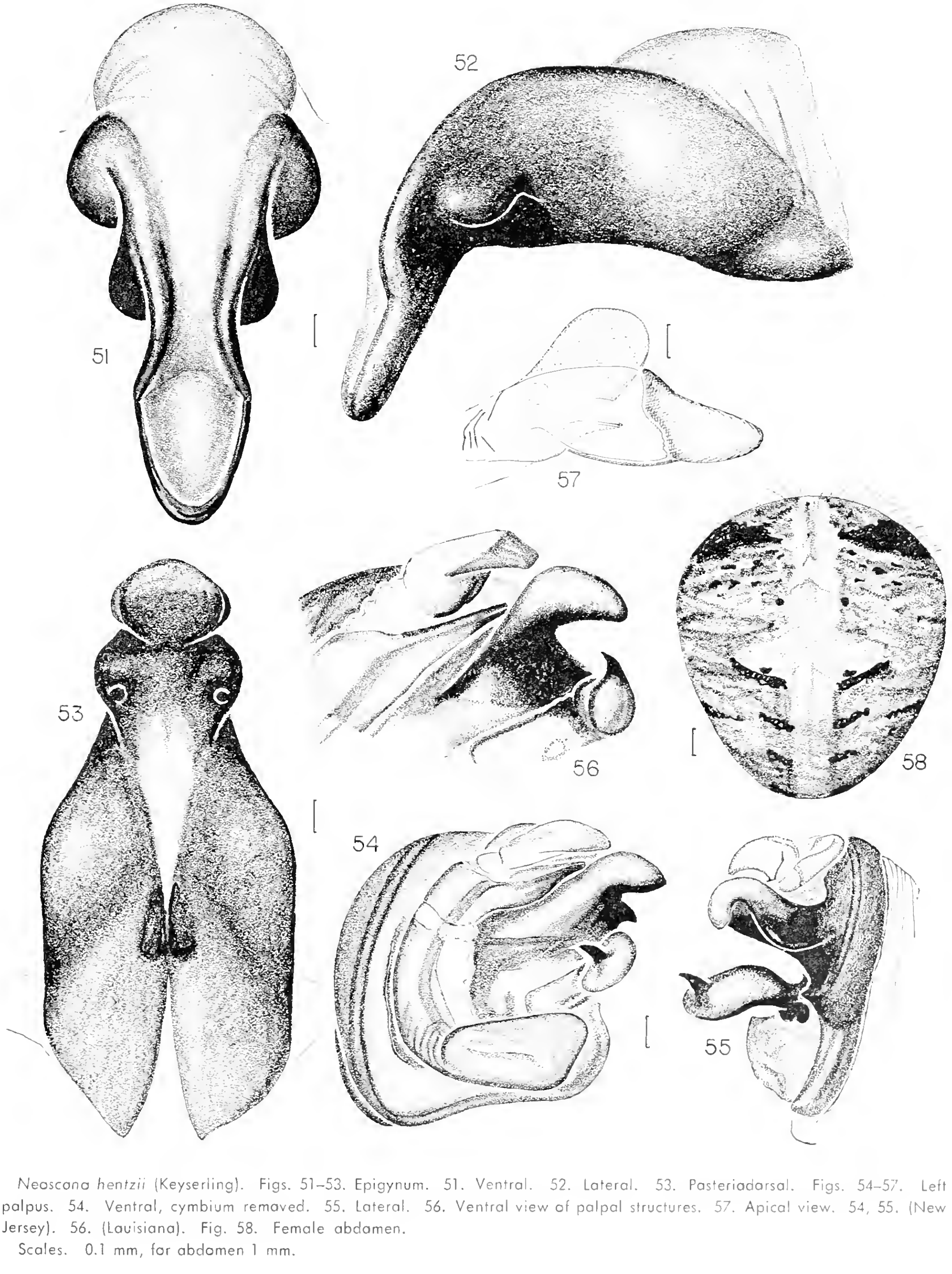
?*Epeira punctigera,* — Keyserling, 1892, Spinnen Amerikas, 4: 136, pl. 7, fig. 100. Not *Epeira punctigera* Doleschall.

Neoscona benjamina, — F. O. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 470, pl. 44, fig. 8, ♀. Comstock, 1912, Spider Book, p. 498, figs. 532–535, ♀, ♂. Comstock, 1940, Spider Book, rev. ed., p. 511, figs. 532–535, ♀, ♂. Archer, 1941, Paper Alabama Mus. Natur. Hist., 14: 48. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 246, figs. 752, 777–778, ♀. (Not *Epeira benjamina* Var. A, Walckenaer.)

Neoscona arkansa Chamberlin and Ivie, 1942, Bull. Univ. Utah, Biol. Ser., 7(1): 77, figs. 217, 218, ♀. Female holotype from Imboden, Arkansas, in the University of Utah collection kept at the American Museum of Natural History, examined. NEW SYNONYMY.

Neoscona nebraskensis Chamberlin and Ivie, 1942, Bull. Univ. Utah, Biol. Ser., 7(1): 77, figs. 219, 220. ♀. Female holotype from Fremont, Nebraska, in the University of Utah collection kept at the American Museum of Natural History, examined. NEW SYNONYMY.

Neoscona sacra, — Chamberlin and Ivie, 1944, Bull. Univ. Utah, Biol. Ser., 8(5): 108. (Not fig. 61; not *sacra* Walckenaer.)



Neoscona hentzii (Keyserling). Figs. 51–53. Epigynum. 51. Ventral. 52. Lateral. 53. Posteriodorsal. Figs. 54–57. Left palpus. 54. Ventral, cymbium removed. 55. Lateral. 56. Ventral view of palpal structures. 57. Apical view. 54, 55. (New Jersey). 56. (Louisiana). Fig. 58. Female abdomen.

Scales. 0.1 mm, for abdomen 1 mm.

Names. Walckenaer described *Epeira benjamina* with two varieties. One, variety A, is light colored and contrastingly marked on the abdomen, the other, variety B, is brown and indistinctly marked. However, he gave variety B the provisional name *rubicunda.* Both forms were descriptions of Abbot manuscript illustrations, var. A, fig. 126, var. B, fig. 351. Marx (1890) first synonymized *domiciliorum* Hentz, and *hentzii* Keyserling with *benjamina* Walckenaer. When McCook illustrated the species, he gave one illustration (pl. 1, fig. 7) for the contrastingly colored specimens, another (pl. 2, figs. 4, 5), for an "old" female that corresponds to var. B of Walckenaer.

Archer (1941) decided, correctly, that two species are involved and used *domiciliorum* Hentz for the one with contrasting colors and *benjamina* for the indistinctly marked one. Had he reversed the names he would have been more convincing. Chamberlin and Ivie (1944) studied Abbot's figures and concluded correctly that Walckenaer's variety A is not what Archer called *benjamina.* They decided to use Walckenaer's name *sacra* instead. This unfortunately added to the confusion. They also claimed "it is doubtful whether the true *benjamina* occurs in the United States." However, since the type of *benjamina* is Abbot's figure 126 from a Georgia spider, it must occur in the United States. They did not use the name *rubicunda,* perhaps because Walckenaer indicated that he had specimens also from the West Indies (presumably *N. nautica* L. Koch).

Unfortunately, the type of *Epeira sacra* Walckenaer, Abbot's manuscript figure 136, has the second legs longer than the first, does not look like an araneid (although it was supposed to come from an orb-web), and the abdomen is a bright orange-brown with narrow black transverse bands on the sides. It is true that Chamberlin and Ivie's photograph of Abbot's figure (fig. 61) looks surprisingly like the photograph of *N. benjamina* in Comstock (1912, 1940). This is the only resemblance. The color alone, also described by Walckenaer, speaks strongly against the synonymy. The transverse bars resemble those of *N. domiciliorum* (Plate 2). Further, the thoracic depression in Abbot's figure (of a male) is Y-shaped. However, in *Neoscona* kept in alcohol, the convex carapace has a longitudinal groove and in fresh, living specimens it may be completely hidden by hairs (Plates 1–3). It is never Y-shaped.

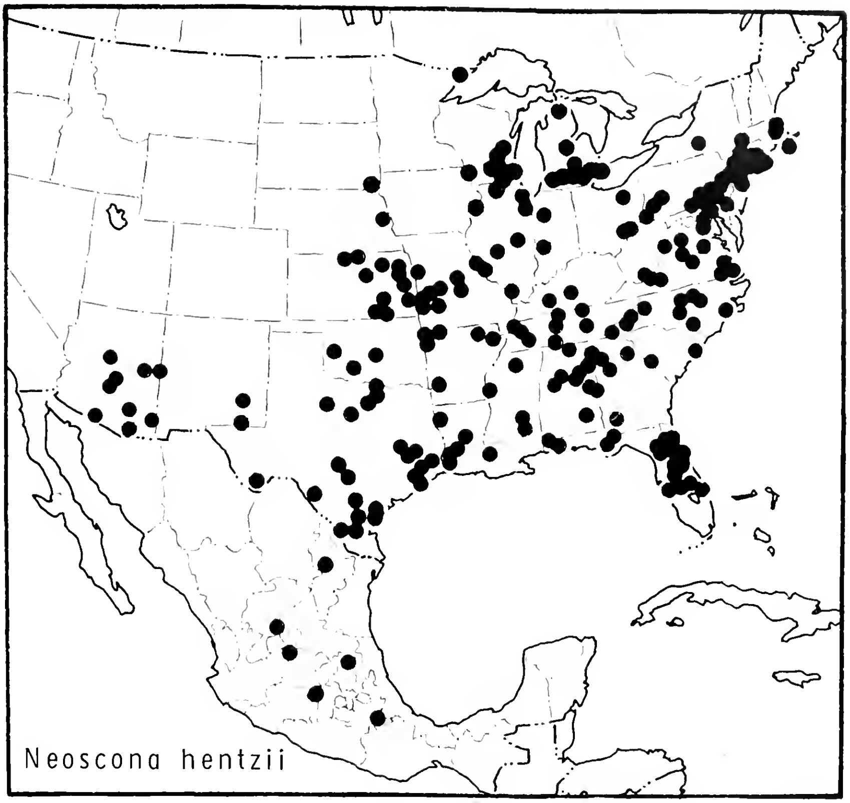
To resolve the problem without switching names and with the hope of providing stability, we have designated a neotype for *Epeira domiciliorum* Hentz, using a specimen determined by Archer. Since the types of both *benjamina* and *sacra* are Abbot illustrations, no neotype can be designated. We therefore use the oldest name with adequate description that leaves no doubt about its interpretation, *Epeira hentzii* Keyserling, for the second and much more common species.

