(US ISSN 0027-4100)

Bulletin OF THE Museum of Comparative Zoology

Spiders of the Orb-Weaver Genus *Parawixia* in America (Araneae: Araneidae)

HERBERT W. LEVI

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 153, NUMBER 1
2 JUNE 1992

(US ISSN 0027-4100)

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

BREVIORA 1952–
BULLETIN 1863–
MEMOIRS 1865–1938
JOHNSONIA, Department of Mollusks, 1941–1974
OCCASIONAL PAPERS ON MOLLUSKS, 1945–

SPECIAL PUBLICATIONS.

1. Whittington, H. B., and W. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. 192 pp.
2. Turner, R. D., 1966. A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia). 265 pp.
3. Sprinkle, J., 1973. Morphology and Evolution of Blastozoan Echinoderms. 284 pp.
4. Eaton, R. J., 1974. A Flora of Concord from Thoreau's Time to the Present Day. 236 pp.
5. Rhodin, A. G. J., and K. Miyata (eds.), 1983. Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams. 725 pp.
6. Angelo, R., 1990. Concord Area Trees and Shrubs. 118 pp.

Other Publications.

Bigelow, H. B., and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprinted 1964.

Brues, C. T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects. (*Bulletin of the M.C.Z.*, Vol. 108.) Reprinted 1971.

Creighton, W. S., 1950. The Ants of North America. Reprinted 1966.

Lyman, C. P., and A. R. Dawe (eds.), 1960. Proceedings of the First International Symposium on Natural Mammalian Hibernation. (*Bulletin of the M.C.Z.*, Vol. 124.)

Ornithological Gazetteers of the Neotropics (1975–).

Peters' Check-list of Birds of the World, vols. 1–16.

Proceedings of the New England Zoological Club 1899–1947. (Complete sets only.)

Proceedings of the Boston Society of Natural History.

Price list and catalog of MCZ publications may be obtained from Publications Office, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A.

This publication has been printed on acid-free permanent paper stock.

SPIDERS OF THE ORB-WEAVER GENUS *PARAWIXIA* IN AMERICA (ARANEAE: ARANEIDAE)

HERBERT W. LEVI[1]

ABSTRACT. *Parawixia* are Neotropical, nocturnal orb weavers related to *Acanthepeira*, *Eriophora*, *Wagneriana*, and *Wixia*. The relationship is based mainly on synapomorphic character states of male and female genitalia.

Of the 26 species of *Parawixia* found in collections, 10 are new, four are known only from males, six from females. There are 24 new synonyms of species and subspecies names. Most *Parawixia* species are found in the Amazon area primarily, and in Central America and eastern Brazil. Many species probably build webs in the canopy. The social nianduti spider (*Parawixia bistriata*), which made such an impression on Darwin, belongs to *Parawixia*.

INTRODUCTION

Among the interesting spiders found in South America by Charles Darwin, as reported in 1839 in *The Voyage of the Beagle*, was a social orb-weaver species. ". . . I found near St. Fé Bajada [present day Paraná] many large black spiders, with ruby-coloured marks on their backs, having gregarious habits. The webs were placed vertically, as is invariably the case with the genus Epeira: they were separated from each other by a space of about two feet, but were all attached to certain common lines, which were of great length, and extended to all parts of the community. In this manner the tops of some large bushes were encompassed by the united nets. Azara [F. de Azara, 1809, *Voyage dans l'Amérique méridionale*] has described a gregarious spider in Paraguay, which Walckenaer thinks must be a Theridion, but probably it is an Epeira, and perhaps even the same species with mine. I cannot, however, recollect seeing a central nest as large as a hat, in which, during autumn, when the spiders die, Azara says the eggs are deposited. As all the spiders which I saw were of the same size, they must have been nearly of the same age. This gregarious habit, in so typical a genus as Epeira, among insects, which are so bloodthirsty and solitary that even the two sexes attack each other, is a very singular fact."

It is a reflection on the current status of spider studies that this spider, though named *bistriata* in 1836 by the Swiss traveler Rengger, and frequently mentioned (Buskirk, 1981), has never been illustrated before. In 1932 Mello-Leitão placed *bistriata* in *Eriophora* and was followed by the catalogers Roewer and Bonnet. Mello-Leitão did not provide illustrations and on receiving some specimens 15 years later did not recognize them and gave them a new name. Only recently Shear (1970) considered that Darwin's spider may have been a *Cyrtophora*, an orb-weaver genus with some social species. Several investigators (Fowler and Diehl, 1978; Fowler and Gobbi, 1988a,b) studied the behavior but were uncertain as to whether there are one or two species that are social. Badcock (1932) realized that a species described and illustrated previously by Tullgren from Bolivia was a social spider also found in Paraguay as reported by Carter (1928), the collector of Badcock's specimens.

This paper is part of the ongoing study of Neotropical orb weavers (Berman and Levi, 1971; Harrod, Levi, and Leibensperger, 1991; Levi, 1968, 1971, 1985, 1986, 1988, 1989, 1991a,b). The primary purpose of my revisions is to help determine

---

[1] Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

species within a given genus, in this case *Parawixia*. Such determinations are needed because spider species are often of economic importance or biological interest (e.g., *Parawixia bistriata*). A secondary function is to provide information aiding in the understanding of evolutionary relationships within the genus. Sequestering this information may be easy in small families but is much more difficult in large and diverse families. Studies on the evolution of small families less diverse than the orb weavers have been published based on an understanding of a few species in the genus (Coddington, 1986).

Before a genus has been revised, it may only be known by its most common species or by the type species to which the generic name is attached. However, the type species is often the most aberrant member of the genus, and has been placed in its own genus specifically because of unusual characters that may not occur in more "average" congenerics. Also, in large diverse families, the study of all species is necessary to determine generic-level characters.

To take examples, when I first worked on *Eriophora* in 1970, I assumed that *Parawixia* belonged to the same genus perhaps as a species group of *Eriophora*. Careful study of *Parawixia* showed this assumption to be erroneous because several characters were found to be apomorphies for *Parawixia* only (see below). In another study, I characterized the genus *Wixia* as lacking a long scape (Levi, unpublished key). I have since found that this absence is only true for Nearctic species; many Neotropical species (which otherwise share apomorphies with Nearctic *Wixia* and can fairly be considered congeneric) do have a long scape (Levi, in prep.). These characters were not elucidated until revisions of the genera in question had been done.

Evolutionary analyses of generic relationships cannot be made until the relevant genera themselves have been revised and the limits of the individual genera defined. Any premature analysis would have to be revised with each successive generic revision. I am currently completing work on a sub-group of the family Araneidae, characterized by the presence of a palpal paramedian apophysis and including the genera *Parawixia*, *Eriophora*, *Acanthepeira*, *Wagneriana*, *Alpaida*, *Wixia*, *Acacesia*, and *Cyclosa*. When the final members of this group, *Wixia* and *Acacesia* (both manuscripts in preparation), are revised, comparison and evolutionary analysis of this group will be possible.

METHODS AND MATERIALS

The methods used are the same ones as those used in previous papers on Neotropical orb weavers. Relative eye sizes were measured by comparing their diameter in profile with that of the anterior median eyes. The distance separating the eyes of the anterior row was measured relative to the diameter of the anterior median eyes in profile; and that the posterior row to the diameter of the posterior median eyes. A forthcoming paper on the genus *Wixia* will describe these methods in some detail.

The specimens used came from the following collections.

AMNH	American Museum of Natural History, New York, New York, United States; N. Platnick, L. Sorkin
BMNH	British Museum (Natural History), London, Great Britain; P. Hillyard, F. Wanless
CAS	California Academy of Sciences, San Francisco, California, United States; W. J. Pulawski, D. Ubick
CS	C. Sandoval, São Paulo, Brazil
CUC	Cornell University Collection, kept in the AMNH; N. Platnick
CV	C. Valderrama A., Bogotá, Colombia
FSCA	Florida State Collection of Arthropods, Gainesville, Florida, United States; G. B. Edwards
HEC	Hope Entomology Collections, Oxford University, Ox-

	ford, Great Britain; D. Spencer-Smith, I. Lansbury
IBNP	Inventario Biológico Nacional, San Lorenzo, Paraguay; J. A. Kochalka
IMPR	I. M. P. Rinaldi, Botucatu, São Paulo, Brazil
INPA	Instituto Nacional de Pesquisas da Amazonia, Manaus, Amazonas, Brazil; J. A. Raphael
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; L. Baert
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; E. A. Maury
MCN	Museu de Ciências Naturais, Porto Alegre, Rio Grande do Sul, Brazil; E. H. Buckup
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts, United States
MECN	Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador; L. Avilés
MEG	M. E. Galiano, Buenos Aires, Argentina
MHNM	Museo de Historia Natural de Montevideo, Uruguay; R. M. Capocasale
MHNMC	Museo de Historia Natural, Medellín, Colombia; M. A. Serna D.
MLP	Museo de Universidad Nacional, La Plata, Argentina; R. F. Arrozpide
MNHC	Museu de História Natural, Curitiba, Paraná, Brazil; S. de F. Caron
MNRJ	Museu Nacional, Rio de Janeiro, Brazil; A. Timotheo da Costa
MUSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; D. Silva D.
MZCR	Museo Zoologico de Universidad de Costa Rica, San José, Costa Rica; C. E. Valerio
MZSP	Museu de Zoologia da Universidade de São Paulo, Brazil; P. Vanzolini, L. Neme, J. L. M. Leme
MZUF	Museo Zoologico de "La Specola," Università, Florence, Italy; S. Mascherini
MHMW	Naturhistorisches Museum, Vienna, Austria; J. Gruber
NRMS	Naturhistoriska Riksmuseet, Stockholm, Sweden; T. Kronestedt
PAN	Polska Akademia Nauk, Warszawa, Poland; A. Riedel, W. Starega, J. Proczynski, A. Slojewska, E. Kierych
RLCB	R. L. C. Baptista, São Paulo, Brazil
SMF	Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; M. Grasshoff
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D. C., United States; J. Coddington
ZMK	Zoologisk Museum, København, Denmark; H. Enghoff

I would like to thank the curators for making the specimens under their care available for this study. I am grateful to J. Kochalka for providing life history information, M. E. Galiano for information on Argentinian collecting localities, R. L. C. Baptista on Brazilian localities, D. Silva D. on Peruvian localities. C. Sandoval sent information and photographs of the nianduti spiders. Evelyn S. de A. Marques sent specimens. V. R. D. von Eickstedt found information on *P. bistriata* venom and bites. E. H. Buckup provided some of the records of *Parawixia* species in the MCN collection that she could determine with my illustrations. C. Stocker and R. Maurer searched unsuccessfully for Rengger's specimens. O. Kraus gave advice on nomenclature. K. Boss and two readers suggested changes to improve the paper. L. R. Levi, L. Leibensperger and W. H. Piel reworded some of the writing and D. Sher-

TABLE 1. DIFFERENTIAL CHARACTERS OF *PARAWIXIA* (PARW), *ERIOPHORA* (ERIO), *ACANTHEPEIRA* (ACAN), *WAGNERIANA* (WAGN), *ALPAIDA* (ALPA). (DATA FROM LEVI, 1971, 1976, 1988, 1991B).

	PARW	ERIO	ACAN	WAGN	ALPA
Pattern					
carap. glabrous	–	–	–	–	[+*]
paired spots on carap.	+*	–	+	–	–
marks betw. ME and LE	+*	–*	+	–	–
black eye rings	–	–	–	–	[+*]
sides of thoracic reg. black	–	–	–	[+*]	–
pattern on sternum	[+*]	–	–	–	–
abd. color pattern	–	–	–	–	[+*]
abd. v. with black rect.	–	[+]	–	–	–
abd. v. black with white spots	+	–	–	–	–
Female Morphology					
LE on sides of tuber.	+	–	+	–	–
PME on slight swelling	–*	–	–	–	–
carap. swollen behind eyes	+	+	+	+	+
abd. with tubers.	4–15	0–3	12+	9–15	–*
ant. median abd. tuber.	–*	–	[+]	–	–
abd. subspherical	+*	+	+	–	–
abd. longer than wide	–*	–	–	+	+
abd. with tail	–	–	–	[+*]	–
3 median post. tubers.	+	–*	+	+	–*
abd. glabrous	–	–	–	–	[+]
Epigynum					
scape	+	+	+	–	–
lobe	–	–	–	+	+
knob at tip	–*	–	–	[+]	–*
notch on face	–	–	–	–	[+*]
post. med. plate round	–	–	[+]	–*	–
post. med. plate oval	–	–	–	+*	+*
post. med. triangular	–	[+]	–	–	–
Male Morphology					
ceph. reg. wide	–	–	[+]	–	–
hook on coxa I	+	+	[–]	+	+*
macrosetae on coxae III, IV	+*	+*	+*	+*	+*
trochanter IV macrosetae	+*	+*	–	–*	–*
tibia II modified	–	–	–	–	–*
Palpus					
patella macrosetae	1**	[2**]	1	1	1*
Y narrow	–	[+]	–	–	–
Y covers PM	–	–	[+]	–	–
PM free	–	+	+	–	–
PM stalk and cap	–	–	–	–	[+*]
PM L- or U-shaped	–	–	–	[+]	–
PM disk with finger	+	+	–	–	–
PM disk with fold	–	–	[+]	–	–
M with base teeth	+	+	–	+	–
base of M with concavity	+	+	–	–	–
long "stipes"	–	[+]	–	–	–
E cone, bullet-shaped	[+*]	–	–	–	–
E knife-shaped	–	–	–	–	[+*]
E razor clam-shaped	–	–	[+]	–	–
A absent	–	–	[+]	–	–
A fused with embolus	–	–		+	+
A-R with hinge	+	+		–	–

ry helped with word-processing. I thank also the anonymous reviewers for suggestions and F. Boisse-Kilgo for meticulous editing. The start of these revisions was supported by NSF grants B-5133, GB-36161, BMS 75-05719, DEB 76-15568, DEB 79-23004, DEB 80-19732 and BSR 83-12771. Publications costs for this study were covered, in part, by the Wetmore-Colles Fund.

Parawixia F. P.-Cambridge

Parawixia F. P.-Cambridge, 1904: 487. Type species by original designation *Epeira destricta* O. P.-Cambridge, 1889.

Diagnosis. Parawixia can be distinguished by the epigynum which, unlike that of *Wagneriana*, has a scape as long as or longer than the width of the base and, unlike that of *Eriophora*, has the scape originating from the posterior margin of the base (Figs. 9, 19, 74). The distal end of the paramedian apophysis in *Parawixia* males is in the shape of a disk with a finger along the distal margin and extending beyond it (Figs. 7, 26, 39). In *Wagneriana* the paramedian apophysis is L-shaped; in *Wixia* and *Acacesia* the paramedian apophysis is a straight prong. In *Acanthepeira* and *Eriophora* the paramedian apophysis is a separate sclerite. Unlike that of *Eriophora*, the palpal patella of *Parawixia* males has only one macroseta.

Coloration, lateral eyes, and abdomen shape are distinctive. There are dark marks between median and lateral eyes (Figs. 2, 4, 12), paired dark spots on the carapace (Figs. 24, 62), and a pattern of paired light patches on the sternum (Fig. 6). In some species, these marks are missing. The lateral eyes are on the sides below tubercles (Figs. 2–5). The spherical to trapezoidal abdomen has 2 to 6 pairs of lateral tubercles and usually 2 to 3 tubercles in a median line posteriorly (Figs. 12, 17).

In collections from Mexico and Guatemala, where the ranges of the two genera overlap, females of *Parawixia* can be separated from those of Nearctic *Acanthepeira* (Levi, 1976; fig. 12) that also have paired spots on the carapace, but have an abdominal median anterior tubercle lacking in *Parawixia* (Figs. 12, 17, 49).

The shape of the embolus of the male palpus and its attachment (soft, lightly sclerotized tissue with a small hematodocha) may be an autapomorphy. The round to trapezoidal shape of the tubercle-bearing abdomen is an autapomorphy of *Parawixia* species, as are the paired light marks on the sternum (Fig. 6, Table 1).

Description. Carapace orange to brown with one or more pairs of spots and characteristic dark marks between median and lateral eyes and behind the lateral eyes (Figs. 12, 17, 37). There are few hairs on the carapace. *Parawixia bistriata*, however, has a hairy carapace and lacks the paired spots. Chelicerae of all are darker distally than proximally. The endite and labium may be dark. The sternum is dark with pairs of lighter patches (Fig. 6) except in *P. baracoa*, *P. undulata*, and *P. bistriata.* The coxae are orange to brown with dusky patches and the legs have indistinct dark rings. The dorsum of the abdomen is variable in individuals of each species but the venter has a species-characteristic pattern. It is black with a distinctive median

---

←

* There are exceptions.

** *P. bistriata* and *E. nephiloides* (Levi, 1971) have a large macroseta and a smaller one on the male palpal patella.

Bracketed characters are autapomorphies for the genus.

Abbreviations: abd., abdomen; ant. anterior; betw., between; carap., carapace; ceph., cephalic; med., median; post., posterior; rect., rectangle; reg., region; tuber(s)., tubercle(s); v., venter; A, terminal apophysis; E, embolus; LE, lateral eyes; M, median apophysis; ME, median eyes; PM, paramedian apophysis; PME, posterior median eyes; R, radix; Y, cymbium; ACAN, *Acanthepeira*; ALPA, *Alpaida*; ERIO, *Eriophora*; PARW, *Parawixia*; WAGN, *Wagneriana*.

white patch (Fig. 31), pairs of white marks (Figs. 18, 44, 140, 147), or other distinctive markings always different from those of related species.

The anterior median eyes are the largest, the lateral eyes the smallest. The posterior median eyes may be on a slight swelling in *Parawixia*, but are not in *Wagneriana*, *Acanthepeira*, or *Eriophora*. In *Wixia* (in prep.) and *Acacesia* (in prep.) the posterior median eyes are on a swelling with the eyes directed toward the sides.

Parawixia have a subspherical to trapezoidal abdomen with four to 15 tubercles, three or four pairs on the sides toward the anterior and middle, one pair posterior on the sides, and two to three single tubercles in a posterior median line (Figs. 12, 17). All individuals of a species have the abdomen about the same shape. Adult *Parawixia bistriata* females lack these tubercles, but immatures and males frequently have three lateral pairs and a faint posterior median tubercle (Fig. 157). Only rarely (in immature and some adult female *P. audax*) does *Parawixia* have a median anterior tubercle as in *Acanthepeira*.

Male coloration is as in females. In males the cephalic region is narrow (Figs. 3, 4) as in males of *Eriophora* and *Wagneriana*. It is not narrow in males of *Acanthepeira*. The abdomen is the same shape as in the female but smaller (Fig. 62). The palpal patella has only one macroseta, except in *P. bistriata*, which has a second smaller, white macroseta. The endite has a tooth facing a tubercle on the proximal end of the palpal femur (Figs. 4, 6). There is always a hook on the distal margin of the first coxa (Fig. 6) fitting into a groove on the second femur. The fourth and sometimes third coxae and trochanters of *Parawixia* males (except in *P. audax*, *P. undulata*, and *P. bistriata*) have one or more macrosetae (Fig. 6), as in males of *Wagneriana*, *Eriophora*, *Acanthepeira*, and *Wixia*. The second tibia is armed with macrosetae and thicker than the first tibia. As in related genera, the palpus has a paramedian apophysis. The base of the median apophysis, just above the radix, is usually modified to resemble a depressed oval with teeth or keels along its margin (Figs. 7, 26, 142, 149, 156), a synapomorphy shared with *Eriophora* and important for separating species of *Parawixia*. In *Wagneriana* and *Wixia* the base is sclerotized, sometimes with a tooth; in other genera it usually is not modified or sclerotized. The embolus is cone- or bullet-shaped (Fig. 7) in all but *P. kochi*. In *Eriophora* it is of various shapes. The terminal apophysis of the *Parawixia* palpus is partly fused to the embolus, as in *Wagneriana* and *Eriophora*. (*Acanthepeira* lacks a terminal apophysis.) This fusion is probably a plesiomorphy.

Variation. The dorsal abdominal pattern and coloration differ among individuals of the same species. The number of macrosetae on the third and fourth trochanters of males is variable and commonly differs on left and right sides of the same specimen.

Relationships. Parawixia is closest to *Eriophora* (Levi, 1971) and *Acanthepeira* (Levi, 1976). The long scape of the epigynum is a synapomorphy with *Acanthepeira* and *Eriophora* species (in *Acanthepeira* the scape is relatively short). But in all *Eriophora* species the scape originates from the anterior margin, and folds back to point posteriorly. The shape of the paramedian apophysis of the male palpus (which is attached to the conductor) and of the abdomen are autapomorphies for the genus *Parawixia*. The tubercles of the lateral eyes and the pairs of dark spots on the carapace are synapomorphies with species of *Acanthepeira*. The dark streaks between median and lateral eyes may also be found in *Eriophora edax*. The usually black underside of the abdomen may have a median white patch or distinctive pairs of light or white patches (Figs. 13, 18, 31, 79) that are also found in species of *Wixia*. The tubercles on the abdomen are homologous with those of *Wagneriana* and

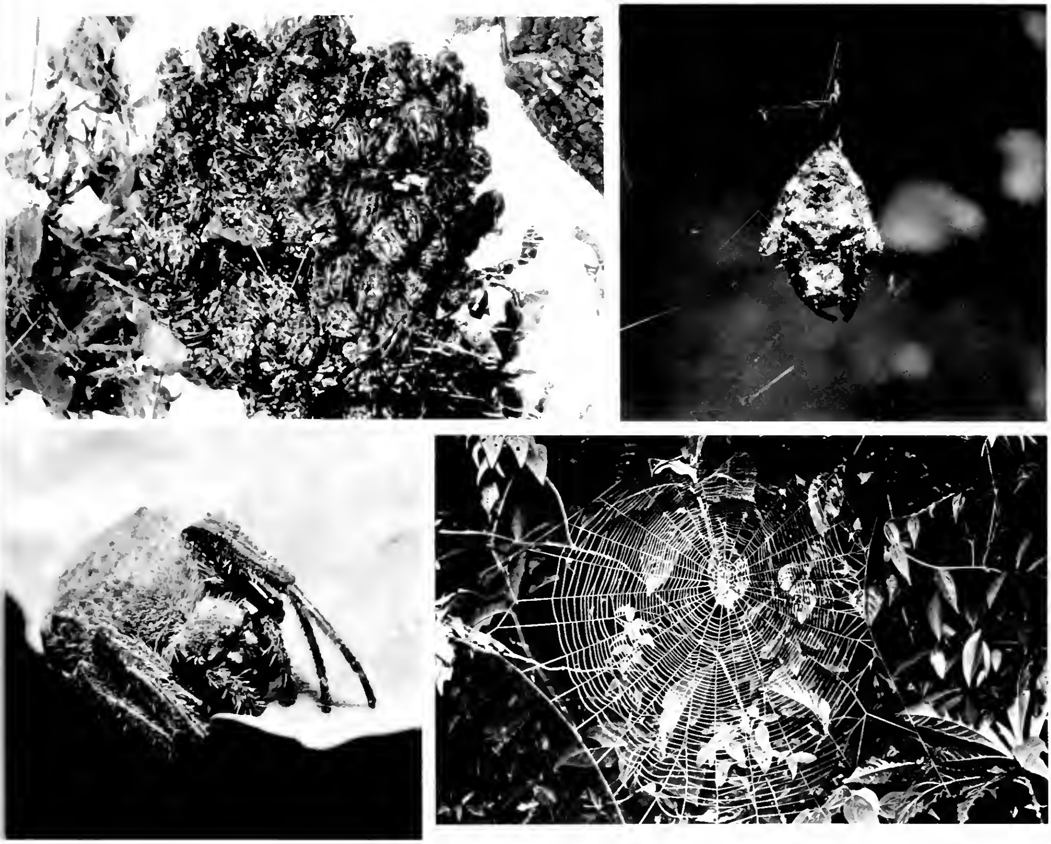


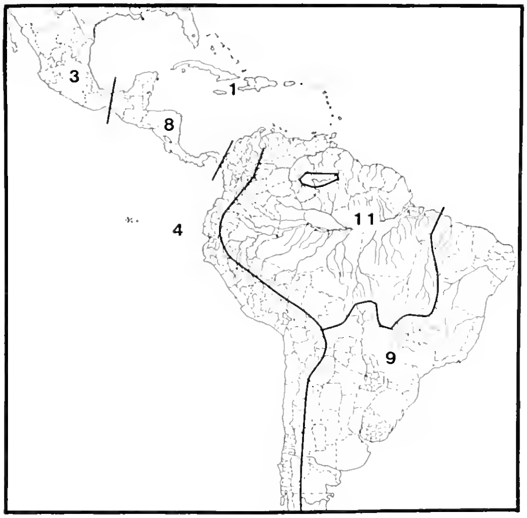
Plate 1. Upper left, *Parawixia bistriata,* sixth instar (photo C. P. Sandoval). Others, *P. audax*. Upper right, female hanging in web. Lower left, female. Lower right, web, orb about 50 cm horizontal diameter.

Acanthepeira, therefore synapomorphic. However, in *Wagneriana*, the abdomen is rectangular, longer than wide and often with a tail above the spinnerets. Macrosetae on the third and fourth coxae and trochanters of males (not always present), presence of a paramedian apophysis, and lack of distal hematodocha are synapomorphies of these various genera: *Parawixia, Acanthepeira, Wagneriana, Wixia, Eriophora, Alpaida, Verrucosa*, and others (Table 1).

Natural History. The best known species is *P. audax*, which makes a loose large web and sits in the hub, cephalic region down, or in a rolled-leaf retreat, one to two meters above the ground. Most species probably live in the canopy and are rarely collected. *Parawixia bistriata* is social and makes webs fairly high up, commonly on telephone poles. All individuals in a colony are of the same age and size and during daytime they cluster together in a shared retreat (Plate 1; see below).

Note. When working on *Eriophora* in 1970 I thought that *Parawixia* might be a synonym of *Eriophora* (Levi, 1971), but this is not the case (see above). The two genera are related. No additional species of *Eriophora* have been found (only one doubtful male from Peru).

Distribution. Parawixia is found



Map 1. Approximate number of *Parawixia* species known from different areas.

throughout the Neotropics, most species being found in the Amazon area (Map 1). It is not certain whether any of the numerous *Epeira* species described from Australia belong to *Parawixia*.

Misplaced Species

Parawixia darlingtoni Bryant, 1945: 382, figs. 14, 16, 21, is a *Wixia*.

P. mastophoroides Mello-Leitão, 1942: 402, figs. 23, 24, imm., is a *Wixia*.

P. tullgreni di Caporiacco, 1955: 348, fig. 31, ♂, is *Alpaida tullgreni* new combination. This species was overlooked in my revision of *Alpaida* (1988).

P. zigzag Mello-Leitão, 1951: 331, figs. 3, 4, ♂, belongs to a new unnamed genus.

KEY TO *PARAWIXIA* FEMALES

1. Scape of epigynum long, reaching at least to midpoint between genital groove and spinnerets (Figs. 50, 79) 2

– Scape not reaching midpoint between genital groove and spinnerets (Figs. 13, 18, 25) 9

2(1). Scape with swelling near tip, tapered most near tip (Figs. 74, 81, 110) 3

– Scape without swelling, evenly tapered (Figs. 46, 123, 136) 5

3(2). Posterior median plate of epigynum narrow (Figs. 75, 76, 111) 4

– Posterior median plate wide; lateral plates short (Figs. 82, 83); southern Brazil (Map 3) ...... *monticola*

4(3). Length of lateral plates about twice their diameter (Fig. 76); Amazon to Misiones Prov., Argentina (Map 3) *velutina*

– Length of lateral plates about one and one-half times their diameter (Fig. 111); Amazon area of Peru, Brazil (Map 3) ...... *ouro*

5(2). Abdomen of adult spherical, without tubercles (Fig. 153); Bolivia, Mato Grosso to northern Argentina (Map 3) ...... *bistriata*

– Abdomen with tubercles 6

6(5). Scape flat and wide (Figs. 46, 48); Mexico, Guatemala, Greater Antilles (Map 3) ...... *tredecimnotata*

– Scape not noticeably flat (Figs. 123, 136, 150); South America 7

7(6). Scape slender, both sides concave and coming to a fine point (Figs. 123–125); base with paired dark spots (Fig. 123); abdomen narrow, longer than wide (Fig. 126); widespread in South America (Map 3) ...... *kochi*

– Scape thicker, base without dark spots (Figs. 136, 143); abdomen subspherical with tubercles (Figs. 139, 146) 8

8(7). Scape thin (Figs. 136, 138); posterior median plate convex, dark brown (Fig. 137); widespread in South America (Map 3) ...... *audax*

– Scape swollen (Figs. 143, 145); posterior median plate flat, usually white (Fig. 144); southern Brazil to Buenos Aires Prov., Argentina (Map 3) ...... *undulata*

9(1). Scape of epigynum swollen at distal end above tip (Figs. 88, 97, 104); taper greatest near tip 10

– Scape without swelling above tip (Figs. 9, 14, 117) 15

10(9). Swelling indistinct; scape long (Figs. 81, 84); southern Brazil (Map 3) ...... *monticola*

– Swelling distinct; scape shorter (Figs. 74, 88) 11

11(10). Posterior median plate much wider than lateral plates (Fig. 105); Amazon (Map 2) ...... *tarapoa*

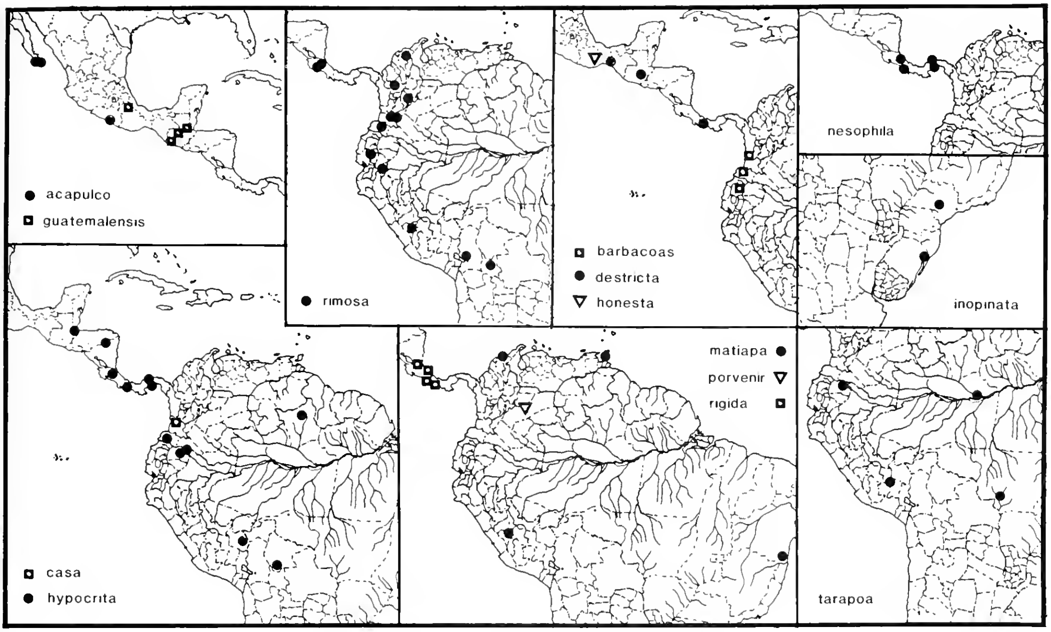
– Posterior median plate equal in width to or narrower than lateral plates (Figs. 76, 89, 98, 111) 12

12(11). Posterior median plate vase-shaped as in Figure 98; Ecuador, Peru to Bahia State, Brazil (Map 3) ...... *divisoria*

– Posterior median plate narrower than lateral plates (Figs. 76, 89, 111) 13

13(12). Median plate with sides almost parallel (Fig. 89); Central America (Map 3) ...... *hoxaea*

– Median plate constricted in middle (Figs. 76, 111); 14



Map 2. Distribution of *Parawixia* species.

14(13). Swelling of scape almost as wide as base of epigynum (Fig. 110); Amazon of Peru, Brazil (Map 3) .... *ouro*

– Swelling half as wide as epigynum base or narrower (Fig. 74); widespread in South America (Map 3) .... *velutina*

15(9). Posterior median plate of epigynum with ventral constriction (top of Fig. 10); Mexico (Map 2) .... *acapulco*

– Posterior plate without ventral constriction (Figs. 15, 22) 16

16(15). Length of scape (from origin with base) about one and one-half times width of base (Fig. 117); Central America (Map 2) .... *rigida*

– Scape barely longer than width of base or shorter (Figs. 14, 56, 63) 17

17(16). Width of posterior median plate equal to or greater than width of a lateral plate (Figs. 15, 28, 33, 41) 20

– Lateral plates each wider than median plate (Figs. 57, 64, 70) 18

18(17). Lateral plates evenly curved in median (Fig. 64); Central America (Map 2) .... *nesophila*

– Lateral plates otherwise (Figs. 57, 70) 19

19(18). Median plate bottle-shaped (Fig. 70); southern Brazil (Map 2) .... *inopinata*

– Median plate square with paired depressions on anterior margin (Fig. 57); Central America to Bolivia, Brazil (Map 2) .... *hypocrita*

20(17). Base of epigynum longer than wide in posterior view (Fig. 41); Mexico, Guatemala (Map 2) .... *guatemalensis*

– Base of epigynum as long as wide or wider than long in posterior view (Figs. 15, 21, 33) 21

21(20). Visible width of each lateral plate less than half width of posterior median plate (Figs. 33–35); Costa Rica and Andes (Map 2) .... *rimosa*

– Visible width of each lateral plate equal to or greater than half width of posterior median plate (Figs. 15, 22, 28) 22

22(21). Base of epigynum tapering evenly into scape (Fig. 27); lateral plates without dorsal lobe (Fig. 28); abdomen with ventral white median patch on black (Fig. 31); Colombia (Map 2) .... *barbacoas*

– Base of epigynum set off from scape (Figs. 14, 19); lateral plates with dorsal lobe (Figs. 15, 21, 22); abdomen with two pairs of ventral white spots (Figs. 18, 25); Mexico, Central America 23

23(22). Posterior median plate as wide as long (Fig. 15); abdomen with anterior tubercles double (Fig. 17); Mexico (Map 2) .... *honesta*

– Posterior median plate longer than wide (Figs. 21, 22); abdomen with single anterior tubercle (Fig. 24); Mexico, Central America (Map 2) .... *destricta*

KEY TO *PARAWIXIA* MALES

1\. Fourth trochanter without macroseta 2

– Fourth trochanter with one or more macrosetae (Fig. 6) 5

2(1). Base of median apophysis with an outer tooth, which is sometimes hidden by radix (Figs. 141, 142, 155, 156), tip of median apophysis pointing away from cymbium (Figs. 141, 149, 155) 3

– Base of median apophysis without outer tooth (Fig. 26); tip of median apophysis curved back, pointing toward tip of cymbium (Fig. 26); Mexico, Central America (Map 2) .... *destricta*

3(2). Median apophysis with a neck or constriction above base (Figs. 155, 156); Bolivia, Mato Grosso to northern Argentina (Map 3) .... *bistriata*

– Median apophysis without neck (Figs. 141, 142, 148, 149) 4

4(3). Median apophysis with an inner tooth on base facing radix (Figs. 141, 142); widespread in South America (Map 3) .... *audax*

– Median apophysis with an inner lobe on base facing radix (Figs. 148, 149); southern Brazil to Buenos Aires Prov., Argentina (Map 3) .... *undulata*

5(1). Embolus club-shaped, with a neck (Figs. 129–135); widespread in South America (Map 3) .... *kochi*

– Embolus pointed at tip, without neck (Figs. 51, 61, 73) 6

6(5). Median apophysis with a distal, fine point and a knob two-thirds along its length (Fig. 61); Central America to Bolivia, Brazil (Map 2) .... *hypocrita*

– Median apophysis otherwise 7

7(6). Median apophysis distally forked into two branches with pointed tips (Figs. 68, 73) 8

– Median apophysis otherwise (Figs. 80, 122) 10

8(7). Southern Brazil (Figs. 73, Map 2) *inopinata*

– Mexico, Central America (Figs. 45, 68, Map 2) 9

9(8). More proximal branch of median apophysis pointed (Fig. 68); underside of abdomen with median white patch .... *nesophila*

– More proximal branch of median apophysis blunt (Fig. 45); underside of abdomen with four white spots .... *guatemalensis*

10(7). Median apophysis with two small distal lobes separated by a notch (Figs. 80, 122) 11

– Median apophysis otherwise (Figs. 39, 51, 87, 93, 95) 12

11(10). Median apophysis with tooth at middle of outer edge (Fig. 80); Amazon to Misiones Prov., Argentina (Map 3) .... *velutina*

– Median apophysis without a tooth on outer edge (Fig. 122); Central America (Map 2) .... *rigida*

12(10). Median apophysis with short, truncate branch as in Figures 52, 109 13

– Median apophysis otherwise (Figs. 50, 54, 102) 14

13(12). Median apophysis with "vertical" keel above its base (Fig. 109); Amazon (Map 2) .... *tarapoa*

– Median apophysis without a keel (Fig. 52); Colombia (Map 2) .... *casa*

14(12). Median apophysis with outer edge swollen at middle (Fig. 54); Colombian Amazon (Map 2) .... *porvenir*

– Median apophysis with about same diameter throughout (Figs. 39, 87) 15

15(14). Median apophysis bent more than 90 degrees and with three knobs below its tip (Fig. 39); Costa Rica and Andes (Map 2) .... *rimosa*

– Median apophysis, if bent more than 90 degrees, with only one or two knobs (Figs. 102, 115) 16

16(15). Visible part of conductor almost as wide as long, subcircular (Fig. 102); median apophysis with 90 degree bend (Fig. 102); Ecuador, Peru (Map 3) .... *divisoria*

– Visible part of conductor longer than wide or mostly hidden (Figs. 51, 115); curvature of median apophysis less than 90 degrees 17

17(16). Median apophysis with "vertical" keel one third its length from base (Figs. 51, 87) or near base (Figs. 93, 95) 18

– Median apophysis without a keel near its base (Fig. 115); Peruvian Amazon (Map 3) .... *maldonado*

18(17). Median apophysis with three distal knobs (Fig. 51); conductor large, longer than wide (Fig. 51); Mexico, Guatemala, Greater Antilles (Map 3) *tredecimnotata*

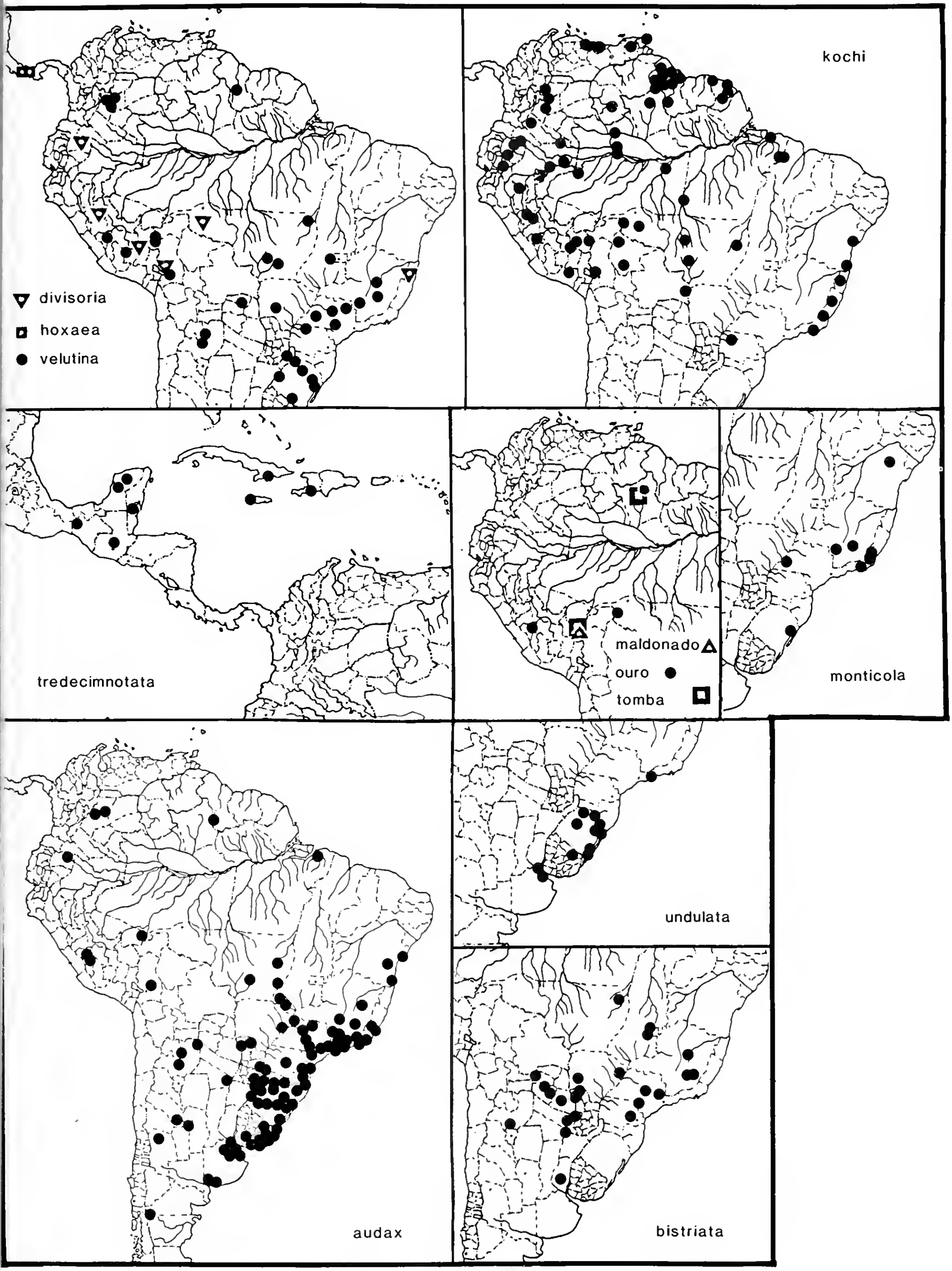
– Median apophysis with only one or two distal knobs (Figs. 87, 93, 95); conductor smaller (Figs. 87, 93, 95) 19

19(18). Embolus equal to or larger in area than small terminal apophysis (Fig. 87); southern Brazil (Map 3) .... *monticola*

– Embolus smaller in area than large terminal apophysis (Figs. 93, 95) 20

20(19). Tip of median apophysis extends beyond most distal part of tegulum (Fig. 95); Peruvian Amazon (Map 3) .... *tomba*

– Median apophysis shorter, not extending beyond tegulum edge (Fig. 93); Trin-



Map 3. Distribution of *Parawixia* species.

idad, Colombia, Peru, Brazil (Map 2)
.... *matiapa*

Parawixia acapulco new species
Figures 9–13; Map 2

Holotype. Female holotype from Revolcadero, Acapulco, Guerrero State, Mexico, July 1959 (N. L. H. Krauss), in AMNH. The specific name is a noun in apposition after the type locality.