Epeira punctigera was a misidentification. The specimens from the Marx collection came from Washington Territory (certainly an error); they may have been *N. nautica.*

Female. Total length 8.5–19.7 mm. Carapace 3.7–8.0 mm long and 3.1–7.3 mm wide. A female from New Jersey, 12.0 mm total length. Carapace 5.9 mm long, 4.5 mm wide. First femur, 6.2 mm; patella and tibia, 7.6 mm; metatarsus, 5.0 mm; tarsus, 1.6 mm. Second patella and tibia, 7.0 mm; third, 4.1 mm; fourth, 6.5 mm.

Male. Total length 4.5–15.0 mm. Carapace 2.3–6.8 mm long, 2.0–6.0 mm wide. A male from Louisiana, 15 mm total length. Carapace 6.2 mm long, 5.4 mm wide. First femur, 6.9 mm; patella and tibia, 9.7 mm; metatarsus, 6.0 mm; tarsus, 1.8 mm. Second patella and tibia, 7.0 mm; third, 4.3 mm; fourth, 6.9 mm.

Variation. Southeastern specimens are much larger than northern ones and those from Arizona. There are individual differences in coloration but all lack a distinct pattern and none has a brightly colored



Map 3. Distribution of *Neoscona hentzii* (Keyserling).

abdomen; the color in alcohol may be white. The variation is greatest in the area outside the range of *N. domiciliorum*. The holotypes of both *N. nebraskensis* and *N. arkansa* are individuals with white abdomens and the proximal epigynal bulges reduced in size.

Diagnosis. The scape of the epigynum is very long and has two pairs of lateral bulges, one pair, often indistinct, near the base and the other pair, very conspicuous, just to the basal side of the midpoint contraction. The position of the second pair, which arises from the margins of the ventral surface and terminates distally beneath (i.e., dorsal to) it, is sufficient to separate *N. hentzii* from all other *Neoscona*, even when the basal pair of lobes cannot be discerned. The narrowing near the midpoint is more pronounced than in other species and the apex is quite pointed, giving the distal segment of the scape a decidedly spoon-shaped appearance (Fig. 51). The second tibia of the male has two rows of straight clasping macrosetae (one row distally sparse), which run the entire length of the prolateral edge (Fig. 128). The conductor of the palpus in lateral view (Fig. 55) is S-shaped and short, and has the distal portion relatively long, quite different from the elongate conductor of *N. domiciliorum*. The terminal apophysis lacks the notch of *N. arabesca* (Fig. 57), but there is a lobe. There is no overlap in size of specimens with sympatric specimens of *Neoscona arabesca*. Unlike the western *N. oaxacensis*, the male lacks spurs on the fourth coxa. In some poorly preserved specimens that have lost most of their color, abdominal spots resembling those of *N. arabesca* appear. Usually these are hidden by other pigment. Color photographs, probably of this species, are on plate 23 in Gertsch, W. J. (1949, *American Spiders*, Van Nostrand).

Natural history. This species is less common than *N. arabesca* but much more common than *N. domiciliorum*. It "occurs in open woods though seldom in grass" according to Kaston (1948). Collections come from palm and high pine—turkey oak trees in Florida, dry sandy area, open hammocks with high water table in Florida, xeromesic hammock, low hammock, all Florida; xeromesic woods and birch maple swamp, Michigan; around houses in woods, Virginia; in tall grass, Ohio; palmetto-cypress swamp in Texas, open pine woods and sparse juniper (*Juniperus pediflorum*) branches on rocky hillside in Arizona; along ditches, Louisiana; rocky slope with oaks, dry second growth in Alabama. Collections of adults are relatively late in the season.

Distribution. Southern Massachusetts, Ontario, Minnesota, east of the Rocky Mountains to Arizona, central Mexico and central Florida in the south (Map 3).

Neoscona orizabensis F. P.-Cambridge

Figures 7, 59–67, 133; Map 4

Neoscona orizabensis F. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 473, pl. 44, fig. 17, ♀. Four female syntypes from Orizaba, [Veracruz], Mexico, in the British Museum, Natural History, examined. Bonnet, 1958, Bibliographia Araneorum 2: 3060.

Neoscona amulensis F. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 472, pl. 64, fig. 15, ♂. Male holotype from Amula, [9.5 km NW of Chilapa, 200 m, Guerrero*], Mexico, in the British Museum, Natural History, examined. Bonnet, 1958, Bibliographia Araneorum, 2: 3055. NEW SYNONYMY.

Note. Because females are easier to recognize than males, I chose the name *orizabensis* for this species. The type of *amulensis* is in poor condition.

Female. Total length, 10.3–15.1 mm; carapace 4.2–5.5 mm long, 3.6–4.9 mm wide. A female syntype measured 13.0 mm total length; carapace 4.3 mm long, 4.3 mm wide. First femur, 6.0 mm; patella and tibia, 7.2 mm; metatarsus, 5.2 mm; tarsus, 1.8 mm. Second patella and tibia, 6.5 mm; third, 3.6 mm; fourth, 6.5 mm.

Male. Total length, 6.1–8.0 mm; carapace 3.3–3.7 mm long, 2.5–3.2 mm wide. A male measured 6.2 mm total length; carapace 3.4 mm long, 2.5 mm wide. First femur, 3.7 mm; patella and tibia, 4.4 mm; metatarsus, 2.9 mm; tarsus, 1.0 mm. Second patella and tibia, 3.5 mm; third, 2.2 mm; fourth, 3.3 mm.

Diagnosis. The carapace is dark brown with two broad longitudinal tan colored bands that join near the thoracic groove (Fig. 7). (In other species the carapace is usually tan with darker areas near the margins and along the median longitudinal line; in *N. hentzii* and *N. nautica* it is usually uniform brown.) The dorsal pattern of the abdomen characteristically contains numerous small, often paired, light colored spots (Fig. 67). The position of lobes on the scape is as in *N. hentzii*, but the scape is considerably shorter and stouter, and the apex less pointed (Fig. 59). The second tibia of the male has a single row of about five clasping macrosetae along the distal portion, more or less disjoined from a more proximal row of longer, curved macrosetae (Fig. 133). The terminal apophysis is very wide with the sides almost parallel, the main part of the embolus is cone-shaped (Fig. 66). The male differs from sympatric *N. oaxacensis* in lacking spurs on the fourth coxae, and from *N. arabesca* in the details of embolus and terminal apophysis mentioned above.

Natural history. No natural history data was found with the collections.

Distribution. Central Mexico (Map 4).

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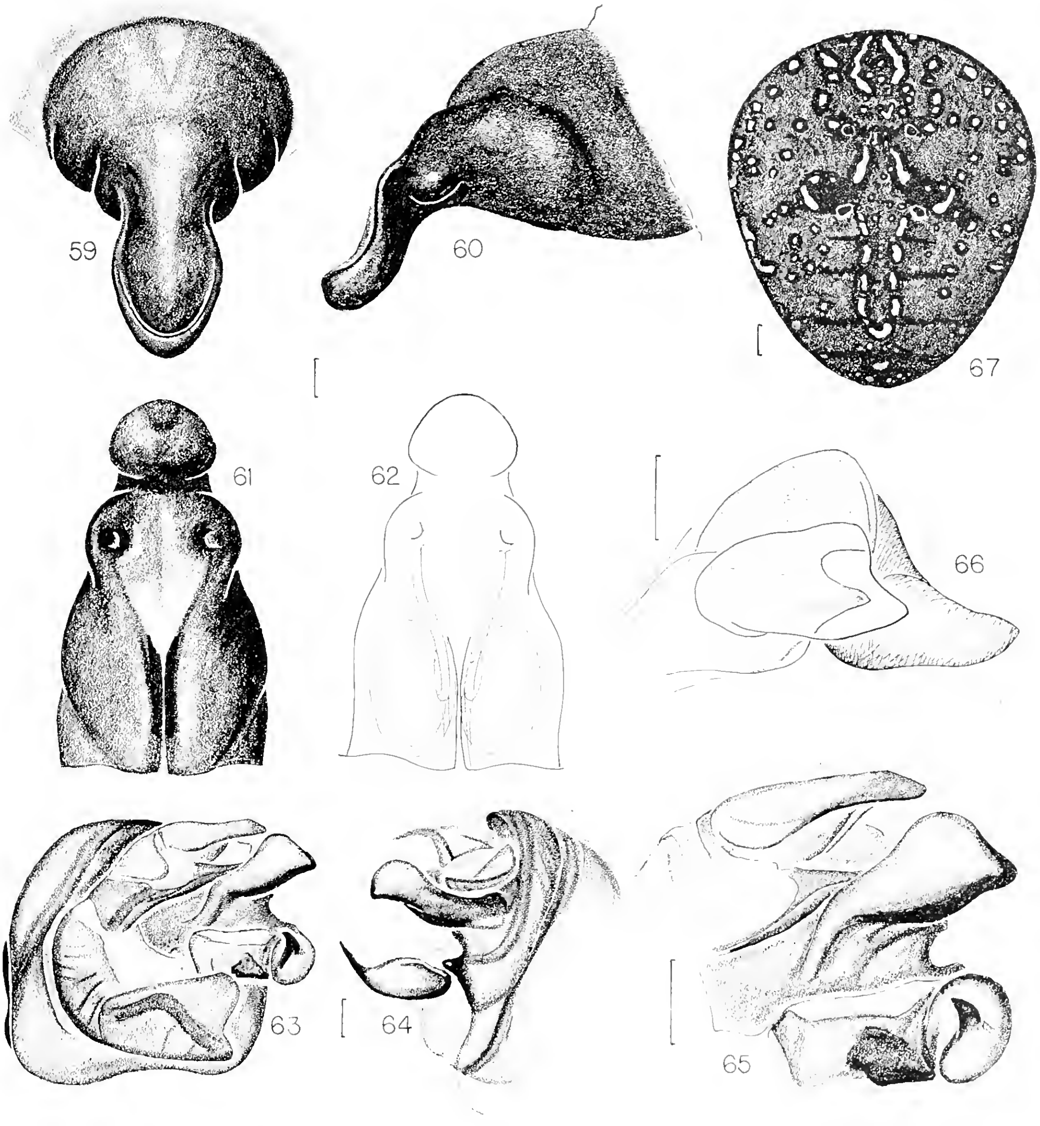
* Selander, R. B., and P. Vaurie, 1962. A gazetteer to accompany the Insecta volumes of the Biologia Centrali-Americana. American Mus. Novitates 2099: 1–70.