Note. The holotype is in poor condition, just molted, with its epigynum not completely hardened.

Description. Female holotype. Carapace orange with brown spots. Chelicerae orange distally brown. Labium, endites brown. Sternum dusky with pairs of clear patches. Coxae, legs orange with brown spots and rings and white setae. Dorsum of abdomen whitish, brown on sides (Fig. 12); venter black with a pair of white spots anterior to spinnerets (Fig. 13). Eyes small. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 1.6 diameters apart. Posterior median eyes 2 diameters apart. Abdomen with 13 tubercles: four pairs on sides and five posterior (Fig. 12). Total length 12 mm. Carapace 4.2 mm long, 3.8 wide. First femur 4.8 mm, patella and tibia 5.8, metatarsus 3.5, tarsus 1.3. Second patella and tibia 5.4 mm, third 3.0, fourth 4.6.

Variation. Total length of females 12.0 to 13.1 mm. The illustrations were made from the holotype.

Diagnosis. The long posterior median plate of the epigynum has a ventral constriction (Fig. 10) unlike that of any other species.

Paratypes. MEXICO *Baja California Sur:* 3.2 km SE Ribera, 26 July 1974, ♀ (R. M. Haradon, W. E. Savary, V. F. Lee, CAS); 19 km S Todos Santos, 12 July 1968, 2♀ (S. Williams, CAS).

Parawixia honesta (O. P.-Cambridge)
Figures 14–18; Map 2

Epeira honesta O. P.-Cambridge, 1899: 300, pl. 37, fig. 6, ♀. Female holotype from Omilteme, [Omiltemi, Guerrero State], Mexico, in BMNH no. 1905.4.28.2834, examined.

Parawixia honesta:—F. P.-Cambridge, 1904: 490, pl. 46, fig. 17, ♀. Roewer, 1942: 871. Bonnet, 1958: 3340.

Description. Female holotype. Carapace orange-brown with paired black patches. Chelicerae orange, distally brown. Sternum dark brown with paired orange patches. Coxae yellow with dark brown; legs orange to yellow with indistinct dark patches and rings. Dorsum of abdomen dark and light brown, with a folium outline (Fig. 17); venter with four indistinct white spots in dusky area (Fig. 18). Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.9 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Abdomen with 13 tubercles: four pairs on sides, and five posterior (Fig. 17). Total length 17 mm. Carapace 6.0 mm long, 4.9 wide. First femur 7.7 mm, patella and tibia 9.2, metatarsus 6.2, tarsus 1.9. Second patella and tibia 7.9 mm, third 4.7, fourth 7.1.

Diagnosis. The posterior median plate of the epigynum (Fig. 15) is wider than that of *P. destricta* (Figs. 21, 22). No additional specimens have been found. This

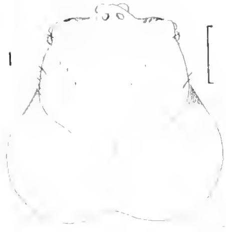
⟶

Figures 1–8. *Parawixia* morphology. 1, 2, female carapace and chelicerae. 3–8, male. 3, carapace. 4, eye region, chelicerae, right palpus. 5, eye region, chelicerae from below. 6, sternum, left endite, coxae, and trochanters. 7, 8, left palpus pulled apart. 1–5, 7, 8, *P. audax*. 6, *P. rimosa*.

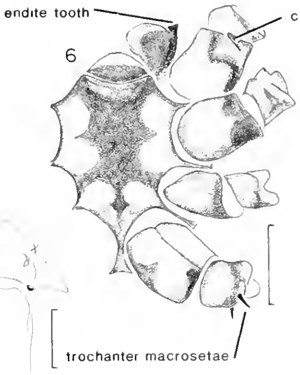
Figures 9–13. *P. acapulco* n. sp., female. 9–11, epigynum. 9, ventral. 10, posterior. 11, lateral. 12, dorsal. 13, abdomen, ventral.

Figures 14–18. *P. honesta* (O. P.-Cambridge), female. 14–16, epigynum. 14, ventral. 15, posterior. 16, lateral. 17, dorsal. 18, abdomen, ventral.

Scale lines 1.0 mm, genitalia 0.1 mm.

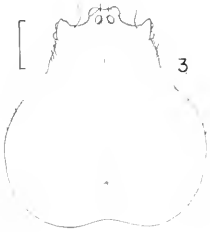


1

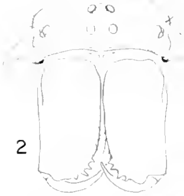


6

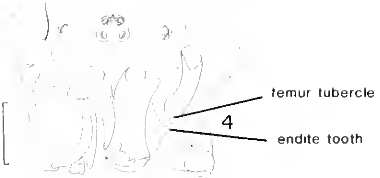
5



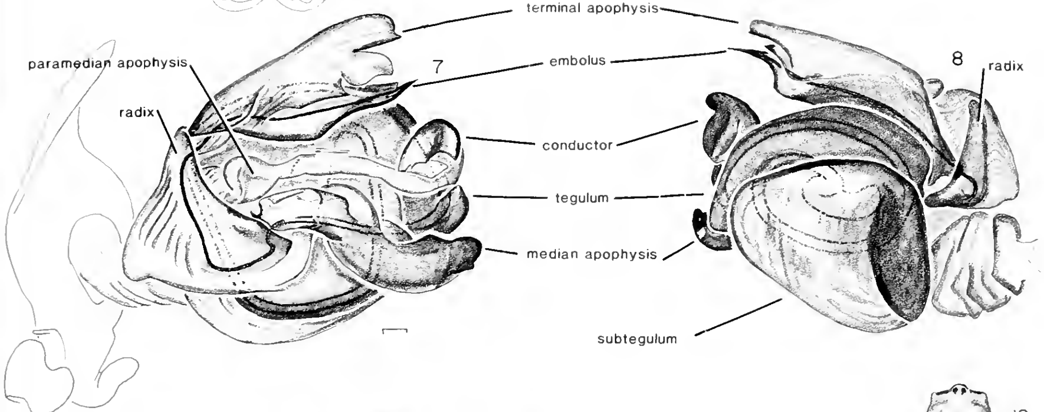
3



2

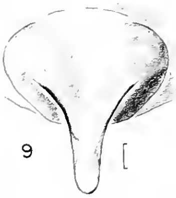


4

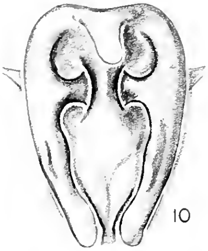


7

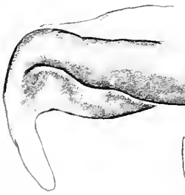
8



9



10

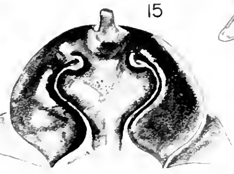


11

12

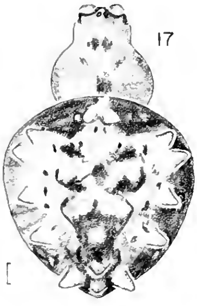
13

14



15

16



17

18

specimen may be conspecific with *P. destricta*.

Parawixia destricta (O. P.-Cambridge)
Figures 19–26; Map 2

Epeira destricta O. P.-Cambridge, 1889: 39, pl. 4, fig. 13, ♂, not 14, ♀. Male holotype from Bugaba, Chiriquí Prov., Panama, not in BMNH, not in HEC, lost. Keyserling, 1892: 105, pl. 5, fig. 78, ♀, ♂.

Parawixia destricta:—F. P.-Cambridge, 1904: 488, pl. 46, figs. 9, 10, ♀, ♂. Roewer, 1942: 870. Bonnet, 1958: 3339.

Note. O. P.-Cambridge (1889) described a male and figured a male and a female, the female of a *Wixia*. F. P.-Cambridge (1904) illustrated the male with the correct female and considered the 1889 male, now lost, to be the type and the correct female a "deuterotype." The British Museum has specimens erroneously marked as types, which come from Guatemala, not from the type locality in Panama. Keyserling (1892) had seen these Guatemala specimens, which were also examined by F. P.-Cambridge; the male undoubtedly is the same species as the lost male holotype.

Description. Female from Guatemala. Carapace orange-brown, lightest between median eyes, with paired dark spots and white setae on cephalic region. Sternum brown with three pairs of orange patches. Coxae orange with brown patches; legs yellowish orange with dark rings and patches. Dorsum of abdomen light and dark orange-brown (Fig. 24); venter with a brown band and two pairs of white spots, the second pair largest (Fig. 25). Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.6 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Abdomen with 11 tubercles: four pairs on sides and three median posterior (Fig. 24). Total length 18 mm. Carapace 9.6 mm long, 5.5 wide. First femur 10.6 mm, patella and tibia 11.7, metatarsus 7.6, tarsus 2.5. Second patella and tibia 10.2 mm, third 6.1, fourth 9.2.

Male from Guatemala. Color as in female. Posterior median eyes 0.6 diameter of anterior medians, anterior laterals 0.5 diameter, posterior laterals 0.6 diameter. Anterior median eyes 0.7 diameter apart. Posterior median eyes their diameter apart. Fourth trochanter without macrosetae. Second femur with ventral row of strong macrosetae, third with a few macrosetae. Second tibia swollen, thicker than first, with prolateral macrosetae. Abdomen with five tubercles: a pair anterior and three posterior. Total length 7.5 mm. Carapace 4.1 mm long, 3.4 wide. First femur 4.8 mm, patella and tibia 6.0, metatarsus 3.5, tarsus 1.4. Second patella and tibia 4.7 mm, third 2.7, fourth 4.0.

Illustrations. Figures 19, 21, 23–26 were made from specimens from Guatemala; Figures 20, 22, from a female from Chiapas.

Note. Males and females were collected together in Guatemala.

Diagnosis. Females differ from those of other species by having the greatest width of the posterior median plate being about equal to the greatest width of the lateral plates in posterior view of the epigynum (Figs. 21, 22). Males differ from those of other species by the strongly curved median apophysis of the palpus (Fig. 26).

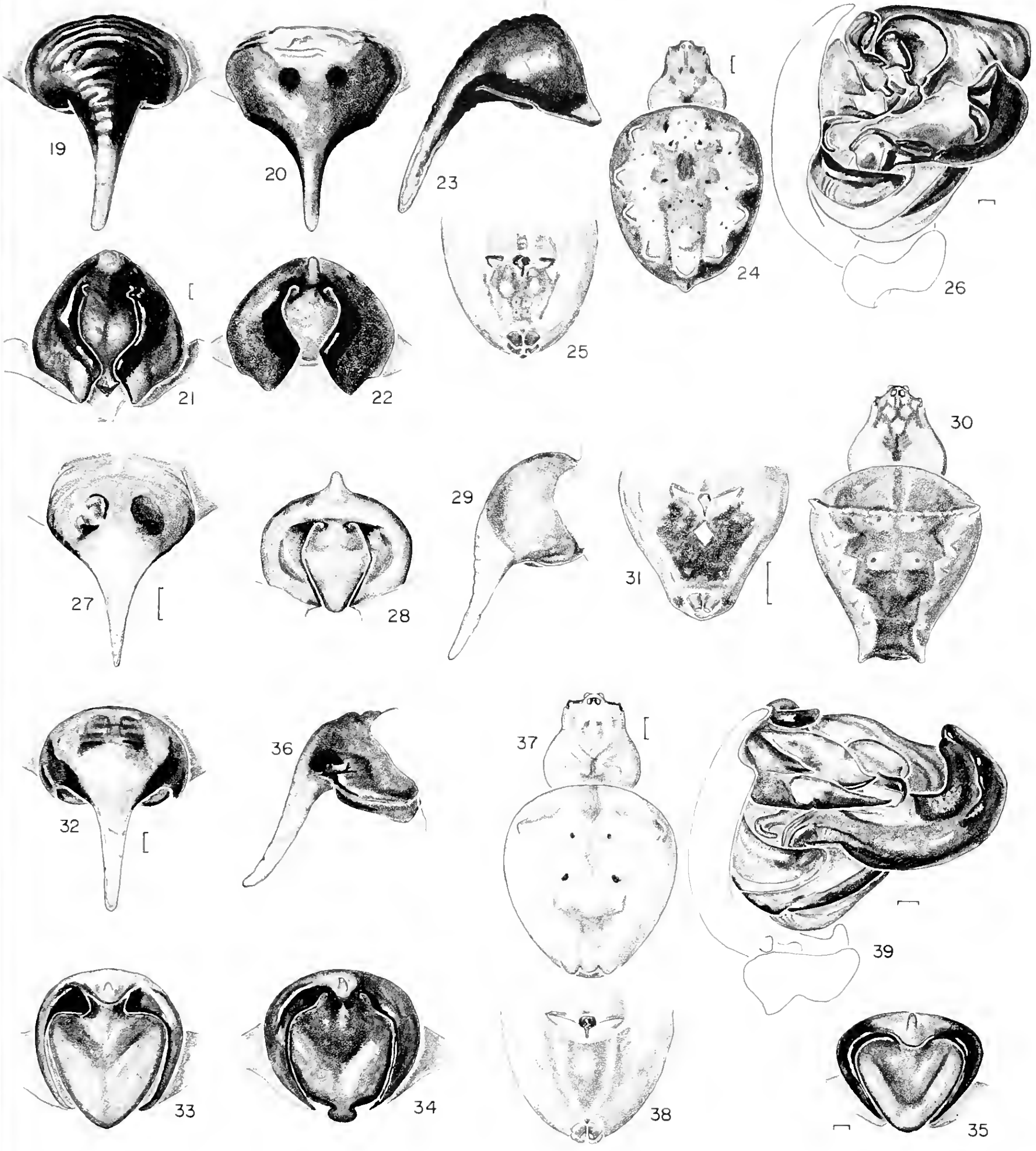
Natural History. The Mexican specimens were collected in a cloud forest.

Records. MEXICO *Oaxaca-Chiapas border:* along ridge SE Cerro Baul, 21 km W Rizo de Oro, 1,615 m, 6–8 Sept. 1972, 2♀ (C. Mullinex, D. E. Breedlove, CAS). GUATEMALA ♀, 2♂ (BMNH, 1905.4.28. 2819–28822 incorrectly marked types).

Parawixia barbacoas new species
Figures 27–31; Map 2

Holotype. Female holotype from near Barbacoas, Depto. Nariño, Colombia, 20 m, 20 Mar. 1974 (W. Eberhard, WE 741), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace orange, cephalic region with symmetrical black markings, but without pairs



Figures 19–26. *Parawixia destricta* (O. P.-Cambridge). 19–25, female. 19–23, epigynum. 19, 20, ventral. 21, 22, posterior. 23, lateral. 24, dorsal. 25, abdomen, ventral. 19, 21, 23, (Guatemala). 20, 22, (Chiapas). 26, left male palpus.

Figures 27–31. *P. barbacoas* n. sp., female. 27–29, epigynum. 27, ventral. 28, posterior. 29, lateral. 30, dorsal. 31, abdomen, ventral.

Figures 32–39. *P. rimosa* (Keyserling). 32–38, female. 32–36, epigynum. 32, ventral. 33–35, posterior. 36, lateral. 32, 33, 36, (syntype). 34, (Cauca, Colombia). 35, (Costa Rica). 37, dorsal. 38, abdomen, ventral. 39, male palpus.

Scale lines 1.0 mm, genitalia 0.1 mm.

of black spots. Chelicerae, labium, endites dusky orange. Sternum clear orange without the usual light patches. Coxae orange, without dusky or darker marks; legs orange, ringed and spotted with black. Dorsum of abdomen with black folium (Fig. 30); venter black with a central white spot and a pair of smaller white spots in front of spinnerets (Fig. 31). Eyes large. Posterior median eyes 0.9 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart, their diameter from laterals. Posterior median eyes their diameter apart, two diameters from laterals. Abdomen with four tubercles (Fig. 30). Total length 7.5 mm. Carapace 3.5 mm long, 2.5 wide. First femur 3.9 mm, patella and tibia 4.7, metatarsus 2.9, tarsus 1.1. Second patella and tibia 4.1 mm, third 2.5, fourth 3.8.

Variation. Total length of females 6.2 to 10.7 mm. The coloration of all four specimens is similar but the Ecuadoran specimen has the posterior median plate less depressed anteriorly. Figures 27–31 were made from the holotype.

Diagnosis. This species differs from others by having marks on the cephalic region, lacking marks on the sternum, and by having only four abdominal tubercles (Fig. 30). The posterior median plate of the epigynum (Fig. 28) is diamond-shaped, unlike that of *P. honesta* (Fig. 15) and *P. destricta* (Figs. 21, 22).

Paratypes. COLOMBIA *Valle:* Cent. Hld. Anchicayá, 400 m, 1978, ♀ (W. Eberhard, MCZ); no date, ♀ (W. Eberhard E77, MCZ). ECUADOR *Pichincha:* Río Corazón, 6.5 km E Río Tandapi, 1,750 m, 18 Feb. 1979, ♀ (L. Burnham, MCZ).

Parawixia rimosa (Keyserling)
Figures 32–39; Map 2

Epeira rimosa Keyserling, 1892: 110, pl. 6, fig. 82, ♀. Three female syntypes and two immatures from Bogotá, Colombia, in BMNH no. 1890.7.1.4674–8, examined.

Parawixia hamata F. P.-Cambridge, 1904: 489, pl. 46, fig. 13, ♂. Parts of male holotype from Costa Rica, in BMNH, examined. Roewer, 1942: 871. Bonnet, 1958: 3340. NEW SYNONYMY.

Aranea destrictoides Strand, 1908: 2. Female holotype from "Popayan oder Cauca" [Popayan, Depto. Cauca], Colombia, in SMF, examined. NEW SYNONYMY.

Parawixia destrictoides:—Roewer, 1942: 870. Bonnet, 1958: 3340.

Parawixia rimosa:—Roewer, 1942: 871. Bonnet, 1958: 3341.

Description. Female from Depto. Cauca, Colombia. Carapace orange with darker spots, darker between median and lateral eyes. Sternum dusky orange with three pairs of lighter patches. Coxae orange with darker streaks; legs dark orange with dusky patches and indistinct dusky rings. Dorsum of abdomen orange brown (Fig. 37); venter black with a median light spot (Fig. 38). Carapace relatively flat and low. Posterior median eyes 0.9 diameter of anterior medians, laterals 0.8 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Abdomen with 10 tubercles (Fig. 37). Total length 11.7 mm. Carapace 4.8 mm long, 3.6 wide. First femur 5.7 mm, patella and tibia 6.9, metatarsus 4.1, tarsus 1.3. Second patella and tibia 6.3 mm, third 3.6, fourth 5.6.

Male from San Pedro, Colombia. Color as in female with distinct, median white patch on black venter of abdomen. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Fourth trochanter with two macrosetae. Second femur with a ventral row of macrosetae. Abdomen as in female. Total length 8.2 mm. Carapace 4.3 mm long, 3.5 wide. First femur 5.1 mm, patella and tibia 6.3, metatarsus 3.9, tarsus 1.5. Second patella and tibia 4.9 mm, third 2.9, fourth 4.5.

Note. Males and females have not been collected together but both sexes have been collected in San Pedro, Colombia, and their distribution is similar.

Variation. The proportions of the epigynum of the syntype illustrated are similar to those of the female from Cauca. In no two individuals is the posterior median plate exactly alike (Figs. 33–35), and the terminal apophysis of males differs slightly among individuals. Some individuals have only four tubercles on the abdomen: two widely separated median anterior tubercles, and two median posterior, close together. Of the three syntypes of *Epeira rimosa*, the epigynum of the one recently molted is illustrated (Figs. 32, 33, 36). Figures 36 to 38 were made from a specimen from Costa Rica; Figure 34 was made from a specimen from Cauca, Colombia, and Figure 39, from Magdalena Dept., Colombia. Total length of females 9.7 to 14 mm, of males 6.2 to 9.5.

Diagnosis. All specimens of this species have a median white patch on the black venter of the abdomen (Fig. 38). Females can be separated from those of *P. destricta* and *P. barbacoas* by the wide posterior median plate and relatively narrow lateral plates in posterior view of the epigynum (Figs. 33–35). Males can be distinguished by the strongly curved median apophysis and from *P. destricta* by the shape of the embolus (Fig. 39).

Natural History. Most specimens come from high elevations, above 1,000 m, but a few are from low elevations. The pair from Ecuador came from a rain forest in Tinalandia.

Distribution. Costa Rica, Colombia to Bolivia (Map 2).

Records. COSTA RICA *Heredia:* La Selva, 50 m, ♀ (W. Eberhard 2756, MCZ). *San José:* nr. Túnel Zurqui, 1,400 m, ♀ (W. Eberhard, MCZ). *Puntarenas:* Monteverde, Campbell's woods, 1,500 m, 5 Apr. 1979, ♂ (J. Coddington, MCZ). COLOMBIA *Magdalena:* San Pedro, 1,160 m, 3 Apr. 1975, ♂ (J. A. Kochalka, MCZ); San Pedro, 500–1,000 m, 1 Aug. 1985, ♀ (H.-G. Müller, SMF); Serra Nueva Granada, 1,300 m, 12 Apr. 1975, ♀ (J. A. Kochalka, MCZ); Pueblo Bello, 1,100 m, 10–17 June 1968, ♂ (B. Malkin, AMNH). *Antioquia:* Ituango, 1,450 m, 26 May 1989, ♀ (M. A. Serna, MNHMC). *Cauca:* between Pienamó and Mondomo, ♀ (W. Eberhard 567, MCZ). *Huila:* 19 km E Station Leticia, 2,300 m, Mar. 1976, ♀ (W. Eberhard, MCZ). *Nariño:* Barbacoas, 20 Mar. 1974, ♀ (W. Eberhard 730, MCZ); La Planada, 1,800 m, 7 km S Choconés, July 1986, 2♀ (W. Eberhard, MCZ). ECUADOR *Pichincha:* Tinalandia, 16 km E Santo Domingo, 680 m, 4 May–25 July 1985, ♀, ♂ (S., J. Peck, AMNH). *Bolívar:* Balzapampa, May to June 1938, ♀ (W. C. Macintyre, MCZ). PERU *Amazonas:* Alto Río Comaina, Pueste de Vigilancia 22, "Falso Paquisha," 850–1,150 m, 21 Oct.–3 Nov. 1987, ♀ (D. Silva D., MUSM). *Junín:* Amable María, ♀ (K. Jelski, PAN). BOLIVIA *La Paz:* Río Zongo, 1,900–2,200 m, 24 Oct.–3 Nov. 1984, ♀ (L. Peña, AMNH). *Cochabamba:* Yungas Chaparé, 1,900–2,800 m, 10–12 Dec. 1984, ♀ (L. Peña, AMNH).

Parawixia guatemalensis (O. P.-Cambridge)
Figures 40–45; Map 2

Epeira guatemalensis O. P.-Cambridge, 1889: 40, pl. 7, fig. 7, ♀, not fig. 8, ♂. Female lectotype (with most legs separated) designated by F. P.-Cambridge from "Livingston, Chicoyoito [?], Polochic Valley near Tamahú [Rio Polochic, Alta Verapaz], Cubilguitz [Gubilguitz, Depto. Alta Verapaz, 15°38′N, 90°22′W], Guatemala," in BMNH no. 1905. 4.28.2826–30. Keyserling, 1892: 112, pl. 6, fig. 83, ♀, not ♂.

Epeira merens O. P.-Cambridge, 1898: 246, pl. 31, fig. 2, ♀. Five female syntypes from Atoyac [18°54′N, 96°46′W], Veracruz State, Mexico, in BMNH no. 1905.4.28.2826–2830, examined. First synonymized by F. P.-Cambridge, 1904.

Parawixia guatemalensis:—F.P.-Cambridge, 1904: 489, pl. 46, fig. 14, ♀. Roewer, 1942: 870. Bonnet, 1958: 3340.

Description. Female lectotype. Carapace orange to brown. Sternum orange with three pairs of light patches. Coxae yellowish with brown patches; legs yellowish with brown patches and rings. Dorsum of abdomen with blackish brown median longitudinal band and white cardiac mark (Fig. 43); venter with black band containing two pairs of white spots (Fig. 44). Posterior median eyes 0.7 diameter of anterior medians, laterals 0.8 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Abdomen with nine tubercles (10 according to F. P.-Cambridge): two pairs on sides and five posterior (Fig. 43). Total length 12 mm. Carapace 5.2 mm long, 4.1 wide. First femur 5.0 mm, patella and tibia 6.6, metatarsus 4.1, tarsus 1.5. Second patella and tibia 6.0 mm, third 3.6, fourth 5.5.

Male. Color as in female but with dark patches on carapace and abdomen darker without cardiac mark. Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.6 diameter. Anterior median eyes 0.6 diameter apart. Posterior median eyes 0.8 diameter apart. Fourth trochanter with three macrosetae. A pair of macrosetae, side by side on proximal end of femur. Second tibia thicker than first, swollen with prolateral macrosetae. Abdomen as in female. Total length 9.3 mm. Carapace 5.2 mm long, 4.3 mm wide. First femur 7.5 mm, patella and tibia 8.5 mm, metatarsus 5.8 mm, tarsus 3.3 mm. Second patella and tibia 6.3 mm, third 3.8 mm, fourth 5.7 mm.

Note. Males and females were matched because of similar size and both having four white spots on the underside of the abdomen.

Variation. The females other than the type have three pairs of lateral abdominal tubercles and five posterior. Total length of females 11.3 to 15.0 mm. The female lectotype and the only male have been illustrated.

Diagnosis. The long, vase-shaped posterior median plate of the epigynum (Fig. 41) and the relatively short scape are diagnostic (Figs. 40, 42). The male differs from that of *P. nesophila* by having four white spots on the underside of the abdomen and details of the palpal sclerites.

Natural History. The male was collected in a cloud forest.

Records. MEXICO *Oaxaca-Chiapas:* ridge SE Cerro Baul, 21 km W Rizo de Oro, 1,615 m, 6–8 Sept. 1972, ♂ (C. Mullinex, D. E. Breedlove, CAS). GUATEMALA *Suchitepequez:* Finca Santa Adelaida, 13 km N Santa Bárbara, 14, 15 July 1959, ♀ (C., P. Vaurie, AMNH).

Parawixia tredecimnotata F. P.-Cambridge
Figures 46–51; Map 3

Parawixia tredecimnotata F. P.-Cambridge, 1904: 490, pl. 46, fig. 16, ♀. Female holotype from Guatemala, in BMNH no. 1905.4.28.2833, examined. Roewer, 1942: 871. Bonnet, 1958: 3341.

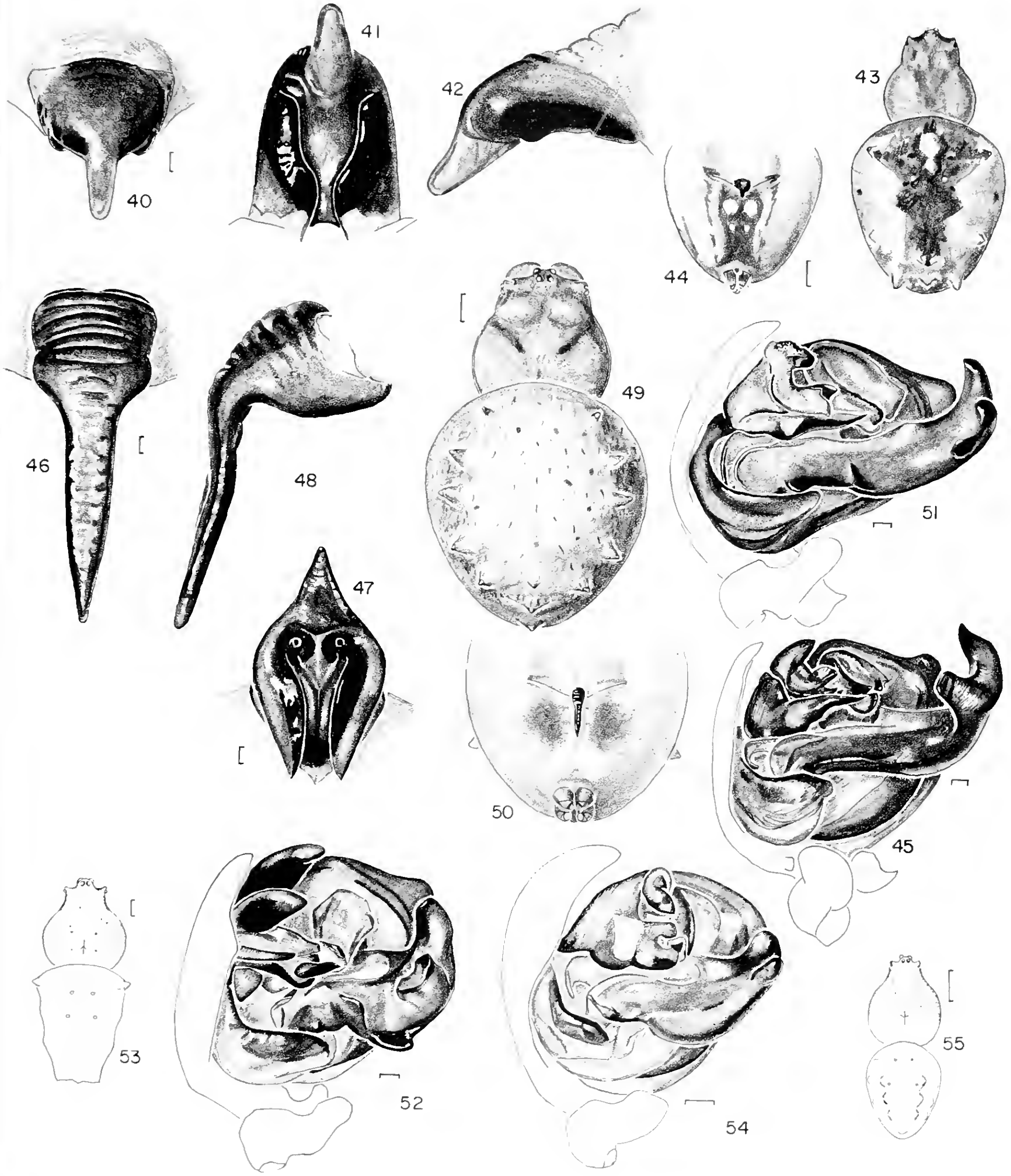
Parawixia cambridgei Bryant, 1940: 342, figs. 104–106, ♀, ♂. Female holotype from coast below Pico Turquino, Santiago de Cuba Prov., Cuba, in MCZ, examined. Brignoli, 1983: 278. NEW SYNONYMY.

Description. Female holotype of *P. tredecimnotata.* Carapace brown with darker brown spots. Sternum brown with pairs of light patches. Coxae lighter than sternum; legs brown with darker patches. Dorsum of abdomen brown, darker on sides (Fig. 49); venter with two dark brown patches side by side (Fig. 50). Eyes subequal. Anterior median eyes slightly less than their diameter apart. Posterior median eyes their diameter apart. Abdomen subspherical, with 13 tubercles (Fig. 49). Total length 12.7 mm. Carapace 5.8 mm long, 4.7 wide. First femur 6.8 mm, patella and tibia 8.4, metatarsus 5.1, tarsus 1.8. Second patella and tibia 7.5 mm, third 4.7, fourth 7.2.

Male from Yucatan, Mexico. Color lighter, more orange than female and with a pair of light patches on venter in front of spinnerets. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 0.8 diameter apart. Posterior median eyes 1.1 diameters apart. Second, third and fourth femora each with a row of ventral macrosetae. Third trochanter with one short macroseta. Abdomen with 13 tubercles. Total length 9.4 mm. Carapace 5.4 mm long, 4.4 wide. First femur 6.7 mm, patella and tibia 8.0, metatarsus 4.9, tarsus 1.7. Second patella and tibia 5.9 mm, third 4.1, fourth 5.8.

Note. The female and the male were collected together in Cuba.

Variation. Total length of females 11.5 to 16.0 mm, of males 8.1 to 9.4. The male paratype of *P. cambridgei* has macrosetae on the third and fourth trochanters. The



Figures 40–45. *Parawixia guatemalensis* (O. P.-Cambridge), female. 40–42, epigynum. 40, ventral. 41, posterior. 42, lateral. 43, dorsal. 44, abdomen, ventral. 45, left palpus.

Figures 46–51. *P. tredecimnotata* F. P.-Cambridge. 46–50, female. 46–48, epigynum. 46, ventral. 47, posterior. 48, lateral. 49, dorsal. 50, abdomen, ventral. 51, male palpus.

Figures 52, 53. *P. casa* n. sp., male. 52, palpus. 53, dorsal.

Figures 54, 55. *P. porvenir* n. sp., male. 54, palpus. 55, dorsal.

Scale lines 1.0 mm, genitalia 0.1 mm.

female holotype and a male from Yucatan have been illustrated.

Diagnosis. Females have a pair of more or less distinct bulges on the cephalic region (Fig. 49). The female can be separated from other Central American *Parawixia* species by the relatively long, flat scape of the epigynum (Figs. 46, 48). In some individuals the scape has been broken off. The male can be separated by the shape of the relatively small terminal apophysis, the large conductor, and the shape of the median apophysis (Fig. 51). This is the only *Parawixia* species known from the Greater Antilles.

Natural History. Specimens were found in a short tropical rain forest in Campeche, Mexico, and on a building in Jamaica.

Distribution. Southern Mexico, Guatemala, and Greater Antilles (Map 3).

Records. MEXICO *Chiapas:* Tampico, 15 July 1909, ♀ (F. A. Schwarz, USNM). *Campeche:* Chicanna Ruins, ca. 8 km W Xpujil, 18°32'N, 89°31'W, 12–14 July 1983, ♀ (W. Maddison, MCZ). *Yucatan:* Chichen Itza, 16 July 1952, ♂ (J., D. Pallister, AMNH). BELIZE Corosal, 28 June 1975, 2♀ (W. C. Sedgwick, MCZ). JAMAICA *Westmoreland:* Negril, 23–30 Mar. 1981, ♂ (H., L. Levi, MCZ). HAITI Damiens, 1931, ♀ (H. L. Dozier, AMNH).

Parawixia casa new species
Figures 52, 53; Map 2

Holotype. Male holotype from Cali, Colombia, on house, 1973, 1974 (W. Eberhard), in MCZ. The specific name is a noun in apposition after the Spanish word for house.

Description. Male holotype. Carapace orange, with paired spots, sides of thoracic region dusky, dark dusky between median and lateral eyes. Sternum dusky orange with three pairs of clear orange patches. Coxae dusky orange; legs orange to mostly gray and black. A white transverse line on dorsum of abdomen (Fig. 53) between anterior tubercles and a folium in middle; venter dusky with two pairs of tiny white spots in center. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 0.9 diameter apart. Posterior median eyes their diameter apart. Fourth trochanter with two short macrosetae. Third femur only with a distinct row of ventral macrosetae. Abdomen with five tubercles: one pair anterior and three posterior in a row (Fig. 53). Total length 8.0 mm. Carapace 4.2 mm long, 3.4 wide. First legs missing. Second patella and tibia 4.5 mm, third 2.7, fourth 4.0.

Note. The male was first thought to be that of *P. barbacoas,* for which only the female is known, but they differ in coloration of the carapace, of the sternum, and of the venter of the abdomen.