Neoscona orizabensis F. P.-Cambridge. Figs. 59–62. Epigynum. 59. Ventral. 60. Lateral. 61. Posteriodorsal. 62. Posteriodorsal, cleared. Figs. 63–66. Left palpus. 63. Ventral view, cymbium removed. 64. Lateral. 65. Ventral view of palpal structures. 66. Apical view. Fig. 67. Female abdomen.
Scales. 0.1 mm, abdomen 1 mm.

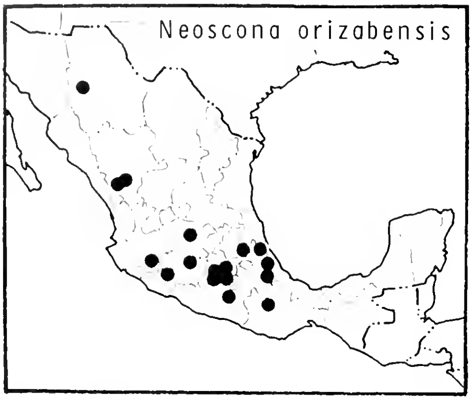
Neoscona utahana (Chamberlin)

Figures 68–77, 135; Map 5

Aranea (*Neoscona*) *utahana* Chamberlin, 1919, Ann. Entomol. Soc. America, 12: 254, p. 19, figs. 1, 2, ♀. Female holotype from Fillmore, Utah, in the Museum of Comparative Zoology, examined.

Neoscona eximia Gertsch and Mulaik, 1936, American Mus. Novitates, 863: 19, fig. 32, ♂. Male holotype and female paratype from Edinburg, Texas, in the American Museum of Natural History, examined. NEW SYNONYMY.

Neoscona jonesi Archer, 1951, American Mus. Novitates, 1487: 22, figs. 35, 50, 58, ♂. Fragments of two male syntypes from Kisatchie



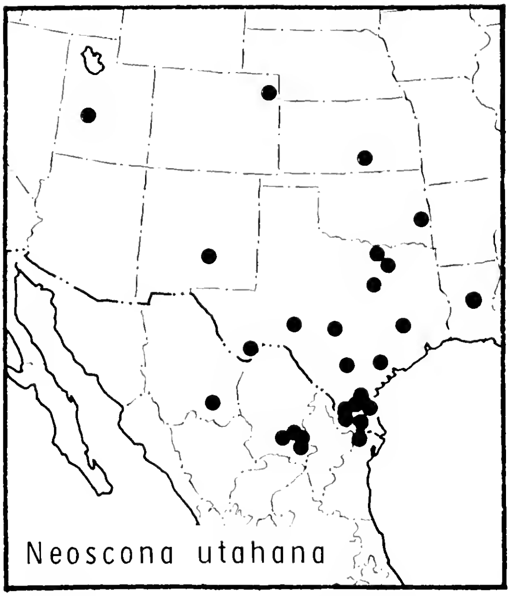
Map 4. Distribution of *Neoscona orizabensis* F. P.-Cambridge.

National Forest, Grant Parish, Louisiana, in the American Museum of Natural History, examined. NEW SYNONYMY.

Female. Total length, 8.8–10.4 mm; carapace 3.2–5.8 mm long, 3.0–4.2 mm wide. A female from Texas, 9.0 mm total length. Carapace 3.6 mm long, 3.3 mm wide. First femur, 5.0 mm; patella and tibia, 6.1 mm; metatarsus, 5.5 mm; tarsus, 1.4 mm. Second patella and tibia, 5.8 mm; third, 3.2 mm; fourth, 4.9 mm.

Male. Total length 6.2–8.0 mm; carapace 3.6–4.0 mm long, 2.9–3.3 mm wide. A male from Texas, 7 mm total length. Carapace 3.7 mm long, 3.0 mm wide. First femur, 5.0 mm; patella and tibia, 5.7 mm; metatarsus, 5.0 mm; tarsus, 1.4 mm. Second patella and tibia, 4.3 mm; third, 2.7 mm; fourth, 4.2 mm.

Diagnosis. In coloration (brown carapace, brown legs and dark brown, triangular abdomen, darker on the sides) *Neoscona utahana* resembles only *N. nautica*. However, the dorsal folium pattern of the abdomen, sharply delimited by a lighter line on its sides (Fig. 77) distinguishes *N. utahana*. The epigynum (Fig. 68) is longer than that of *N. nautica* and, unlike that of *N. arabesca*, is narrowed above the tip and is rounded at its tip. The flaplike terminal apophysis (Fig. 76) separates males from those of *N. nautica*. The shape and pattern on the abdomen (Fig. 77), present on all males examined, separates males from related and sympatric species. The main part of the embolus is cone-shaped and extends slightly beyond the lamella.



Map 5. Distribution of *Neoscona utahana* (Chamberlin).

Natural history. Specimens have been taken under eaves in Texas.

Distribution. From Utah, Colorado, and Kansas south to northern Mexico (Map 5).

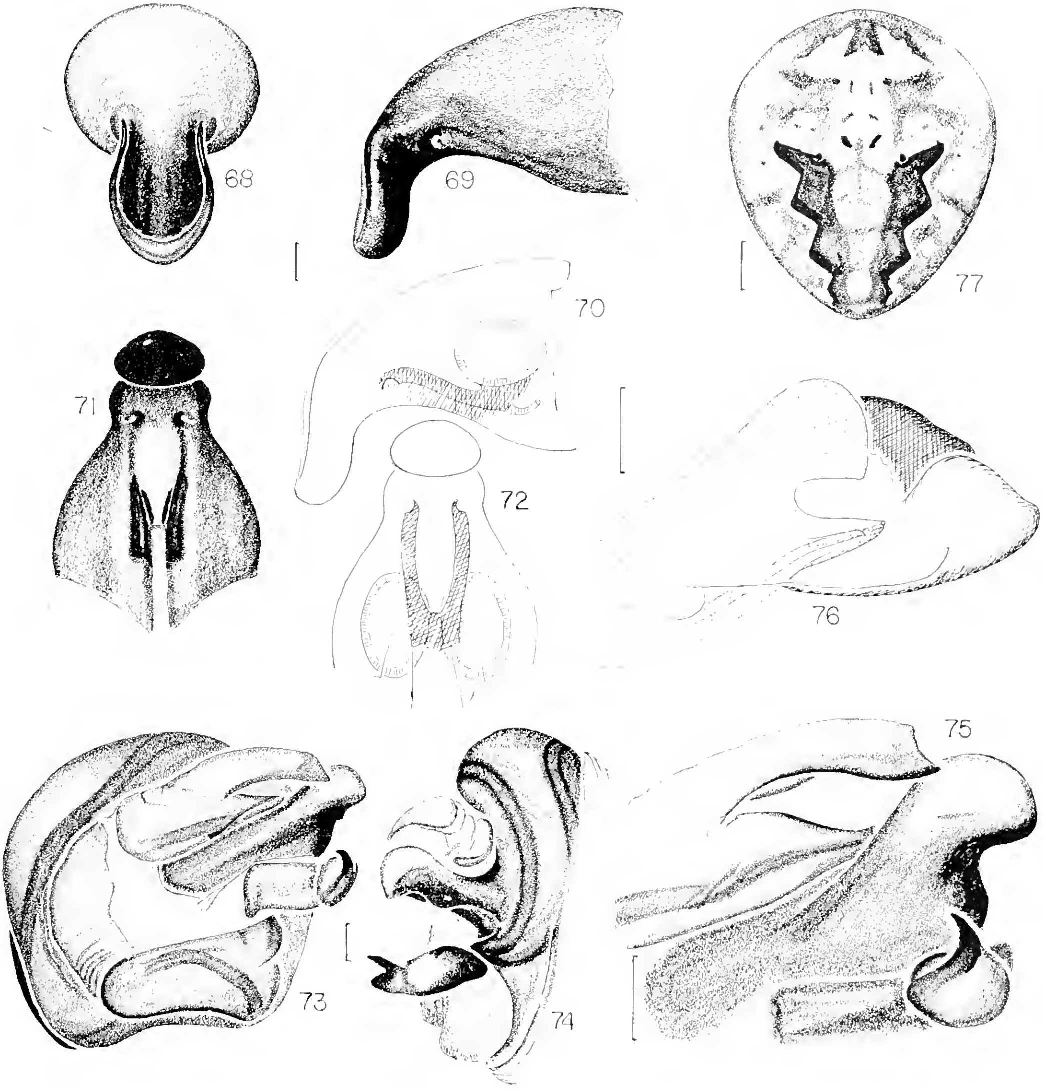
Neoscona oaxacensis (Keyserling)

Plate 4; Figures 4, 9, 11, 78–90, 129; Map 6

Epeira oaxacensis Keyserling, 1863, Sitzungsber. Naturwiss. Ges., Isis, Dresden, p. 121, pl. 5, figs. 15, 16, ♀. Female holotype from Oaxaca, Mexico, in the British Museum, Natural History, lost. Keyserling, 1893, Spinnen Amerikas, 4: 238, pl. 12, fig. 178, ♀ ["oaxensis"].