Diagnosis. The peculiar shape of the median apophysis of the palpus (Fig. 52) distinguishes the male from males of other species.

Parawixia porvenir new species
Figures 54, 55; Map 2

Holotype. Male holotype from Finca Chenevo, ca. 20 km N Río Muco, 20 km S El Porvenir, 170 m, Depto. Meta, Colombia, no date (W. Eberhard), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Male holotype. Carapace yellowish with a dusky patch on each side extending posteriorly from below lateral eyes to anterior of thoracic region, and lacking paired dark spots (Fig. 55). Chelicerae yellowish with a dusky streak. Endites, labium dusky yellowish. Sternum dusky with three pairs of clear yellowish patches. Coxae yellowish; legs yellow with dusky marks and rings. Dorsum of abdomen spotted, with folium outlined with black. Venter dusky with three pairs of small white spots. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Fourth trochanter with two short macrosetae on one side, one on the other. Second, third, and fourth femora each with ventral row of macrosetae. Abdomen with five tubercles: one pair anterior and three posterior median. Total length 5.5 mm. Carapace 2.7 mm long, 2.1 wide. First femur 3.1 mm, patella and tibia 3.5, metatarsus 2.1, tarsus 0.3. Second patella and tibia 2.7 mm, third 1.5, fourth 2.7.

Diagnosis. The first tarsus only, on both sides, is minute. This may be a character of the species or a malformation of the male. The C-shaped embolus, which appears to have a cap, and the distal lobe of the median apophysis make the palpus distinct from that of other species (Fig. 54).

Parawixia hypocrita (O. P.-Cambridge)
Figures 56–62; Map 2

Epeira hypocrita O. P.-Cambridge, 1889: 38, pl. 5, fig. 8, ♂. Male holotype from Bugaba, Chiriquí Prov., Panama, in BMNH, examined. The male was on a pin in alcohol, which was removed. Keyserling, 1892: 109, pl. 5, fig. 81, ♂.

Parawixia hypocrita:—F. P.-Cambridge, 1904: 489, pl. 46, fig. 12, ♂. Roewer, 1942: 871. Bonnet, 1958: 3340.

Description. Female from Barro Colorado Island, Panama. Carapace orange-brown with darker spots. Sternum, coxae, legs orange-brown. Dorsum of abdomen black-brown and white (Fig. 59); venter black with a white spot in center (Fig. 60). Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Abdomen with about 10 tubercles (Fig. 59). Total length 11.7 mm. Carapace 5.0 mm long, 4.0 wide. First femur 6.2 mm, patella and tibia 7.7, metatarsus 4.6, tarsus 1.5. Second patella and tibia 6.8 mm, third 4.0, fourth 6.2.

Male holotype. Color as in female, except for abdominal pattern of the holotype (Fig. 62). Posterior median eyes 0.6 diameter of anterior medians, anterior laterals 0.6 diameter, posterior laterals 0.5 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Fourth trochanter with two short macrosetae. Total length 6.4 mm. Carapace 3.6 mm long, 2.7 wide. First femur 5.2 mm, patella and tibia 6.1, metatarsus 3.4, tarsus 1.1. Second patella and tibia 5.3 mm, third 2.5, fourth 3.7.

Note. The species is common in Panama, and males and females were collected together.

Variation. Total length of females from 10.2 to 15.0 mm, of males 6.2 to 7.2. Specimens from Napo, Ecuador, lack the median ventral white spot. The male holotype and a female from Barro Colorado Island, Panama, were illustrated.

Diagnosis. The abdomen of the females is trapezoidal (Figs. 59, 62). Females can be separated from similar species by the small, square, posterior median plate of the epigynum (Fig. 57). The palpus of the male differs from that of any other species in having a pointed median apophysis bearing a small knob on its margin (Fig. 61).

Distribution. Guatemala to Roraima Terr., Brazil, and Beni Prov., Bolivia (Map 2).

Records. GUATEMALA Livingston, May, ♀ (USNM). NICARAGUA Musawas, 10–31 Oct. 1955, ♀ (B. Malkin, AMNH). COSTA RICA *Heredia:* La Selva, Dec. 1980, imm. (W. Eberhard 2175, MCZ); Feb. 1986, ♀ (W. Eberhard 3229, MCZ). PANAMA *Panamá:* Barro Colorado Island, 16 July 1954, numerous ♀♀, ♂♂ from several collections (AMNH, MCZ); Experimental Gardens, Chilibre, Fort Sherman, (all A. M. Chickering, MCZ); Gamboa (W. Eberhard, MCZ). COLORADO *Nariño:* La Planada, 1,800 m, 7 km S Choconés, Aug. 1986, ♀ (W. Eberhard, MCZ). ECUADOR *Napo:* Cuyabeno, Puce Field Sta., 1–7 Aug. 1988, ♀ (W. Maddison, MCZ); Cuyabeno, Laguna Grande, 25–29 June 1988, ♀ (W. Maddison, MCZ); Dureno, S. Río Aguarico, 25–30 Sept. 1977, ♀ (L. Peña, AMNH). PERU *Madre de Dios:* Zona Reservada Pakitza, 20 Sept. 1987, ♀ (I. Bohorquez M., MUSM). BRAZIL *Roraima:* Ilha do Maracá, 21 July 1987, 2♀ (A. A. Lise, MCN). BOLIVIA *Beni:* Estac. Biol. Beni, 9 Sept. 1987, ♀ (J. Coddington, S. Larcher, USNM).

Parawixia nesophila Chamberlin and Ivie
Figures 63–68; Map 2

Parawixia nesophila Chamberlin and Ivie, 1936: 52, pl. 16, figs. 141–143, ♀. Female holotype from Barro Colorado Island, Lago Gatún, Panama, in AMNH, examined. Roewer, 1942: 871. Bonnet, 1958: 3340.

Description. Female holotype. Carapace orange with symmetrical dark marks, darkest between median and lateral eyes, lightest between median eyes (Fig. 66). Sternum dusky with paired orange patches on sides. Coxae orange with dusky patches; legs orange with brown spots and rings. Dorsum of abdomen orange-brown with brown streaks and spots, and folium outlined with dark brown (Fig. 66). Venter black with a white patch in middle (Fig. 67). Posterior median eyes 0.8 diameter of anterior medians, laterals 0.8 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Abdomen with 12 tubercles; the anterior lateral tubercle is double and the tubercle above the spinnerets is missing (Fig. 66). Total length 12.0 mm. Carapace 6.1 mm long, 4.8 wide. First femur 6.8 mm, patella and tibia 8.5, metatarsus 5.3, tarsus 1.5. Second patella and tibia 7.7 mm, third 4.4, fourth 7.0.

Male from Barro Colorado Island. Color as in female, but carapace without dark marks. Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.6 diameter. Anterior median eyes 0.7 diameter apart. Posterior median eyes their diameter apart. Fourth trochanter with two short macrosetae. Abdomen with 12 tubercles: the second, third, and fourth pairs small. Total length 8.0 mm. Carapace 4.7 mm long, 3.9 wide. First femur 6.0 mm, patella and tibia 7.0, metatarsus 4.2, tarsus 1.4. Second patella and tibia 5.4 mm, third 3.1, fourth 4.8.

Note. The male was collected at the type locality.

Variation. Total length of females 9.0 to 14.4 mm, of males 8.0 to 8.8. All illustrations were made from Barro Colorado Island specimens.

Diagnosis. The 13 abdominal tubercles, with anterior laterals double (Fig. 66), and the narrow median posterior plate of the epigynum, bordered on each side by convex margins of the lateral plates (Fig. 64), distinguish this species from the Brazilian *P. inopinata* (Fig. 70). The male differs from *P. guatemalensis* (Fig. 45) and *P. inopinata* (Fig. 73) by the shape of the terminal apophysis and median apophysis of the palpus (Fig. 68), and from *P. guatemalensis* by having a median white patch on the underside of the abdomen.

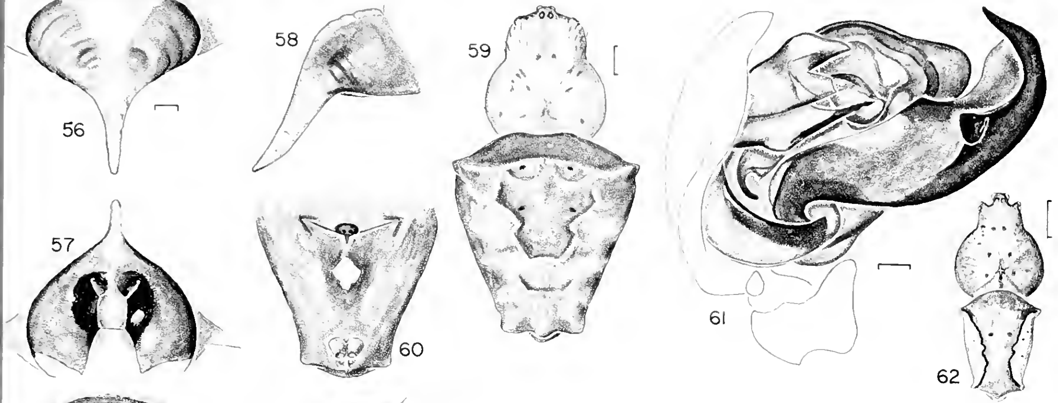
Natural History. Parawixia nesophila is apparently found in forested areas. A male was found in Costa Rica in leaf litter.

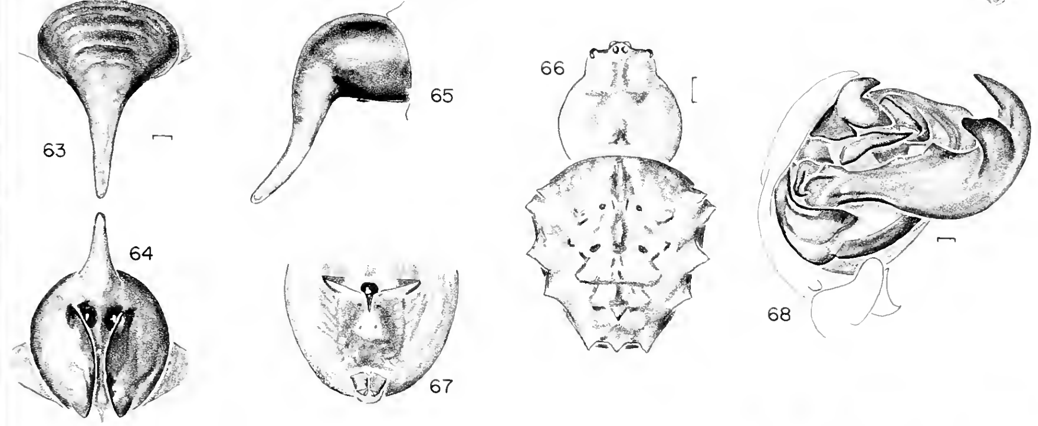
Records. COSTA RICA Hacienda de Limón [?, unknown locality], ♀ (USNM). *Puntarenas:* Rincón de Osa, 15 Aug. 1966, ♂ (S. Peck, AMNH). PANAMA *Colon:* Paraíso, Feb. 1911, ♀ (E. A. Schwarz, USNM). *Panamá:* Barro Colorado Island, Lago Gatún, Aug. 1928, 2♀ (A. M. Chickering, AMNH); July 1936, ♀; Aug. 1939, 2♀; July 1950, ♀; July 1954, ♀; Aug. 1954, ♂, imm. (all A. M. Chickering, MCZ); ♀ (Y. Lubin, MCZ).

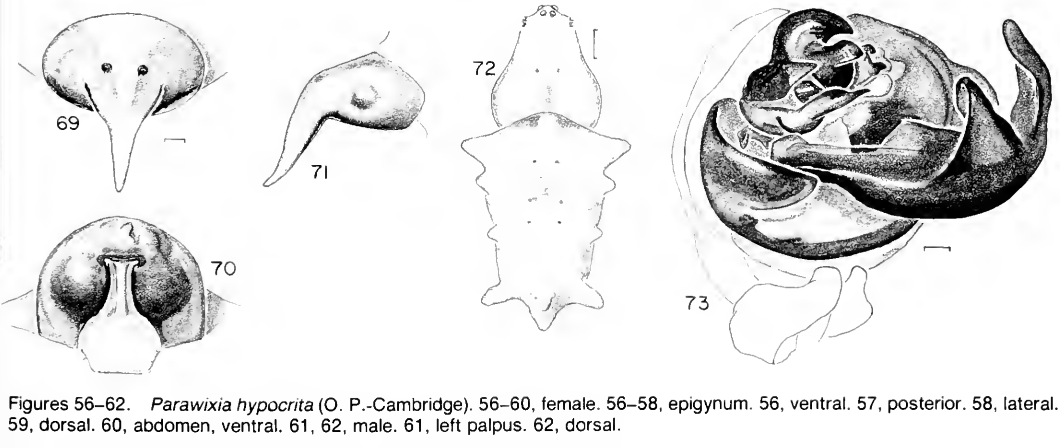
Parawixia inopinata Camargo
Figures 69–73; Map 2

Parawixia inopinata Camargo, 1950: 223, pl. 2, figs. 7–9, pl. 13, figs. 2, 3, ♂. Male holotype from Boracéia, Mun. Salesópolis, Est. São Paulo, Brazil, in MZSP no. 1347, examined. Brignoli, 1983: 278.

Description. Female from Rio Grande do Sul, Brazil. Carapace orange with a pair of darker spots on cephalic region and a thin dusky line on each side of thoracic region (Fig. 72). Sternum dusky orange. Coxae orange with dusky distal patch; legs orange with black rings on first two femora and at ends of tibiae and tarsi. Dorsum of abdomen yellowish with black patches (Fig. 72); venter black behind epigynum, white in front of spinnerets. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 0.8 diameter apart. Posterior median eyes their diameter apart. Abdomen narrow with three pairs of lateral tubercles,







Figures 56–62. *Parawixia hypocrita* (O. P.-Cambridge). 56–60, female. 56–58, epigynum. 56, ventral. 57, posterior. 58, lateral. 59, dorsal. 60, abdomen, ventral. 61, 62, male. 61, left palpus. 62, dorsal.

Figures 63–68. *P. nesophila* Chamberlin and Ivie. 63–67, female. 63–65, epigynum. 63, ventral. 64, posterior. 65, lateral. 66, dorsal. 67, abdomen, ventral. 68, male palpus.

Figures 69–73. *P. inopinata* Camargo. 69–72, female. 69–71, epigynum. 69, ventral. 70, posterior. 71, lateral. 72, dorsal. 73, male palpus.

Scale lines 1.0 mm, genitalia 0.1 mm.

four posterior (Fig. 72). Total length 12.0 mm. Carapace 4.7 mm long, 3.5 wide. First femur 6.9 mm, patella and tibia 8.0, metatarsus 6.0, tarsus 1.9. Second patella and tibia 4.7 mm, third 3.9, fourth 6.7.

Male holotype. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 1.3 diameters apart. Posterior median eyes 1.5 diameters apart. Fourth trochanter with three short macrosetae. Abdomen with tubercles as in female. Total length 7.8 mm. Carapace 4.2 mm long, 3.3 wide. First femur 5.8 mm, patella and tibia 7.3, metatarsus 5.5, tarsus 1.6. Second patella and tibia 5.0 mm, third 3.0, fourth 5.0.

Note. Male and female are matched on the basis of their similar abdomen shape (Fig. 72). Also the genitalia of both sexes (Figs. 69–71, 73) resemble those of *P. nesophila*.

Diagnosis. Both the male and the female are close to the Panamanian *P. nesophila*. The female differs by having a bottle-shaped posterior median plate of the epigynum (Fig. 70). The male differs by having longer prongs of the median apophysis of the palpus (Fig. 73).

Record. BRAZIL *Rio Grande do Sul:* Caracol, Canela, 27 Dec. 1972, ♀ (M. Fernandez, MCN 0689).

Parawixia velutina (Taczanowski), new combination
Figures 74–80; Map 3

Epeira velutina Taczanowski, 1878: 159, pl. 1, fig. 10, ♀. Female lectotype here designated from wasp nest from Amable María, Depto. Junín, Peru, in PAN, examined.

Aranea velutina:—Roewer, 1942: 855.

"*Araneus*" *eriophoroides* di Caporiacco, 1954: 111, figs. 29, 29a. Female from *Trypoxylon* wasp nest from Charvein, French Guiana, lost (not in MNHN, MZUF). Brignoli, 1983: 262. NEW SYNONYMY.

Araneus velutinus:—Bonnet, 1955: 627.

Note. The type collection from a wasp nest contains the female lectotype and one female and one immature paralectotype of *E. velutina*, three female paralectotypes, that are probably *P. ouro*, and a male and an immature paralectotype, that are *Wagneriana jelskii.*

Measurements and illustrations of *A. eriophoroides* suggest that it is this species.

Description. Female lectotype. Carapace orange with a pair of dusky spots, darker on clypeus and lateral to median eyes. Sternum dusky with three pairs of light patches. Coxae yellowish with dusky patches; legs yellowish with darker rings. Dorsum of abdomen with faint indications of a folium (Fig. 78); venter dusky with three to four pairs of indistinct white round spots (Fig. 79). Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Abdomen with 15 tubercles: four pairs on sides, one small anterior median, and six posterior. Of these, one pair and four medians above spinnerets. Posterior tubercles with cap (Fig. 78). Total length 9.6 mm. Carapace 4.7 mm long, 3.6 wide. First femur 4.5 mm, patella and tibia 6.2, metatarsus 3.6, tarsus 1.3. Second patella and tibia 5.6 mm, third 3.1, fourth 5.0.

Male from near Puerto Lleras, Meta, Colombia. Carapace orange with paired dark spots and white setae. Sternum dusky with pairs of clear orange patches on sides. Coxae, legs orange. Dorsum of abdomen speckled white, venter dusky white. Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.6 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Fourth trochanter with three stout macrosetae. All femora with ventral row of macrosetae. Abdomen with at least 11 tubercles. Total length 7.8 mm. Carapace 4.7 mm long, 3.8 wide. First femur 5.2 mm, patella and tibia 6.4, metatarsus 3.7, tarsus 1.3. Second patella and tibia 5.4 mm, third 3.1, fourth 4.3.

Note. Males and females were collected together in Mato Grosso, and both were collected at a second locality in Mato Grosso although not together.

Variation. Total length of females 11 to 13.6 mm, of males 6.2 to 9.2. The anterior median tubercle of the abdomen and the most posterior tubercle above the spinnerets may be present or absent. Figures 74–79 were made from a female from Diamantina, Minas Gerais, Brazil; Figure 80 was made from a male from Meta Dept., Colombia.

Diagnosis. Females can be separated from most *Parawixia* species by the shape of the scape, which has a knob above its tip. From *P. monticola* they are separated by another feature of the epigynum: the lateral plates overhang the median plate, forming a slit with almost parallel edges in posterior view (Figs. 75, 76). The male can be separated from males of most species by the three macrosetae on the fourth trochanter, by having the median apophysis distally bilobed, and having proximally a small tooth just above the radix (Fig. 80).

Natural History. A male was collected by sweeping shrubs in Colombia, and from a forest in Argentina.

Distribution. Amazon area, Guianas to Misiones Prov., Argentina (Map 3).

Records. GUYANA nr. Yupukarri, Rupununi Riv., 10 Nov. 1937, ♀ (W. G. Hassler, AMNH). COLOMBIA *Meta:* Monte Redondo, 1,500 m, 45 km W Villavicencio, June 1949, ♂ (L. Richter, AMNH); Lomalinda, nr. Puerto Lleras, 3°16′N, 73°23′W, 26 Sept. 1985, ♂ (B. Carroll, MCZ); 6 km SW Puerto Lopez, ♀ (W. Eberhard 1480, MCZ). PERU *Apurímac:* Ninabamba, Río Pampas, [2,135 m, ca. 13°28′N, 73°49′W], 129 km SE Ayacucho, 2 Oct. 1947, ♀ (W. Weyrauch, AMNH). *Madre de Dios:* Zona Reservada Tambopata, 25 July 1987, ♀ (D. Silva D., MUSM); Reserva Cuzco Amazonico, 15 km NE Puerto Maldonado, 14 July 1989, ♀, imm. (D. Silva D., MUSM). BOLIVIA *La Paz:* Miguilla, 1,800 m, 2–3 Dec. 1984, ♀ (L. E. Peña, AMNH). BRAZIL *Goiás:* Fazenda Mongolinho, Corumbá, 8 June 1942, ♂ (K. Lenko, MZSP 6663). *Mato Grosso:* Chapada dos Guimarães, 18 Nov. 1983, 2♂ (M. Hoffman, MCN 11982, 11984); Barra dos Bugres, Nov. 1983, ♀ (A. Cerrutti, MNRJ); no date, ♂ (A. Cerrutti, MNRJ); Barra do Tapirapé, Jan. 1963, 2♂ (B. Malkin, AMNH); 17 Jan.–2 Feb., ♀ (B. Malkin, MZSP 3403). *Mato Grosso do Sul:* 50 km S Campo Grande, 17 July 1988, ♂ (P. Salinas, AMNH). *Minas Gerais:* Carmo do Rio Claro, 3♂ (J. C. Carvalho, MNRJ); Minas Serinha Diamantina, Jan.–Mar. 1943, ♀ (E. Cohn, AMNH); Morro da Graça, 18–20 Oct. 1964, ♀ (Exped. Zool. MZSP 4180). *São Paulo:* 6 km N Paraguaçu Paulista, Feb. 1965, ♂ (G. Eiten, AMNH); Botucatu, 12 Feb. 1987, ♀ (I. M. P. Rinaldi, IMPR); Fazenda Itaquere, 25 Nov. 1963, ♂ (K. Lenko, MZSP 6962); Fazenda Graciosa, Piraçununga, 31 May 1947, ♂ (Schubart, MZSP 6442). *Paraná:* Rôlandia, 1948, ♂ (A. Maller, AMNH). *Rio Grande do Sul:* Tenente Portela, 29 Nov. 1978, ♂ (H. Bischoff, MCN 8436); Garruchos, São Borja, 11 Dec. 1975, ♀, 2♂ (A. A. Lise, MCN 10978); Itapua, Viamão, 5 Feb. 1975, ♀ (A. A. Lise, MCN 2446); Ponta Grossa, Porto Alegre, 13 Sept. 1975, ♀ (A. A. Lise, MCN 3013); Bage, 28 Oct. 1981, ♀ (A. A. Lise, MCN 9966); Farroupilha, 29 Sept. 1978, ♀ (H. Bischoff, MCN 8320); Passo Fundo, 12 Oct. 1985, 2♀ (A. A. Lise, MCN 14341). PARAGUAY *Chaco:* Parque Nac. Defensores del Chaco, 18–27 Nov. 1984, ♂ (J. Kochalka, IBNP). ARGENTINA *Misiones:* ♀ (R. V. Partridge, MACN); Eldorado, 1964, ♂ (A. Kovacs, AMNH). *Jujuy:* Calilegua Natl. Park, 18–28 Dec. 1987, ♀ (S., J. Peck, AMNH). *Salta:* El Rey Natl. Park, 1,000 m, 5–15 Dec. 1987, ♀ (S., J. Peck, AMNH).

Parawixia monticola (Keyserling), new combination

Figures 81–87; Map 3

Epeira monticola Keyserling, 1892: 94, pl. 4, fig. 70, ♀. Female holotype and four early instar paratypes from Serra Vermelha, Est. Rio de Janeiro, Brazil, in BMNH, examined and labeled.

Aranea monticola:—Roewer, 1942: 847.

Araneus monticola:—Bonnet, 1955: 546.

Description. Female holotype. Carapace orange-brown with dark patches and light and dark setae (Fig. 85). Sternum dark brown with pairs of light patches on sides. Legs with darker rings. Dorsum of abdomen with patches of different shades of brown (Fig. 85); venter dusky to black

(Fig. 86). Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.8 diameter, posterior 0.7 diameter. Anterior median eyes slightly less than their diameter apart. Posterior median eyes their diameter apart. Abdomen with three pairs of lateral tubercles and five posterior (Fig. 85). Total length 12 mm. Carapace 5.2 mm long, 3.7 wide. First femur 5.7 mm, patella and tibia 7.1, metatarsus 4.5, tarsus 1.5. Second patella and tibia 6.4 mm, third 3.9, fourth 6.1.

Male from Minas Gerais, Brazil. Color as in female. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Fourth trochanter with two macrosetae on right, three on left. Abdomen as in female. Total length 7.8 mm. Carapace 4.2 mm long, 3.6 wide. First femur 5.1 mm, patella and tibia 6.4, metatarsus 3.2, tarsus 1.2. Second patella and tibia 5.1 mm, third 3.0, fourth 4.7.

Note. The males were not collected with females but with two males of *P. velutina*. Their similarity to females in appearance and being collected within the same range suggested the match.

Variation. Total length of females 9.6 to 13.6 mm. The female from Bahia had the posterior median plate narrower than the one illustrated (Figs. 82, 83). Females from Itabapoana and Porto Cabral had the epigynum with a larger base relative to the length of the scape. Both females belonging to the MNRJ had their scapes broken off. Figures 81, 82, 85, 86 were made from the holotype; Figures 83, 84, from a specimen from Sumaré, Rio de Janeiro, in AMNH.

Diagnosis. In posterior view (Figs. 82, 83), the epigynum of *P. monticola* has a round posterior median plate, constricted dorsally, while that of *P. velutina* is very narrow over most of its length (Figs. 75, 76). But there is considerable variation in the shape of the posterior median plate and the shape of its base.

Natural History. A female was collected in Espírito Santo in an orb on a shrub in woods, another in Itabapoana hanging on a thread from a leaf of a shrub in woods at night.

Records. BRAZIL *Bahia:* Rio Jacuípe, ♀ (MNRJ). *Espírito Santo:* Apiacá, 26 July 1987, ♀ (R. L. C. Baptista, RLCB). *Minas Gerais:* Lagôa Santa, ♀ (Reinhardt, ZMK); Carmo do Rio Claro, 2♂ (J. C. Carvalho, MNRJ). *Rio de Janeiro:* Sumaré, Rio de Janeiro, Jan., Feb. 1946, 2♀ (H. Sick, AMNH); Rio de Janeiro, 26 May 1979, ♀ (C. J. Becker, MCN 8579), 14 Sept. 1987, ♀ (R. Sanches, RLCB); Botanical Garden, Rio de Janeiro, Nov. 1983, ♀ (R. Domingues, RLCB); Bom Jesus do Itabapoana, 14 June 1987, ♀ (R.L.C. Baptista, RLCB). *São Paulo:* Porto Cabral, 1941, ♀ (L. Travassos Filho, MZSP 9579). *Rio Grande do Sul:* Porto Alegre, ♀ (MNRJ).

Parawixia hoxaea (O. P.-Cambridge)
Figures 88–92; Map 3

Epeira hoxaea O. P.-Cambridge, 1889: 35, pl. 5, fig. 6, ♀. Two female syntypes and one abdomen from Tolé, Chiriquí Prov., Panama, in BMNH no. 1905.4.28.2831–2832, examined. Keyserling, 1892: 87, pl. 4, fig. 65, ♀.

Parawixia hoxaea:—F. P.-Cambridge, 1904: 490, pl. 46, fig. 15, ♀. Roewer, 1942: 871. Bonnet, 1955: 3340.

Note. There are two female syntypes and one abdomen. The abdomen may be of a different species but it may be the epigynum of this abdomen that was illustrated by O. P.-Cambridge. Here I follow Keyserling (1892) and F. P.-Cambridge (1904), who illustrated the epigynum of a complete specimen (but with cephalothorax and abdomen separated). The third specimen, with the abdomen attached to the carapace, has the scape of the epigynum broken. All had been on pins in alcohol and are in poor condition. The pins were carefully removed.

Description. Female syntype. Carapace dull orange with brown marks. Chelicerae, dark orange. Labium brown, endites orange to brown. Sternum orange-brown with three pairs of light patches. Coxae orange with brown; legs orange with indistinct brown rings and spots. Dorsum of abdomen brown and white (Fig. 91); venter with indistinct white pigment spots (Fig. 92). Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.8 diameter, posterior laterals 1 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Abdomen with 11 tubercles: three pairs on sides, one pair posterior and three median posterior (Fig. 91). Total length 9 mm. Carapace 3.4 mm long, 2.7 wide. First femur 4.8 mm, patella and tibia 5.4, metatarsus 3.4, tarsus 1.1. Second patella and tibia 4.4 mm, third 2.2, fourth 4.0.

Illustrations. A syntype was illustrated.

Diagnosis. All specimens are smaller and have a shorter scape (Figs. 88, 90) than *P. velutina* (Figs. 74, 77).

Record. PANAMA *Chiriquí:* El Volcán, 28 Feb. 1936, ♀ (W. J. Gertsch, AMNH).

Parawixia matiapa new species
Figures 93, 94; Map 2

Holotype. Male holotype from Hacienda Matiapa, Camacã, Bahia State, Brazil, 14 Oct. 1978 (J. S. Santos), in MCN no. 11099a. The specific name is a noun in apposition after the type locality.

Description. Male holotype. Carapace orange. Chelicerae, endites orange. Labium brown. Sternum orange, dusky only in center. Legs orange with indistinct darker patches. Abdomen dorsum darkest in median area; venter dusky with a pair of white spots behind genital groove. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.5 diameter. Anterior median eyes slightly less than their diameter apart. Posterior median eyes slightly more than their diameter apart. Fourth trochanter with two short macrosetae on right, three on left. Second, third, and fourth femora with a ventral row of macrosetae. Abdomen with one pair of tubercles anterior, four tubercles posterior, and three pairs of bulges on sides; no caps on tubercles (Fig. 94). Total length 7.5 mm. Carapace 4.1 mm long, 3.2 wide. First femur 5.6 mm, patella and tibia 6.6, metatarsus 3.5, tarsus 0.5. Second patella and tibia 4.7 mm, third 2.8, fourth 4.2.

Variation. Total length of males 5.5 to 7.8 mm. The male from Colombia has macrosetae on the fourth trochanters as in the holotype; the other males have only two macrosetae. Figure 93 of the palpus was made from the male from Utcuyacu, Peru; Figure 94, from the holotype.

Diagnosis. This male differs from those of *P. monticola* and *P. divisoria* by the sculpturing of the base of the median apophysis and the position of the conductor in the palpus (Fig. 93).

Distribution. Trinidad, northern Colombia, to Junín Dept., Peru, and Bahia States, Brazil (Map 2).

Paratypes. TRINIDAD Piarco, 3–6 Jan. 1955, ♂ (A. M. Nadler, AMNH). COLOMBIA *Magdalena:* Pueblo Bello, 1,100 m, Sierra Nevada de Santa Marta, 10, 11 June 1968, ♂ (B. Malkin, AMNH). PERU *Junín:* Utcuyacu, Mar. 1948, ♂ (F. Woytkowsky, AMNH).

Parawixia tomba new species
Figures 95, 96; Map 3

Holotype. Male holotype from Explorer's Inn, Tambopata Reserve, Depto. Madre de Dios, Peru, 30 Mar. 1988 (J. Palmer, D. Smith), in MUSM. The specific name is an arbitrary combination of letters.

Description. Male holotype. Carapace orange-yellow with black spots. Chelicerae, endites orange-yellow. Sternum dusky in center. Legs yellowish with black spots. Abdomen whitish, dusky on sides; venter with black spots underlain by white. Posterior median eyes 0.6 diameter of anterior medians, anterior laterals 0.5 diameter, posterior laterals 0.4 diameter. Anterior median eyes slightly less than their diameter apart. Posterior median eyes their diameter apart. Fourth trochanter with five macrosetae on right, three on left. Second, third, and fourth femora each with ventral row of macrosetae. Abdomen with one pair of tubercles anterior and four distinct tubercles posterior (Fig. 96). Total length 9.6 mm. Carapace 4.5 mm long, 3.4 wide. First femur 6.3 mm, patella and tibia 7.2, metatarsus 4.2, tarsus 1.4. Second patella and tibia 5.4 mm, third 3.1, fourth 4.6.

Illustration. The holotype was illustrated.

Diagnosis. This male differs from those of *P. monticola* and *P. divisoria* by the sculpturing of the base of the median apophysis and the position of the conductor in the palpus (Fig. 95).

Paratype. BRAZIL *Roraima:* Estação Ecologica de Maracá, Ilha de Maracá, Rio Uraricuera, 17 July 1987, ♂ (A. A. Lise, MCN 19281).

Parawixia divisoria new species
Figures 97–103; Map 3

Holotype. Female holotype and male paratype from Divisoria, Huánuco [La Divisoria, Dpto. Ucayali, 09°05'S, 75°46'W], 1,700 m, Peru, 23 Sept. to 3 Oct. 1946 (W. Woytkowski), in AMNH. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace orange with paired dark patches and dark area between median and lateral eyes. Sternum brown with pairs of light orange patches. Coxae orange with brown; legs orange with indistinct brown rings. Dorsum of abdomen gray with brown patches (Fig. 100); venter black with a pair of white spots (Fig. 101). Posterior median eyes 0.9 diameter of anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.8 diameter. Anterior median eyes slightly more than their diameter apart. Posterior median eyes slightly more than their diameter apart. Abdomen with 10 tubercles, none posterior above spinnerets (Fig. 100). Total length 9.5 mm. Carapace 4.2 mm long, 3.3 wide. First femur 4.9 mm, patella and tibia 6.0, metatarsus 3.3, tarsus 1.2. Second patella and tibia 5.1mm, third 3.0, fourth 4.8.

Male paratype from Divisoria, Peru. Coloration as in female. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 0.7 diameter apart. Posterior median eyes their diameter apart. Third trochanter with one macroseta on one side, fourth with three short macrosetae, two thick, one thin. Second and third femora each with a ventral row of macrosetae. Abdomen with 5 tubercles: two anterior, three posterior (Fig. 103). Total length 7.0 mm. Carapace 3.5 mm long, 3.1 wide. First femur 5.2 mm, patella and tibia 6.0, metatarsus 3.1, tarsus 1.2. Second patella and tibia 4.2 mm, third 2.5, fourth 3.9.

Variation. Total length of females 7.0 to 8.8 mm. The male paratype has only two macrosetae on the fourth trochanter, none on the third. The female holotype and the male paratype collected with it were illustrated.

Diagnosis. Females differ from those of *P. tarapoa* by having a longer scape and a narrower posterior median plate in the epigynum (Fig. 98). The male differs from those of similar species by the nearly round conductor and shorter median apophysis (Fig. 102).

Natural History. A male was found in a rain forest in Rondônia.

Paratypes. ECUADOR *Napo:* Dureno, 200 m, Río Aguarico, 00°04'S, 76°34'W, 23–30 Sept. 1977, ♀ (L. Peña, AMNH).

⟶

Figures 74–80. *Parawixia velutina* (Taczanowski). 74–79, female. 74–77, epigynum. 74, ventral. 75, 76, posterior. 77, lateral. 78, dorsal. 79, abdomen, ventral. 80, male left palpus.

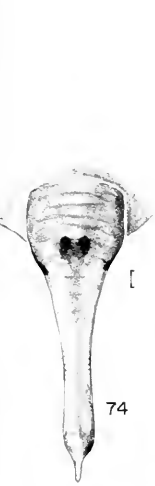
Figures 81–87. *P. monticola* (Keyserling). 81–86, female. 81–84, epigynum. 81, ventral. 82, 83, posterior. 84, lateral. 85, dorsal. 86, abdomen, ventral. 87, male palpus.

Figures 88–92. *P. hoxaea* (O. P.-Cambridge), female. 88–90, epigynum. 88, ventral. 89, posterior. 90, lateral. 91, dorsal. 92, abdomen, ventral.

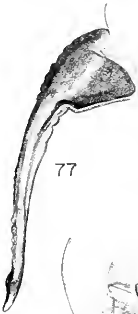
Figures 93, 94. *P. matiapa* n. sp., male. 93, palpus. 94, dorsal.

Figures 95, 96. *P. tomba* n. sp., male. 95, palpus. 96, dorsal.

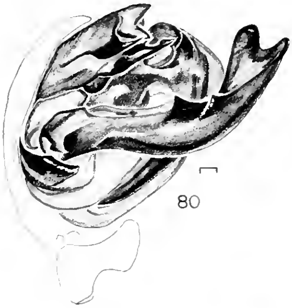
Scale lines 1.0 mm, genitalia 0.1 mm.

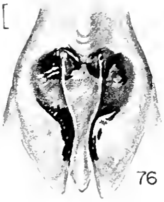

74

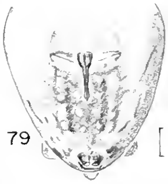

75

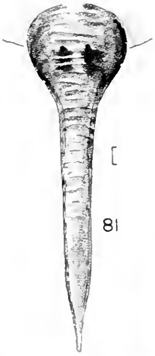

77


78


80


76

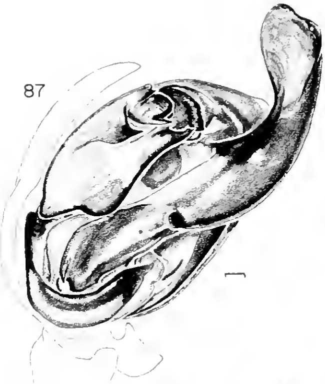

79

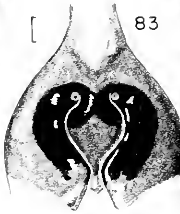

81


82

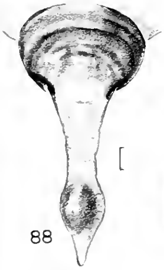

84


85

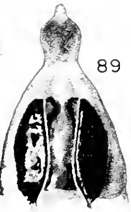

87

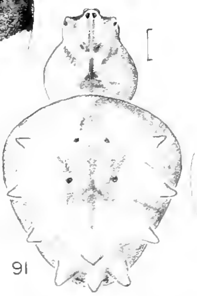

83

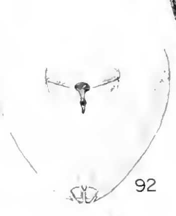

86

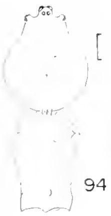

88


90


89


91


92


94


93


95


96

PERU *Cuzco:* Sayllapampa, 3,800 m, 13°25'S, 71°40'W, 23 Sept. 1987, ♂ (D. Silva D., MUSM). BRAZIL *Bahia:* Fazenda N. Senhora das Neves, Itamaraju, 9 Oct. 1978, ♀ (J. S. Santos, MCN 11021). *Rondônia:* Fazenda Rancho Grande, NE Cacaulandia, 6–15 Dec. 1990, ♀ (G. B. Edwards, FSCA). BOLIVIA *La Paz:* Guanay, N La Paz, Tres Esteros, 19–25 Aug. 1989, ♀, ♂ (L. Peña, AMNH).

Parawixia tarapoa new species
Figures 104–109; Map 2

Holotype. Female holotype from Tarapoa, Cuyabeno, 0°07'S, 76°20'W, Napa Prov., Ecuador, 23 June to 1 July 1988 (W. Maddison), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female from Manaus, Brazil. Carapace orange with paired darker spots. Sternum dusky yellow. Coxae yellowish with dusky marks; legs light orange with dusky rings, which are darker on proximal articles. Dorsum of abdomen with dark brown median band bordered by white (Fig. 107); venter black with a pair of small white spots, spots almost touching (Fig. 108). Tubercles of lateral eyes small and indistinct. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart. Posterior median eyes slightly more than their diameter apart. Abdomen narrow, with five tubercles, and two pairs of swellings on sides (Fig. 107). Total length 8.0 mm. Carapace 3.4 mm long, 2.6 wide. First femur 4.0 mm, patella and tibia 4.8, metatarsus 2.9, tarsus 1.1. Second patella and tibia 4.0 mm, third 2.5, fourth 4.0.