Epeira cooksonii Butler, 1877, Proc. Zool. Soc. London, p. 76, pl. 13, fig. 2, ♀. Six female syntypes from Albemarle Island, 9 female syntypes from Charles Island, Galapagos, in the British Museum, Natural History, examined. NEW SYNONYMY.

Epeira adiantoides Taczanowski, 1878, Horae Soc. Entomol. Rossicae 14: 148, pl. 1, fig. 4, ♀. Four female syntypes from Chorillos [now



Neoscona utahana (Chamberlin). Figs. 68–72. Epigynum. 68. Ventral. 69. Lateral. 70. Lateral, cleared. 71. Posteriodorsal. 72. Posteriodorsal, cleared. Figs. 73–76. Left palpus. 73. Ventral view, cymbium removed. 74. Lateral. 75. Ventral view of palpal structures. 76. Apical view. Fig. 77. Female abdomen.
Scales. 0.1 mm, abdomen 1 mm.

suburb of Lima], Peru, and numerous juvenile female and juvenile male specimens from this locality in the Polish Academy of Sciences, Warsaw, examined. NEW SYNONYMY.

Epeira vertebrata McCook, 1888, Proc. Acad. Natur. Sci. Philadelphia, p. 196, figs. 6–10, ♀, ♂. Syntypes from San Diego, California, in the Academy of Natural Sciences, Philadelphia. McCook, 1893, American Spiders, 3: 151, pl. 3, figs. 6, 7, pl. 4, fig. 1, pl. 5, fig. 4, ♀, ♂.

Neoscona oaxacensis, — F. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 468, pl. 44, figs. 4, 5, ♂, ♀. Gertsch and Mulaik, 1936, American Mus. Novitates, 863: 21. Bonnet, 1958, Bibliographia Araneorum, 2: 3059.

Neoscona cooksoni, — F. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 473, pl. 44, fig. 16, ♀.

Neoscona conifera F. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 469, pl. 44, figs. 6, 7, ♀, ♂. Two female, 4 male syntypes from Chilpancingo, Mexico, examined. Bonnet, 1958, Bibliographia Araneorum, 2: 3057. NEW SYNONYMY.

Neoscona salaeria Chamberlin, 1920, Entomol. News, 31: 167, figs. 1, 2, ♀. Male holotype from Saltair Beach, Utah, in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Neoscona lativulva Chamberlin and Ivie, 1942, Bull. Univ. Utah, Biol. Ser., 7(1): 78, figs. 221, 222, ♀. Female holotype from Laguna Beach, California, in the University of Utah collection kept at the American Museum of Natural History, examined. NEW SYNONYMY.

Note. Gertsch (1936) suspected the synonymy of some names listed above. Specimens of *N. conifera* differ by being smaller. The holotype of *Neoscona lativulva* is a small individual having only two ventral spots rather than the more common four and having a narrower, more pointed epigynum, an epigynal variation that occasionally appears in individuals throughout the range of *N. oaxacensis.*

Female. Total length 8.9–18.0 mm. Carapace 3.8–7.7 mm long, 3.3–5.5 mm wide. A female from southern California, 13 mm total length. Carapace 5.3 mm long, 4.5 mm wide. First femur, 6.1 mm; patella and tibia, 8.0 mm; metatarsus, 6.2 mm; tarsus, 1.8 mm. Second patella and tibia, 7.2 mm; third, 4.3 mm; fourth, 7.2 mm.

Male. Total length 6.3–12.7 mm. Carapace 3.5–6.3 mm long, 2.9–5.0 mm wide. A male from southern California, 10 mm total length. Carapace 5.3 mm long, 4.5 mm wide. First femur, 6.3 mm; patella and tibia, 8.0 mm, metatarsus, 6.5 mm; tarsus, 1.8 mm. Second patella and tibia, 5.8 mm; third, 4.2 mm; fourth, 6.5 mm.

Variation. There is variation in size. Mexican, and Central and South American specimens have a more distinct light median dorsal band on the abdomen as well as a slenderer abdomen than North American specimens. In some specimens the epigynal scape is constricted and more pointed (Fig. 83). These specimens may belong to a different species. They have been named *N. lativulva* by Chamberlin and Ivie.

Diagnosis. The black and white dorsal pattern on the narrow abdomen separates all but the most faded females (Figs. 89, 90). The single pair of lobes on the scape is positioned somewhat beneath (dorsal to) the ventral surface (Figs. 78, 79). In specimens that have heavily sclerotized epigyna the lobes are sometimes obscured, but in such cases the abdominal pattern generally suffices to separate the species. The males, like those of the allopatric *N. pratensis* and *N. neotheis,* have a spur on coxa IV (Fig. 9) that distinguishes them from all sympatric species. The second tibia is strongly curved, with the prolateral surface concave. Two rows of clasping macrosetae run the length of the tibia (some additional similar macrosetae may be present near the proximal end). The macrosetae are characteristically curved toward the dorsal surface of the tibia (Fig. 129). The dorsal abdominal pattern resembles that of certain *Aculepeira* with which the species has been confused.

Natural history. In California specimens have been taken from citrus trees and from carrot seed heads and in Arizona from an alfalfa field. It has been collected from shrubs and tall grass in Texas, on a bridge in Arizona, on cedars in a cemetery in Kansas and on the outside wall of a house

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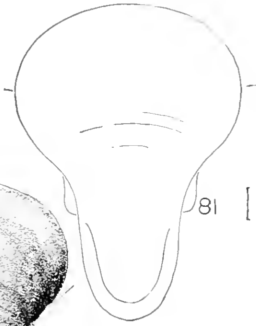
Neoscona oaxacensis (Keyserling). Figs. 78–83. Epigynum. Figs. 78, 81, 82, 83. Ventral. 79. Lateral. 80. Posteriodorsal. 78–80. (California). 81. Syntype of *Epeira adiantoides* (Peru). 82. Syntype of *Epeira cooksoni* (Galapagos Isl.). 83. (Mexico City). Figs. 84–87. Left palpus. 84. Ventral, cymbium removed. 85. Lateral. 86. Ventral view of palpal structures. 87. Apical view. Figs. 88–90. Female abdomen. 88. Syntype of *Epeira adiantoides* (Peru). 89. (Michoacan). 90. (California). Scales. 0.1 mm, abdomens 1 mm.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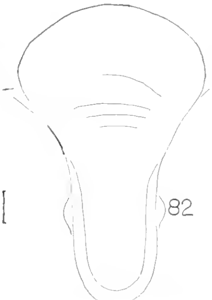
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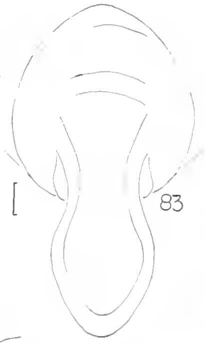
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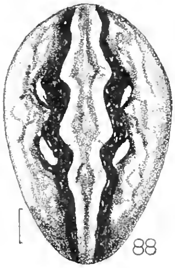
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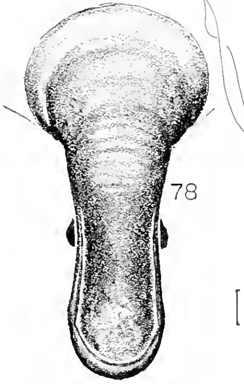
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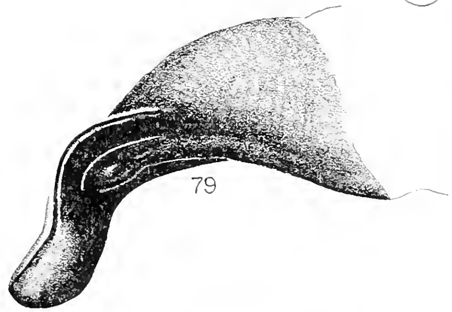
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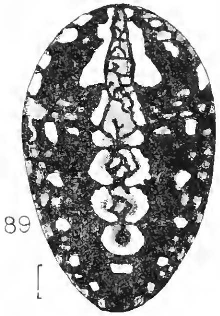
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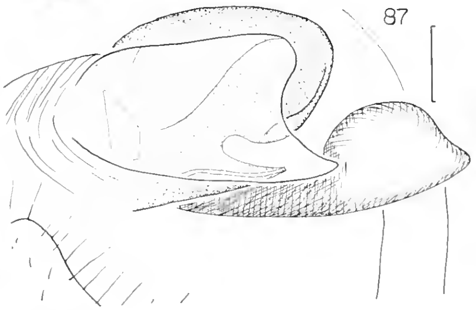
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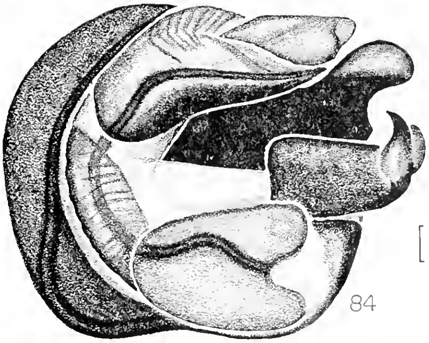
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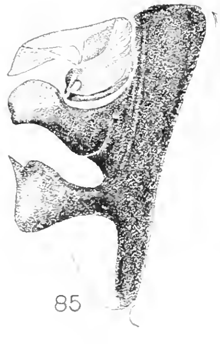
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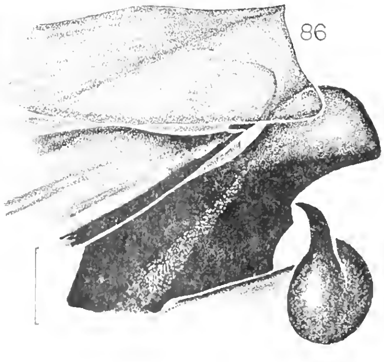
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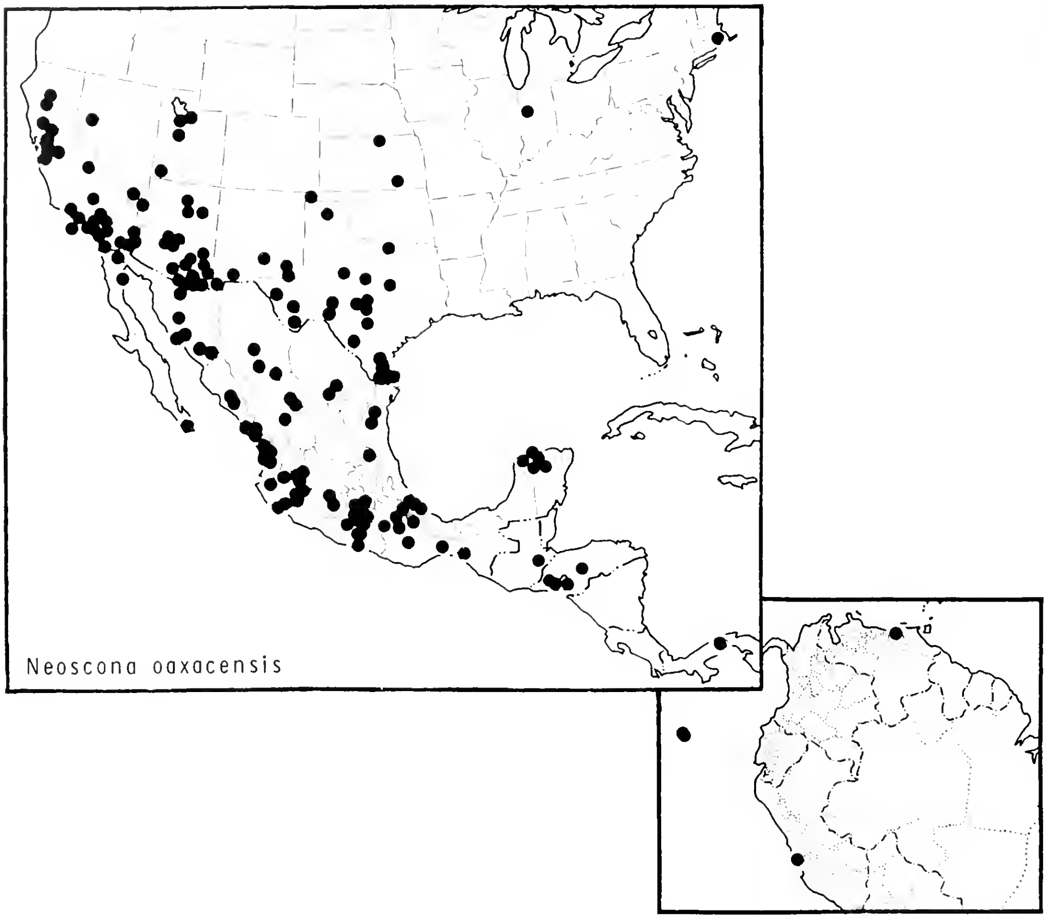


Map 6. Distribution of *Neoscona oaxacensis* (Keyserling).

in Sonora. *Colias* butterflies have been found in its web in California. Chamberlin (1920) reports the spider to be a nuisance because of the abundant webs at Saltair Beach Resort, Utah.

Distribution. California and Utah, Kansas south probably to Peru (Map 6) and Galapagos Islands. There are some collections from isolated localities: Providence, Rhode Island (N. Banks); Lafayette, Indiana, 16 August 1920; and Wawawai, Washington Territory (N. Banks). It probably is also found on Hawaii.

Neoscona neotheis (Petrunkevitch)

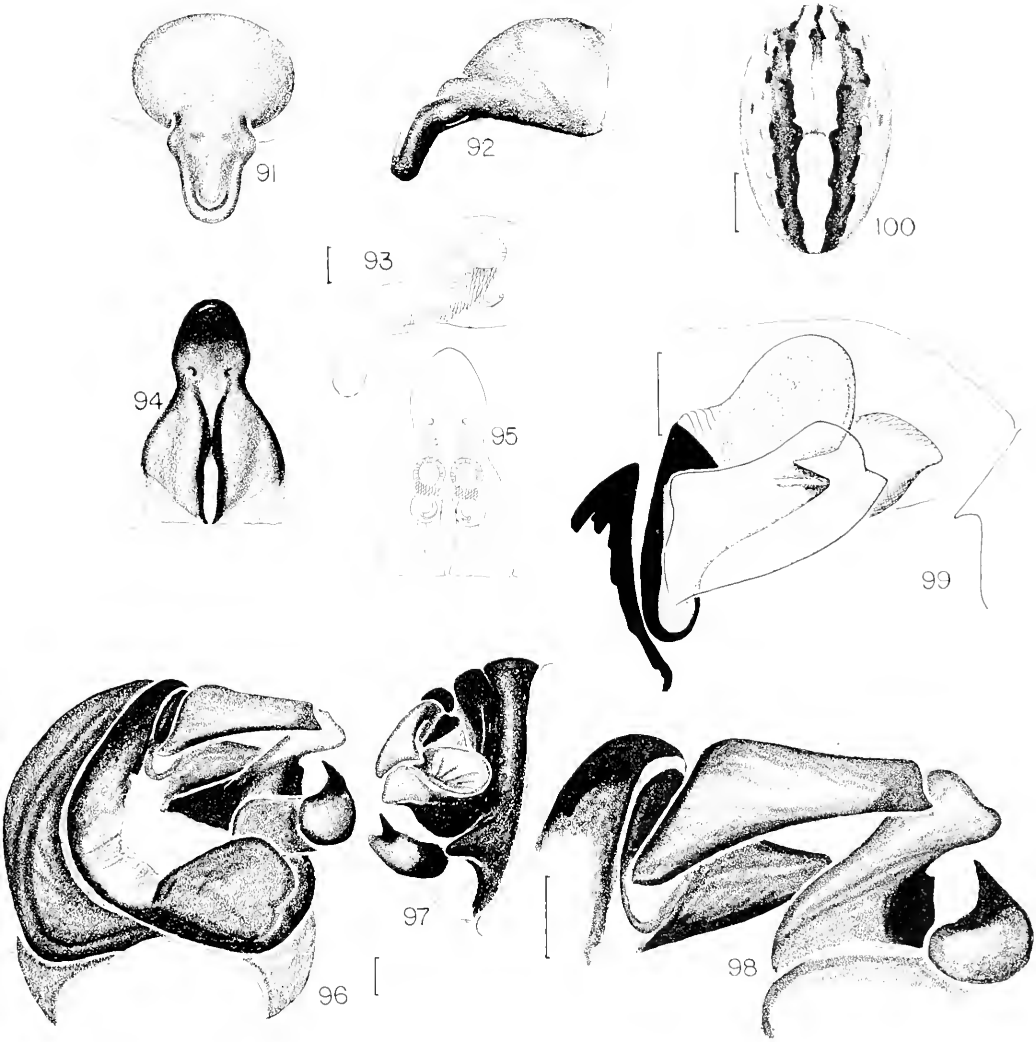
Figures 12, 91–100, 130, 131; Map 7

Epeira theisii, — Keyserling, 1893, Spinnen Amerikas, 4: 246, pl. 12, fig. 184, ♀, ♂. McCook, 1893, American Spiders, 3: 166, pl. 6, figs. 8, 9, ♀, ♂. Not *Epeira theis* Walckenaer.

Araneus neotheis Petrunkevitch, 1911, Bull. American Mus. Natur. Hist., 29: 305. New name for *Epeira theisii*, Keyserling.

Cubanella nidicola Franganillo, 1926, Cuba Contemporare, 41(161): 15, fig. 6, ♂. The Franganillo collection is in the Cuban Academy of Sciences, Havana, but the index to vial numbers is lost. NEW SYNONYMY.

Neoscona oaxacensis, — Petrunkevitch, 1930,



Neoscona neotheis (Petrunkevitch). Figs. 91–95. Epigynum. 91. Ventral. 92. Lateral. 93. Lateral, cleared. 94. Posteriodorsal. 95. Posteriodorsal cleared. Figs. 96–99. Left palpus. 96. Ventral, cymbium removed. 97. Lateral. 98. Ventral view of palpal structures. 99. Apical view. Fig. 100. Female abdomen.
Scales. 0.1 mm, abdomen 1 mm.