Male from Manaus. Color as in female, except for a transverse white line between anterior lateral tubercles on dorsum of abdomen. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes their diameter apart. Posterior median eyes slightly more than their diameter apart. Fourth trochanter with two thick macrosetae. Abdomen with an anterior pair of lateral tubercles, three posterior tubercles in a median row, and two pairs of slight humps on each side. Total length 6.4 mm. Carapace 3.5 mm long, 2.9 wide. First femur 4.5 mm, patella and tibia 5.2, metatarsus 2.7, tarsus 1.0. Second patella and tibia 3.6 mm, third 2.1, fourth 3.4.

Note. The male and the female were collected together in Manaus.

Variation. The holotype is darker than the specimen described and figured (Fig. 107) and 9.3 mm in total length. All illustrations were made from specimens from Manaus.

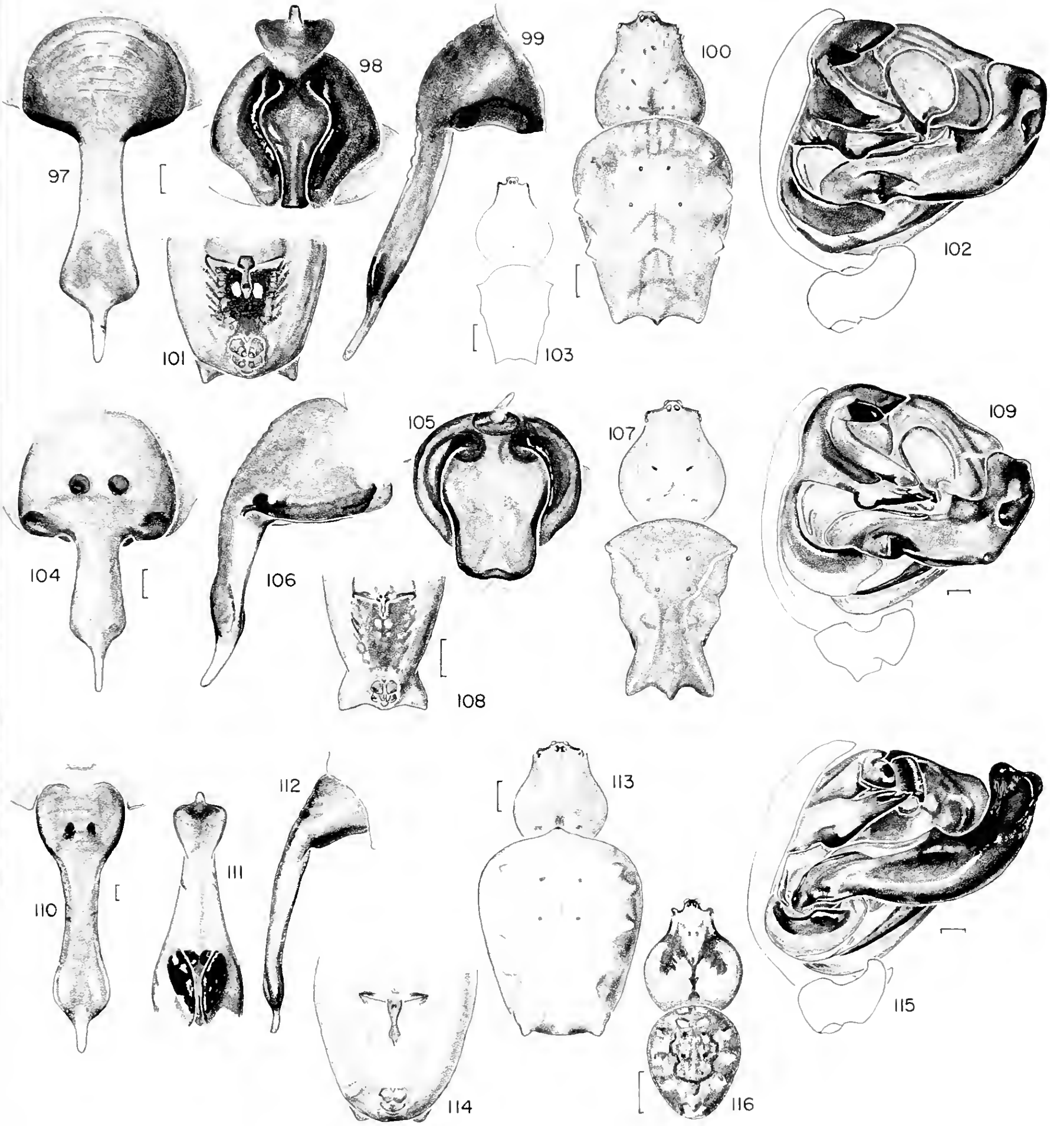
Diagnosis. The large, wide median plate of the epigynum (Fig. 105) separates females of *P. tarapoa* from those of *P. divisoria*, which has a narrower median plate (Fig. 98). The male is separated by the wider base of the median apophysis and the slightly different shape of the embolus of the palpus (Fig. 109).

Paratypes. PERU *Pasco:* Villa America, nr. Quebrada Castillo, 298 m, 28 Oct. 1986, ♂ (D. Silva D., MUSM). *Cuzco:* Sayllapampa, 3,800 m [13°25'S, 71°40'W], 23 Sept. 1987, ♂ (D. Silva D., MUSM). BRAZIL *Amazonas:* Manaus, 3 Sept. 1986, ♀, ♂ (M. B. Barcia, MCN 19658). *Mato Grosso:* NE Cáceres, 20 July 1988, ♀ (P. Salinas, AMNH).

Parawixia ouro new species
Figures 110–114; Map 3

Holotype. Female holotype from Ouro Prêto do Oeste, Rondônia State, Brazil, Oct. 1982 (W. Roth), in MZSP ex RLCB. The specific name, the Portuguese word for gold, is a noun in apposition after the type locality.

Description. Female holotype. Carapace orange-yellow. Chelicerae orange. Labium, endites brown. Sternum dusky with pairs of light patches. Coxae orange-yellow; legs orange-yellow with indistinct dusky rings. Dorsum of abdomen mostly whitish, sides brown (Fig. 113); venter with a white rectangular patch between genital groove and spinnerets (Fig. 114). Posterior



Figures 97–103. *Parawixia divisoria* n. sp. 97–101, female. 97–99, epigynum. 97, ventral. 98, posterior. 99, lateral. 100, dorsal. 101, abdomen, ventral. 102, 103, male. 102, left palpus. 103, dorsal.

Figures 104–109. *P. tarapoa* n. sp. 104–108, female. 104–106, epigynum. 104, ventral. 105, posterior. 106, lateral. 107, dorsal. 108, abdomen, ventral. 109, male palpus.

Figures 110–114. *P. ouro* n. sp., female. 110–112, epigynum. 110, ventral. 111, posterior, 112, lateral. 113, dorsal. 114, abdomen, ventral.

Figures 115–116. *P. maldonado* n. sp., male. 115, palpus. 116, dorsal.

Scale lines 1.0 mm, genitalia 0.1 mm.

median eyes 0.7 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Abdomen with four pairs of tubercles on sides, one anterior median, and three posterior (Fig. 113). Total length 11 mm. Carapace 4.2 mm long, 3.1 wide. First femur 5.4 mm, patella and tibia 6.7, metatarsus 4.3, tarsus 1.4. Second patella and tibia 5.8 mm, third 2.7, fourth 5.0.

Variation. The paratype from Ilha de Maracá is much darker than the holotype, the abdomen as long as wide, and lacking the anterior median tubercle, but having two posterior median tubercles. Its total length is 10 mm. The holotype was illustrated.

Diagnosis. The shorter, wider scape of the epigynum (Figs. 110, 112) separates this species from *P. velutina*.

Paratypes. PERU The paralectotypes of *P. velutina* from Amable María, Junín, may be this species. BRAZIL *Roraima:* Ilha de Maracá, 25 July 1987, ♀ (A. A. Lise, MCN 19657).

Parawixia maldonado new species
Figures 115, 116; Map 3

Holotype. Male holotype from Reserva Cuzco Amazonico, 12°33′S, 69°03′W, 200 m, Río Madre de Dios, 15 km NE Puerto Maldonado, Depto. Madre de Dios, Peru, 29 June 1989, male paratype 13 July 1989 (D. Silva D.), in MUSM. The specific name is a noun in apposition after the type locality.

Description. Male holotype. Carapace orange with dark brown marks and white setae (Fig. 116). Chelicerae dusky, endites brown, labium orange. Sternum orange, slightly darker in midline. Legs orange with wide dark brown rings and patches. Abdomen black with two pairs of white spots anteriorly and white marks behind tubercles, and a faint darker black outline of a folium (Fig. 116). Sides and venter black. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 0.6 diameter apart. Posterior median eyes their diameter apart. Endite with tooth, palpal femur with tubercle. Palpal patella with one macroseta on left, two on right. Fourth trochanter with two macrosetae on right. Second and third femora each with a ventral row of macrosetae. Abdomen with three pairs of lateral tubercles and two posterior, median tubercles (Fig. 116). Total length 6.7 mm. Carapace 3.5 mm long, 2.9 wide. First femur 3.9 mm, patella and tibia 4.6, metatarsus 2.7, tarsus 1.1. Second patella and tibia 3.7 mm, third 2.0, fourth 3.2.

Variation. In the paratype both palpal patellae have one macroseta.

Diagnosis. This male differs from those of *P. monticola*, *P. divisoria*, and *P. tomba* by the sculpturing of the base of the median apophysis and the position of the conductor in the palpus (Fig. 115), and by the ovoid outline of the abdomen (Fig. 116).

Parawixia rigida (O. P.-Cambridge)
Figures 117–122; Map 2

Epeira rigida O. P.-Cambridge, 1889: 36, pl. 5, fig. 5, ♀. Two female syntypes in poor condition from Bugaba, Chiriquí Prov., Panama, in BMNH no. 1905.4.28.2835–2836, examined.

Epeira armata O. P.-Cambridge, 1889: 41, pl. 4, fig. 17, ♂. Male holotype from Bugaba, Panama, in BMNH, examined. Keyserling, 1892: 107, pl. 5, fig. 79, ♂. NEW SYNONYMY.

Epeira rivalis Keyserling, 1892: 103, pl. 5, fig. 76, ♀. Female holotype from Guatemala, in BMNH, lost. NEW SYNONYMY.

Parawixia rigida:—F. P.-Cambridge, 1904: 491, pl. 46, fig. 18, ♀. Roewer, 1942: 871. Bonnet, 1958: 3341.

Parawixia armata:—F. P.-Cambridge, 1904: 489, pl. 46, fig. 11, ♂. Roewer, 1942: 870. Bonnet, 1958: 3339.

Aranea rivalis:—Roewer, 1942: 851.

Araneus rivalis:—Bonnet, 1955: 586.

Note. The syntypes of *E. rigida* and the holotype of *E. armata* were on pins in alcohol and are in poor condition with the legs separate. The pins were carefully removed. The female type of *E. rivalis* is lost, but illustration and description match only this species.

Description. Female from Costa Rica. Carapace light orange with black marks on thoracic region. Labium, endites black. Sternum black with an orange patch on each side. Coxae orange and black; legs light orange with black spots, streaks and rings. Dorsum of abdomen brown and white with a folium outline (Fig. 120); venter with white spots on brown (Fig. 121). Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.6 diameter. Anterior median eyes 0.9 diameter apart. Posterior median eyes 0.8 diameter apart. Abdomen with 10 tubercles: three pairs of laterals, the second and third pairs barely distinct, and four posterior; the median dorsal one indistinct (Fig. 120). Total length 17 mm. Carapace 5.9 mm long, 4.9 wide. First femur 6.9 mm, patella and tibia 8.0, metatarsus 5.0, tarsus 1.8. Second patella and tibia 7.5 mm, third 4.4, fourth 7.2.

Male holotype of *E. armata*. Carapace mottled brown with paired spots. Sternum, coxae olive-brown. Legs brown. Abdomen (damaged by insect pin) with trapezoidal, lighter area, widest anteriorly; venter dark with a median light spot. Posterior median eyes 0.7 diameter of anterior medians; laterals 0.7 diameter. Anterior median eyes 0.6 diameter apart. Posterior median eyes slightly less than their diameter apart. Fourth trochanter with three macrosetae. Abdomen with five tubercles. Total length 7.4 mm. Carapace 4.1 mm long, 3.4 wide. First femur 4.9 mm, patella and tibia 6.2, metatarsus 5.9, tarsus 1.2. Second patella and tibia 3.2 mm, third 3.1, fourth 4.2.

Note. The male and the female were not collected together, but they have the same type locality and distribution.

Variation. Total length of females 12 to 17 mm, of males 7.4 to 8.8. The females have nine or 10 tubercles on the abdomen: the last tubercle, the posterior median, may be missing. The fourth trochanter of the male from Sirena has two macrosetae on one side, three on the other. Figures 117–121 were made from a female from La Selva, Costa Rica; Fig. 122, from the holotype of *E. armata*.

Diagnosis. *Parawixia rigida* differs from other Central American species by having a median white spot on the venter of the abdomen (Fig. 121). The female differs from those of *P. hypocrita* and *P. nesophila*, which also have a white spot, by having the scape of the epigynum long (Figs. 117, 119, 121) and laterally flattened (Fig. 119). The male differs by the shape of the large curved median apophysis with a distal notch (Fig. 122).

Records. COSTA RICA Hacienda de Limón [?, not located], ♀ (Burgdorf, Schild, USNM). *Heredia:* La Selva, nr. Puerto Viejo, 22 Mar. 1979, ♀ (J. Coddington, MCZ), Feb. 1981, ♀ (W. Eberhard 2204, MCZ). *Puntarenas:* Osa Peninsula, ♂ (MZCR); Sirena, Osa Peninsula, Feb. 1984, ♂ (W. Eberhard, MCZ).

Parawixia kochi (Taczanowski)
Figures 123–135; Map 3

Epeira opuntiae:—C. L. Koch, 1845: 102, pl. 383, fig. 909, ♀. Specimens probably from Brazil, lost. Misidentification, not *Epeira opuntiae* Walckenaer, 1841 = *Cyrtophora citricola* (Forskål).

Epeira kochii Taczanowski, 1873: 134. New name for *E. opuntiae* C. L. Koch, not Walckenaer.

Epeira minas Keyserling, 1892: 95, pl. 5, fig. 71, ♀, ♂. Three female, two male syntypes from Rio Minas, Est. Espírito Santo [?, unknown locality], Brazil, in BMNH, examined. NEW SYNONYMY.

Aranea kochii:—Roewer, 1942: 845.

Aranea minas:—Roewer, 1942: 847.

Molinaranea setosa Mello-Leitão, 1948: 169, fig. 11, ♂. Male holotype from Guest [? house] near Moraballi River, Essequibo River, 24 km above Bartica, Guyana (W. Hingston) [locality from label], in BMNH, examined. NEW SYNONYMY.

Parawixia kochi albozonata di Caporiacco, 1948: 655. Female holotype, without abdomen from Conwarook near Potaro River, Guyana, in MZUF, examined; 1954: 99. Brignoli, 1983: 278. NEW SYNONYMY.

Parawixia kochi maculilatera di Caporiacco, 1948: 655. Female holotype from Two Mouths near Essequibo River, Guyana, in MZUF, examined. Brignoli, 1983: 278. NEW SYNONYMY.

Parawixia kochi nigrohumeralis di Caporiacco, 1948: 655. Female holotype from Guyana, in MZUF, examined. Brignoli, 1983: 279. NEW SYNONYMY.

Araneus kochi:—Bonnet, 1955: 525.

Araneus minas:—Bonnet, 1955: 544.

Araneus setosus:—Brignoli, 1983: 263.

Note. C. L. Koch's illustration shows a *Parawixia* with a relatively narrow body and Koch considered the 5-mm-long, curved scape characteristic of this species:

"zwei Linien langen, geschweift gebogenen nadelförmigen Legestachel." Most other *Parawixia* species with a long scape have a more spherical abdomen. *Parawixia kochi albozonata* is presumably the same species as the other two "subspecies" described by di Caporiacco even though the abdomen is missing. *Parawixia kochi maculilatera* has the characteristic abdomen shape and epigynum of *P. kochi*. *Molinaranea setosa* has the characteristic embolus with a round tip and neck of males of *P. kochi*.

Description. Female syntype of *E. minas*. Carapace brown, clypeus darkest. Sternum maculated light and dark brown. Legs brown, indistinctly ringed. Dorsum of abdomen shades of brown with folium outlined with dark (Fig. 126); venter brown with indistinct light patches and some paired white pigment patches (Fig. 127). Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes slightly less than their diameter apart. Posterior median eyes their diameter apart. Abdomen longer than wide, with three pairs of lateral tubercles and five posterior (Fig. 126). Total length 16 mm. Carapace 6.6 mm long, 5.4 wide. First femur 7.8 mm, patella and tibia 9.5, metatarsus 6.2, tarsus 2.1. Second patella and tibia 9.2 mm, third 5.5, fourth 8.7.

Male syntype of *E. minas*. Carapace orange, less distinctly marked than carapace of female. Fourth trochanter with one short macroseta. Abdomen oval, humps indistinct. Total length 10.5 mm. Carapace 6.2 mm long, 4.8 wide. First femur 6.9 mm, patella and tibia 8.4, metatarsus 5.2, tarsus 1.7. Second patella and tibia 6.7 mm, third 4.2, fourth 6.7.

Variation. Some individuals have a spherical abdomen, but usually the abdomen is longer than wide (Fig. 126). There always are an anterior pair of tubercles and five posterior, with two smaller pairs on the sides. One female from Peru had the anterior lateral tubercles double. There are many individual differences but there is no consistent geographical variation. However, there are consistent geographical differences in the shape of the terminal apophysis, embolus, and base of the median apophysis (Figs. 128–135). Nevertheless, in all palpi the tip of the embolus is round and has a neck, and in all palpi the base of the median apophysis has a similar tooth pointing at the radix (Figs. 128–135). Total length of females 12.8 to 18.8 mm, of males 8.3 to 10.8. Figures 123 to 128 were prepared from a female from the Meta Dept., Colombia; Figure 129 was prepared from a male from Guyana; Figure 130, from the male syntype of *Epeira minas*.

Diagnosis. The female can be recognized by the long, slender scape of the epigynum with concave sides (Figs. 123–125), and usually by the slightly elongate abdomen (Fig. 126). The base of the epigynum has two characteristic dark spots (Fig. 123). This is the only *Parawixia* species in which the male palpus has a round embolus tip above a neck (Figs. 128–135). The fourth trochanter of the male almost always has one macroseta; only one Peruvian male lacked the seta.

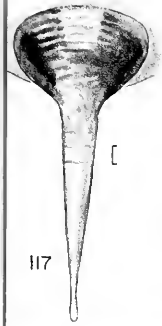
Natural History. The species has been collected in its web at night in rain forest, in secondary forest, savanna, and swamp forest, and also on a burned out tree. Specimens collected by H. Höfer near Manaus

→

Figures 117–122. *Parawixia rigida* (O. P.-Cambridge). 117–121, female. 117–119, epigynum. 117, ventral. 118, posterior. 119, lateral. 120, dorsal. 121, abdomen, ventral. 122, male left palpus.

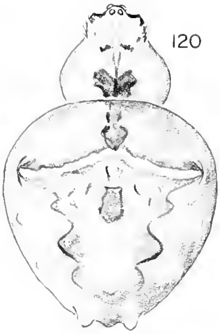
Figures 123–135. *P. kochi* (Taczanowski). 123–127, female. 123–125, epigynum. 123, ventral. 124, posterior. 125, lateral. 126, dorsal. 127, abdomen, ventral. 128–130, male palpus. 128, (Meta, Colombia). 129, (Guyana). 130, (Espírito Santo, Brazil). 131–135, tip of embolus, terminal apophysis, and base of median apophysis. 131, (Trinidad). 132, (Caripito, Venezuela). 133, (Puerto Lopez, Meta, Colombia). 134, (Cuzco Amazonica, Madre de Dios, Peru). 135, (Barra dos Bugres, Mato Grosso, Brazil).

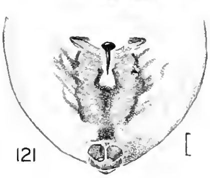
Scale lines 1.0 mm, genitalia 0.1 mm.

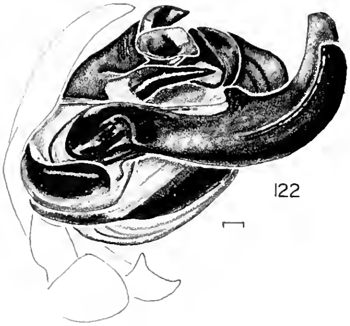

117


119


118

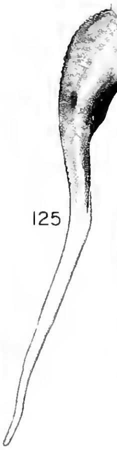

120

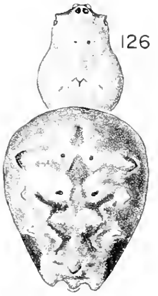

121


122

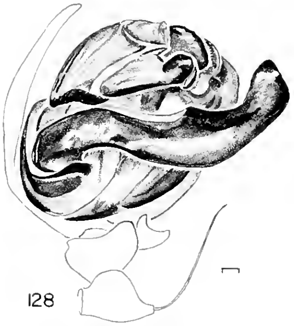

123

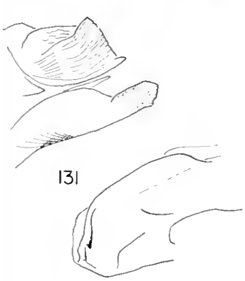

124

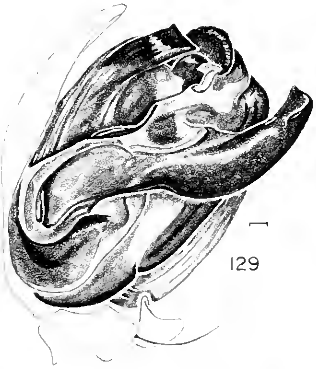

125

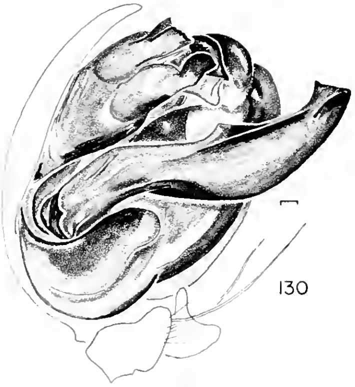

126

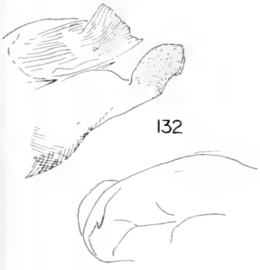

127


128

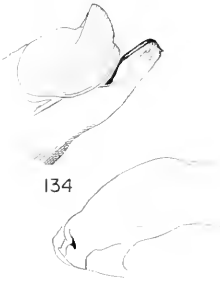

131

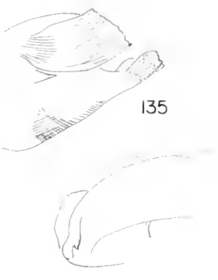

129


130


132


133


134


135

came from a vertical web, 80 cm in diameter, with an open hub and a mesh of 0.7 to 2 cm. If disturbed the spider flees upward and tries to escape on the tree trunk to the side of the web.

Distribution. Trinidad, Venezuela, Amazon area to Paraná State, Brazil (Map 3).

Records. LESSER ANTILLES *Trinidad:* Arima, St. George's Co. (AMNH); Navy Base (AMNH); Port of Spain (MCZ); Los Banguizales, Cedros (AMNH); Maracas Valley (AMNH). VENEZUELA *Monagas:* Caripito (AMNH). *Miranda:* Santa Cruzita, 450 m, Guatopo Nat. Park (USNM). *Araqua:* Rancho Grande (USNM). *Carabobo:* San Esteban (AMNH). *Bolívar:* Maripa, Río Caura (MCZ). *Amazonas:* Cerro Duida (AMNH). GUYANA *Mazaruni-Potaro:* Kaieteur Fall (CUC); Kartabo (CUC); Kamakusa (AMNH); Tumatumari Riv., Potaro (CUC); nr. Mazaruni Riv., Pakaraima Mts. (AMNH). *Rupununi:* Upper Essequibo Riv. (AMNH). *East Berbice-Corentyne:* Canje, Ikuruwa Rivers (AMNH). *East Berbice-Demerara:* "Opora region" [Ororo Marali], (AMNH). SURINAM *Marowijne:* "Langaman" [Langamankondre, 5°42′N, 54°00′W] (AMNH). FRENCH GUIANA nr. Placer Tresor, Roura Mts. (MCZ); Sautero, Matoury (MCZ); nr. Cayenne (MCZ); Saül, Mont Bœuf Mort (AMNH). COLOMBIA *Boyacá:* Río Upia, 850–950 m (AMNH). *Meta:* 15 km SW Puerto Lopez (MCZ); Lomalinda, nr. Puerto Lleras (MCZ). *Caquetá:* Río Orteguaza (AMNH). *Amazonas:* Araracuara (CV). ECUADOR *Napo:* Pompeya (MCZ); Río Coca nr. Río Napo (MCZ); Cuyabeno, Río Tarapuy (MCZ, MECN); Cuyabeno, Laguna Grande (MCZ, MECN). *Pastaza:* 4.1 km SE Puyo (MCZ). *Morona-Santiago:* Los Tayos Santiago, Río Santiago (MCZ); Tayos caves (MCZ). PERU northern Peru: Reanrer [? unknown locality] (AMNH). *Loreto:* Parque Nacional Pacaya-Samiria, Pithecia, 05°06′S, 74°50′W, Río Samirio (MUSM); Estiron, Río Ampiyacu (AMNH); Iquitos (MCZ). *San Martín:* Río Tanbo [Tambo Río Negro, Pósic, 05°59′S, 77°12′W] (AMNH); 32 km SE Moyobamba (AMNH). *Huánuco:* Dantos-La Molina, SW Puerto Inca, (MUSM); Panguana, 260 m (MUSM); Tingo María (AMNH); 100 km E Tingo María (CAS). *Junín:* Rio Tarma, Huacapistana (CUC). *Cuzco:* Atalaya (MUSM). *Madre de Dios:* Reserva Cuzco Amazonico, 12°33′S, 69°03′W, 15 km NE Puerto Maldonado (MUSM); Parque Nacional Manu (MUSM, USNM); Reservada Tambopata (MCZ, MUSM); Zona Reservada Pakitza (MUSM). BRAZIL *Roraima:* Mt. Roraima (MCZ). *Pará:* Canindé, Rio Gurupi (AMNH); Rio Gurupiuna, 50 km E Canindé (AMNH); Belém (MCZ); Jacara-Acanga (AMNH). *Amazonas:* Cururuzinko, Rio Autas (NRMS); Sta. Amelia, Rio Autas (NRMS); Benjamin Constant (MNRJ); 60 km N Manaus (INPA); Canal Janauari, Manaus (INPA); Igapo Tarumã Minim, Manaus (INPA); Ilha da Marchanttia (INPA); Reserva Ducke, Manaus (INPA, MCN); Tapurucuara (MZSP); Tobatinga (MNRJ). *Rondônia:* Ouro Prêto do Oeste (MNRJ); NE Cacaulandia (FSCA). *Bahia:* Conceição do Almeida (MCN); Ilhéus (RLCB); Faz. Nossa Senhora das Neves, Itamarajú (MCN). *Espírito Santo:* Apiocá (RLCB); Colatina (MNRJ). *Rio de Janeiro:* Rio de Janeiro (MNRJ). *Paraná:* Reserva Estadual Vila Rica, Fênix (MCN). *Mato Grosso:* Barra do Bugres (MNRJ); 260 km N Xavantina (MCZ); Utiariti (MZSP). BOLIVIA *Beni:* Chacobo Indian Village, Río Benicito (AMNH); Estacion Biologico Beni (USNM). *La Paz:* Guanay (AMNH). *Santa Cruz:* Cachuela (USNM).

Parawixia audax (Blackwall)

Plate 1; Figures 136–142; Map 3

Epeira audax Blackwall, 1863: 29. Specimens from Rio de Janeiro, Brazil, lost. Keyserling, 1892: 85, pl. 4, fig. 64, ♀.

Epeira meridionalis Keyserling, 1865: 810, pl. 19, figs. 19, 20, ♀. Female from Uruguay, in BMNH. First synonymized by Keyserling, 1892: 85.

Epeira amaurophila Holmberg, 1876: 17. Female from northern Argentina, lost. First synonymized by Houssay, 1917 (not seen).

Epeira duodecimtuberculata Bertkau, 1880: 91, pl. 2, fig. 33, ♀. Females from Tijuca, Rio de Janeiro, Cap Irmao, Cap Gavia, and Copacobana, Brazil, lost. First synonymized by Keyserling, 1892: 85.

Epeira coronigera Taczanowski, 1878: 157, pl. 1, fig. 9, imm. One immature female, two immature males, and three smaller immature syntypes from Amable María, Depto. Junín, Peru, from wasp nest, in PAN, examined. NEW SYNONYMY.

Parawixia eumeniphila Strand, 1915: 115. Male holotype from Joinville, Jaragua, Itapocú, Est. Santa Catarina, Brazil, in SMF, examined. Roewer, 1942: 870. Bonnet, 1958: 3340. NEW SYNONYMY.

Araneus ribeiroi Mello-Leitão, 1917: 89, figs. 11, 12. Female from Belo Horizonte, Minas Gerais, Brazil, lost. DOUBTFUL NEW SYNONYMY.

Araneus rugosa Badcock, 1932: 24. Immature holotype from Corcovado, Rio de Janeiro, Brazil, in BMNH, examined. Bonnet, 1955: 588. NEW SYNONYMY.

Verrucosa audax:—Mello-Leitão, 1933: 42. Roewer, 1942: 880. Bonnet, 1959: 4790.

Aranea coronigera:—Roewer, 1942: 840.

Aranea rugosa:—Roewer, 1942: 851.

Araneus coroniger:—Bonnet, 1955: 470.

Note. I follow Keyserling in the interpretation of *P. audax*, as the species was not illustrated by Blackwall and Blackwall's specimens are lost. The immature specimens of *Epeira coronigera* have the abdomen circular, almost as wide as long, and with a distinct anterior median tubercle as may be characteristic of this species. Mello-Leitão's *A. ribeiroi* was perhaps an immature female of *P. audax*, having a soft projection in place of the future scape of the epigynum. Badcocks's immature specimens of *P. eumeniphila* have a pair of white spots on the venter of the abdomen as do some immature *P. audax* and adult *P. undulata*; they may belong to either this or the other species. Mello-Leitão (1942) correctly placed *E. audax* in *Parawixia*. Bonnet (1956: 1783) erroneously synonymized the name *Epeira duodecimtuberculata* Bertkau with *Eriophora socialis* [=*Parawixia bistriata*].

Description. Female from Pinhal, Santa Catarina, Brazil. Carapace orange with white hair and a few dark hairs; clypeus brown. Sternum, coxae orange; legs orange with dark spots. Dorsum of abdomen yellowish with brown marks (Fig. 139); venter dusky with three pairs of small white spots and a white streak on each side (Fig. 140). Cephalic area of carapace with a pair of swellings. Posterior median eyes 0.9 diameter of anterior medians, anterior laterals 0.9 diameter, posterior laterals 0.8 diameter. Anterior median eyes slightly more than their diameter apart. Posterior median eyes their diameter apart. Abdomen with 13 tubercles: one anterior median, four pairs on sides and four posterior (Fig. 139). Total length 12.0 mm. Carapace 5.6 mm long, 4.5 wide. First femur 5.4 mm, patella and tibia 7.2, metatarsus 4.5, tarsus 1.7. Second patella and tibia 6.0 mm, third 3.5, fourth 5.4.

Male from Pinhal, Santa Catarina, Brazil. Color as in female. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.5 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Lateral eyes 0.6 diameter apart. Fourth trochanter without macroseta. Second and third femora with ventral row of strong macrosetae, first and fourth with two rows. Abdomen with 13 tubercles as in female. Total length 8.4 mm. Carapace 4.1 mm long, 3.7 wide. First femur 4.1 mm, patella and tibia 5.6, metatarsus 3.3, tarsus 1.3. Second patella and tibia 4.5 mm, third 2.5, fourth 3.7.

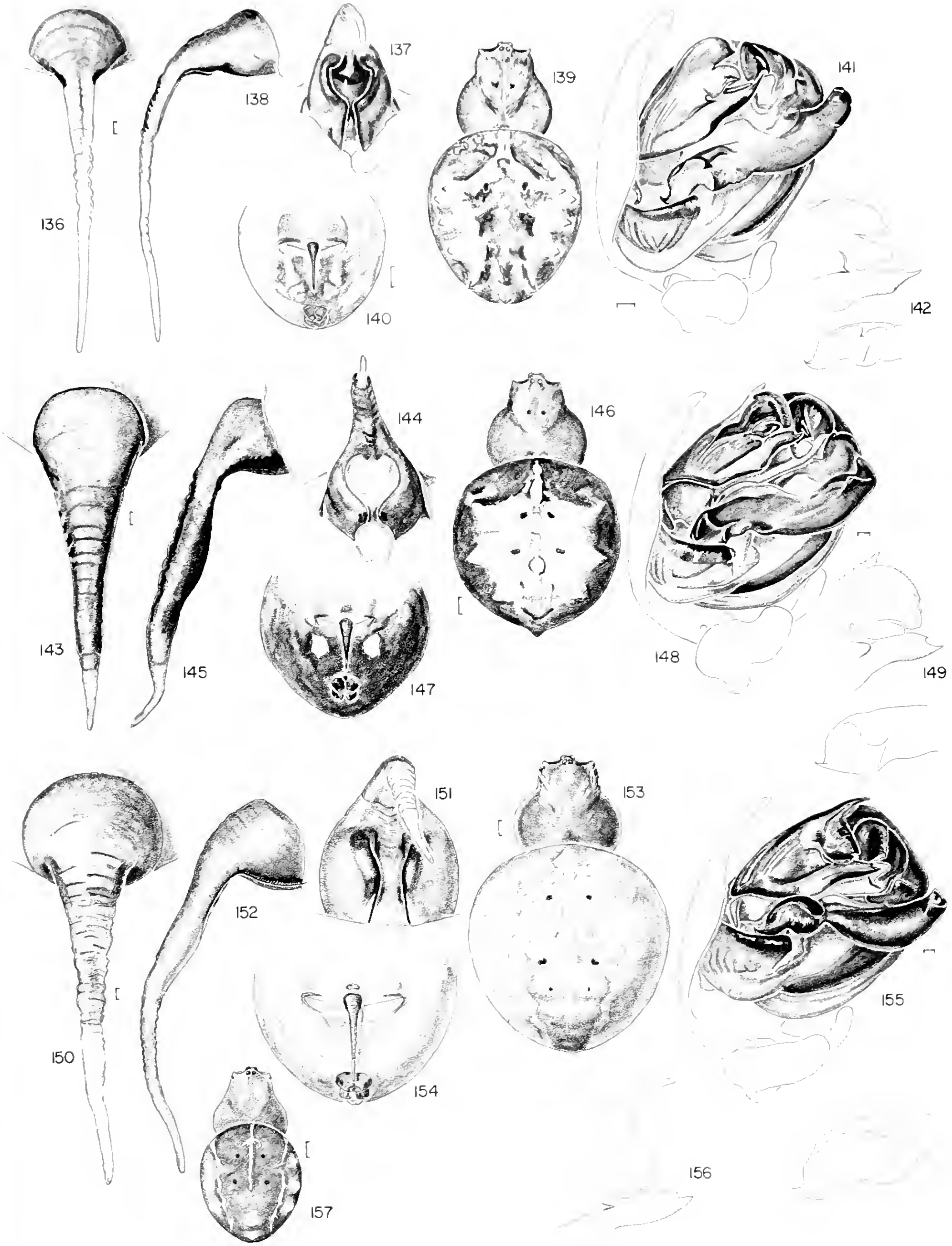
Variation. The anterior, median tubercle of the abdomen is frequently missing. Some females have the anterior lateral tubercles double. The photograph of a female from S of Jujuy, Argentina, shows her to be mostly green and white with some brown spots and brown patellae matching the lichens of the substrate. Immatures may have a pair of white patches on the venter of the abdomen. Total length of females 10.0 to 20.8 mm; of males 7.7 to 9.6. Figures 136–139 were made from specimens from Canela, Rio Grande do Sul, Brazil; Figures 140–142, from Pinhal, Santa Catarina, Brazil.

Diagnosis. Females differ from those of *P. bistriata* by having distinct tubercles on the abdomen (Fig. 139), from those of *P. undulata* by having the posterior median plate of the epigynum swollen, sclerotized, and dark in color (Fig. 137), and from those of both by the pattern on the venter of the abdomen (Fig. 140). Males differ from most species of *Parawixia* by lacking macrosetae on the fourth trochanter, from *P. bistriata* by having tubercles on the abdomen, and from both *P. bistriata* and *P. undulata* by the shape of the base of the median apophysis and the shape of the terminal apophysis of the palpus (Figs. 141, 142).

Natural History. This is perhaps the most common araneid orb weaver in southern Brazil. I made the following notes on 22 March 1985 at Cataratas do Iguaçu, Brazil. This *Parawixia* is very common and makes an enormous web, with a bridge about 2 m long, the web 50 to 90 cm in horizontal diameter, with very loose, wide mesh (Plate 1). The bottom of the orb is about 1 to 2 m above the ground. The spider hangs in the middle, cephalic region down (Plate 1), or hides in a silk retreat within a curled leaf near a radius or a frame line. The spider walks to the retreat when disturbed and if touched there, drops slowly on a thick silk rope. If handled the female tries to throw silk on the hand. I watched individuals feed on grasshoppers 3.5 cm long, longer than the spider. The viscous silk is very sticky. No two specimens have the same dorsal coloration of the abdomen or similar humps; the reddish and green coloration of some individuals is washed out in alcohol. The spider is probably mostly nocturnal and builds at night.

Distribution. Amazon area to Chubut Province, Argentina (Map 3).