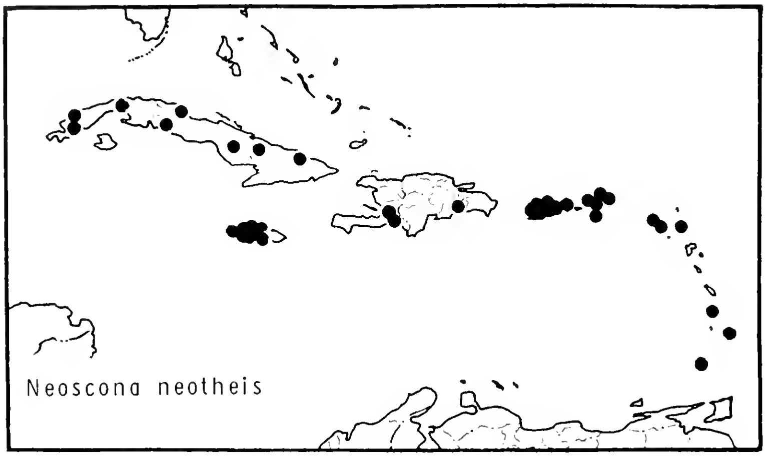
Trans. Connecticut Acad. Sci., 30: 322, figs. 200–204, ♀, ♂. Not *Neoscona oaxacensis* Keyserling.

Cubanella recta Franganillo, 1930, Mem. Inst. Nac. Habana, 1 (1): 66, fig. 8, ♂. 1936, Los Arácnidos de Cuba hasta 1936, p. 77, figs. 35, 36, ♂. Type not examined, see above. NEW SYNONYMY.

? *Neoscona parallela* Franganillo, 1931, Rev. Belén, 1: 44. Type not examined, see above. Franganillo, 1936, Los Arácnidos de Cuba hasta 1936, p. 78. *Nomen dubium.*

Neoscona nidicola, — Franganillo, 1936, Los Arácnidos de Cuba hasta 1936, p. 76, fig. 34, juv. ♀.

Neoscona neotheis, — Gertsch and Mulaik, 1936, American Mus. Novitates, 863: 21, pl. 31, ♂. Bonnet, 1958, Bibliographia Araneorum, 2: 3059.



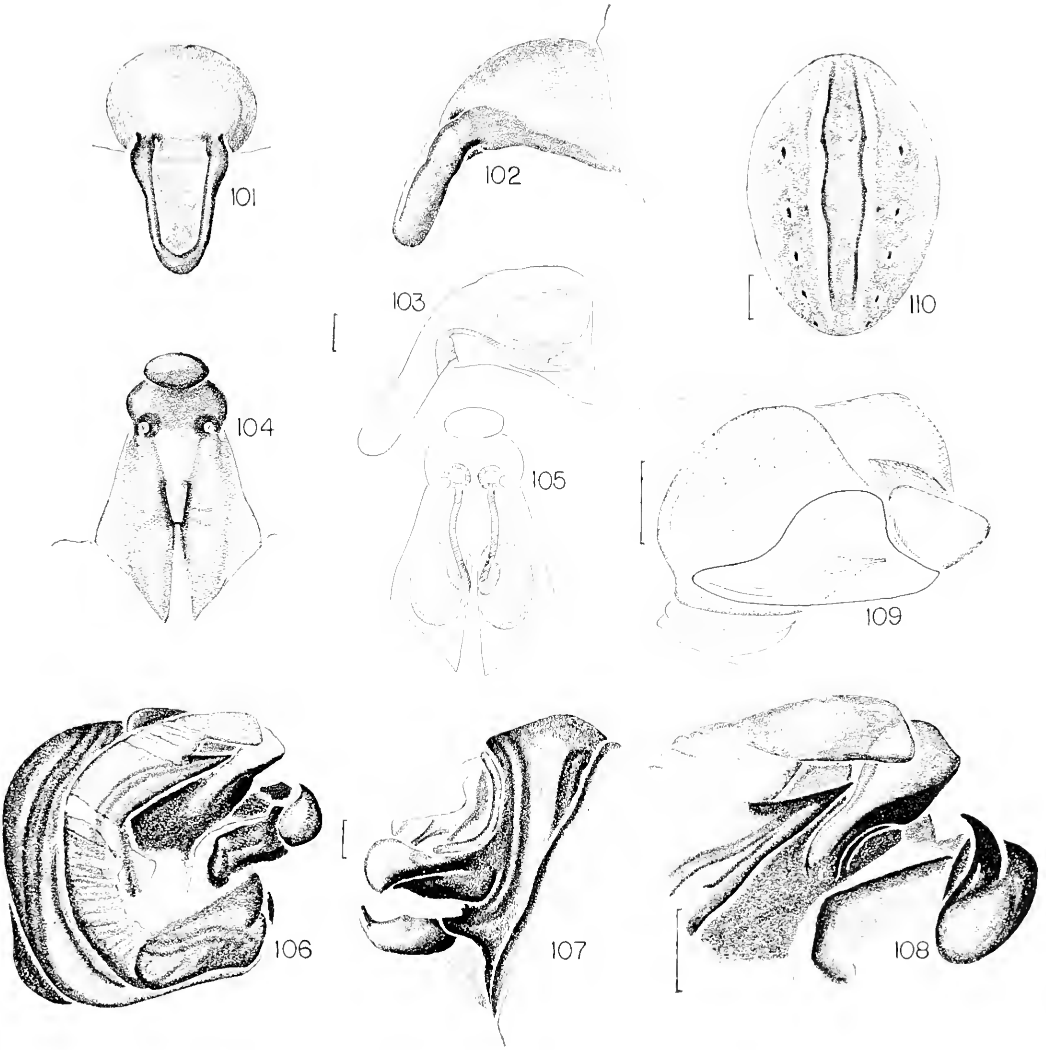
Map 7. Distribution of *Neoscona neotheis* (Petrunkevitch).

Female. Total length 5.7–17.0 mm. Carapace 2.2–6.3 mm long, 1.7–4.8 mm wide. A female from Puerto Rico, 6.5 mm total length. Carapace 2.4 mm long, 1.9 mm wide. First femur, 3.2 mm; patella and tibia, 3.7 mm; metatarsus, 2.9 mm; tarsus, 0.9 mm. Second patella and tibia, 3.2 mm; third, 1.8 mm; fourth, 3.1 mm.

Male. Total length 5.8–11.8 mm. Carapace 2.5–6.0 mm long, 2.3–5.4 mm wide. A male from Jamaica, 7.2 mm total length. Carapace 3.7 mm long, 2.9 mm wide. First femur, 4.5 mm; patella and tibia, 5.5 mm; metatarsus, 4.6 mm; tarsus, 1.3 mm. Second patella and tibia, 4.0 mm; third, 2.5 mm; fourth, 4.7 mm.

Variation. Some specimens, mostly from Cuba and Jamaica, are almost twice the size of others. At first it was thought these were hybrids. Small and large specimens are generally not found together. Certain collecting sites have large specimens, others small ones. Perhaps the larger size is due to the spider's undergoing more molts before maturity, possibly a result of competition with a similar sized species. Both large and small specimens show the diagnostic features of the species. The largest came from Camagüey, Cuba.

Diagnosis. Both sexes of this light colored species can be recognized by the dorsal abdominal pattern, which consists of a median longitudinal white band with straight margins between two bold black longitudinal stripes (Fig. 100). The ventral abdominal pattern is less variable in this species than in most others and consists of two white bands on each side of the black central area with each band partly or completely constricted about a third of its length posteriorly from the epigastric furrow (Fig. 12). The scape of the female epigynum is not constricted near the midpoint, instead a single pair of lateral lobes is present between the midpoint and the apex, positioned so that each one arises proximally beneath the ventral surface and terminates distally by joining the margin of that surface (Fig. 91). The second tibia of the male is nearly straight with three rows of clasping macrosetae tapering to a single row of macrosetae near the proximal end (Figs. 130, 131). Unlike those of *N. oaxacensis*, the macrosetae of this species are triangular and not heavily curved. The macrosetae of a small male are illustrated by Figure 130, those of a large one by Figure 131. The male is separate from other species not only by markings but also by the unique sclerotized attachment of the terminal division of the palpus (Figs. 96, 98, 99).

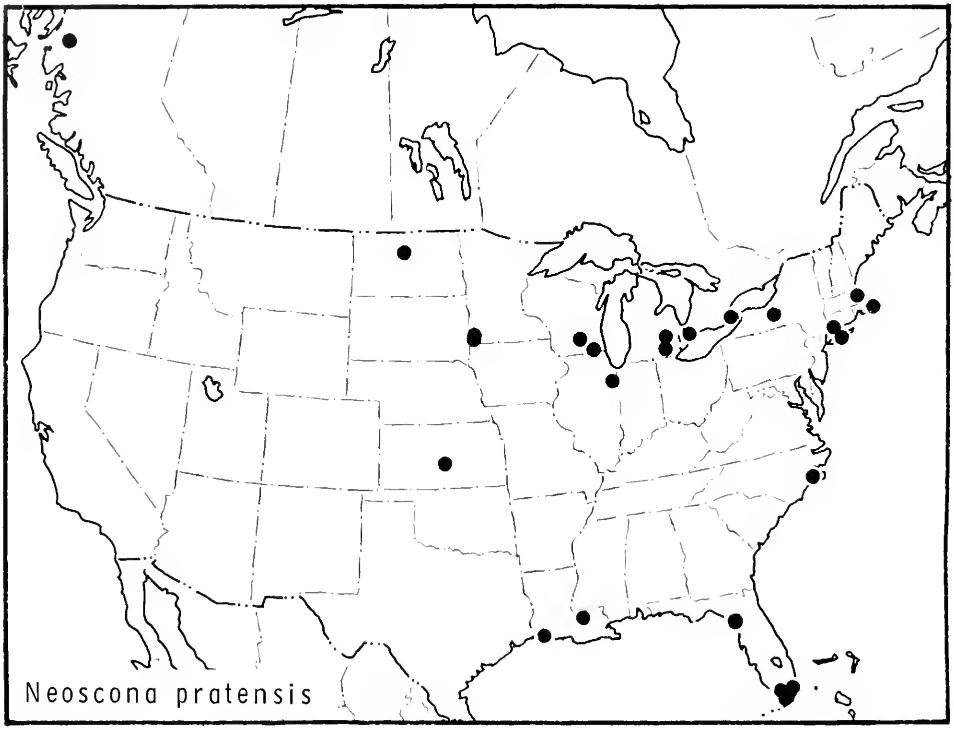


Neoscona pratensis (Hentz). Figs. 101–105. Epigynum. 101. Ventral. 102. Lateral. 103. Lateral, cleared. 104. Posteriodorsal. 105. Posteriodorsal, cleared. Figs. 106–109. Left palpus. 106. Ventral, cymbium removed. 107. Lateral. 108. Ventral view of palpal structures. 109. Apical view. Fig. 110. Female abdomen.
Scales. 0.1 mm, abdomen 1 mm.