Records. GUYANA *Rupununi:* Rupununi River betw. Dadanawa and Isherton, ♀ (AMNH). COLOMBIA *Meta:* 15 km SW Puerto Lopez, ♂ (MCZ); 20 km S El Porvenir, ♂ (MCZ). ECUADOR *Napo:* Cuyabeno, ♀, ♂ (MCZ). PERU *Junín?:* Mejorada, Río Mantaro, ♀ (AMNH). BOLIVIA *La Paz:* Coroico, imm. (MCZ). BRAZIL *Pará:* Belém (MCZ, MEG). *Acre:* Rio Branco (MZSP). *Bahia:* Ilhéus (RLCB); Mucuri (MCN); Rio Una, 74 km SW Salvador (MCN); Salvador (ZMK). *Goiás:* Jataí (MZSP); 40 km from Porto Landia nr. Mineiros (MCZ). *Mato Grosso:* Chavantina (MZSP); Rosário Oeste (AMNH); 260 km N Xavantina (MCZ). *Mato Grosso do Sul:* Três Lagoas (MZSP). *Minas Gerais:* Belo Horizonte (AMNH); Caxambú (MCZ); Lagoa Santa (ZMK); Lavras (MCZ); Pouso Alegre (MZSP); Santa Barbara, Reserva Flores (RLCB); Serra do Cipó (RLCB); Reserva Ecológica do Panga, Uberlândia (MCN). *Espírito Santo:* Apiao (RLCB); Colatina (MNRJ); Guaraparí (MZSP); Santa Teresa (MZSP); Vitória (MNRJ). *Rio de Janeiro:* Açude de Solidão (MCZ); Angra dos Reis (MZSP); Bom Jesus do Itabapoane (RLCB); Campos Itatiana (MZSP); Ilha Santana Macaé (RLCB); Itaipava (RLCB); Parque Nacional Itatiaia (RLCB); Magé (RLCB); Parati (RLCB); Rio de Janeiro (AMNH, MCZ, MNRJ); São João da Barra (RLCB); Teresópolis (AMNH, RLCB); Pico da Tijuca (MCZ); Barra da Tijuca (MCZ, RLCB). *São Paulo:* Alto do Leno; Barueri; Boracéia (all MZSP); Botucatu (IMPR, MZSP); Caraguatatuba; Carvalho Arayo; Castelho; Cocaia; Eldorado; Guarulhos (all MZSP); Ilha Comprida (AMNH); Ilha Vitória; Itapetininga; Itaquera Nova Europa (all MZSP); Itu (MCN); Jaboticabal (MCN); Juquiá (MZSP); Maua (AMNH); Mogi dos Cruces (MZSP); Monte Alegre (MZSP); Praia do Santos (MNRJ, MZSP); Rio Claro (MCZ); São Paulo (AMNH, MZSP, NHMW); São Roque (AMNH, MZSP); Serra da Cantareira (MZSP); Salesópolis (AMNH); Ubatuba (RLCB). *Paraná:* Cavinna (AMNH); Engelheiro Lange (MZSP); Ponte Rio Coutinho, Guarapuava (MZSP); Curitiba (MNRJ, MZSP); Salta do Iguaçu (MCZ); Parque Estad. Marumbi, Morretes (RLCB); Rio Branco (MCN); Rôlandia (AMNH); Serra Negra (MNRJ). *Santa Catarina:* Alto da Serra, estrada São Bento Corupá (MZSP); Blumenau (MZSP, NHMW); Mono dos Cionventos Araranguá (MCN); Pinhal (AMNH). *Rio Grande do Sul:* Barra do Ribeiro; Bom Jesus; Cambara do Sul; Campo Bom; Canela; Canoas; Capão da Canoa; Catuipe; Caxias do Sul; Charqueadas; Dois Irmãos; Encantado; Estaio; Garruchus São Borja; Garibaldi; Guaíba; General Câmara; Irai; Gravataí; Montenegro; Morro do Côco Viamão; Morro São Pedro; Niterói; Nonai; Novo Ham-



Figures 136–142. *Parawixia audax* (Blackwall). 136–140, female. 136–138, epigynum. 136, ventral. 137, posterior. 138, lateral. 139, dorsal. 140, abdomen, ventral. 141, male left palpus. 142, tip of embolus, terminal apophysis, and base of median apophysis.

Figures 143–149. *P. undulata* (Keyserling). 143–147, female. 143–145, epigynum. 143, ventral. 144, posterior. 145, lateral. 146, dorsal. 147, abdomen, ventral. 148, male palpus. 149, tip of embolus, terminal apophysis, and base of median apophysis.

Figures 150–157. *P. bistriata* (Rengger). 150–154, female. 150–152, epigynum. 150, ventral. 151, posterior. 152, lateral. 153, dorsal. 154, abdomen, ventral. 155, male palpus. 156, tip of embolus, terminal apophysis, and base of median apophysis. 157, immature, dorsal.

Scale lines 1.0 mm, genitalia 0.1 mm.

burgo; Osório; Palmares do Sul; Passo Fundo (all MCN); Porto Alegre (MCN, MCZ); Pelotas (AMNH, MCN, MCZ); Portão; Rio Grande; Rio Pardo; Saint Hilaire; Santa Cruz do Sul; Santa Maria; São Francisco de Paula; São Jeronimo (all MCN); São Leopoldo (MCN, MZSP); São Vincente do Sul; Santa Maria; Santa Vitória do Palmar; Est. Ecol. do Taim; Tenente Portela; Tôrres; Triunfo; Vacaria; Viamão (all MCN); Vila Oliva (MCN, MNRJ). URUGUAY *Canelones:* Las Piedras (MHNM); Pando (MHNM). *Lavaleja:* Fuente del Puma (FSCA). *Maldonado:* Sierra de las Animas (MHNM). *Montevideo:* Carrasco (MHNM); Cerro (MHNM); Montevideo (MHNM); Sayago (CAS). *Rocha:* Chuy (MHNM); Palmares de Castillos (MHNM). *Treinta y Tres:* Arrozal [?] (MHNM). PARAGUAY *Amambay:* Bella Vista (IBNP); nr. Pedro Juan Caballero (MCZ). *Concepción:* Fonciere (MHNW). *Alto Paraná:* Itabo Reserve (IRSNB); Mision Nueva Tribu Cerro León (IRSNB); km 12 de Stroessner, Centro Forestal de Alto Paraná (IBNP); Tatiyupi Reserve (IRSNB). *Paraguarí:* Cerro Acahaí, 500–570 m (IBNP). *Itapúa:* 20 km NNE Puerto Capitán Meza (MCZ). ARGENTINA *Misiones:* Colonia Acaraguá, Rt. 8, km 26 (MACN); Iguazú (CAS, MEG); Eldorado (AMNH); Gral. Manuel Belgrano (MEG); Posadas (MEG); Rt. 12, Gruta India, Dpto. Libertador San Martín, (MEG). *Jujuy:* Yuto (MEG). *Salta:* 5 km S Jujuy (MCZ); Oran (MEG). *Chaco:* Resistencia (MACN). *La Rioja:* Iliar, 7 km S Olta (MACN). *Córdoba:* Calamuchita (MACN); Palamuelita (MACN). *Buenos Aires:* Azul (AMNH); Buenos Aires (ZMK); Delta del Paraná (MEG); La Plata (MZSP); Moreno (MACN); Pte. Samborombón (MACN); Sierra de la Ventana (MEG); Tigre (MACN); Villa Ballester (AMNH); Zelaya (MACN); Zubiaurre (ZMK). *Mendoza:* 8 km SSW Estación Cacheuta, 1,500 m (MCZ); Mendoza (MACN, NHMW). *Río Negro:* El Bolson (AMNH). *Chubut:* El Rlesempeiro [?] (MACN).

Parawixia undulata (Keyserling), new combination
Figures 143–149; Map 3

Mahadeva undulata Keyserling 1892: 67, pl. 3, fig. 52, ♀. Four female syntypes from Rio Grande do Sul, Brazil, in BMNH, examined.

Aranea undulata:—Roewer, 1942: 855.

Verrucosa undulata:—Bonnet, 1959: 4791.

Description. Female from Vacaria, Rio Grande do Sul. Carapace orange-brown, with a pair of dark spots and a few light colored setae. Sternum dark orange without marks. Coxae dark orange; legs orange, distal articles ringed with black. Dorsum of abdomen black, brown, and white (Fig. 146); venter black with two white patches (Fig. 147). Posterior median eyes 0.7 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Laterals separated by their radius. Abdomen with 9 tubercles: Three pairs on sides and three posterior median (Fig. 146). Total length 16.0 mm. Carapace 6.8 mm long, 5.7 wide. First femur 5.6 mm, patella and tibia 7.8, metatarsus 4.7, tarsus 1.7. Second patella and tibia 7.0 mm, third 4.2, fourth 6.4.

Male from Vacaria, Rio Grande do Sul. Lighter in color than female, with faint indications of folium on abdomen. Posterior median eyes 0.5 diameter of anterior medians, laterals 0.5 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Laterals separated by their radius. Fourth coxa and trochanter without macroseta. Second and third femur with ventral row of macrosetae, scattered ventral macrosetae on first and fourth femora. Abdomen as in female. Total length 11.5 mm. Carapace 6.4 mm long, 5.2 wide. First femur 5.8 mm, patella and tibia 8.0, metatarsus 4.5, tarsus 1.7. Second patella and tibia 6.5 mm, third 3.7, fourth 5.5.

Variation. Total length of females 11.2 to 18.0 mm, of males 7.7 to 11.5. The illustrations were made from specimens from Vacaria, Rio Grande do Sul, Brazil.

Diagnosis. Females differ from those of *P. bistriata* by having tubercles on the abdomen (Fig. 146), from those of *P. audax* by having the posterior median plate of the epigynum not sclerotized, flat, and usually white (Fig. 144). The venter of the abdomen, unlike that of *P. bistriata* and of adult *P. audax*, has a pair of white patches on black (Fig. 147). Males differ from those of *P. bistriata* by having tubercles on the abdomen and from males of *P. bistriata* and *P. audax* by the shape of the terminal apophysis and the proximal end of the median apophysis (Figs. 148, 149).

Natural History. One female from São Paulo State came from a shrub in a field along the road; the web was 40 cm in diameter.

Distribution. From São Paulo State, Brazil, to Buenos Aires Province, Argentina (Map 3).

Records. BRAZIL *São Paulo:* Ubatuba, 7 June 1985, ♀ (R. L. C. Baptista, RLCB). *Rio Grande do Sul:* São Francisco de Paula, ♀ (P. P. Buck, MNRJ), 18 Jan. 1981, ♀ (T. de Lema, MCN 9497); Canela, 10 Feb. 1966, 3♀, 11 May 1974, 2♀ (A. A. Lise, MCN 709, 2099); Esc. Ecologico do Taim, Vitória, 3 Dec. 1986, ♀ (M. Rosenau, MCN 16538); Est. Ecol. do Esmeralda, Esmeralda, 12 Dec. 1978, 2♀ (C. J. Becker, MCN 8461); Gramado, 20 Mar. 1976, 2♀ (P. C. Braun, MCN 3822); Itaimbézinho, Cambará do Sul, 18 May 1985, ♀ (A. A. Lise, MCN 13300); Pelotas, 12 Apr. 1964, 4♀ (C. Biezanco, MCZ), 26 Sept. 1975, ♀ (A. A. Lise, MCN 3463); Porto Alegre, 6 July 1973, ♀ (M. Moraes, MCN 1476); Rio Grande, 8 Dec. 1976, 2♀, ♂ (H. Bischoff, MCN 4864), 4 Nov. 1986, ♀ (C. Biezanko, MCZ); Santana Guiaba, 21 Jan. 1977, 2♀ (A. A. Lise, MCN 4998); Vacaria, 14 Jan. 1974, 14♀, 7♂, 23 May 1982, 4♀ (A. A. Lise, MCN 309, 10151). URUGUAY *Cerro Largo:* nr. Melo, 1926, ♀ (Sanborn, AMNH). ARGENTINA *Buenos Aires:* Boulogne, ♂ (Prosen, MLP); Tigre, 2♀ (Viana, MACN).

Parawixia bistriata (Rengger), new combination; Nianduti Spider

Plate 1; Figures 150–157; Map 3

Epeira bistriata Rengger, 1836: 131. Specimens from Paraguay, lost.

Epeira socialis Rengger, 1836: 131. Specimens from Paraguay, lost.

Epeira bicolor:—C. L. Koch, 1839: 57, fig. 374, ♀.

Epeira socialis:—Holmberg, 1874: 95.

Epeira burmeisteri Holmberg, 1874: 95. Specimens from Barrancas de Obligado, Argentina, lost. NEW SYNONYMY.

Araneus nordenskiöldii Tullgren, 1905: 29, figs. 9a–h, ♀, ♂. Eighteen female and eight male syntypes from Tatarenda [600 m, Tarija, 21°50'S, 63°37'W, NE of Aguairenda], Bolivia, in NRMS, examined. Badcock, 1932: 22. Bonnet, 1955: 552. NEW SYNONYMY.

Araneus horizontinus Mello-Leitão, 1917: 87, fig. 9, ♀. Specimens lost. First synonymized by Mello-Leitão, 1932: 124.

? *Araneus paraopeba* Mello-Leitão, 1917: 92, fig. 10, ♀. Specimens lost. NEW SYNONYMY.

Eriophora bistriata:—Mello-Leitão, 1932: 124. Roewer, 1942: 866. Sandoval, 1987. Fowler and Diehl, 1978. Fowler and Gobbi, 1988a,b.

Araneus sermoniferus Mello-Leitão, 1932: 124. New name for *Araneus socialis:*—Burmeister, [?] 1872: 492 [not seen] allegedly not Rengger. Bonnet, 1955: 598 (*A. sermonifer*). NEW SYNONYMY.

Aranea bicolorata Roewer, 1942: 837. New name for *Epeira bicolor* preoccupied by *Aranea bicolor* Walckenaer (a European salticid *Carrhotus bicolor*). NEW SYNONYMY.

Aranea nordenskiöldii:—Roewer, 1942: 849.

Aranea sermonifera:—Roewer, 1942: 852.

Eriophora burmeisteri:—Roewer, 1942: 866. Bonnet, 1956: 784.

Eriophora acronavis Mello-Leitão, 1947: 241, fig. 8, ♀. Female holotype from Ponta Grossa, Paraná, Brazil, in MNHC, examined. Brignoli, 1983: 268. NEW SYNONYMY.

Eriophora socialis:—Bonnet, 1956: 1785.

Note. Rengger gave the name "*Epeira bistriata* oder [or] *socialis*" to this species. *Epeira bistriata* has never been illustrated before. According to Rengger its main characters are that it is a "social *Epeira* with a hazelnut-shaped abdomen having red spots." Only one species fits this description, the one illustrated here. Rengger's specimens are not in NHMB or in the Naturmuseum Aarau, Switzerland (R. Maurer, C. Stocker, personal communication).

C. L. Koch's *Epeira bicolor* (Fabricius) is a large spider from Brazil. Critical features are a spherical abdomen with transverse marks, no distinct marks on the underside of the abdomen and a 5-mm-long scape ("2 Linien langen, über dieselbe rückwärts gebogenen Legstachel"). This fits *Parawixia bistriata*. But this is probably a misidentification of *Aranea bicolor* Fabricius (1798: 230), which has a worthless, unrecognizable description of a spider from "America." *Aranea bicolor* Fabricius (1798) is also a junior homonym of *Aranea bicolor* Olivier (1789: 230). Olivier's *Aranea bicolor* is a worthless description without a holotype for a spider from Guadeloupe, Lesser Antilles (see also Petrunkevitch, 1911).

Holmberg (1874) writes that the scape of *E. burmeisteri* reaches the center of the spinnerets. This is characteristic for this species, but not known for any others. Mello-Leitão (1932) thought Burmeister's and Holmberg's descriptions fit a different social species, common in Argentina. This could not be verified.

The spider is known in Spanish as the "ñandutí" spider, derived from the word for "spider-web" in the Guaraní language (Fowler and Diehl, 1978; Kochalka, 1989, personal communication), in Portuguese as *aranha do cerrado* (C. Sandoval, 1990, personal communication).

Description. Female from Depto. Central, Paraguay. Carapace with dark orange cephalic region, sides of carapace red-brown; cephalic region with long white hairs. Sternum dark orange. Coxae dusky dark orange; legs orange-brown. Dorsum of abdomen dark gray with indistinct folium (Fig. 153); venter dark gray with indistinct paired lighter patches (Fig. 154). Posterior median eyes 0.7 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 1.3 diameters apart. Posterior median eyes their diameter apart. Lateral eyes their diameter apart. Abdomen spherical, without tubercles (Fig. 153). Total length 22 mm. Carapace 9.4 mm long, 8.1 wide. First femur 8.8 mm, patella and tibia 11.1, metatarsus 7.1, tarsus 2.7. Second patella and tibia 10.5 mm, third 6.5, fourth 9.6.

Male from Formosa, Argentina. Darker than female in coloration. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Laterals their diameter apart. Palpal patella with one dark macroseta and one light-colored smaller seta. Fourth trochanter without macroseta. Abdomen oval. Total length 13 mm. Carapace 7.7 mm long, 6.7 wide. First femur 7.5 mm, patella and tibia 9.4, metatarsus 5.9, tarsus 1.8. Second patella and tibia 7.6 mm, third 5.0, fourth 7.1.

Variation. Total length of females 16.7 to 27 mm, of males 11.7 to 18.5. In adult females preserved in alcohol the abdomen is variable in color. In immature specimens the abdomen has a diagnostic pattern and three to four pairs of lateral tubercles, and two posterior, median tubercles (Fig. 157). The tubercles may be visible on the abdomen of males. Early instars are almost all black; later instars have light stripes, a longitudinal row of dark red dots on the tubercles on each side, and a faint red spot in the cardiac area. Adults are mostly dark gray with a little red anterior lateral on the abdomen dorsum (Kochalka, 1989, personal communication; and color photographs by C. P. Sandoval, Plate 1). Figures 150, 151 were prepared from the holotype of *E. aeronavis*, Figure 152 was made from a female from Tucumán, Argentina, 153–155 were made from syntypes of *A. nordenskiöldi*, and 157 was prepared from an immature from Barra da Tapirapé, Mato Grosso, Brazil.

Diagnosis. Females differ from those of *P. audax* and *P. undulata* by having a spherical abdomen sometimes with only three faint pairs of lateral tubercles, indistinctly marked on the venter (Figs. 153, 154). The scape of the epigynum is less sclerotized than in *P. audax* and *P. undulata* and the posterior median plate may be white (Fig. 151). Males differ from those of the similar two species by having a proximal constriction of the median apophysis, and by the shapes of the base of the median apophysis and the distal end of the terminal apophysis (Figs. 155, 156).

Natural History. The species has communal webs 2 to 5 m above the ground, just beyond reach, often on telephone poles in urban and suburban areas, in open woodland and orchard, in the lower Pantanal, and in isolated trees in dry areas, but never in a forest having a closed canopy. Individuals cluster during daytime in a common shaded retreat "as big as a hat," constructed with relatively little silk (Plate 1). At dusk the spiders move out on thick silk lines that stretch as far as 30 m and build orbs. Within an hour all orbs are completed, and may cover a 100 m^2 area. The orbs are taken down at dawn. Marked spiders do not return to the same spot as that of the previous night, but build in the vicinity. Large prey ensnared are overpowered and fed on by many spiders, the number in proportion to prey size. Reproductive casts of ants are a common prey item, but are not the only food. All spiders in a colony are of the same age and molt during the same week. Spiders transferred to another colony are not attacked and neighboring colonies may fuse. Males and females mature in late January in southern Brazil. The number of males is approximately equal to that of females. Following the final molt, females disperse and deposit egg-sacs with a mean of 551 eggs, less than half the number laid by related araneids of equal size. Spiderlings emerge in May. In the laboratory there are eight postembryonic instars. (J. Kochalka, C. Sandoval, personal communications; Fowler and Diehl, 1978; Fowler and Gobbi, 1988a,b). Rengger gives colony size as between 30 to 40 individuals; Azara in 1808 estimated less than 100 individuals (Fowler and Diehl, 1978; Kochalka, 1989, personal communication). In 1965, when visiting Rio de Janeiro, I saw what I believed to be webs of this species, high up on telegraph poles outside the entrance of the Parque da Cidade, too high up to collect. I could not find any webs on a return visit to the same spot in 1987. Carter (1928) claims that the spiders' bite is venomous. They can kill beetles larger than 2.5 cm in a few minutes and there are records of birds trapped in their webs (C. Sandoval, personal communication).

Venom. The Hospital Vital Brazil of the Instituto Butantan has recorded only three accidents, all of persons living in the area surrounding the city of São Paulo: In 1964, a 7-year-old girl was bitten on the hand with only slight pain. In 1966, an 18-year-old man was bitten on the foot; no treatment was necessary. In 1970, a baby of eight months was bitten on the buttock with moderate local pain, edema and mild erythema. In all cases punctures of fangs were visible. The first and last victims were treated with antihistamines and analgesics. Vellard, in his book on spider venoms (1936: 262), did not cite any accidents with the species, but expressed the belief that they do occur and are not serious. In recent years, V. P. D. von Eickstedt has received, from the São Paulo State Central Electrical Co. from Andradina and from Pirassununga, requests for help in removing the spiders because workers were afraid to work on poles with webs (Vera P. D. von Eickstedt, 1990, personal correspondence).

Distribution. From Mato Grosso, Minas Gerais States, Brazil, to Bolivia and Buenos Aires Prov., Argentina (Map 3).

Records. BRAZIL *Districto Federal:* Brasilia, 27 Mar. 1964, 2♀ (C., E., E. S. Ross, CAS); Sobradinho, 3 Apr. 1971, 3♀, 2♂ (A. Carlos, C. Sandoval, CS). *Minas Gerais:* Diamantina, Minha Serinha, Jan.–Mar. 1945, 6♀ (E. Cohn, AMNH); Serra do Cipó, 1977, ♀, ♂ (V. R. D. von Eickstedt, MCZ); Mariana, ♀ (P. Forseca, MZSP 7615); Lagao Santa, imm. ♀ (ZMK), 12 Jan. 1965, 21 imm. (J. Morgante, MZSP 3893). *Mato Grosso:* Barra do Tapirapé, 23 Dec. 1962, 43 imm., 12 Jan. 1963, 20 imm. (B. Malkin, AMNH); Tapirapé, 23 Nov. 1960, 91 imm. (AMNH). *Mato Grosso do Sul:* Miranda, 17 Jan. 1985, 33 imm. (B. A. M. Soares, MZSP 157); Três Lagoas, 26–27 Mar. 1964, ♀ (P. Vanzolini, MZSP 3179). *São Paulo:* Rincão, 1942, 5♀ (B. A. M. Soares, MZSP 7616); Itirapina, imm., 29 Nov. 1984, imm. (C. Sandoval, CS); Piraju, 12 June 1985, ♀ (C. Sandoval, CS); Campinas, 15 Mar. 1990, 2♀, 3♂ (J. Vascocellos-Neto). PARAGUAY *Boquerón:* Laguna Negra, Transchaco km 470, 17 May 1984, ♀; Filadelfia, 16 May 1984, ♀. *Nueva Asunción:* Transchaco km 709, 25 May 1984, ♀; 1984 (all L. Baert, J. P. Maelfait, IRSNB). *Concepción:* Concepción, 7 Mar. 1989, 3♀, 3♂ (J. A. Kochalka, MCZ); San Lorenzo, 24 July 1976, ♀, ♂ (H. Fowler, MCZ), 9 Jan. 1982, 4♀, 2♂ (J. A. Kochalka, IBNP). *Central:* Villeta, Feb., Mar. 1983, ♀ (L. Fogarty, MCZ); Asunción, Jan. 1892, 6 imm. (Dr. Bohls, BMNH). ARGENTINA *Formosa:* Formosa, Mar. 1918, 2♂ (P. Jorgensen, MCZ), ♀ (MACN). *Chaco:* Resistencia, July 1934, 9♀ (J. B. Daguerre, MACN). *Salta:* Rosario de la Frontera, Los Baños, 8 May 1979, 9♀, 3♂ (Mision Scient. Danesa, ZMK). *Tucumán:* Tucumán, 1987, 45♀, 88♂, 4 imm. (J. A. Kochalka, MCZ). *Entre Ríos:* Rosario, 2♀ (W. Sörensen, ZMK).

LITERATURE CITED

Badcock, H. D. 1932. Reports of an Expedition to Paraguay and Brazil in 1926–27. Arachnida from the Paraguayan Chaco. Journal of the Linnean Society of London, **38**(257): 1–48.

Berman, J. D., and H. W. Levi. 1971. The orb-weaver genus *Neoscona* in North America (Araneae: Araneidae). Bulletin of the Museum of Comparative Zoology, **141**(8): 465–500.

Bertkau, P. 1880. Verzeichniss der von Prof. Ed. van Beneden auf seiner im Auftrage der belgischen Regierung unternommenen wissenschaftlichen Reise nach Brasilien und La Plata i. J. 1872–73 gesammelten Arachniden. Mémoires couronnés et mémoires des savants étrangers, publiés par l'Académie royale des sciences, des lettres et des beaux-arts de Belgique, **43**(2): 1–120.

Blackwall, J. 1863. Description of newly discovered spiders captured in Rio de Janeiro. The Annals and Magazine of Natural History. Series 3, **11:** 29–45.

Bonnet, P. 1955. Bibliographia Araneorum. Toulouse, **2**(1): 1–918.

———. 1956. Bibliographia Araneorum. Toulouse, **2**(2): 919–1925.

———. 1958. Bibliographia Araneorum. Toulouse, **2**(4): 3027–4230.

———. 1959. Bibliographia Araneorum. Toulouse, **2**(5): 4231–5058.

Brignoli, P. 1983. A Catalogue of the Araneae Described Between 1940 and 1981. Manchester: Manchester Univ. Press. 755 pp.

Bryant, E. B. 1940. Cuban spiders in the Museum of Comparative Zoology. Bulletin of the Museum of Comparative Zoology, **86:** 247–554.

———. 1945. The Argiopidae of Hispaniola. Bulletin of the Museum of Comparative Zoology, **95**(4): 357–418.

Burmeister, H. 1861[?1872]. Reise durch die La Plata-Staaten, Halle [not seen].

Buskirk, R. E. 1981. Sociality in the Arachnida. Social Insects, **2:** 281–367.

Camargo, H. F. de A. 1950. Contribuição ao estudio das aranhas brasileiras (Arachnida-Aranea). Três espécies novas e uma pouco conhecida. Papéis Avulsos do Departamento do Zoologia, **9**(15): 223–248.

Cambridge, F. P.-. 1897–1905. Arachnida, Araneidea and Opiliones, **2:** 1–610. *In* Biologia Centrali–Americana, Zoologia, London.

Cambridge, O. P.-. 1889–1902. Arachnida, Araneidea, **1:** 1–317. *In* Biologia Centrali–Americana, Zoologia, London.

Caporiacco, L. di. 1948. Arachnida of British Guiana collected in 1931 and 1936 by Professors Beccari and Romiti. Proceedings of the Zoological Society of London, **118**(3): 607–747.

———. 1954. Araignées de la Guyane Française du Muséum d'Histoire Naturelle de Paris. Commentationes Pontifica Academia Scientiarum, **16:** 45–193.

———. 1955. Estudios sobre los Arácnidos de Venezuela, 2ª Parte: Araneae. Acta Biologica Venezuelica, Universidad Central, **1:** 265–448.

Carter, G. S. 1928. A naturalist's journey in South America. Proceedings of the Royal Philosophical Society of Glascow, **56:** 82–107.

Chamberlin, R. V., and W. Ivie. 1936. New spiders from Mexico and Panama. Bulletin of the University of Utah, Biological Series, **27**(5): 1–103.

Coddington, J. 1986. The genera of the spider family Theridiosomatidae. Smithsonian Contributions to Zoology, Washington, **422:** 1–96.

Darwin, C. 1839. The Voyage of the Beagle. Edited by L. Engel, 1962, Doubleday and Co. 524 pp.

Fabricius, J. C. 1798. Supplementum Entomologiae systematicae. Hafniae. 572 pp.

Fowler, H. G., and J. Diehl. 1978. Biology of a Paraguayan colonial orb-weaver, *Eriophora bistriata* (Rengger) (Araneae, Araneidae). Bulletin British Arachnological Society, **4**(6): 241–250.

Fowler, H. G., and N. Gobbi. 1988a. Cooperative prey capture by an orb-web spider. Die Naturwissenschaften, **75:** 208, 209.

———. 1988b. Communication and synchronized molting in a colonial araneid spider, *Eriophora bistriata*. Experientia, **44**(8): 720–722.

Harrod, J. C., H. W. Levi, and L. B. Leibensper-

GER. 1991. The Neotropical orbweavers of the genus *Larinia* (Araneae: Araneidae). Psyche, **97:** 241–265 (for 1990).

HOLMBERG, E. L. 1874. Descriptions et notices d'arachnides de la République argentine. Periódico Zoológico, **1:** 283–302.

———. 1876. Los Arácnidos argentinos. Anales de agricultura de la República Argentina, Buenos Aires, **4:** 95.

HOUSSAY, B. A. 1917. Activación por los huevos de Araña de la acción hemolitica de los venenos de Víboras. La Prensa médica argentina, **1917:** 382–385 [not seen].

KEYSERLING, E. 1865. Beiträge zur Kenntniss der Orbitelae Latrl. Verhandlungen der k. k. zoologischen und botanischen Gesellschaft in Wien, **15:** 799–856.

———. 1892–1893. Die Spinnen Amerikas, Epeiridae. Nürnberg, **4:** 1–377.

KOCH, C. L. 1839. Die Arachniden. Nürnberg, **5:** 1–158.

———. 1845. Die Arachniden. Nürnberg, **11:** 1–174.

LEVI, H. W. 1968. The spider genera *Gea* and *Argiope* in America (Araneae: Araneidae). Bulletin of the Museum of Comparative Zoology, **136**(9): 319–352.

———. 1971. The *Ravilla* group of the orbweaver genus *Eriophora* in North America. (Araneae: Araneidae). Psyche, **77**(3): 280–302 (for 1970).

———. 1976. The orb-weaver genera *Verrucosa, Acanthepeira, Wagneriana, Acacesia, Wixia, Scoloderus* and *Alpaida* north of Mexico (Araneae: Araneidae). Bulletin of the Museum of Comparative Zoology, **147**(8): 351–391.

———. 1985. The spiny orb-weaver genera *Micrathena* and *Chaetacis* (Araneae: Araneidae). Bulletin of the Museum of Comparative Zoology, **150**(8): 429–618.

———. 1986. The orb-weaver genus *Witica* (Araneae: Araneidae). Psyche, **93**(1–2): 35–46.

———. 1988. The Neotropical orb-weaving spiders of the genus *Alpaida* (Araneae: Araneidae). Bulletin of the Museum of the Comparative Zoology, **151**(7): 365–487.

———. 1989. The Neotropical orb-weaver genera *Epeiroides, Bertrana* and *Amazonepeira* (Araneae: Araneidae). Psyche, **96**(1–2): 75–99.

———. 1991a. The Neotropical and Mexican species of the orb-weaver genera *Araneus, Dubiepeira,* and *Aculepeira.* Bulletin of the Museum of Comparative Zoology, **152**(4): 167–315.

———. 1991b. The Neotropical orb-weaver genera *Edricus* and *Wagneriana* (Araneae: Araneidae). Bulletin of the Museum of Comparative Zoology, **152**(6): 363–415.

MELLO-LEITÃO, C. 1917. Notas arachnologicas, V. Especies novas ou pouco conhecidas do Brasil. Broteria, **15:** 74–102.

———. 1932. Sobre *Eriophora bistriata* (Rengger) o a presença do genero *Hyptiotes* na America do Sul. Boletim do Museu Nacional do Rio de Janeiro, **8:** 117–126.

———. 1933. Catalogo das Aranhas argentinas. Archivos da Escola superior de agricultura e medicina veterinaria, Rio de Janeiro, **10:** 3–63.

———. 1942. Arañas del Chaco y Santiago del Estero. Revista del Museo de La Plata, (Nueva Serie Zoología), **2:** 381–426.

———. 1947. Aranhas do Paraná e Santa Catarina, das Coleções do Museu Paranaense. Arquivos do Museu Paranaense, **6:** 231–304.

———. 1948. Contribuição ao conhecimento da Fauna Araneológica da Guianas. Anais da Academia Brasileira de Ciencias, **20:** 151–196.

———. 1951. Arañas de Maullin colectadas por el ingeniero Rafael Barros V. Revista chilena de historia natural, **51–53:** 327–338.

OLIVIER, G. A. 1789. Araignée, pp. 173–240. *In* Encyclopédie Méthodique. Histoire Naturelle, Insectes. Paris, Vol. 4.

PETRUNKEVITCH, A. 1911. A synonymic index-catalogue of spiders of North, Central and South America with all adjacent islands. Bulletin of the American Museum of Natural History, **29:** 1–791.

RENGGER, J. R. 1836. Ueber Spinnen Paraguay's. Archiv für Naturgeschichte, Zweiter Jahrgang, **1:** 130–132.

ROEWER, C. F. 1942. Katalog der Araneae von 1758 bis 1940. Bremen, **1:** 1–1040.

SANDOVAL, C. P. 1987. Aspectus da Ecologia e Socialidade de Uma Aranha Colonial: *Eriophora bistriata* (Rengger, 1836) (Araneidae). Thesis, Universidade Estadual de Campinas, São Paulo, Brazil.

SHEAR, W. A. 1970. The evolution of social phenomena in spiders. Bulletin British Arachnological Society, **1**(5): 65–76.

STRAND, E. 1908. Diagnosen neuer aussereuropäischer Argiopiden. Zoologischer Anzeiger, **33**(1): 1–4.

———. 1915. Systematisch-faunistische Studien über paläarktische, afrikanische und amerikanische Spinnen des senckenbergischen Museums. Archiv für Naturgeschichte, Abteilung A, **81**(9): 1–153.

TACZANOWSKI, L. 1873. Les Aranéides de la Guyane française. Horae Societatis entomologicae Rossicae. St.-Petersburg, **9:** 64–150.

———. 1878. Les Aranéides du Pérou central. Horae Societatis entomologicae Rossicae. St.-Petersburg, **14:** 140–175.

TULLGREN, A. 1905. Araneida from the Swedish Expedition through the Gran Chaco and the Cordilleras. Arkiv för zoologi, Stockholm, **2:** 1–81.

VELLARD, J. 1936. Le venin des Araignées, Paris. 312 pp.

INDEX

Valid names are printed in italics. Page numbers refer to main references, starred page numbers to illustrations.

(US ISSN 0027-4100)

Bulletin OF THE Museum of Comparative Zoology

The Neotropical Orb-Weaving Spiders of the Genera *Wixia*, *Pozonia*, and *Ocrepeira* (Araneae: Araneidae)

HERBERT W. LEVI

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 153, NUMBER 2
14 APRIL 1993

(US ISSN 0027-4100)

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

BREVIORA 1952–
BULLETIN 1863–
MEMOIRS 1865–1938
JOHNSONIA, Department of Mollusks, 1941–1974
OCCASIONAL PAPERS ON MOLLUSKS, 1945–

SPECIAL PUBLICATIONS.

1. Whittington, H. B., and W. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. 192 pp.
2. Turner, R. D., 1966. A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia). 265 pp.
3. Sprinkle, J., 1973. Morphology and Evolution of Blastozoan Echinoderms. 284 pp.
4. Eaton, R. J., 1974. A Flora of Concord from Thoreau's Time to the Present Day. 236 pp.
5. Rhodin, A. G. J., and K. Miyata (eds.), 1983. Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams. 725 pp.
6. Angelo, R., 1990. Concord Area Trees and Shrubs. 118 pp.

Other Publications.

Bigelow, H. B., and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprinted 1964.

Brues, C. T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects. (*Bulletin of the M.C.Z.*, Vol. 108.) Reprinted 1971.

Creighton, W. S., 1950. The Ants of North America. Reprinted 1966.

Lyman, C. P., and A. R. Dawe (eds.), 1960. Proceedings of the First International Symposium on Natural Mammalian Hibernation. (*Bulletin of the M.C.Z.*, Vol. 124.)

Ornithological Gazetteers of the Neotropics (1975–).

Peters' Check-list of Birds of the World, vols. 1–16.

Proceedings of the New England Zoological Club 1899–1947. (Complete sets only.)

Proceedings of the Boston Society of Natural History.

Price list and catalog of MCZ publications may be obtained from Publications Office, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A.

THE NEOTROPICAL ORB-WEAVING SPIDERS OF THE GENERA *WIXIA, POZONIA,* AND *OCREPEIRA* (ARANEAE: ARANEIDAE)

HERBERT W. LEVI[1]

ABSTRACT. The species previously placed in *Wixia* fall into three distinct genera: *Wixia*, *Pozonia*, and *Ocrepeira*. *Wixia* is known from only one pair of adults collected recently and the holotype collected in the last century, and several immatures, all from the Amazon region. Three species of *Pozonia*, all previously known, are distributed from Mexico and the West Indies to Paraguay. *Ocrepeira* contains 67 species, two north of Mexico and 65 from Mexico to Argentina and Chile. Forty-six of the *Ocrepeira* species are new (70% of the species) while 18 (30%) were previously known. There are eight new synonyms of the 18 previously known names. Two North American species of *Wixia* are transferred to *Ocrepeira*.

The species of the three genera differ in the shape of the carapace and the abdomen.

The few webs that are known, made by species of *Pozonia* and *Ocrepeira*, are complete orbs placed almost vertically.

INTRODUCTION

The family of araneid orb weavers, Araneidae, is the third largest spider family. The only larger ones are the jumping spiders (Salticidae) and the mainly Holarctic Linyphiidae. Comprehensive revisions and keys covering the whole Neotropics are not available for either of these families. Perhaps half of the Neotropical araneid orb weavers have now been revised. The first revisions of Neotropical species were made together with the Nearctic species: *Gea* and *Argiope* (Levi, 1968), *Neoscona* (Berman and Levi, 1971), and *Eriophora* (Levi, 1971). These will eventually be updated. The first revision of the Neotropical araneids was that of *Micrathena* and *Chaetacis* (Levi, 1985), followed by *Alpaida* (Levi, 1988), *Witica* (Levi, 1986), *Epeiroides*, *Bertrana*, and *Amazonepeira* (Levi, 1989), *Araneus*, *Dubiepeira*, and *Aculepeira*, (Levi, 1991a), *Larinia* (Harrod *et al.*, 1991), *Edricus* and *Wagneriana* (Levi, 1991b), and *Parawixia* (Levi, 1992).

My goal has always been to make it possible to determine animals so that they can be used for research. When I started work, it was a longstanding tradition that systematists would determine animals for biologists in other fields. However, it seemed absurd to me that systematists spent their time identifying specimens, rather than working on revisions and making this knowledge directly available to these specialists. Revisions allow the identification of specimens and also provide a context for the naming of new species. Naming of new species should not be attempted before the genus has been revised and common species, named in the last century, illustrated and their variation noted.

When I started work, there were few spider specialists in North America. When Jocelyn Crane worked on the behavior of Venezuelan jumping spiders (1948), she first had to do the taxonomic work herself. At the same time, Kaston published *Spiders of Connecticut* (1948). This work showed the value of a clear text and good illustrations in taxonomic work. Spiders can readily be identified with short, well-illustrated descriptions such as these, but not with lengthy, elaborate descriptions accompanied by poor illustrations (for example, Petrunkevitch, 1925). Therefore, my descriptions of Neotropical orb weavers are accompanied by drawings of sev-

---

[1] Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

eral views of the spider. To answer questions about my working and drawing methods for these revisions, a description is provided below.

MATERIALS AND ACKNOWLEDGMENTS

Specimens from the following collections were used whose curators I thank for making the material available.

AMNH	American Museum of Natural History, New York, United States; N. Platnick, L. Sorkin
BMNH	Natural History Museum, London, Great Britain; P. Hillyard, F. Wanless
CAS	California Academy of Sciences, San Francisco, California, United States; W. J. Pulawski, D. Ubick
CUC	Cornell University Collection, kept in the AMNH; N. Platnick
CV	Carlos Valderrama A., Bogotá, Colombia
DAD	D. A. Dean, College Station, Texas, United States
DU	D. Ubick, San Francisco, California, United States
FSCA	Florida State Collection of Arthropods, Gainesville, Florida, United States; G. B. Edwards
HECO	Hope Entomology Collections, Oxford University, Oxford, Great Britain; D. Spencer-Smith, I. Lansbury
IESC	Instituto de Ecologia, Academia de Ciencias, Cuba; G. Alayón
IBNP	Inventario Biológico Nacional, San Lorenzo, Paraguay; J. A. Kochalka
INPA	Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil; J. A. Raphael
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; L. Baert
JAK	J. A. Kochalka
JMM	J. M. Maes, León, Nicaragua
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; E. A. Maury
MCN	Museu de Ciências Naturais, Porto Alegre, Rio Grande do Sul, Brazil; E. H. Buckup
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts, United States
MECN	Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador; L. Avilés
MEG	M. E. Galiano, Buenos Aires, Argentina
MHNM	Museo de Historia Natural de Montevideo, Uruguay; R. M. Capocasale
MLJ	Maria-Luisa Jiménez, La Paz, Mexico
MLP	Museo de Universidad Nacional, La Plata, Argentina; R. F. Arrozpide
MNHN	Muséum National d'Histoire Naturelle, Paris, France; C. Rollard, J. Heurtault, J. Kovoor
MNRJ	Museu Nacional, Rio de Janeiro, Brazil; A. Timotheo da Costa
MNSD	Museo Nacional de Historia Natural, Santo Domingo, Dominican Republic; F. Del Monte
MUSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; D. Silva D.
MZSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; P. Vanzolini, L. Neme, J. L. M. Leme
MZUF	Museo Zoologico de la Specola, Università di Firenze, Florence, Italy; S. Mascherini
NMB	Naturhistorisches Museum, Basel, Switzerland; C. Stocker
NRMS	Naturhistoriska Riksmuseet, Stockholm, Sweden; T. Kronestedt
PAN	Polska Akademia Nauk, Warszawa, Poland; A. Riedel, W. Starega, J. Prószynski, A. Slojewska, E. Kierych
RLCB	Renner L. C. Baptista, São Paulo, Brazil

SMF	Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; M. Grasshoff
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., United States; J. Coddington
ZMB	Zoologisches Museum der Humboldt Universität, Berlin, Germany; M. Moritz
ZMK	Zoologisk Museum, København, Denmark; H. Enghoff

I want to thank numerous individuals for helping. L. Leibensperger helped with various tasks including rewording the manuscript. L. R. Levi reworded sentences. D. Sherry word processed and assembled the paper. F. Boisse-Kilgo edited meticulously. M. A. Serna D. and E. H. Buckup provided locality information. R. Baptista, W. Eberhard, J. Kochalka, and Y. Lubin gave ecological and behavioral data. J. Prószynski supplied information on the Taczanowski collection. O. Kraus gave advice on a nomenclature problem. Various readers of previous manuscripts made suggestions to improve these papers and two anonymous readers suggested improvements and corrections in this paper. NSF grant GB–36161 supported the start of the revisions of *Wixia* and related genera. Publication costs of this study were covered in part by the Wetmore Colles Fund.

Equipment. 1. American Optical dissecting microscope with Greenough optics (ca. 1950) with 0.7×, 4×, and 8× objectives. The 12× ocular gives magnifications of 8.4×, 48×, and 96×. The right reticule has a 20 by 20 (400 square) grid. Other oculars available for higher magnification are 18× and 30×.

2. Leitz dissecting microscope also with Greenough optics, 1×, 4×, and 10× objectives and 15×, 25×, and 32× oculars. In the reticule of the American Optical microscope, alternate rows of squares are numbered, which makes this reticule easier to use than the Leitz reticule with unnumbered squares.

3. Leitz Smith interference compound microscope: used rarely for small genitalia. Used sometimes with reflected light provided by a fiber light system (a method first suggested by J. Coddington). The optics of a compound microscope are far superior to those of any dissecting microscope. The genitalia are in a depression slide covered with alcohol.

4. Dolan-Jenner Fiber Light (Series 180) with two arms, one lighting from the left, the other from the right. Both lights are used to see outlines; for shading and sculpturing illustrations, only the left is used.

Containers. 1. Syracuse watch glasses (with grooved and beveled edges for stacking) are used for preliminary examination of specimens. I prefer them with ground rims so they can be stacked.

2. Stender glass dishes (22 mm deep, 52 mm inside diameter) with ground glass lids are used for detailed examination and illustration. One Stender dish is filled to one-quarter depth with light-colored washed sand, another with black silicon carbide (Carborundum, B. Opell, 1983), lapidary grade, 80 grit size. A third dish is filled on one side with white paraffin and on the other with black paraffin (made by blackening paraffin with lampblack). When making the dish, a temporary cardboard divider keeps the hot paraffin from mixing and is removed when it solidifies. While the paraffin is soft, depressions of various sizes are made, some in the black-white border.

Art Materials. 1. Papers. Tracing paper (letter-size onion skin), coquille board no. 3, two-ply Strathmore board, for line illustrations and Bainbridge board (38 by 51 cm) for mounting illustrations. The sculptured coquille board, which used to be used widely for illustrations of newspaper advertisements, is increasingly difficult to find in art stores and in consistent quality, whiteness, and evenness of texture.

2. Drawing Supplies. Rapidograph or other technical pen, sizes 000 (0.25 mm), 00 (0.3 mm), 2, 3, and 4. Black India ink: Rapidograph or Pelikan drawing ink A. Opaque white water paint (Steig's Pro-White). Good quality no. 2 pencils. Wil-

liam Corn's lithographic crayons in pencil shape no. 3, 4, and 5. Black Staedtler Omnichrom pencils that can be sharpened (first suggested by R. Forster). Sandpaper for sharpening crayons. Camel-hair brushes, sizes 1, 00, 000. Crow-quill pen tip and holder and a desk fluorescent light having a magnifying lens.

3. Cards approximately 13 by 20 cm. Each card is gridded into squares of a given size: 5, 6, or 7 mm etc., up to 15, 18, 21, and 25 mm. Grids are drawn with no. 00 Rapidograph pens.

4. Fixative: Krylon no. 1303 Crystal Clear Spray or Krylon no. 1306, Workable Fixative.

5. 3M Scotch Positional Mounting Adhesive rolls for mounting illustrations on Bainbridge board.

Illustrations. In males, the left palpus is amputated (and stored in a 2 by 6 mm vial stoppered with cotton). In females, the epigynum is left attached, but pulled out slightly with a needle for examination of posterior and lateral views.

The following conventions are used in making illustrations. The illumination comes from the upper left. The anterior end of the animal is placed toward the top of the page, the posterior end toward the bottom. In side view, the head is on the left, the tail end on the right. The left side and the structures are illustrated. In illustrating epigyna and palpi, I modify the convention to ease visualization of structures, e.g., in posterior view of the epigynum, the venter is up, the dorsum is down as you would expect if you flipped it over.

A grid card is selected so as to produce a finished illustration of 6 to 9 cm in size, about 2 to 3 times the published size. The card grid corresponds to the microscope reticule grid. A piece of tracing paper is folded in half and placed over the grid card. The pencil outline is drawn on the tracing paper. If the illustration is symmetrical, only half of the structure need be drawn; the drawing can be folded and the other half traced. Great care is required when folding to avoid distortion. When the outline is completed, the back of the tracing paper is blackened by rubbing with a graphite pencil. The paper is put blackened-side down on a piece of Coquille board. Tracing the outline with a sharp graphite pencil transfers it to the board. Care must be taken not to dent the texture of the board.

The outline is corrected with pencil while referring to the specimen. The outline is then inked with a no. 00 Rapidograph pen, with the help of a magnifying glass under a fluorescent light. The inked outline is placed next to the microscope for completion. No. 3 and 4 Rapidograph pens are used to blacken totally the darkest areas. Cleaning brushes used for this purpose is time-consuming. The white of the reflections, the lightest areas, is surrounded lightly with Omnichrome pencil. Dimmer areas are shaded in with no. 4 lithographic crayon and Omnichrome pencils, darker areas with softer crayons. Fine white lines are made around sclerites with water color white. A camel-hair brush is used, drawn to a point by lightly twisting the wet point while touching paper. There may be problems differentiating transparent areas and borders of sclerites; for example, palpal structures close to the cymbium may be obscured by long cymbial setae. The palpus (or other structure) should be turned slightly and compared with the drawing to make sure the shape of the sclerites is correct. The palpus should be pulled apart only if many specimens are available.

The illustration is cleaned under the magnifying light. Areas covered by lithographic pencil are difficult to correct: small white dots can be made to make dark areas lighter, or some black can be lifted up with 3M Scotch Magic Tape (a G. Hormiga invention). When completed, the illustration is sprayed with artist's fixative and later mounted on Bainbridge board. After mounting, the illustrations are individually numbered with a Rapidograph lettering set. Illustrating techniques are described in some detail in Zweifel (1988) and Hodges (1988).

Line illustrations are made on smooth Strathmore board, 2 to 3 times larger than the coquille illustrations, and are reduced to the desired size by photocopying. The photocopies are mounted with the coquille illustrations.

When illustrating and measuring, one is faced with a dilemma between pulling the specimen apart in order to be highly accurate or measuring less accurately and leaving the specimen intact for the next study. It is usually preferable to avoid damaging the specimen. Genitalia or other parts are never left on microscope slides. If a structure such as the female genitalia must be cleared with Hoyer's Medium (Krantz, 1970) and mounted between two large coverslips, they are taken off afterward and the structure is stored in a small vial with the rest of the specimen.

Type specimens. The original specimens, the types of early describers, are often not labeled as such. The concept of a holotype to which the species name is attached was not applied until early this century. The type method is quite recent, appearing after 1850. The original Code of Nomenclature of 1901 had no directions for types (Mayr, 1969; Mayr and Ashcroft, 1991). Often it is not known if the specimens examined and labeled as types are really the original specimens. The labeling of specimens as types of the Emerton collection in the MCZ was done by E. B. Bryant, not by Emerton. The American specimens of Taczanowski at the Polish Academy of Science had only numbers that were matched to notebooks in the 1930's by Zolzislaw Raabe, who later became professor at the university in Warszawa; Raabe could not locate all specimens and some file cards indicate missing specimens (J. Prószynski, personal communication). Eugène Simon, and perhaps also N. Banks, placed additional spiders into the vials that contained the original specimens, sometimes of similar but different species. In the British Museum, many neat, inked labels of O. P.- and F. O. P.-Cambridge were made by E. Browning and others.

Lectotypes here are only designated when a mixture of species is suspected among the syntypes. Neotypes are designated only where essential to avoid later confusion. In previous revisions all adult specimens examined for the revision were designated as paratypes. In this paper only specimens from the type locality or nearby are designated as such.

Descriptions. Descriptions are made following a standard format. An outline to be filled in later is in the computer. Notation of colors: white on the carapace and sternum in these araneid genera is usually a result of pigment granules under the exoskeleton. Fine black pigment spots are referred to as dusky. Eye measurements are expressed as ratios of the diameter (with cornea in profile) to that of the anterior median eyes (Figs. 27, 28). Distances between eyes of the anterior row are expressed as diameters of the anterior median eyes (in profile); distances between eyes of the posterior row are given as diameters of the posterior median eyes. The height of the clypeus, the distance between anterior median eyes and the edge of the carapace, is given in diameters of an anterior median eye and measured below the eye (Fig. 28f). These measurements are approximate as araneid eyes are quite variable and difficult to measure; often one side is slightly different from the other. Grasshoff (1968) discusses some of the difficulties in measuring araneid spiders and their eyes.

Other measurements are made using the ocular reticule with 400 squares and, while accurate to about one-tenth of a millimeter, the measurements must be regarded as approximate for several reasons. The total length of the specimen depends on the angle of the abdomen to the carapace. In *Wixia*, *Pozonia*, and *Ocrepeira* the abdomen is at an angle to the cephalothorax (Fig. 40). A slight dorsal pressure makes the animal longer. [Often, as in *Ocrepeira* (Fig. 44), when illustrating the abdomen the carapace is pushed slightly down to make the abdomen more level to better show the pattern.] Measuring carapace length cannot be done accurately without removing the abdomen, which usually covers the posterior of the thoracic region. To avoid amputation, the measurement of carapace length (Fig. 27) is best made with the specimen on sand and viewed at an angle, but the legs may obscure the view. The width of the carapace is measured at the widest part (Fig. 27), and the measurement is more accurate in specimens having a sclerotized carapace. If the carapace is soft it may be warped. In the group of genera studied here, the width of the cephalic region is measured directly behind the posterior lateral eyes (Fig. 27). However, if the longest setae of the carapace are behind the lateral eyes, they interfere with very accurate measurement. The leg articles are measured along their dorsal length; as they are not amputated and placed on a horizontal slide, there may be small errors due to parallax.

Illustrations, descriptions, and measurements were made from one specimen, and photocopies of all illustrations are kept. A more sclerotized or a softer specimen may show features not visible in other specimens. If there is considerable variation, additional illustrations are made. Notes on variation in color, pattern, or morphology are recorded on a second sheet for records and collections. Also noted on this sheet are the total lengths of about 10 females and 10 males from different localities. Total length is helpful for determining spiders, although less consistent than the length of the leg articles (see also Levi, 1985).

When only a few specimens are available, it is difficult to decide whether some small variation actually means that the specimen belongs to a different species. I expect a separate species to exhibit not only consistent differences in genitalia, but also in color or morphology, and show similar differences in the opposite sex. Nevertheless, even with care, lumping or splitting mistakes are unavoidable.

Mapping. Our own outline maps are used and photocopied to reduce their size. The dots are transfer dots; labeling of maps is done with a Kroy machine. The most valuable references for finding old Neotropical localities are Selander and Vaurie (1962) for Mexico and Central America, and the collection of gazetteers of Neotropical bird collecting localities by R. Paynter (1975–1991). [Several collectors of South American spiders specialized in birds as well as spiders: K. Jelski and J. Sztolcman (who collected for L. Taczanowski), E. Goeldi (who collected for E. Simon), and Graf Keyserling, E. Simon himself, and more recently, H. Sick (Levi, 1964).] Other localities cited in the Paynter gazetteers were collecting localities frequented by collectors of various animals in the 19th century. Modern automobile maps of individual countries, especially those with gazetteers, are useful and available from map stores. Automobile maps are available for individual Mexican states and for separate regions of Argentina.

Literature citations of collection records are ignored since too many specimens in collections are misidentified.

Systematics of Neotropical orb weavers. It is not possible to estimate the number of araneid orb-weaver species based on our current knowledge. (While I anticipated about twenty species in the genus *Wixia*, the collections had close to 70 species and actually fell clearly into three genera.) The phylogenetic relationships among the orb weavers are currently unknown but certain features could turn out to be conclusive. The paramedian apophysis may be absent, present as a separate sclerite, or fused to the conductor. In *Wixia*, *Pozonia*, and *Ocrepeira*, the presence of a paramedian apophysis attached to the conductor in the male palpus (Figs. 23, 32, 46, 47) may indicate that they are related. Other genera of the Neotropics whose males have a paramedian apophysis attached to the conductor are: *Acacesia*, *Alpaida*, *Cyclosa*, *Edricus*, *Molinaranea*, *Parawixia*, *Scoloderus*, *Verrucosa*, *Wagneriana*, and *Xylethrus*. Others probably have not been examined or their males are not known. In *Eriophora*, *Gasteracantha* *cancriformis*, and *Acanthepeira* the paramedian apophysis is a separate sclerite. Some *Micrathena* species have a paramedian apophysis attached to the conductor, others a free sclerite, others lack this structure (*M. funebris, M. sagittata, M. gracilis*, Levi, 1985): apparently it is secondarily lost. But is absence of the paramedian apophysis in other genera due to secondary loss or did they never evolve this structure? Of the genera that have a paramedian apophysis, *Molinaranea* and *Xylethrus* have not been revised. A. A. Lise is currently revising *Verrucosa*. Most of these genera are American. *Parawixia* may also be found in Australia, and only *Cyclosa* species are found worldwide (see Table 1).

Other characters that support this grouping are: the positions of the conductor in the palpus, the attachment of the median apophysis, the number of patellar setae, the structure of the epigynum, and the frequent median, posterior (row of) tubercles on the abdomen in the *Alpaida* group of genera (but not in *Ocrepeira*).

The conductor is on the edge of the tegulum in *Araneus* (Levi, 1991a, fig. 3) and in *Larinia* (Harrod *et al.*, 1991, fig. 15), while in the *Ocrepeira* and *Alpaida* group of genera it is attached to the center of the bulb, away from the edge, closer to the cymbium (Figs. 23, 32). The median apophysis, whose attachment is offset behind the sclerite in *Araneus* (Levi, 1991a, fig. 3) and *Larinia* (Harrod *et al.*, 1991, figs. 14, 15), is on the side of the sclerite in the *Ocrepeira*, *Alpaida* group of genera (Figs. 23, 32). While most average-sized species of the *Araneus, Larinia* group have 2 palpal patellar setae, there is only one in the *Ocrepeira*, *Alpaida* group. [However, dwarf males of *Kaira* lack these setae, and giant males of *Eriophora* (allied to *Alpaida*) have two. The smallest *Eriophora* male, *E. nephiloides* O. P.-Cambridge, and the largest of the *Parawixia* species, *P. bistriata* Rengger, have one large macroseta and one small.]

The scape of the epigynum has evolved numerous times in various araneoid families. In *Araneus* it has a pocket at its tip (Levi, 1991a, fig. 1). In *Larinia* this pocket may be behind a thick lip (Harrod *et al.*, 1991, fig. 1). In *Aculepeira* (allied to *Araneus*) the tip is pointed (Levi, 1991a, fig. 543). It rarely, if ever, has a pocket in *Eriophora*, *Parawixia*, and *Ocrepeira* (Figs. 7, 29); if flat and rounded, it may have a plain, ventral depression at the tip.

At present, it is still too early to assess whether further evidence will agree or conflict with these characters.

Wixia O. P.-Cambridge

Wixia O. P.-Cambridge, 1882: 437. Type species by monotypy *Wixia abdominalis* O. P.-Cambridge. The generic name is feminine.

Diagnosis. *Wixia* differs from most araneid genera by having the pedicel attached to the posterior third of the abdomen (Fig. 4b). It differs from *Pozonia* and *Ocrepeira* by having the carapace high and the clypeus about 2 to 4 diameters of the anterior median eyes, and from *Pozonia* by the cephalic region being almost as wide as the thoracic region (Figs. 4 a–c, 6). It differs from *Scoloderus* by having the thoracic region only slightly higher than the cephalic region (Fig. 4b).

Relationship. The shape of the carapace is an apomorphy, the swollen posterior median eye area and the palpal structure are synapomorphies shared with *Ocrepeira* and *Pozonia*, and the shape of the abdomen is a synapomorphy with *Pozonia*.

Description. The posterior median eyes face almost to the sides, being on a joint swelling (Figs. 4, 6). The first patella and tibia are as long as the carapace (Figs. 5, 6). The abdomen is anteriorly drawn out in both sexes, the female with two tubercles on its anterior tip (Figs. 4, 6). The epigynum appears to be as in *Ocrepeira* or *Pozonia* (Figs. 1–3).

The male is smaller than the female and similar in appearance (Fig. 6). Its endite has a tooth, the first coxa has a hook (Fig. 6), the palpal patella one macroseta (Fig. 6). The palpus (Figs. 5a,b) is *Ocrepeira*-like with a large median apophysis (M), a

TABLE 1. DIFFERENTIAL CHARACTERS OF *PARAWIXIA* (PARW), *ERIOPHORA* (ERIO), *ACANTHEPEIRA* (ACAN), *WAGNERIANA* (WAGN), *EDRICUS* (EDRI), *ACACESIA* (ACAC), *ALPAIDA* (ALPA), *WIXIA* (WIXI), *POZONIA* (POZO), *OCREPEIRA* (OCRE), *CYCLOSA* (CYCL), *SCOLODERUS* (SCOL). (DATA FROM LEVI, 1971, 1976, 1977, 1988, 1992).

	PARW	*ERIO*	*ACAN*	*WAGN*	*EDRI*	*ACAC*	*ALPA*	*WIXI*	*POZO*	*OCRE*	*CYCL* (prov.)	*SCOL* (prov.)
Pattern												
carap. glabrous	–	–	–	–	–	–	[+*]	–	–	–	–	–
paired spots on carap.	+*	–	+	–	–	–	–	–	–	–	–	–
marks betw. ME and LE	+*	–*	+	–	–	–	–	–	–	–*	–	–
black eye rings	–	–	–	–	–	–	[+*]	–	–	–	–	–
sides of thoracic reg. black	–	–	–	[+*]	–	–	–	–	–	–*	–	+
pattern on sternum	[+*]	–	–	–	–	–	–	–	–	–	–	–
abd. pattern	–	–	–	–	–	[+]	[+*]	–	–	+*	[+]	–
abd. v. with black rect.	–	[+]	–	–	–	–	–	–	–	–	–	–
abd. v. black with white spots	+	–	–	–	–	–	–	–	+	+*	[+]	–
Female Morphology												
clypeus high	–	–	–	–	[+]	–	–	[+]	–	–	–	[+]
ceph. reg. narrow	–	–	–	–	–	[+]	–	–	[+]	–	+	–
LE on sides of tuber.	+	–	+	–	–	–	–	–	–	–	–	–
PME on slight swelling	–*	–	–	–	+	+	–	+	+	+*	–	+
PME touch	–	–	–	–	–	–	–	–	–	–	+	–
PME large	–	–	–	–	[+]	–	–	–	–	–	–	–
carap. swollen behind eyes	+	+	+	+	–	–	+	+	–	+*	–	+
carap. and sternum modified	–	–	–	–	[+]	–	–	–	–	–	–	–
abd. with tubers.	4–15	0–3	12+	9–15	11	–	–*	[2]	[2]	[2*]	0–2	0–2
leg IV longer than I	–	–	–	–	[+]	–	–	–	–	–	–	–
ant. median abd. tuber.	–*	–	+	–	–	–	–	–	–	–	–	+
abd. subspherical	+*	+	+	–	–	–	–	–	–	–	–	–
abd. oval	–*	–	–	+	–	+	+	–	–	–*	+	–
abd. with tail	–	–	–	+*	+*	–	–	–	–	–	+*	–
3 median post. tubers.	+	–*	+	+	+	–	–	–	–*	–	–	–
abd. glabrous	–	–	–	–	–	–	[+]	–	–	–	–	–
abd. attached post.	–	–	–	–	–	–	–	+	+	–	–	+*
Epigynum												
scape	+	+	+	–	–	+	–	+	+	+*	+	–
lobe	–	–	–	+	+	–	+	–	–	–*	–	+
knob at tip	–*	–	–	+	+	–	–*	–	?	–	–	–
notch on face	–	–	–	–	–	–	[+*]	–	–	–	–	–
post. med. plate round	–	–	[+]	–*	+	–	–	–	–	–	–	–
post. med. plate oval	–	–	–	+*	+	–	+*	–	–	–	–	–
post. med. triangular	–	[+]	–	–	–	–	–	–	–	–	–	–

TABLE 1. (*CONTINUED*)

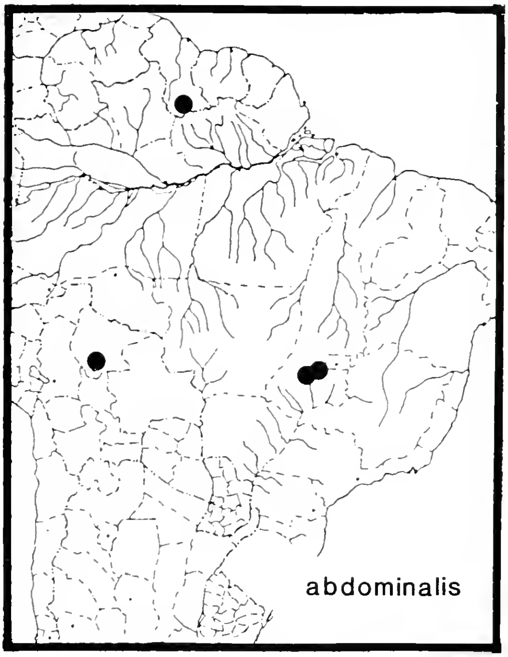
	PARW	*ERIO*	*ACAN*	*WAGN*	*EDRI*	*ACAC*	*ALPA*	*WIXI*	*POZO*	*OCRE*	*CYCL* (prov.)	*SCOL* (prov.)
Male Morphology												
ceph. reg. wide	–	–	[+]	–	+	–	–	–	–	–	–	+
hook on coxa I	+	+	–	+	+*	+	+*	+	+	+	+*	+
macrosetae on coxa III, IV	+*	+*	+*	+*	–	+*	+*	+	–	+*	+*	–
trochanter IV macrosetae	+*	+*	–	–*	+	–	–*	+	–	–	–	–
tibia II modified	–	–	–	–	+	+	–*	+	–	–	–	+
Palpus												
much wider than long	–	–	–	–	–	–	–	–	–	–	[+]	–
patella macrosetae	1**	[2**]	1	1	1	1	1*	1	1	1	1	1
Y narrow	–	[+]	–	–	–	–	–	–	–	–	–	–
Y covers PM	–	–	[+]	–	–	–	–	–	–	–	–	–
PM absent	–	–	–	–	–	–	–	–	–	–	–	+
PM free	–	+	+	–	–	–	–	–	–	–	–	–
PM stalk and ap	–	–	–	–	+	–	+*	–	–	–	+*	–
PM L- or U-shaped	–	–	–	[+]	–	–	–	–	–	–	+*	–
PM disk with finger	+	+	–	–	–	–	–	–	–	–	–	–
PM disk with fold	–	–	[+]	–	–	–	–	–	–	–	–	–
PM a prong	–	–	–	–	–	+	–	+	+	+	+*	–
M with base teeth	+	+	–	+	–	–	–	–	+	+	–	–
M with projection to Y	–	–	–	–	–	–	[+]	–	–	–	–	–
base of M with concavity	+	+	–	–	–	–	–	–	–	–	–	+
base of M stalk with knob	–	–	–	–	–	–	+*	–	–	–	–	–
long "stipes"	–	[+]	–	–	–	–	–	–	–	–	–	–
E cone-, bullet-shaped	+*	–	–	–	+	–	–	–	–	–	–	–
E knife-shaped	–	–	–	–	–	–	[+*]	–	–	–	–	–
E razor clam-shaped	–	–	[+]	–	–	–	–	–	–	–	–	–
E filiform	–	–	–	–	–*	–	–*	–	–	–	[+]	–
A absent	–	–	[+]	–	–	–	–	–	–	–	–	–
A fused with embolus	–	–	–	+	+	–	+	+	+	+	+	+
A fused with R	–	–	–	+	+	–	+	–	–	–	–	–
R with an outgrowth	–	–	–	–	–	–	–	–	–	[+*]	–	–

* There are exceptions.

** *P. bistriata* and *E. nephiloides* (Levi, 1971) have a large macroseta and a smaller one on the male palpal patella.

Bracketed characters are autapomorphies for the genus.

Abbreviations: abd., abdomen; ant., anterior; betw., between; carap., carapace; ceph., cephalic; med., median; post., posterior(ly); prov., provisionally; rect., rectangle; reg., region; tuber(s)., tubercle(s); v., venter; A, terminal apophysis; E, embolus; LE, lateral eyes; M, median apophysis; ME, median eyes; PM, paramedian apophysis; PME, posterior median eyes; R, radix; Y, cymbium.



Map 1. Distribution of *Wixia abdominalis*.

light-colored conductor (C) with a prong-like paramedian apophysis (PM) with its tip tucked under the radix (R).

Misplaced North American Species.

Wixia ectypa (Walckenaer, 1841) = *Ocrepeira ectypa* (Walckenaer).

Wixia georgia (Levi, 1976) = *Ocrepeira georgia* (Levi). NEW COMBINATION.

Misplaced species. The following species have been misplaced in *Wixia*, other than those placed here in *Pozonia* and *Ocrepeira*:

acrosomoides (Mello-Leitão, 1939: 109), is *Wagneriana acrosomoides*, see Levi, 1991b: 404.
albotaeniata Mello-Leitão, 1942: 403, is *Alpaida rubellula* (Keyserling, 1892), see Levi, 1988: 395.
destricta (O. P.-Cambridge, 1889: 39) is a *Parawixia* not *Wixia* as thought in Levi, 1991a: 179.
fissifasciata Mello-Leitão, 1945: 244, is *Alpaida bicornuta* (Taczanowski), see Levi, 1988: 387.
gavensis Camargo, 1950: 231, is *Wagneriana gavensis* (Camargo), see Levi, 1991b.
infelix Soares and Camargo, 1948: 378, fig. 35, ♂, is a *Mecynogea*.
nigropunctata Mello-Leitão, 1941: 214, is *Alpaida rubellula* (Keyserling, 1892), see Levi, 1988: 395.
rubellula (Keyserling, 1892: 81), is *Alpaida rubellula* (Keyserling, 1892).
tatarendensis (Tullgren, 1905: 34) belongs to a new genus, close to *Wixia*.

Unrecognizable Species.

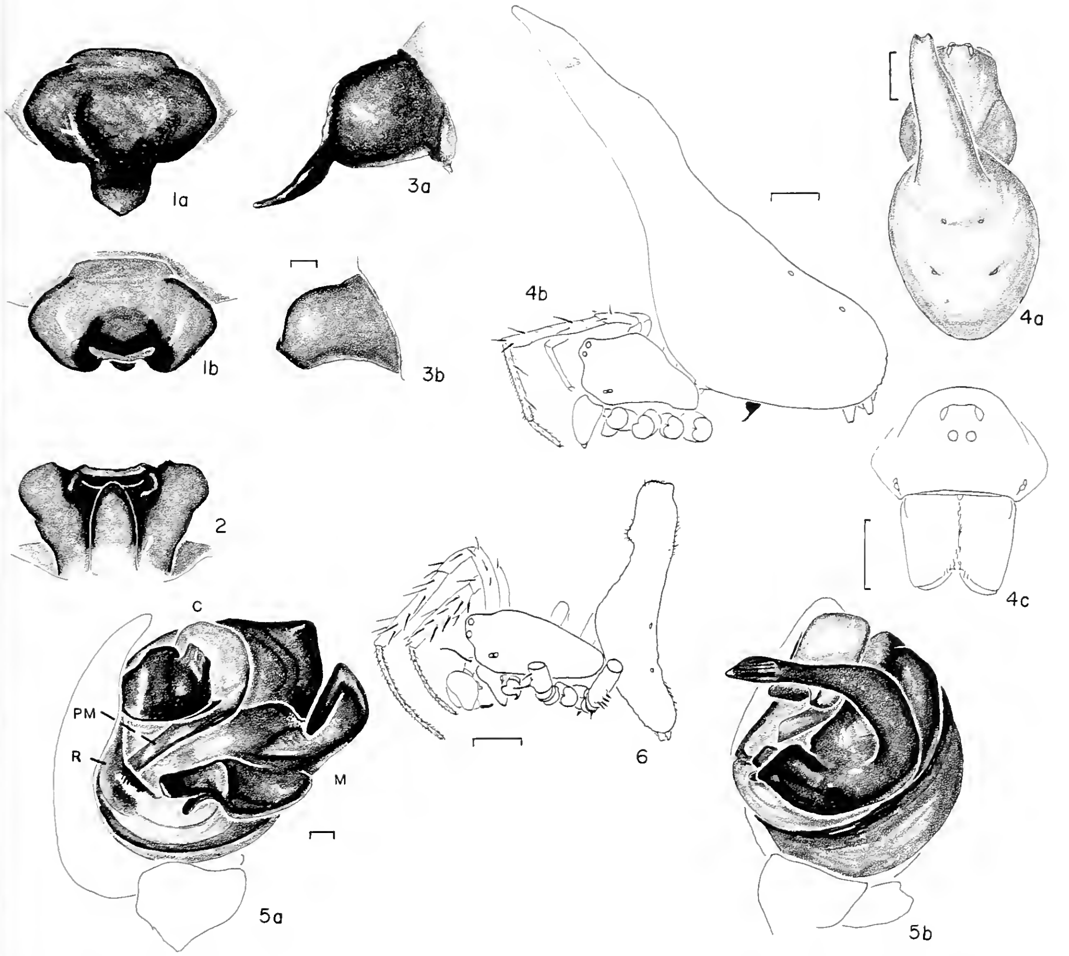
proxima Mello-Leitão, 1940: 207, type specimens lost.

Wixia abdominalis O. P.-Cambridge
Figures 1–6; Map 1

Wixia abdominalis O. P.-Cambridge, 1882: 438, pl. 31, fig. 13, ♀. Female holotype from "the Amazon," in HECO, examined. Roewer, 1942: 881. Bonnet, 1959: 4828.

Description. Female holotype. Carapace orange-brown with short setae. Chelicerae, labium, endites, sternum, legs orange-brown. Dorsum of abdomen white with some dusky marks (Fig. 4a); venter dusky. Posterior median eyes 1.2 diameters of anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart. Posterior median eyes two diameters apart. Ocular quadrangle wider behind than in front. Height of clypeus equal to 3.5 diameters of anterior median eyes. There is a tooth on the anterior margin of the chelicera, on each side of which is a smaller one. Abdomen drawn out anteriorly with two points (Figs. 4a,b). Total length 5.4 mm. Carapace 3.1 mm long, 2.3 wide, 1.9 wide behind eyes, 1.6 high in thoracic region. Abdomen 8.8 mm long. First femur 2.7 mm, patella and tibia 3.1 mm, metatarsus 2.0 mm, tarsus 0.9 mm. Second patella and tibia 3.1 mm, third 1.8 mm, fourth 2.5 mm.

Male. Coloration darker than female with yellow-orange and dark patches posteriorly on each side of carapace. Legs with dark rings, abdomen spotted with venter black. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 0.7 diameter apart. Posterior median eyes 1.4 diameters apart. The abdomen has a bulge anteriorly on the underside (Fig. 6). The fourth coxa has a macroseta on a tubercle, the fourth trochanter has a macroseta. There is a large, long macroseta on a tubercle at the proximal end of the second femur and several macrosetae at the proximal end of the fourth femur (Fig. 6). The second tibia is



Figures 1–6. *Wixia abdominalis* (O. P.-Cambridge). 1–4, female. 1–3, epigynum. 1a, ventral with scape. 1b, ventral, scape torn off. 2, posterior. 3a, lateral with scape. 3b, lateral, scape torn off. 4a, dorsal. 4b, lateral. 4c, eye region and chelicerae. 1b, 2, 3b, 4a, 4c, holotype. 5, 6, male. 5, left male palpus. 5a, mesal. 5b, ventral. 6, lateral.

Abbreviations. C, conductor; M, median apophysis; PM, paramedian apophysis; R, radix.

Scale lines. 1.0 mm, genitalia 0.1 mm.

proximally swollen with several long macrosetae (Fig. 6). Total length 5.5 mm. Carapace 3.4 mm long, 2.9 wide, 1.8 mm wide behind eyes, 1.6 mm high in thoracic region. Abdomen 6.2 mm. First femur 3.2 mm, patella and tibias 3.8 mm, metatarsus 2.4 mm, tarsus 0.9 mm. Second patella and tibia 2.9 mm, third 1.9 mm, fourth 2.7 mm.

Variation. The second female collected was 7.5 mm total length, abdomen 14 mm high (Fig. 4b). It was collected with the male after completion of the revision and its illustration was added before printing.

Specimens Examined. GUYANA Kuyuwini Landing, Kuyuwini River, 20–21 Nov. 1937, imm. (W. G. Hassler, AMNH). BRAZIL *Goiás:* Porteria, Pirenópolis, 20 July 1942, imm. (F. Lane, MZSP 8023); Jaraguá, 12 July 1942, imm. (F. Lane, MZSP 7273); Fazenda Aceiro [?], Oct. 1962, imm. male (MZSP 7864). BOLIVIA *Beni:*

Estac Biológica Beni, 225 m, 14°47′S, 66°15′W, 8–14 Nov. 1989, ♀, ♂ (J. Coddington, S. Larcher, E. Pañaranda, C. Griswold, D. Silva D.).

Pozonia Schenkel

Pozonia Schenkel, 1953: 24. Type species by designation and monotypy *Pozonia cornuta* Schenkel, 1953: 25, fig. 23, imm. Brignoli, 1983: 279. The generic name is feminine.

Note. The holotype of *P. cornuta* is immature. It is believed to be *P. nigroventris* but might be *P. bacillifera*.

Diagnosis. Pozonia species differ from those of *Ocrepeira* by having the pedicel attached to the posterior half, and rarely to the middle of the abdomen (Figs. 10, 14, 19). Females of the *Pozonia* species differ from those of *Wixia* and *Ocrepeira* by the width of the cephalic region of the carapace, which is less than half that of the thoracic region (Fig. 18). The abdomen, unlike that of most other araneids, has scattered spindle-shaped setae (Figs. 10, 19). The sternum of the male has a median tubercle, unlike that of any other araneid male (Fig. 25).

The placement of the pedicel on the abdomen is a synapomorphy with *Wixia*. The shape of the carapace, the spindle-shaped setae, and the structure of the male sternum are autapomorphies of *Pozonia*.

Specimens of *Pozonia* had erroneously been placed in *Kaira*. *Kaira* has the posterior median eyes facing straight up, while those of *Pozonia* are on a bulge and face at an angle, forward and sideways (Figs. 19, 24). *Kaira* has a minute, slightly sclerotized epigynum with a median keel; the epigynum of *Pozonia* is large and sclerotized, with a scape (Figs. 7–9, 11–13, 15–17). The male of *Kaira* is minute and has a median apophysis with denticles and two flagella; the median apophysis of *Pozonia* is relatively large, bearing two prongs distally (Fig. 23), and the palpus has a paramedian apophysis, which is absent in *Kaira*.

Description. The carapace is higher in the thoracic region than in the cephalic region (Figs. 10, 14, 19). The posterior median eyes face forward and laterally and are on a swelling, a synapomorphy with *Wixia* and *Ocrepeira*. The carapace has short setae behind the eyes and long hair-like setae on the anterior of the thoracic groove (Fig. 18). The abdomen has pairs of tubercles or swellings, some long setae and some spindle-shaped setae (Figs. 10, 14, 19). Spindle-shaped setae are also found in the Australian *Dicrostichus* (Mastophorinae) and the theridiid genus *Chrysso* (*Meotipa*) and are believed a homoplasy. The first patella and tibia are longer than the carapace. The tibia of the first leg is curved or slightly S-shaped with dense, light-colored macrosetae on the underside (Figs. 10, 14, 19). Both are autapomorphies of *Pozonia*. The scape of the epigynum is flat with indistinct or no wrinkles and no distal pockets (Figs. 7–9, 11–13, 15–17).