The pattern and spur on the fourth coxa of the male separate *N. neotheis* from all sympatric species. The genitalic characters separate it from the related *N. oaxacensis*, with which it has been confused. At times the pattern is like that of some Mexican *N. oaxacensis*.

Natural history. Specimens have been taken from a beach grove in Puerto Rico.

Distribution. West Indies (Map 7). One female from Costa Rica had an epigynum resembling that of *N. neotheis*. A male from Alto Parana, Taquararaza, Paraguay, had the radix-stipes hinge sclerotized and may be this species. It is possible that this is only a subspecies of *N. oaxacensis* connecting through intermediates in Venezuela. But no such specimens are known.



Map 8. Distribution of *Neoscona pratensis* (Hentz).

Neoscona pratensis (Hentz)

Plate 1; Figures 101–110, 134; Map 8

Epeira pratensis Hentz, 1847, J. Boston Natur. Hist. Soc., 5: 475, pl. 31, fig. 11, ♀. Female type from Massachusetts, destroyed. Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 310, pl. 33, fig. 15, pl. 36, fig. 9, ♀, ♂. Keyserling, 1892, Spinnen Amerikas, 4: 184, pl. 9, fig. 136, ♀. McCook, 1893, American Spiders, 3: 142, pl. 1, fig. 6, ♀, ♂. Emerton, 1902, Common Spiders, p. 167, fig. 396, ♀.

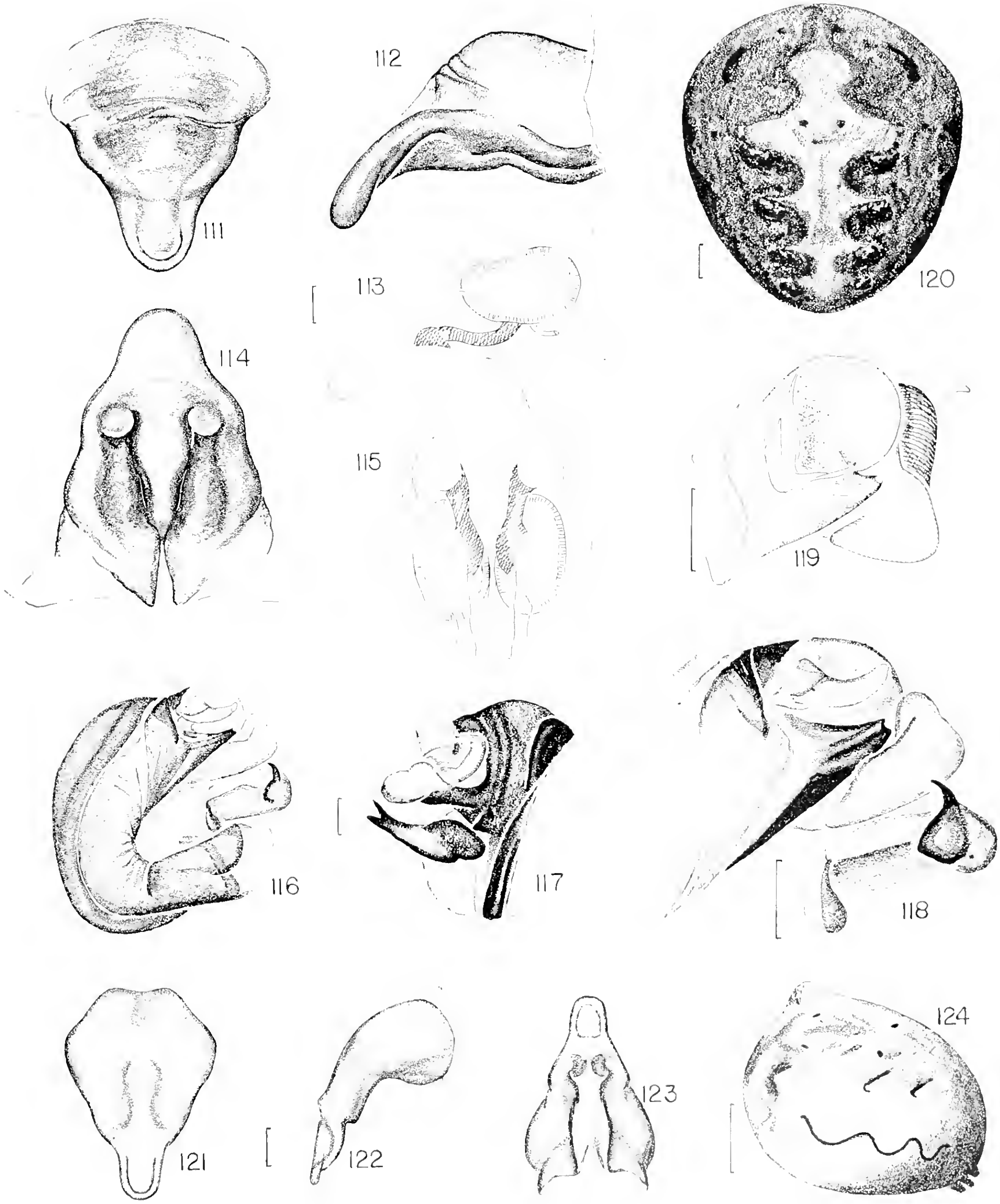
Neoscona pratensis, — Comstock, 1912, Spider Book, p. 502, fig. 537, ♀. 1940, Spider Book, rev. ed., p. 515, fig. 537, ♀. Kaston, 1947, Bull. Connecticut Natur. Hist. Surv., 70: 247, fig. 774, ♀.

Female. Total length 6.5–10.2 mm. Carapace 2.9–4.4 mm long, 2.3–3.3 mm wide. A female from Long Island, New York, 9.5 mm total length. Carapace 3.6 mm long, 2.8 mm wide. First femur, 3.3 mm; patella and tibia, 4.3 mm; metatarsus, 3.0 mm; tarsus, 1.0 mm. Second patella and tibia, 3.9 mm; third, 2.1 mm; fourth, 3.6 mm.

Male. Total length 6.7–7.9 mm. Carapace 3.4–4.1 mm long, 2.8–3.3 mm wide. A male from Long Island, New York, 7.0 mm total length. Carapace 3.7 mm long, 3.2 mm wide. First femur, 4.0 mm; patella and tibia, 5.2 mm; metatarsus, 3.9 mm; tarsus, 1.3 mm. Second patella and tibia, 4.3 mm; third, 2.7 mm; fourth, 4.3 mm.

Variation. There is considerable variation in size.

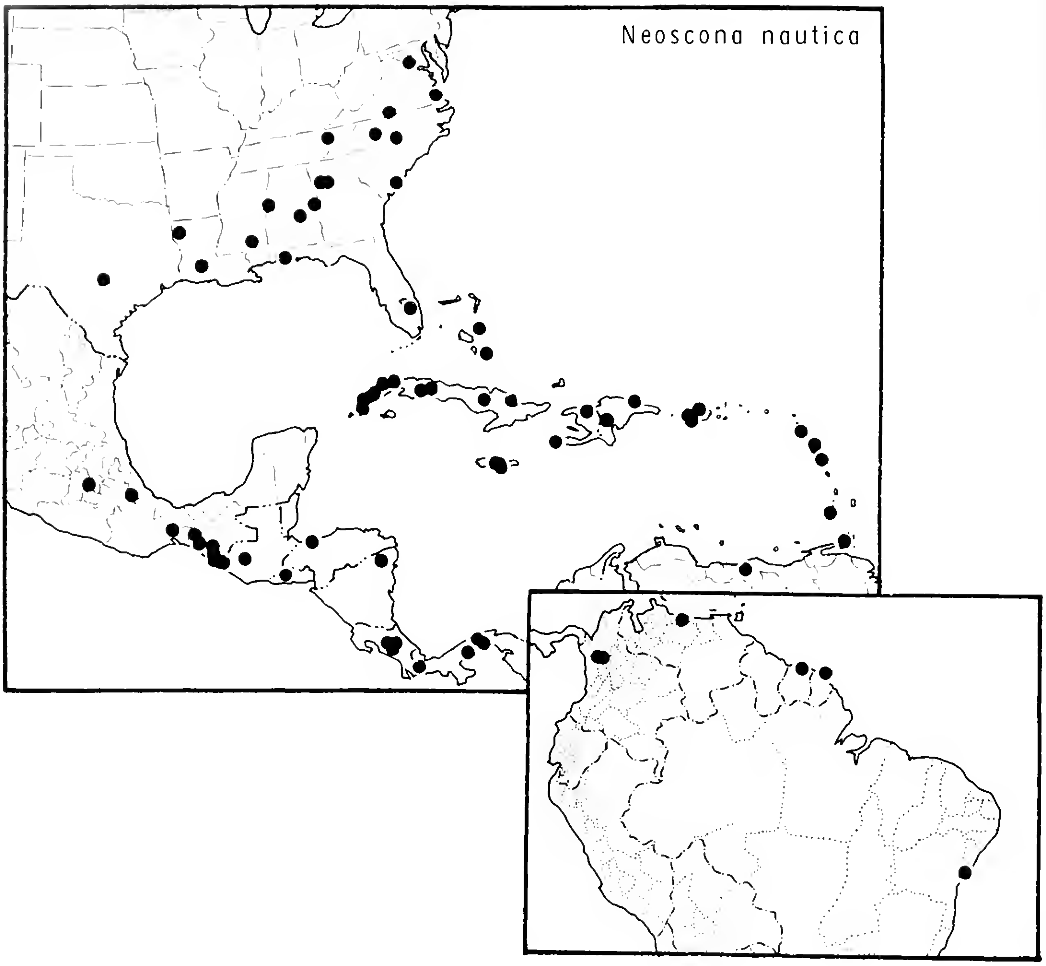
Diagnosis. Both sexes can easily be separated from related allopatric *N. neotheis* and *N. oaxacensis* and sympatric *Neoscona* species by the dorsal abdominal pattern, which consists of a median, longitudinal dark band bordered by light colored longitudinal lines extending from the anterior end two-thirds to three-quarters of the way to the posterior end, and a



Neoscona nautica (L. Koch). Figs. 111–115. Epigynum. 111. Ventral. 112. Lateral. 113. Lateral, cleared. 114. Posteriodorsal. 115. Posteriodorsal, cleared. Figs. 116–119. Left palpus. 116. Ventral, cymbium removed. 117. Lateral. 118. Ventral view of palpal structures. 119. Apical view. Fig. 120. Female abdomen.

Neoscona redempta (Gertsch and Mulaik). Figs. 121–123. Epigynum. 121. Ventral. 122. Lateral. 123. Posteriodorsal. Fig. 124. Female abdomen, dorsolateral.

Scales. 0.1 mm, abdomens 1 mm.



Map 9. Distribution of *Neoscona nautica* (L. Koch).

row of black spots to the side of each band, all on a solid, generally brownish to greenish background (Fig. 110). The scape has no lateral bulges and is not narrowed near the midpoint, but the margins of the ventral surface tend to be somewhat ragged along the proximal half of the scape (Fig. 101). The second tibia has three rows of clasping macrosetae (Fig. 134).

Natural history. The species has been collected from salt marshes in New England and on Long Island, on a bridge in Minnesota, and in pine-palmetto in Everglades National Park; from a salt marsh, Levy County, Florida, and by sweeping upland fields in the George Reserve, Michigan. It seems to have a preference for marshes and swamps. Specimens are

→

Left second tibia of male in prolateroventral view. Figs. 125, 126. *Neoscona arabesca.* Fig. 127. *N. domiciliorum.* Fig. 128. *N. hentzii.* Fig. 129. *N. oaxacensis.* Figs. 130, 131. *N. neotheis.* Fig. 132. *N. nautica.* Fig. 133. *N. orizabensis.* Fig. 134. *N. pratensis.* Fig. 135. *N. utahana.*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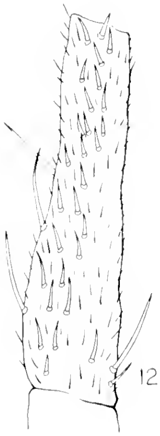
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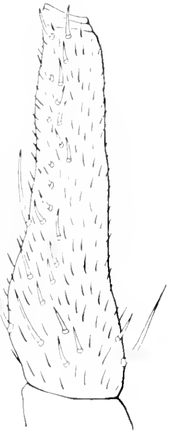
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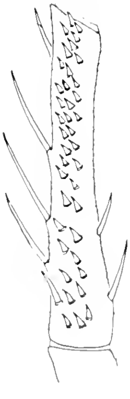
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mature from May on in Florida, from August in Michigan.

Distribution. From Terrace, British Columbia, to New England, south to Florida (Map 8).

Neoscona nautica (L. Koch)

Figures 13, 111–120, 132; Map 9

Epeira vulgaris Hentz, 1847, Proc. Boston Soc. Natur. Hist., 5: 469, pl. 30, fig. 6, ♀. Female holotype from South Carolina, destroyed. *Nomen dubium.* Not *Aranea vulgaris* Linnaeus, 1858 [=*Tegenaria domestica*]. The generic names *Aranea* and *Epeira* are objective synonyms.

Epeira tristis Taczanowski, 1873, Horae Soc. Entomol. Rossicae, 9: 131. Female holotype from Iles du Salut, French Guiana, in the Polish Academy of Sciences, Warsaw, examined. NEW SYNONYMY. Not *Epeira tristis* Blackwall, 1862.

Epeira nautica L. Koch, 1875, Aegyptische und Abyssinische Arachniden, p. 17, pl. 2, fig. 2, ♀. Female holotype from Suakin, [Sudan], in the British Museum, Natural History, examined.

Epeira volucripes Keyserling, 1885, Verhandl. Zool. Bot. Ges. Wien, 34: 528, pl. 13, fig. 27, ♀. Female syntypes from Panama and Haiti in the Museum of Comparative Zoology, examined. 1892, Spinnen Amerikas, 4: 199, pl. 9, fig. 147, ♀, ♂. McCook, 1893, American Spiders, 3: 162, pl. 6, figs. 1, 2, ♀, ♂.

Neoscona volucripes, — F. P. Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 473, pl. 44, fig. 18, ♀.

Epeira tristimoniae Petrunkevitch, 1911, Bull. American Mus. Natur. Hist., 29: 320. New name for *Epeira tristis* Taczanowski. NEW SYNONYMY.

Neoscona nautica, — Petrunkevitch, 1930, Trans. Connecticut Acad. Sci., 30: 321, figs. 197–199, ♀, ♂. Comstock, 1940, Spider Book, rev. ed., p. 513, fig. 536, ♀. Bonnet, 1958, Bibliographia Araneorum, 2: 3058.

Neoscona vulgaris, — Comstock, 1912, Spider Book, p. 500, fig. 536, ♀. Archer, 1940, Paper Alabama Mus. Natur. Hist. 14: 50. Bryant, 1945, Bull. Mus. Comp. Zool. 95: 380.

Araneus marcuzzii DiCaporiacco, 1955, Acta Biol. Venezuelica, 1(16): 355, fig. 35, ♀. Female holotype from Carúpano, Sucre, Venezuela, in Museo di Biología, Universidad Central de Caracas, examined. NEW SYNONYMY.

Note. This widespread species has been cited many times with the specific name *nautica* (Bonnet, 1958). Archer (1940) designated a neotype for *Epeira vulgaris* Hentz and deposited it in the Alabama Natural History Museum. There were three specimens marked neotype that had dried. Archer's neotype meets only a few of the conditions of Article 75 of the International Code of Zoological Nomenclature. The specimens have been sent to the American Museum where other Archer specimens are kept.

Female. Total length 7.0–11.5 mm. Carapace 3.2–4.4 mm long, 2.6–3.5 mm wide. A female from Alabama, 8.0 mm total length. Carapace 2.9 mm long, 2.4 mm wide. First femur, 3.2 mm; patella and tibia, 4.3 mm; metatarsus, 3.2 mm; tarsus, 1.0 mm. Second patella and tibia, 3.5 mm; third, 2.2 mm; fourth, 3.6 mm.

Male. Total length 4.5–5.4 mm. Carapace 2.3–2.9 mm long, 2.0–2.3 mm wide. A male from Alabama, 4.7 mm total length. Carapace 2.3 mm long, 2.2 mm wide. First femur, 3.3 mm; patella and tibia, 3.9 mm; metatarsus, 2.9 mm; tarsus, 0.9 mm. Second patella and tibia, 2.8 mm; third, 1.8 mm; fourth, 2.9 mm.

Variation. There is little variation in color and shape. The bars on the abdomen are at times more distinct.

Diagnosis. The scape of the female is extremely broad and triangular (Fig. 111), unlike that of any other American species. The carapace is dark brown, the legs are dark brown, the dorsal abdomen is dark olive or brown with a characteristic pattern (Fig. 120). The sides are black with a distinct lobed edge toward the lighter dorsum, and the ventral abdomen has a fairly consistent pattern that resembles two music notes facing each other (Fig. 13). The black sides separate the species from *N. hentzii.* The male is lighter in color. The second tibia of the male has a strangely haphazard row of prolateral macrosetae and a large median ventral macroseta that is diagnostic (Fig. 132). The terminal apophysis of the palpus (Figs. 118, 119) is a small, narrow, bent structure, very different from the flap present in all native American species.

Natural history. The species has been collected from cliffs in Puerto Rico, from a pigpen in Panama, a stable in North Carolina, buildings in Louisiana, and a market in Tennessee.

Distribution. Cosmotropical; Southeastern United States as far north as Virginia; Mexico, Central America, West Indies, and South America (Map 9). The species is also common in Hawaii and Guam, Mariana Islands. The fact that a cosmopolitan species is present in the Southeast but seems absent from California is of interest. Its closest relatives are found in the South Pacific area.

Neoscona redempta (Gertsch and Mulaik), New Combination

Figures 121–124

Aranea redempta Gertsch and Mulaik, 1936, American Mus. Novitates, 863: 18, fig. 39, ♀. Female holotype from Edinburg, Texas, in the American Museum of Natural History, examined.

Description. Female holotype. Carapace brown, dark on sides. Sternum with white pigment, dark around edge. The legs are banded. The abdomen has a gray folium and a black wavy line on each side (Fig. 124). The venter has a pair of white spots side by side. The median eyes are on slight tubercles. Total length, 5.2 mm. Carapace 2.0 mm long, 2.1 mm wide. First femur, 2.1 mm; patella and tibia, 2.8 mm; metatarsus, 1.7 mm; tarsus, 0.5 mm. Second patella and tibia, 2.5 mm; third, 1.7 mm; fourth, 2.3 mm.

Diagnosis. The humped abdomen (Fig. 124) is unusual for *Neoscona* species. The epigynum (Figs. 121–123) is also unique.

Records. No specimens other than the type have been found.

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