The male has a tooth on the endite, a hook on the distal margin of the first coxae, and macrosetae on the fourth coxa and trochanter (Fig. 25). The second tibia has large macrosetae on the anterior surface (Fig. 26). The abdomen is shorter than that of the female (Fig. 24). The structure of the palpus is similar to that of *Ocrepeira* with a pointed paramedian apophysis attached to the conductor, but the median apophysis is distally forked and the terminal apophysis is a small scale (Fig. 23).

All known species are Neotropical.

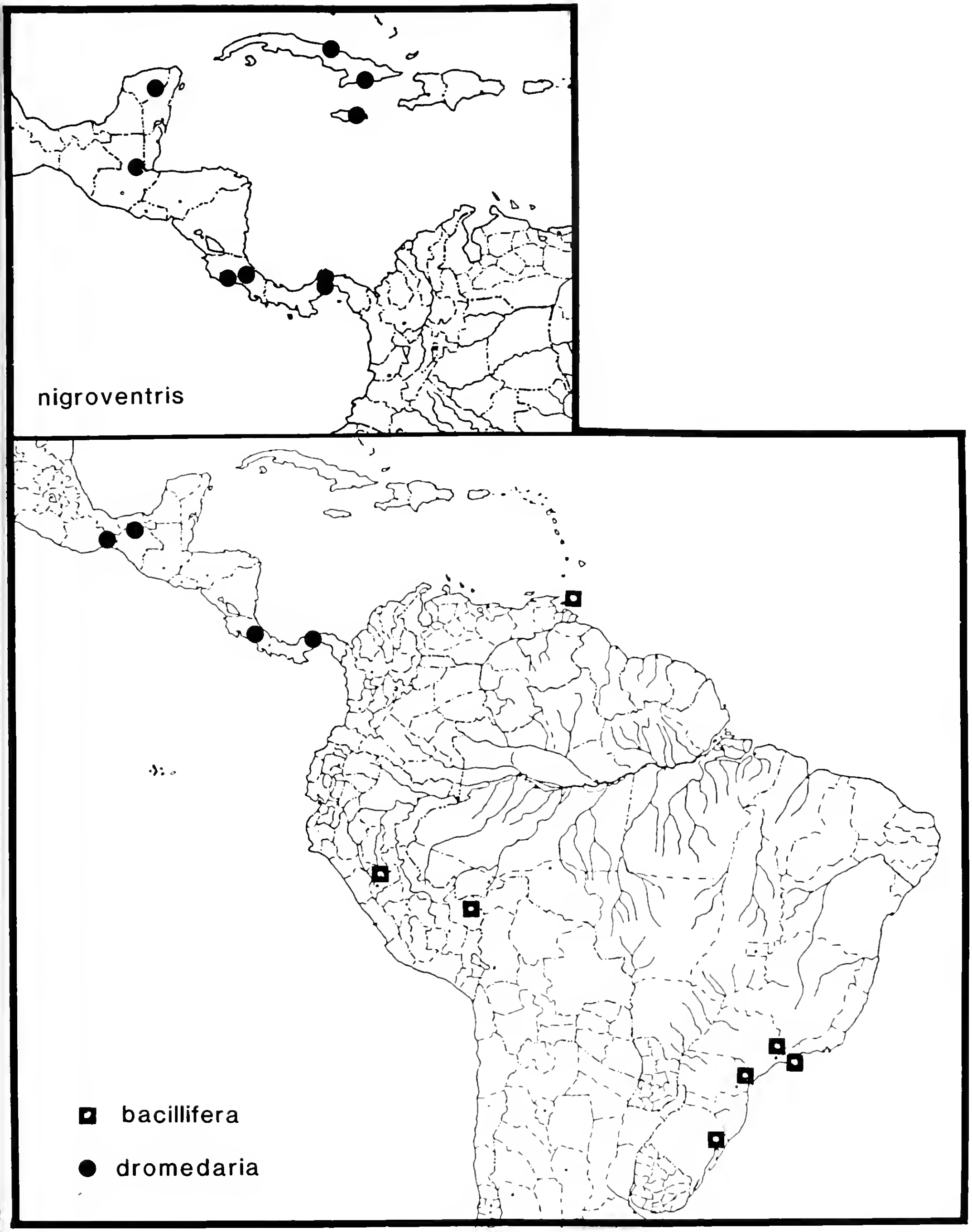
Natural History. Females make a nocturnal orb web (*P. dromedaria*) and are probably found in the canopy (*P. nigroventris*). The web illustrated by Eberhard (1986, p. 74, fig. 4.2i), as *Wixia* "species 573," is that of an immature *Pozonia* from Cali, Colombia, total length 5 mm, abdomen, 4.7 mm high. The plane of its orb web was at a 90° angle with the horizontal plane, the orb having a 7 cm horizontal diameter, 8.8 cm vertical.

Immature specimens are fairly common in collections, but adults are not.

KEY TO *POZONIA* FEMALES

1. Scape of epigynum short, less than twice as long as wide (Figs. 7, 9); Mexico, Central America .... *dromedaria*

– Scape longer, more than twice as long as wide (Figs. 11, 15) 2



Map 2. Distribution of *Pozonia* species.

2(1). Posterior median plate bottle-shaped, much wider than long (Fig. 12); Trinidad to Paraguay .... *bacillifera*
– Posterior median plate roughly hexagonal, four margins concave, posteriorly narrower than lateral plates (Fig. 16); Mexico, Central America, Cuba, Jamaica .... *nigroventris*

Pozonia dromedaria (O. P.-Cambridge), new combination
Figures 7–10; Map 2

Kaira dromedaria O. P.-Cambridge, 1893: 115, pl. 14, fig. 9, ♀. Female holotype from Teapa, Tabasco, Mexico, in BMNH, examined. F. P.-Cambridge, 1904: 522, pl. 51, fig. 11, ♀. Roewer, 1942: 904.
Caira dromedaria:—Bonnet, 1956: 925.

Description. Female from Escazu, Costa Rica. Carapace orange with a pair of black patches behind the eyes with some short black setae and long, white hair-like setae behind the black patches and around the sides of the thoracic region. Chelicerae orange. Labium, endites orange-brown. Sternum bright orange-brown. Coxae orange-brown, distally lighter; legs orange with brown to black rings and patches, coxae and legs with white hair-like setae. Dorsum of abdomen white and gray, posterior with black transverse bars, some spindle-shaped black setae and some long, white hair-like setae (Fig. 10); venter black. Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes their diameter apart, 2.2 diameters from laterals. Posterior median eyes 1.5 diameters apart, 3 diameters from laterals. Height of clypeus equal to 1 diameter of the anterior median eyes. Abdomen with pair of dorsal humps and five humps in middle (Fig. 10). Total length 8.3 mm. Carapace 4.7 mm long, 4.0 wide, 1.7 behind eyes. First femur 5.7 mm, patella and tibia 6.8, metatarsus 3.6, tarsus 1.7. Second patella and tibia 6.2 mm, third 3.9, fourth, 5.8. Abdomen 9.6 mm high.

Variation. The female holotype has the posterior median plate of the epigynum wider than the illustrated specimen from Costa Rica. Total length of females 7.4 to 8.3 mm.

Diagnosis. The epigynum of the female differs from that of *P. nigroventris* by the short, tongue-shaped scape which is barely twice as long as wide.

Natural History. Pozonia dromedaria was collected in an orb at night in Costa Rica. The orb had closely spaced, sticky spirals reminiscent of webs of *Ocrepeira* species observed in Colombia. The web was slanted, at about 45° and was about 2.5 m above the ground in relatively open habitat near the house (W. Eberhard, personal communication.)

Specimens Examined. MEXICO *Oaxaca:* 3.2 km NE Tehuantepec, 31 Aug. 1964, ♀ (J., W. Ivie, AMNH). COSTA RICA *San José:* San Antonio de Escazu, 1,300 m, Feb. 1981, ♀ (W. Eberhard 2177, MCZ). PANAMA *Panamá:* Barro Colorado Island, Lago Gatún, 19 Aug. 1939, ♀ (A. M. Chickering, MCZ).

Pozonia bacillifera (Simon), new combination
Figures 11–14; Map 2

Araneus (Vixia) bacillifer Simon, 1895: 819, fig. 870, ♀. Simon, 1897: 475. Two immature syntypes from Paraguay, in MNHN no. 8459, examined.
Wixia bacillifera:—Roewer, 1942: 881. Bonnet, 1959: 4828.

Note. Simon's figure 870 is a mature female showing the scape of the epigy-

---

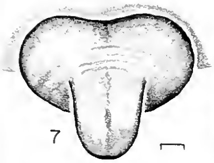
⟶

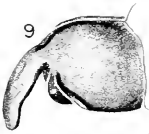
Figures 7–10. *Pozonia dromedaria* (O. P.-Cambridge), female. 7–9, epigynum. 7, ventral. 8, posterior. 9, lateral. 10, lateral.

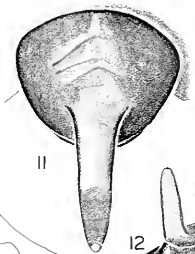
Figures 11–14. *P. bacillifera* (Simon), female. 11–13, epigynum. 11, ventral. 12, posterior. 13, lateral. 14, lateral.

Figures 15–26. *P. nigroventris* (Bryant). 15–20, female. 15–17, epigynum. 15, ventral. 16, posterior. 17, lateral. 18, carapace. 19, lateral. 20, posterior. 21–26, male. 21–23, left palpus. 21, mesal. 22, paracymbium. 23, pulled apart. 24, dorsal. 25, sternum and left coxae. 26, left second tibia, ventral.

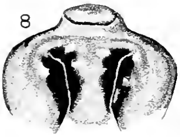
Scale lines. 1.0 mm, genitalia 0.1 mm.


7

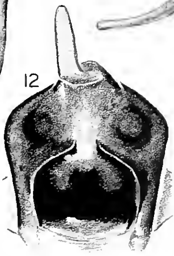

9

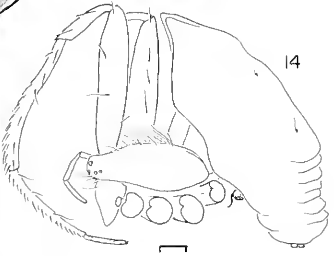

11

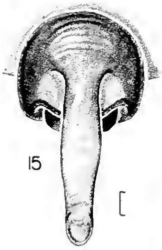

13

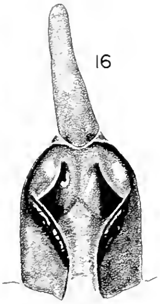

8

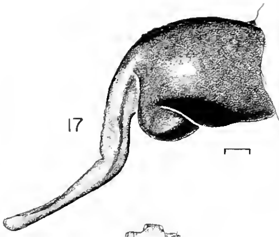

10

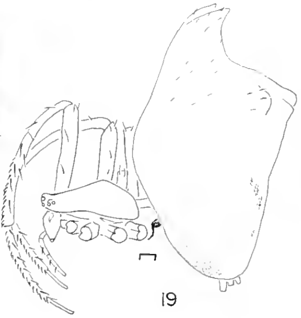

12


14

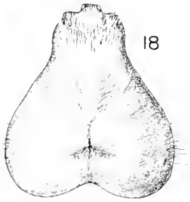

15

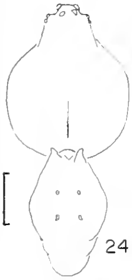

16

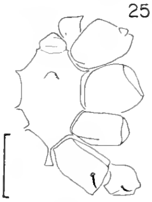

17

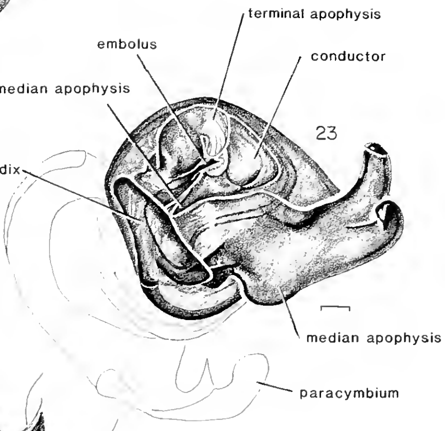

19

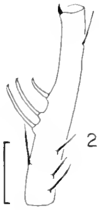

20

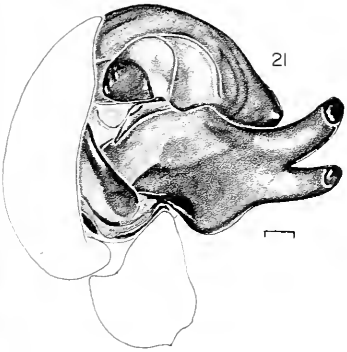

18


24


25


23


26


21


22

num. The description was published two years later and the surviving syntypes are immature.

The posterior median eyes of Simon's immature syntype have the same diameter as the anterior medians, laterals 0.6 diameter. Anterior median eyes 1.1 diameters apart, 1.4 diameters from laterals. Posterior median eyes 1.5 their diameter apart, 1.6 diameters from laterals. Lateral eyes separated by 0.6 their diameter. Ocular rectangle is slightly wider than long and wider behind than in front. Height of clypeus equal to one-third diameter of anterior median eyes. Abdomen with three anterior tubercles. Total length 7.0 mm. Carapace 3.4 mm long, 2.7 wide, 1.2 wide behind eyes. First femur 4.4 mm, patella and tibia 5.4 , metatarsus 2.7, tarsus 1.4. Second patella and tibia 4.9 mm, third 2.9, fourth 3.5. Abdomen 11.5 mm high.

Description. Female from Trinidad. Cephalic region dusky with long white hairs. Chelicerae orange. Labium, endites dusky orange. Sternum bright orange. Coxae dusky orange; legs dusky orange-brown. Dorsum of abdomen white and black; venter black. Posterior median eyes 1.2 diameters of anterior medians, laterals 1 diameter. Anterior median eyes 1.2 diameters apart, 2.2 diameters from laterals. Posterior median eyes 1.8 diameters apart, 2.2 diameters from laterals. Ocular quadrangle wider behind than in front. Height of clypeus equal to 0.9 diameter of anterior median eyes. Abdomen with two anterior tubercles (Fig. 14). Total length 8.7 mm. Carapace 4.9 mm long, 4.1 wide, 2.1 wide behind eyes. First femur 6.2 mm, patella and tibia 7.5, metatarsus 4.2, tarsus 1.8. Second patella and tibia 7.2 mm, third 4.2, fourth 6.2. Abdomen 10.2 mm high.

Variation. The adult female from São Paulo measured 8.7 mm total length, the abdomen 8.0 mm high; the one from Peru 13.4 total length, abdomen 17 mm high. The Peruvian female from Puerto Maldonado was darker than the others with the cephalothorax orange-brown, abdomen dusky, except for its anterior region, which was black underneath. The posterior median plate of the epigynum of the same female was more angular than that of other specimens. The illustrations were made from the female collected in Trinidad.

Diagnosis. The epigynum differs from that of *P. nigroventris* by the bottle-shaped posterior median plate, from that of *P. dromedaria* by the longer scape (Fig. 11).

Specimens Examined. TRINIDAD Maracas Valley, Feb. 1972, ♀ (J. A. L. Cooke, AMNH). PERU *Huánuco:* Cueva de Las Lechuzas, Tingo María, 31 June 1967, ♀ (A. F. Archer, W. Sherbrooke, AMNH). *Madre de Dios:* Cuzco Amazonica Lodge, nr. Puerto Maldonado, 8 Mar. 1990, ♀ (D. Silva D., MUSM); Zona Reservada Tambopata, 3 June 1988, ♀ (J. Coddington, USNM). BRAZIL *São Paulo:* Amparo, Fazenda Santa Maria, 25 Nov. 1942, imm. (F. Lane, MZSP 8071); Ilha Vitória, 16 Mar.–7 June 1965, ♀ (Exped. Depto. Zool., MZSP 4141). *Paraná:* Serra Negra, imm. (A. Mayer, MNRJ). *Rio Grande do Sul:* Porto Alegre, imm. (P. Buck, MNRJ); imm., 1984 (A. A. Lise, MCN).

Pozonia nigroventris (Bryant), new combination
Figures 15–26; Map 2

Wixia nigroventris Bryant, 1936: 329, pl. 23, fig. 10. Immature female holotype from Loma del Gato, 2,600–3,325 ft [790–1,010 m], Sierra de Cobre, Santiago Prov., Cuba, in MCZ, examined. Bryant, 1940: 346, fig. 113, ♂ (incorrect secondary spelling *nigriventris*). Roewer, 1942: 882. Bonnet, 1959: 4829 (as *nigriventris*).

? *Kaira granadensis* Mello-Leitão, 1941: 118. Immature holotype from Cucuta [Depto. Norte de Santander], Colombia, in MNRJ, examined. Brignoli, 1983: 271. NEW DOUBTFUL SYNONYMY.

? *Pozonia cornuta* Schenkel, 1953: 25, fig. 23, imm. Immature male holotype from El Pozón, Falcon Prov., Venezuela, in NMB no. 1815a, examined. NEW DOUBTFUL SYNONYMY.

Nomenclatural note. Although the holotype of *nigroventris* Bryant is immature, it is certain that the male collected later in Cuba is conspecific since we can expect that there is only one species belonging to

Pozonia in the Greater Antilles. Males and mature females were found in Mexico and Central America. The immature holotype of *granadensis* Mello-Leitão is similar to the immature holotype of *nigroventris* but it might be *A. dromedaria*. *Pozonia cornuta* is probably this species but it might be *P. bacillifera*.

Description. Female from Barro Colorado Island, Panama. Carapace, chelicerae, labium, endites, sternum orange-yellow. Carapace darker behind median eyes and with long, white hair-like setae. Coxae, legs yellowish. Dorsum of abdomen white with black streaks (Fig. 20), with some spindle-shaped black setae; venter black (Fig. 19). Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter of anterior medians. Anterior median eyes 1.2 diameters apart, 1.6 diameters from laterals. Posterior median eyes 1.3 diameters apart, 2.3 from laterals. Ocular rectangle wider than long. Clypeus height equal to 0.6 diameter of anterior median eyes. The first and second legs have many macrosetae on distal part of tibia and along metatarsus. Abdomen long and narrow (Figs. 19, 20). Total length 14 mm. Carapace 5.1 mm long, 4.1 wide, 2.1 behind eyes. First femur 6.5 mm, patella and tibia 8.0, metatarsus 4.7, tarsus 2.0. Second patella and tibia 7.5 mm, third 4.5, fourth 6.4. Abdomen 16 mm high.

Male from Sierra de Cobre, Cuba. Carapace orange-brown, cephalic region lighter. Chelicerae dusky brown. Labium, endites brown. Sternum orange with dusky knob. Legs dusky orange. Venter of abdomen black. Posterior median eyes 0.7 diameter of right anterior median, anterior laterals 0.7 diameter, posterior laterals 0.4. Anterior median eyes their diameter apart. Posterior median eyes with only right one on a tubercle. Ocular quadrangle a transverse rectangle. Height of clypeus equal to 1 diameter of anterior median eyes. Sternum with a median knob (Fig. 25). First coxa with hook and dorsal tubercle, fourth with macroseta. Fourth trochanter with one macroseta. Second tibia thicker than first, slightly flattened, swollen, with prolateral macrosetae (Fig. 26). Abdomen seen in Figure 24. Total length 5.6 mm. Carapace 3.1 mm long, 2.3 wide, 1.1 wide behind eyes. First femur 4.1 mm, patella and tibia 4.8, metatarsus 2.8, tarsus 1.5. Second patella and tibia 4.1 mm, third 2.9, fourth 3.8.

Note. Males and females were matched because both were uniquely found in the Greater Antilles.

Variation. The immature holotype of *A. nigroventris* (Fig. 20) is only 4.5 mm long, and has posterior median eyes larger than anterior medians, and the ocular rectangle wider than long. Carapace 2.5 mm long, 2.2 wide, 1.1 behind eyes. First patella and tibia 3.8 mm, abdomen 4.8 high. The specimen from Guatemala has the clypeus less than half the AME diameter. Total length of females 8.4 to 14 mm, of males 5.5 to 6.5. Illustrations of the female (Figs. 15–19) were made from specimens from Barro Colorado Island, Panama, and of the male (Figs. 21–26) from a specimen from Cuba.

Diagnosis. The epigynum of the female differs from that of *A. dromedaria* by the long scape (Figs. 15–17); it differs from that of both *A. dromedaria* and *A. bacillifera* by the hexagonal shape of the posterior median plate (Fig. 16).

Natural History. A male from Panama came from a canopy sample.

Specimens Examined. MEXICO *Yucatan:* Kabah [Kabá], 19 July 1964, ♂ (J. C. Pallister, AMNH). GUATEMALA *Peten:* Poptún, Finca Ixobel, 7 Feb. 1980, ♂ (V. Roth, AMNH). COSTA RICA *Puntarenas:* nr. Tárcoles, Reserva Carara, 23 Nov. 1984, imm. (W. Eberhard 2682, MCZ). *Cartago:* Turrialba, 23 July–13 Aug. 1965, imm. (A. M. Chickering, MCZ). PANAMA *Panamá*: Summit, July 1939, ♀, Aug. 1950, 2♂ (both A. M. Chickering, MCZ); Barro Colorado Isl., 23 May, 1952, ♀ (T. C. Schneirla, AMNH); Pipeline Rd. nr. Gamboa, 25 July 1979, ♂ (M. K. Stowe, MCZ); 12 July 1976, ♂ (Y. Lubin, JAK); Fort Sherman, Aug. 1939, ♂ (A. M. Chickering, MCZ); Chiva Chiva, Oct. 1946, ♂ (N. L.

H. Krauss, AMNH); Chilibre, July 1950, imm. (A. M. Chickering, MCZ).

CUBA Sierra del Cobre, 3,000–3,800 ft [900–1,200 m], 3–7 July 1936, ♂ (P. J. Darlington, MCZ); Loma de la Alegría, Cayo Sabinal, Camagüey, 28 Jan. 1989, imm. (A. Avila Calvo, IESC). JAMAICA *St. Thomas:* 6.5 mi [10.4 km] NE Bath, 10 Oct. 1957, imm. (A. M. Chickering, MCZ).

Ocrepeira Marx

Ocrepeira Marx, 1883: 22. Type species by monotypy *Epeira ectypa* Walckenaer.

Amamra O. P.-Cambridge, 1889: 55. Type species by monotypy *Amamra bituberosa* O. P.-Cambridge, 1889.

Notes. Marx failed to indicate that he was introducing a new generic name and only listed *ectypa* in a list of species in combination with a previously unknown generic name: *Ocrepeira.* Neave (1939–1975) does not list this generic name. According to the *International Code of Zoological Nomenclature* (1985) Art. 12 b (5), *Ocrepeira* is an available name, and the identity of the type species *Epeira ectypa* Walckenaer, 1841 is not in doubt.

F. P.-Cambridge (1904) synonymized *Amamra* with *Wixia* and has been followed by others including Bryant (1936: 329, 330) and myself (1976), although Bryant questioned this synonymy. The shape of the carapace is a very good generic character in the orb weavers and the carapace shape of *Wixia abdominalis* differs from that of other species previously placed in the genus (Figs. 5, 6).

Diagnosis. The carapace differs from that of *Pozonia* and *Acacesia* (Levi, 1976, fig. 78) by being wide in the eye region (Fig. 27), with some exceptions, and differs from that of *Wixia* by being relatively low, with the clypeus height equal to one or at most two diameters of the anterior median eyes (Fig. 28). The abdomen, unlike that of *Parawixia* and *Wagneriana*, has only two anterior humps (with some exceptions), and the attachment of the pedicel, unlike that of *Wixia* and *Pozonia*, is at the anterior half of the abdomen (Fig. 40).

The paramedian apophysis of the palpus is a straight rod, as is that of *Pozonia*, with the tip rounded (Fig. 32), sometimes pointed (Fig. 106), rarely short (PM in Fig. 46). The paramedian apophysis of *Wagneriana* is L-shaped, and that of *Parawixia* and *Eriophora* is enlarged, distal to the conductor, and disk-shaped (Levi, 1991b).

Ocrepeira females have been confused with those of *Neoscona* (Berman and Levi, 1971, figures 121–124). Differences are that the *Neoscona* carapace is less sclerotized, with more hair-like setae, the cephalic region is narrower than that of *Ocrepeira*, and the posterior median eyes face dorsally. *Neoscona* females can be separated by the oval abdomen from the few *Ocrepeira* whose eyes face dorsally; *Ocrepeira* whose eyes face "up" have a shield-shaped abdomen or an oval pattern-less abdomen with a dark frame (Fig. 390). In addition, the venter of the abdomen of *Neoscona* has two to four pairs of white patches on black, while that of *Ocrepeira* has only one pair of white patches. African *Pararaneus* (Grasshoff, 1968) species differ by having only a short lobe on the conductor which might be a paramedian apophysis; the median apophysis has a proximal projection and has the eyes facing dorsally. Its coloration and palpal structures (Grasshoff, 1968) are similar to *Ocrepeira's.*

Description. The cephalic region is often darker than the thoracic. The sternum may be darker than the coxae or may have some white pigment, the legs are ringed and the pattern on the dorsum of the abdomen is variable among specimens of the same species. In a number of species, however, the anterior part of the abdomen is dark in color to a distinct line between the tubercles (Figs. 148, 189, 357). Many of the species with a light-colored abdomen in alcohol and with few dorsal marks probably are green when alive (as is *O. albopunctata*). The venter of the abdomen is marked gray to black, frequently with species-characteristic white spots or patches. This ventral pattern can be used to match males with females.

Two species, *O. hirsuta* and *O. lapeza*, have the sternal color pattern with paired light patches otherwise characteristic of *Parawixia*. *Ocrepeira lapeza* (Fig. 343) has paired dark spots on the carapace, as is also characteristic of *Acanthepeira* and *Parawixia* species.

Males are usually darker than females, have a darker cephalic region than the female, and often have dark, radiating streaks from the thoracic groove toward the cephalic region (Fig. 368). Males are more likely than females to have white pigment under the sternum and a white cardiac mark on the abdomen.

The carapace is low, the clypeus height equal to one to two diameters of the anterior median eyes. The cephalic region is relatively wide in females. The posterior median eyes are on a swelling, the eyes facing anterolaterally. This posterior median eye position is more pronounced in *Ocrepeira* than in related genera. However, several species lack this swelling (*O. yaelae* Fig. 357, *O. comaina* Fig. 368, *O. herrera* Fig. 390, *O. covilli* Fig. 399). These same species have a narrow cephalic region (*camaca* Fig. 97, *yaelae* Fig. 357, *herrera* Fig. 390, *covillei* Fig. 399). The narrow head and eyes "facing up" is considered as secondary since some species show intermediate stages (*gulielmi* Fig. 239, *viejo* Fig. 384). The genitalia of these species are similar to those of other *Ocrepeira*. The anterior or posterior median eyes are the largest, the laterals always the smallest. The lateral eyes may be slightly separated from each other. There are some setae on the carapace, usually a bunch of setae above the lateral eyes. The first leg is the longest, the third the shortest. Usually the second leg is slightly longer than the fourth. The abdomen, unlike that of *Pozonia*, has only two anterior tubercles. These tubercles are rarely absent (*comaina* Fig. 368, *herrera* Fig. 390, *covillei* Fig. 399). Only *O. rufa* (Fig. 51), *O. arturi* (Fig. 104), and *O. mastophoroides* (Fig. 140) have numerous tubercles. It is certain that all *O. mastophoroides* have these many tubercles, but perhaps only some individuals in *O. rufa* and *O. chickeringi* do. Few have an anterior median tubercle (*darlingtoni* Fig. 332, *atuncela* Fig. 256). Some have the anterior tubercles projecting, others have them pointing laterally, and in some this character is variable, differing among individuals of the same species. The abdomen is attached slightly vertically to the cephalothorax, the anterior overhang is greater than in species of some other genera, but less than in *Wixia* and *Pozonia*.

Males appear similar to females, but have a narrow cephalic region, and a smaller abdomen, with less distinct tubercles. The endite of all males has a tooth facing a tubercle on the proximal end of the palpal femur. The sternum of *O. covillei* has several short macrosetae, but many specimens lack these setae. The first coxa has a hook on the distal margin (Fig. 34); there is a groove on the second femur. The third and fourth coxae frequently have one or more short macrosetae, sometimes on a tubercle. The third and fourth trochanters may also have macrosetae (Fig. 34). These macrosetae are quite variable, often of different number on left and right sides, sometimes absent in individuals of species that have them. The palpal patella of all species has one long macroseta. The second tibia is always thicker than the first, sometimes swollen, bearing sometimes long macrosetae, but never having outgrowths or branches (Fig. 35).

The epigynum is heavily sclerotized with a broad lobe-shaped scape usually attached posteriorly to the base. The scape may be longer than the width of the base (Fig. 29). In posterior view there are median and lateral plates (Fig. 30). The sclerites in posterior view of the epigynum are diagnostic for many species.

The palpus is similar to that of *Parawixia* (Levi, 1992, figs. 7, 8). It has a large conductor, to which is attached the paramedian apophysis. The paramedian apophysis is of characteristic shape, usually rounded at its distal end with parallel sides. In *O. subrufa* (Fig. 46), it is a flat, rectangular extension of the conductor. In *O. rufa* (Fig. 69) and *O. potosi* (Fig. 75) it is shoe-shaped, and in others it is a long, tapering, pointed structure (*gulielmi* Fig. 241, *anta* Fig. 262, *jacara* Fig. 364, *comaina* Fig. 367, *heredia* Fig. 369, *albopunctata* Fig. 378, *herrera* Fig. 391, *covillei* Fig. 402). In two species the paramedian apophysis is a gutter, a repository for the embolus (*abiseo* Fig. 319, *tinajillas* Fig. 327). In most species there is an outgrowth from the radix toward the embolus and the paramedian apophysis, barely visible in some, prominent in others (*yaelae* Fig. 359, *jacara* Fig. 364, *albopunctata* Fig. 377, *viejo* Fig. 385). Both the paramedian apopysis and the radix outgrowth seem to support the embolus. The median apophysis is always large, often distally forked, and its insertion into the radix is less modified than that of *Parawixia* and *Wagneriana* species. The embolus is short and scale-like, or pointed, except in *O. magdalena* (Fig. 338), which has a long embolus. Emboli are generally similar in related species. Beyond the embolus is a tripartite structure (Fig. 46). While one can call the part closest to the embolus the embolar lamella and the most distal, the terminal apophysis, these parts are difficult to homologize with similar parts in other araneids. The outgrowth of the radix is an autapomorphy. The *O. albopunctata* and *O. viejo* embolus has a large, scale-like structure (Fig. 379) that is transferred to the female when mating, and once in the epigynum (on left in Figs. 372, 373) the scale is difficult to remove. Other species may have a similar, less conspicuous, structure.

Many species with a narrow cephalic region also lack the posterior median eye swelling, have an oval or shield-shaped abdomen, a tapering, pointed paramedian apophysis, and a prominent radix outgrowth. However, there is also considerable overlap: not all species with a narrow cephalic region have posterior median eyes facing "up." Other species have a pointed paramedian apophysis, and the outgrowth from the radix, though less distinct, is found in yet other species.

Relationships. The position of the posterior median eyes, their placement on a slight swelling with the eyes facing sideways to forward is a character shared by the species of the three genera, *Wixia, Pozonia*, and *Ocrepeira*. This character is also found in some *Parawixia* and in *Acacesia* and is believed a synapomorphy of these groups. In some species of unrelated genera (e.g., *Eustala*) the posterior median eyes are similarly placed, and in several species of *Ocrepeira* it appears this peculiar placement of eyes has been secondarily lost. The position of the posterior median eyes, the abdomen shape, and the pointed paramedian apophyses are synapomorphies of *Ocrepeira* and related genera. The outgrowth of the radix is an autapomorphy of *Ocrepeira*.

Natural History. Stowe (1978) described a specialized scaffold-like, reduced web for *Ocrepeira ectypa*. This observation may have been an error, or the observation of a temporary day-time web. All the specimens collected with web notes in vials indicated that the spider had made a complete orb web; the orb is nearly vertical.

Ocrepeira salidito (no. 1139) and *O. atuncela* (no. 173) have a fine-meshed orb with the hub closed; *O. lapeza* (no. 1491) and *O. planada* (no. 3347, 3358) have a loose mesh with a wide central hole (Plate 1); they build the orbs at night and the spider rests in the hub face down (Eberhard, voucher numbers of specimens in MCZ and personal communication).

Distribution. Most species are Neotropical and many species come from high elevations in the Andes (Map 3). The Andean species, many isolated from each other, may be very localized and of limited distribution. Species occuring north of Mexico (see Levi, 1976) are *O. globosa*, *O. redempta* (see Levi, 1976), *Ocrepeira ectypa* (Walckenaer, 1841), and *Ocrepeira georgia* (Levi, 1976), NEW COMBINATION.

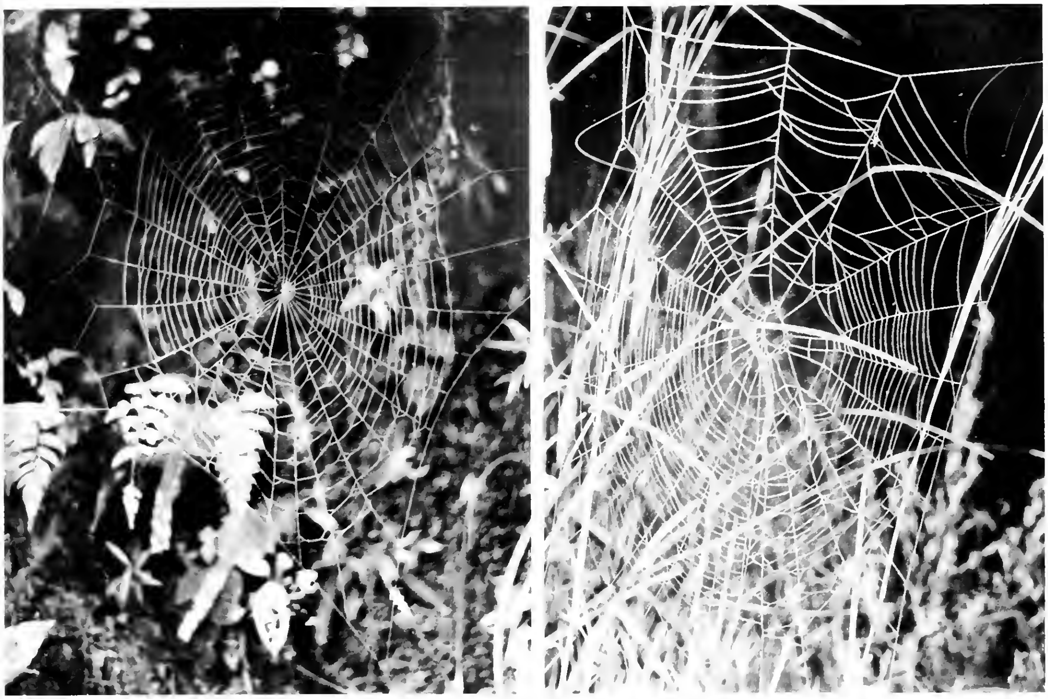
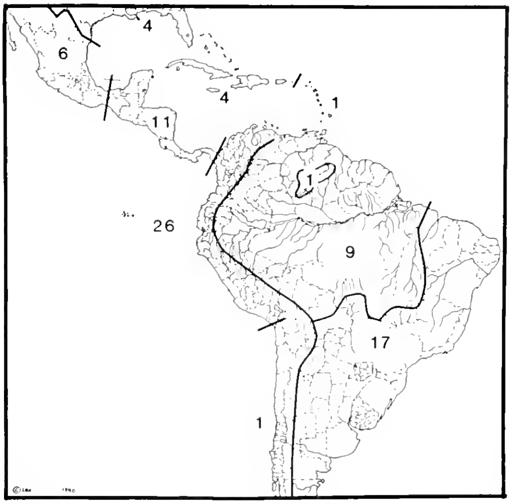


Plate 1. Left, *Ocrepeira atuncela*, horizontal diameter of orb 24 cm. Right, *O. lapeza*, horizontal diameter of orb 18.6 cm (photo, W. Eberhard).

Keys. The keys were more difficult to construct than those for species of other genera. Most species are relatively uncommon and few specimens were available. Often, the variability of color patterns or tubercles is unknown. The availability of these features would have simplified the key.

KEY TO FEMALES OF *OCREPEIRA* SPECIES

1. Abdomen with many humps evenly distributed (Figs. 51, 104, 140) 2
– Abdomen with only a pair of anterior tubercles or humps, sometimes an anterior median tubercle (Figs. 39, 44, 63, 332) 4
2(1). Epigynum as in Figures 137–139; Argentina (Map 5) .... *mastophoroides*
– Epigynum as in Figures 48, 101; Mexico and Central America 3
3(2). Epigynum pointed posteriorly in ventral view (Fig. 101); Panama (Map 4) .... *arturi*
– Epigynum rounded posteriorly in ventral view (Fig. 48); Mexico to Panama (Map 4) .... *rufa*
4(1). Epigynum (base and scape) in ventral and posterior views as long as wide or wider than long (Figs. 71, 72, 302, 303, 322, 323, 340, 341, 372, 373) 5
– Epigynum (base and scape) longer than wide in ventral and posterior views (Figs. 160, 161, 167, 168) 19
5(4). Scape forming a lobe of posterior margin of base (Figs. 36, 37, 41, 42, 52, 53, 340, 341) 15
– Scape set off from base (Figs. 257, 264, 278, 372, 403) 6
6(5). Scape originating at anterior of base (Figs. 372, 375), posterior view of epigynum as in Figure 373; Guyana, Amazon area (Map 6) .... *albopunctata*
– Scape originating on ventral face or posterior of base (Figs. 257, 264, 278, 302, 403) 7
7(6). Scape longer than wide (Figs. 264, 272, 302) 11
– Scape as long as or shorter than wide (Figs. 257, 308) 8
8(7). In posterior view of epigynum lateral plates touch dorsally (bottom of Fig. 258); Colombia (Map 5) .... *anta*
– In posterior view lateral plates separated (Figs. 309, 316); Peru 9



Map 3. Approximate number of *Ocrepeira* species in different areas.

9(8). In posterior view median plate overhanging lateral plates (Fig. 404) ...... *sorota*

– In posterior view lateral plates overhanging medians (Figs. 309, 316); Bolivia (Map 6) 10

10(9). Posterior area of base, behind scape, depressed (Figs. 308, 309); (Map 6) ...... *cuy*

– Posterior area of base otherwise (Figs. 315, 316); (Map 6) ...... *abiseo*

11(7). Dorsum of abdomen with pairs of black spots having light rings (Fig. 305); Colombian Andes (Map 6) ...... *saladito*

– Dorsum of abdomen without such spots 12

12(11). Posterior median plate of epigynum subdivided into anterior and posterior plates, anterior one with a median longitudinal groove (Fig. 265); Peru (Map 6) ...... *barbara*

– Posterior median plate otherwise (Figs. 273, 279, 323) 13

13(12). Posterior median plate circular (Fig. 273); Ecuador (Map 6) ...... *tungurahua*

– Posterior median plate with parallel sides (Fig. 279) or with median constriction (Fig. 323) 14

14(13). Posterior median plate with sides parallel (Fig. 279); Colombian Andes (Map 6) ...... *valderramai*

– Posterior median plate constricted (Fig. 323); Ecuador (Map 6) ...... *tinajillas*

15(5). Posterior median plate of epigynum much wider than long (Figs. 37, 42) 16

– Posterior median plate longer than wide (Figs. 53, 72, 341) 17

16(15). Epigynum in ventral view with a transverse depression (Fig. 36); posterior median plate trapezoidal (Fig. 37); Mexico (Map 4) ...... *globosa*

– Ventral view of epigynum convex (Fig. 41); posterior median plate dorsally rounded, lateral plates extending dorsally beyond median plate (Fig. 42); Mexico, Guatemala (Map 4) ...... *subrufa*

17(15). Jamaica (Map 4); epigynum as in Figures 71–73 ...... *branta*

– Mexico, Central and South America 18

18(17). Colombia, epigynum with a small lobe (Figs. 340–342); Colombia (Map 6) ...... *lapeza*

– Mexico to Panama (Map 4), epigynum with wide lobe (Figs. 48–50, 52–54, 56–58, 60–62, 64–66) ...... *rufa*

19(4). Abdomen oval with indistinct humps and without dorsal folium or transverse streaks (Figs. 390, 399), sometimes with dark dorsal patch (Fig. 400) 20

– Abdomen with a pair of humps or tubercles or with dorsal folium or streak markings 22

20(19). Posterior median plate triangular and with granulated surface (Fig. 388); Peruvian Amazon (Map 6) ...... *herrera*

– Posterior median plate with a constriction or with sides parallel (Figs. 95, 393) 21

21(20). Epigynum with long scape as in Figures 392, 395, 397; Central America to Amazon area (Map 6) ...... *covillei*

– Epigynum with short scape as in Figure 94; Bahia to Paraná States, Brazil (Map 5) ...... *camaca*

22(19). Abdomen dorso-anteriorly dark, dark area sharply demarcated at a line extending between tubercles, posterior without folium, sometimes with a dark patch (Figs. 183, 384) 23

– Abdomen marked otherwise 34

23(22). Anterior dark area of abdomen covering anterior pair of muscle scars (Figs. 183, 189, 208) 24

– Anterior pair of muscle scars outside the dark area (Figs. 148, 150, 337) 28

24(23). Scape laterally flattened or torn off (Figs. 193, 195, 206) 25

– Scape otherwise 26

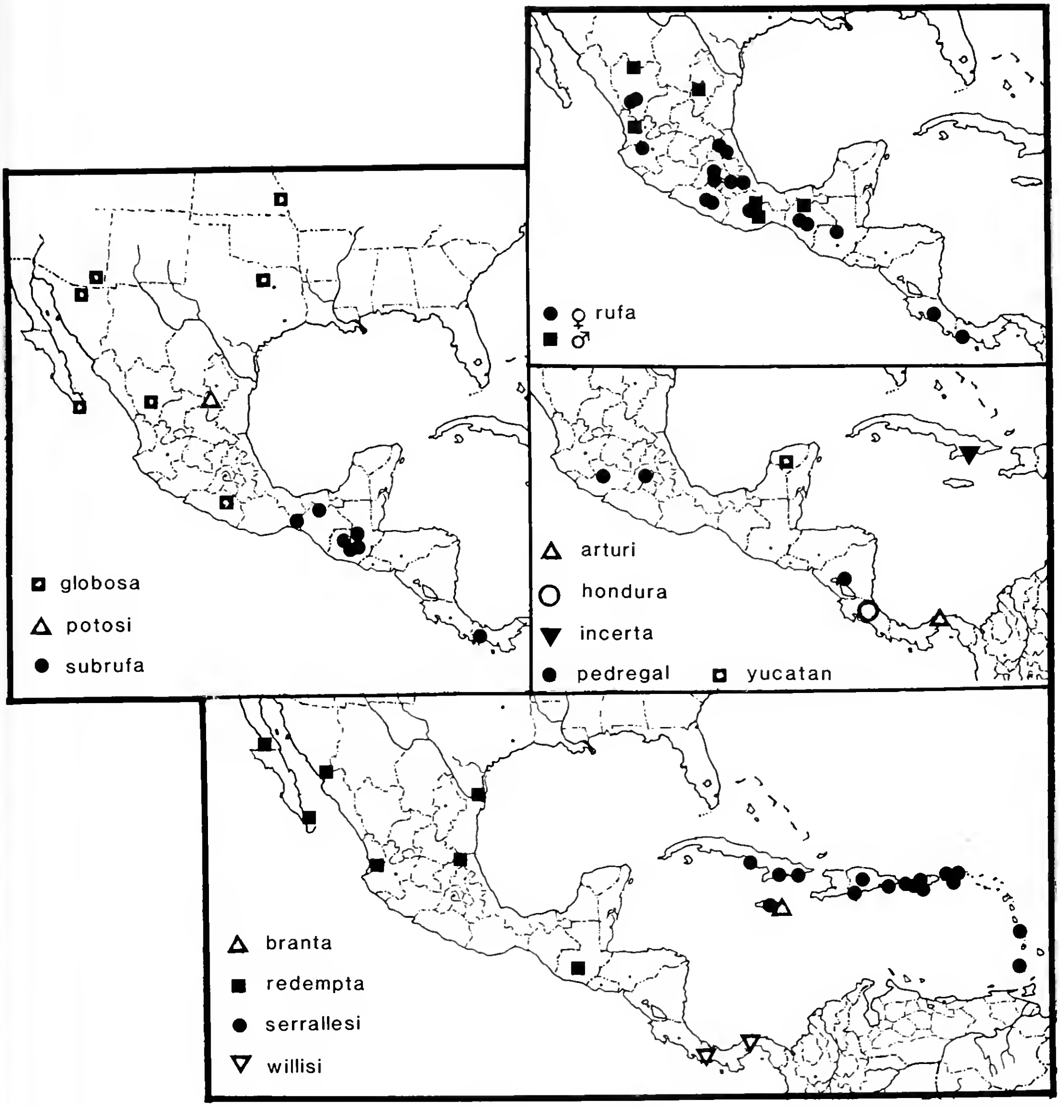
25(24). In posterior view scape (or scar) touching median plate (Fig. 206); Mato Grosso State, Brazil (Map 5) ...... *gima*

– In posterior view scape some distance from median plate (Fig. 195); Brazil, Paraguay (Map 5) ...... *fiebrigi*

26(24). Sides of scape with median swelling (Fig. 180); southern Brazil (Map 5) ...... *malleri*

– Sides of scape almost parallel (Figs. 186, 201) 27

27(26). Length of epigynum and scape less than



Map 4. Distribution of *Ocrepeira* species.

1.5 times its width (Fig. 200); Bolivia, N. Argentina (Map 5) .... *molle*

– Length of epigynum more than twice its width (Fig. 186); São Paulo State, Brazil to Buenos Aires Prov., Argentina (Map 5) .... *galianoae*

28(23). Hispaniola (Map 6), epigynum as in Figures 329–331 .... *darlingtoni*

– Central and South America; epigynum otherwise 29

29(28). Epigynum large and flat as in Figures 360–362; Peru (Map 6) .... *duocypha*

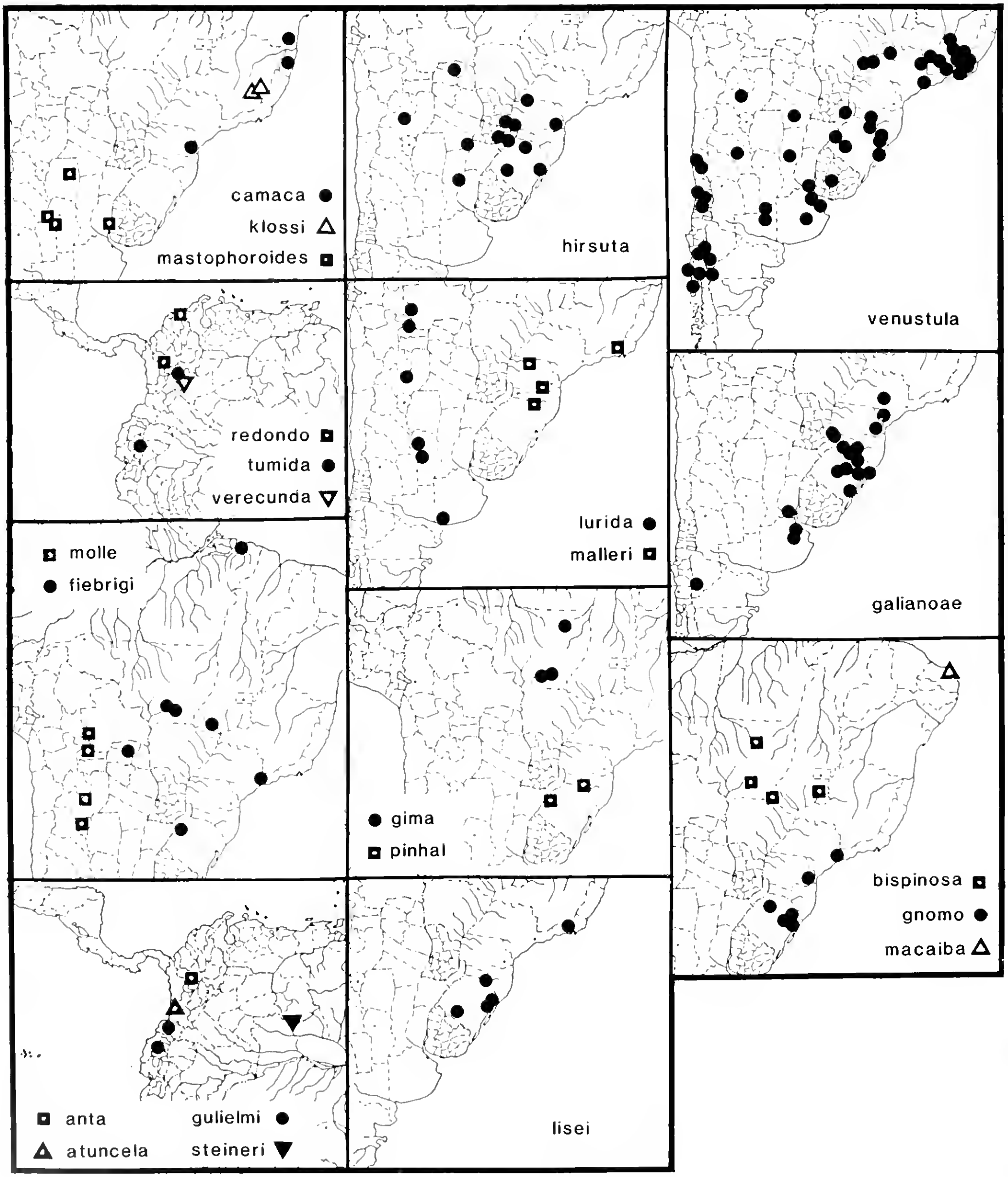
– Epigynum otherwise (Figs. 143, 354, 380) 30

30(29). Scape with parallel sides (Figs. 354, 380) 31

– Scape tapering or rounded (Figs. 143, 334, 348) 32

31(30). Scape smooth, posterior view of epigynum as in Figure 381; Central America, Venezuela to Peru (Map 6) .... *viejo*

– Scape wrinkled, posterior view of epi-



Map 5. Distribution of *Ocrepeira* species.

gynum as in Figure 355; Ecuador (Map 6) .... *yaelae*

32(30). Epigynum in posterior view with deep pit at ventral end of median plate (center of Fig. 349); Venezuela, Colombia, and Amazon area (Map 6) .... *maraca*

– Epigynum without pit (Figs. 144, 335) 33

33(32). Sides of scape convex (Fig. 334) .... *magdalena*

– Sides of scape concave (Fig. 143); Minas Gerais State, Brazil to Chile (Map 5) ..... *venustula*

34(22). Origin of scape on ventral surface of base as in Figures 236, 238, 243, 245, 297, 299 35

– Base gradually narrowing posteriorly into a scape (Figs. 143, 146, 167, 212) 40

35(34). Lateral plates of epigynum in posterior view touching (Figs. 244, 250, 298) 36

– Lateral plates separated by the median plate (Figs. 237, 254, 291) 38

36(35). Tubercles of abdomen directed anteriorly (Figs. 246, 252) 37

– Tubercles of abdomen directed laterally (Fig. 300); Colombia (Map 6) ..... *ituango*

37(36). Lateral plates of epigynum with median, dorsal projections (Fig. 244); Amazon area, Venezuela (Map 5) ..... *steineri*

– Lateral plates without such projections (Fig. 250); northeastern Brazil (Map 5) ..... *macaiba*

38(35). Posterior lateral plates of epigynum (and base) having a lateral anterior-posterior groove (Figs. 237, 238); Colombia, Ecuador (Map 5) ..... *gulielmi*

– Base and lateral plates without groove (Figs. 254, 255, 291, 292) 39

39(38). Abdomen with anterior median tubercle (Fig. 256); sides of posterior median plate parallel (Fig. 254); Colombia (Map 5) ..... *atuncela*

– Abdomen without median anterior tubercle (Fig. 293) sides of posterior median plate convex (Fig. 291); Colombia, Ecuador (Map 6) ..... *planada*

40(34). Epigynum triangular (Fig. 114); posterior median plate bottle-shaped (Fig. 115); Cuba (Map 4) ..... *incerta*

– Epigynum otherwise 41

41(40). Tubercles of abdomen pointing anteriorly (Figs. 177, 228, 235) 42

– Tubercles or humps of abdomen pointing laterally (Figs. 122, 129, 151) 46

42(41). Posterior base of epigynum grading into broad lobe with median, longitudinal groove (Figs. 174, 218) 44

– Scape set off from base of epigynum (Figs. 224, 232); Brazil 43

43(42). Posterior lateral plates separated by median plate (Fig. 225); São Paulo to Rio Grande do Sul States, Brazil (Map 5) ..... *gnomo*

– Posterior lateral plates overlapping (Fig. 233); Rio de Janeiro to Rio Grande do Sul States, Brazil (Map 5) ..... *lisei*

44(42). Posterior lateral plates touching as in Figure 213; Paraná, Rio Grande do Sul States, Brazil (Map 5) ..... *pinhal*

– Posterior lateral plates separated by a median plate (Figs. 175, 219) 45

45(44). Posterior median plate triangular (Fig. 175); Colombia, Ecuador (Map 5) ..... *tumida*

– Posterior median plate constricted in middle (Fig. 219); Mato Grosso, Goiás States, Brazil (Map 5) ..... *bispinosa*

46(41). Scape slightly swollen above tip (Figs. 131, 133); Minas Gerais State, Brazil (Map 5) ..... *klossi*

– Scape not swollen (Figs. 119, 126, 167) 47

47(46). Epigynum subtriangular, lobe with a pocket (Fig. 126); Costa Rica (Map 4) ..... *hondura*

– Epigynum otherwise (Figs. 88, 143, 160, 167) 48

48(47). Posterior of epigynum with a wide, deep depression behind scape (Fig. 168); Panama (Map 4) ..... *willisi*

– Epigynum without such a depression, or with a narrow pit (Figs. 120, 144, 161) 49

49(48). Abdomen with a pair of white squares their diameter apart on underside (Fig. 82); West Indies (Map 4) ..... *serrallesi*

– Abdomen otherwise or with a pair of white spots (Fig. 164) 50

50(49). Mexico (Map 4); epigynum as in Figures 88–90 ..... *redempta*

– South America 51

51(50). Ventral view of epigynum with a bulge on each side, scape behind bulge hardly longer than length of base above bulge (Figs. 119–121); southern Brazil, Paraguay, northern Argentina (Map 5) ..... *hirsuta*

– No bulges on sides of epigynum (Fig. 160), or if bulges, scape behind bulge longer than length of base (Fig. 143) 52

52(51). Posterior median plate vase-shaped (Fig. 161); Bolivia to Buenos Aires Prov., Argentina (Map 5) ..... *lurida*

– Sides of posterior median plate almost parallel, sometimes slightly constricted (Figs. 144, 146); Minas Gerais, Brazil to Chile (Map 5) ..... *venustula*

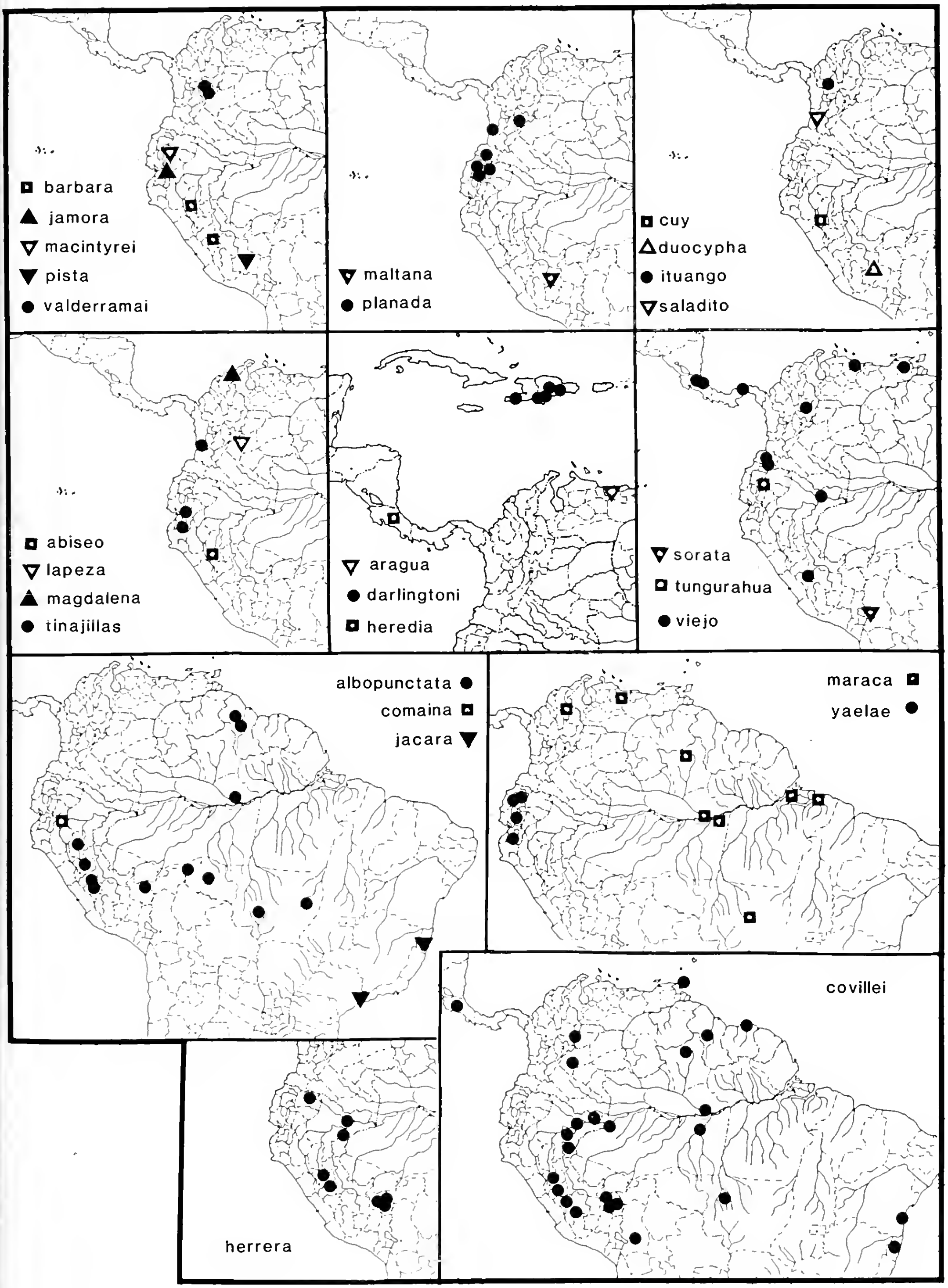
KEY TO MALES OF *OCREPEIRA* SPECIES

Ocrepeira verecunda from Colombia (Figs. 155, 156) is not included in the key.

1. Median apophysis of palpus (Figs. 32, 33, M in 46, 47) with two prongs of equal length or "lower" one longer than "upper." Length of one of the prongs at least one quarter length of median apophysis (Figs. 223, 231, 242, 248, 263, 270, 277, 283, 288, 296, 306, 307, 314, 320, 328, 333) 2

– Median apophysis with one prong or "lower" one much shorter than "upper" (Figs. 46, 47, 100, 109), or prongs very short or absent (Figs. 285, 353) 16

2(1). West Indies (Map 6); palpus as in Figure 333 *darlingtoni*
– South America; palpus otherwise 3
3(2). Palpus as in Figures 247, 248; Amazon area, Venezuela (Map 5) *steineri*
– Palpus otherwise; Andes to Brazil 4
4(3). Brazil 5
– Andes 6
5(4). Base of median apophysis with two parallel lengthwise, curved ridges (Figs. 230, 231); São Paulo to Rio Grande do Sul States (Map 5) *gnomo*
– Base of median apophysis with one "vertical" ridge (Figs. 222, 223); Mato Grosso, Goiás States (Map 5) *bispinosa*
6(4). Palpus in ventral view with lower prong about twice as long as upper prong (Figs. 287, 288, 306, 307) 7
– Prongs of more equal length (Figs. 262, 263, 277, 319, 320, 327, 328) 8
7(6). "Upper" prong short, blunt (Figs. 306, 307); Colombia (Map 6) *saladito*
– "Upper" prong long, acute (Figs. 287, 288); Peru (Map 6) *pista*
8(6). "Upper" prong at its origin wider than "lower" prong; palpus as in Figures 262, 263; Colombia (Map 5) *anta*
– Prongs of equal width or "lower" prong wider (Figs. 242, 270, 277, 283, 296, 314, 319, 328) 9
9(8). "Lower" edge of median apophysis with a proximal bulge (Figs. 313, 319, 327) 10
– "Lower" edge of median apophysis without bulge (Figs. 241, 269, 276, 282, 295) 12
10(9). Base of median apophysis with a semicircular offset (Fig. 313); Peru *cuy*
– Base of median apophysis otherwise (Figs. 319, 327) 11
11(10). Base of median apophysis with a triangular offset (Fig. 319) *abiseo*
– Base of median apophysis with little sculpturing (Fig. 327) *tinajillas*
12(9). Base of median apophysis with a semicircular offset (Figs. 276, 295) 13
– Base of median apophysis otherwise (Figs. 241, 269, 282) 14
13(12). Prongs of median apophysis long (Figs. 295, 296) *planada*
– Prongs of median apophysis short (Figs. 276, 277) *tungurahua*
14(12). Base of median apophysis with a triangular offset (Fig. 282) *valderramai*
– Base of median apophysis otherwise (Figs. 241, 269) 15
15(14). Base of median apophysis with boomerang-shaped offset (Fig. 269) *macintyrei*
– Base of median apophysis with a "diagonal" ridge (Fig. 241) *gulielmi*
16(1). Median apophysis "higher" than long as in Figures 338, 339; northern Colombia (Map 6) *magdalena*
– Median apophysis otherwise (Figs. 184, 284, 352) 17
17(16). Embolus thread-shaped (Fig. 216); Peru (Map 6) *maltana*
– Embolus various shapes, never thread-shaped 18
18(17). Median apophysis with a narrow neck and dark round spot in its base (Fig. 359); Ecuador (Map 6) *yaelae*
– Median apophysis otherwise 19
19(18). Terminal apophysis surrounding minute conductor; terminal apophysis in submesal view larger than conductor (Fig. 385); Central and South America (Map 6) *viejo*
– Terminal apophysis and conductor otherwise 20
20(19). Median apophysis with a distal notch (Figs. 210, 285, 353, 365, 369, 370, 377, 378) 21
– Median apophysis without notch (Figs. 47, 93, 141) 26
21(20). Distal notch of median apophysis narrow and with parallel sides (Fig. 285); Ecuador (Map 6) *jamora*
– Distal notch shallow or triangular (Figs. 210, 353, 378) 22
22(21). Palpus as in Figures 369, 370; Central America (Map 6) *heredia*
– Palpus otherwise 23
23(22). Terminal apophysis large and overhanging conductor as in Figures 210, 211 *gima*
– Terminal apophysis otherwise 24
24(23). Terminal apophysis small and pointed as in Figure 352 *maraca*
– Terminal apophysis otherwise 25
25(24). Terminal apophysis surrounding conductor as in Figures 364, 365 *jacara*
– Terminal apophysis pincer-shaped as in Figure 377 *albopunctata*
26(20). Median apophysis having a long tube-shaped (with parallel sides) pointed projection or two with "upper" one longer (Figs. 47, 70, 76, 87, 93, 100, 107, 109, 112, 306, 307) 27
– Median apophysis otherwise (Figs. 141, 142, 172, 173) 36
27(26). Palpus as in Figures 99, 100; Paraná State, Brazil (Map 5) *camaca*
– Palpus otherwise; Colombia, Mexico, Central America, West Indies 28
28(27). Palpus as in Figures 306, 307; Colombia *saladito*
– Palpus otherwise; Mexico, Central America, West Indies 29
29(28). Paramedian apophysis shoe-shaped (Figs. 69, 75) 30
– Paramedian apophysis otherwise 31
30(29). Prong of median apophysis thick as in Figures 69, 70 (Map 4) *rufa*
– Prong thin and curved "up" as in Figures 75, 76; Mexico (Map 4) *potosi*
31(29). Prong of median apophysis with a distal bend as in Figures 111, 112; Mexico (Map 4) *yucatan*



Map 6. Distribution of *Ocrepeira* species.

– Prong evenly curved (Figs. 47, 87, 93, 107, 109) ... 32

32(31). Prong relatively short, about three times as long as wide (Fig. 47); paramedian apophysis rectangular (PM in Fig. 47); Mexico, Central America (Map 4) ... *subrufa*

– Prong much longer and paramedian apophysis otherwise (Figs. 76, 93, 107, 109) ... 33

33(32). Base of median apophysis with an offset area the shape of a semicircle (Fig. 93); Mexico, Guatemala (Map 4) ... *redempta*

– Base of median apophysis otherwise ... 34

34(33). Base of median apophysis with a large offset area the shape of a tooth (Fig. 87); West Indies (Map 4) ... *serrallesi*

– Base of median apophysis otherwise ... 35

35(34). Terminal apophysis distally forked as in Figure 106; Panama (Map 4) ... *arturi*

– Terminal apophysis distally pointed as in Figure 108; Mexico (Map 4) ... *pedregal*

36(26). Median apophysis short and in submesal view surrounded by the tegulum as in Figure 391; Peru (Map 6) ... *herrera*

– Median apophysis longer (Figs. 124, 135, 184, 190, 198) ... 37

37(36). Median apophysis in ventral view distally with a bulge or keel "above," beyond the tegulum (Figs. 124, 125, 135, 136, 184, 185, 190, 191, 198, 199, 204) ... 38

– Median apophysis without bulge or keel (Figs. 142, 153, 158, 166, 179, 211, 346, 386) ... 43

38(37). Terminal apophysis overhanging conductor (Figs. 124, 190) ... 39

– Terminal apophysis not reaching "top" of conductor (Figs. 135, 184, 198) ... 40

39(38). Terminal apophysis distally rounded, and median apophysis short (Fig. 124); São Paulo State, Brazil, Paraguay, northern Argentina (Map 5) ... *hirsuta*

– Terminal apophysis pointed, median apophysis long (Fig. 190); São Paulo State, Brazil to Buenos Aires Prov., Argentina (Map 5) ... *galianoae*

40(38). Bulge on "upper" margin of median apophysis evenly rounded (Figs. 136, 185) ... 42

– Bulge on "upper" margin pointed or keel-shaped (Figs. 199, 204) ... 41

41(40) Bulge on "upper" surface of median apophysis keel-shaped (Figs. 198, 199); Amazon to Rio Grande do Sul State, Brazil (Map 5) ... *fiebrigi*

– Bulge on "upper" margin pointed (Fig. 204); Bolivia, Argentina (Map 5) ... *molle*

42(40). Median apophysis wide and terminal apophysis as in Figure 184 ... *malleri*

– Median apophysis narrow and terminal apophysis as in Figure 135; Minas Gerais State, Brazil (Map 5) ... *klossi*

43(37). Terminal apophysis strongly curved and pointed overhanging the conductor as in Figure 210; Mato Grosso State, Brazil (Map 5) ... *gima*

– Terminal apophysis otherwise ... 44

44(43). Terminal apophysis surrounding small conductor as in Figure 385; Costa Rica (Map 6) ... *viejo*

– Terminal apophysis and conductor otherwise ... 45

45(44). Terminal apophysis small, cone-shaped as in Figure 367; Peru ... *comaina*

– Terminal apophysis otherwise ... 46

46(45). Terminal apophysis reaching "top" of conductor or overhanging conductor (Figs. 141, 152, 157, 165, 172, 178, 345) ... 47

– Terminal apophysis barely touching conductor (Figs. 198, 367, 369, 402) ... 53

47(46). Distal part of terminal apophysis triangular as in Figure 345; Venezuela (Map 6) ... *aragua*

– Terminal apophysis otherwise ... 48

48(47). Tip of terminal apophysis with upper edge straight as in Figure 172; Panama (Map 4) ... *willisi*

– Tip of terminal apophysis with upper edge curved and pointing to median apophysis (Figs. 141, 152, 157, 165, 178) ... 49

49(48). Abdomen with about 14 tubercles (Fig. 140); Argentina (Map 5) *mastophoroides*

– Abdomen with only an anterior pair of tubercles or humps ... 50

50(49). Median apophysis with neck, widening towards tip (Figs. 178, 179); Colombia, Ecuador (Map 5) ... *tumida*

– Median apophysis otherwise ... 51

51(50). Median apophysis distally blunt (Figs. 157, 158); Colombia, Ecuador (Map 5) ... *redondo*

– Median apophysis distally pointed (Figs. 153, 166); Brazil, Argentina ... 52

52(51). Overhanging portion of terminal apophysis wide as in Figure 152; Minas Gerais State, Brazil to Chile (Map 5) ... *venustula*

– Overhanging portion of terminal apophysis narrow as in Figure 165; Bolivia to Buenos Aires Prov., Argentina (Map 5) ... *lurida*

53(46). Distal end of terminal apophysis with shallow notch (Figs. 369, 402) ... 54

– Distal end of terminal apophysis pointed (Figs. 198, 345, 367) ... 55

54(53). Distal end of median apophysis prong slightly wider than section immediately below and prong fairly straight (Fig. 369); Costa Rica (Map 6) .... *heredia*

– Median apophysis with an even taper and bent "up" (Fig. 402); Costa Rica to Amazon area (Map 6) .... *covillei*

55(53). Conductor extending above and beyond terminal apophysis (Fig. 198); Amazon to Rio Grande do Sul State, Brazil and Paraguay (Map 5) .... *fiebrigi*

– Conductor and terminal apophysis tips touching (Fig. 345); Venezuela (Map 6) .... *aragua*

Ocrepeira globosa (F. P.-Cambridge), new combination

Figures 36–40; Map 4

Wixia globosa F. P.-Cambridge, 1904: 486, pl. 46, fig. 4, ♀. Female holotype from Tepetlapa, Guerrero State, Mexico, in BMNH no. 1905.4.28.2811, examined. Roewer, 1942: 882. Bonnet, 1959: 4829. Levi, 1976: 382, figs. 116–120, ♀ (not figs. 112, 121, 122, ♂).

Note. The male for *globosa* is unknown. Levi (1976) matched the male of *rufa* with *globosa* and matched the male of *clivosa* with *rufa* on the basis of a dorsal abdominal pattern. But now I find the pattern variable, and am uncertain if the match was correct.

Description. Female from Baja California Sur, Mexico. Cephalic region streaked gray and black on orange, eye tubercle and sides of thoracic region orange. Chelicerae light orange. Labium, endites brown. Sternum dusky orange underlain by white pigment. Coxae light orange; legs dusky orange with indistinct dark rings. Dorsum of abdomen with posterior paired curved black marks (Fig. 39); venter light dusky without marks. Posterior median eyes 1.3 diameters of anterior medians, laterals 0.6 diameter. Anterior median eyes 1.3 diameters apart. Posterior median eyes 2 diameters apart. Ocular quadrangle slightly wider behind than in front. Height of clypeus equal to 2 diameters of anterior median eyes. Abdomen oval, with large cone-shaped, forward-pointing tubercles (Fig. 39). Total length 6.6 mm. Carapace 3.0 mm long, 2.7 wide, behind lateral eyes 1.6 wide. First femur 3.0 mm, patella and tibia 3.6, metatarsus 2.2, tarsus 0.7. Second patella and tibia 3.4 mm, third 2.1, fourth 3.4.

Variation. No two epigyna are alike. They vary in the shape of the outline and the extent of the ventral depression (Levi, 1976, figs 116–118; Figs. 36–38). However, all have the wide convex median plate in posterior view (Fig. 37) and a thin ventral posterior lip (Fig. 38). Total length of females 5.0 to 7.8 mm. Figures 36–38 were made from a female from Baja California Sur.

Diagnosis. As in *O. rufa*, all females of *O. globosa* have the clypeus height about equal to 2 diameters of the anterior median eyes, higher than that of most other species. The ventral depression of the epigynum (Fig. 36) and the shape of the posterior median plate (Fig. 37) separate *O. globosa* from *O. subrufa* (Figs. 41, 42).

Specimens Examined. UNITED STATES KANSAS *Bourbon Co:* Redfield, 15 Oct. 1963, ♀ (W., J. Ivie, AMNH). TEXAS *Dallas Co*: Dallas, ♀, Whire Creek, Dallas, ♀ (both S. Jones, MCZ). ARIZONA *Cochise Co:* South Fork, Cave Creek, Chiricahua Mts., 11 Sept. 1950, ♀ (W. J. Gertsch, AMNH). MEXICO *Sonora:* N end of Sierra de los Ajos, head Canyon de Evans, 28 Aug. 1970, ♀ (V. Roth, AMNH). *Baja California Sur:* Sierra de la Laguna, Cañon de la Zorra, 840 m, Paso de Cecilia Selva, ♀ (M. L. Jiménez, MLJ). *Durango:* Palos Colorado, 5 Aug. 1947, ♀ (W. J. Gertsch, AMNH).

Ocrepeira subrufa (F. P.-Cambridge), new combination

Figures 41–47; Map 4

Wixia subrufa F. P.-Cambridge, 1904: 486, pl. 46, fig. 6, ♀. Female holotype from Chiacam [Depto. Alta Verapaz, 26 km E of Cobán, 700 m, 15°34′N, 90°06′W, old coffee plantation], Guatemala, in

BMNH, 1904: 486, examined. Roewer, 1942: 882. Bonnet, 1959: 4830.

Wixia sicula F. P.-Cambridge, 1904: 487, pl. 46, fig. 8, ♂. Male holotype from Teapa, Tabasco State, Mexico, in BMNH no. 1905.4.28.2818, examined. Roewer, 1942: 882. Bonnet, 1959: 4830. NEW SYNONYMY.

Wixia vulcani Kraus, 1955: 25, pl. 4, figs. 72–74, ♀. Female holotype from top of San Salvador Volcano, 1,965 m, El Salvador, in SMF, not examined. Brignoli, 1983: 281. NEW SYNONYMY.

Synonymy. The holotype of *W. subrufa* is damaged by insect pin holes. F. P.-Cambridge did not consider *W. sicula* and *W. subrufa* as belonging together, presumably because they came from different localities and had different dorsal markings. In 1976, I thought erroneously that because of dorsal markings the *sicula* male must belong to *W. rufa* and the male of *W. clivosa* to *W. globosa* (Levi, 1976).

The illustration for *W. vulcani* shows the characteristic features of *O. subrufa.*

Description. Female from Sacatepequez, Antigua, Guatemala. Carapace dark orange-brown with some white setae, sides of thoracic region darkest. Chelicerae, labium, endites orange-brown. Sternum dark orange-brown. Coxae dark orange; legs orange-brown with darker rings and patches. Dorsum of abdomen blackish brown anteriorly; posterior with some transverse dark bars; a light line between dark and light areas, and some scattered long black hairs (Fig. 44); venter black with two discrete white spots (Fig. 45). Posterior median eyes same diameter as anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart. Posterior median eyes 1.4 diameters apart. Ocular quadrangle slightly narrower behind than in front. Height of clypeus equal to one diameter of anterior median eyes. Abdomen with tubercles directed toward sides (Fig. 44). Total length 7.7 mm. Carapace 3.7 mm long, 3.1 wide, 1.8 wide behind lateral eyes. First femur 3.5 mm, patella and tibia 4.4, metatarsus 2.8, tarsus 1.0. Second patella and tibia 4.0 mm, third 2.7, fourth 3.9.

Male holotype of *W. sicula.* Color as in female, but sternum yellow with brown border and abdomen dorsum with a white anterior cardiac mark. Posterior median eyes 0.9 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes slightly more than their diameter apart. Posterior median eyes 1.5 diameters apart. Height of clypeus equal to 0.9 diameter of anterior median eye. Third coxa with two macrosetae on right, one on left, fourth with one macroseta. Fourth trochanter with one macroseta. Total length 4.0 mm. Carapace 2.9 mm long, 2.4 wide. First femur 3.1 mm, patella and tibia 3.6, metatarsus 2.1, tarsus 0.9. Second patella and tibia 2.9 mm, third 1.9, fourth 2.5.

Note. The male was matched with the female because of similar ventral markings on the abdomen (Fig. 45). One collection has males and females together.

Variation. Total length of females 6.2 to 9.0 mm, of males 4.0 to 6.4. The male from Guatemala had the ocular quadrangle slightly narrower behind than in front and the carapace 2.7 mm wide, 1.7 behind

→

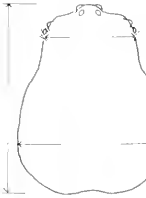
Figures 27–35. *Ocrepeira* morphology. 27–31, female *O. venustula* (Chile). 27, carapace. 28, eye region and clypeus. 29–31, epigynum. 29, ventral. 30, posterior. 31, lateral. 32, 33, male *O. venustula* (Chile), left palpus pulled apart. 34, 35, male *O. serrallesi.* 34, left coxae. 35, left second tibia, ventral.

Figures 36–40. *O. globosa* (F. P.-Cambridge), female. 36–38, epigynum. 36, ventral. 37, posterior. 38, lateral. 39, dorsal. 40, lateral.

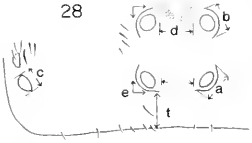
Figures 41–47. *O. subrufa* (F. P.-Cambridge). 41–45, female. 41–43, epigynum. 41, ventral. 42, posterior. 43, lateral. 44, dorsal. 45, abdomen, ventral. 46, 47, male palpus.

Abbreviations. A, terminal apophysis; C, conductor; M, median apophysis; PM, paramedian apophysis; T, tegulum.

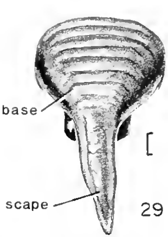
Scale lines. 1.0 mm, genitalia 0.1 mm.



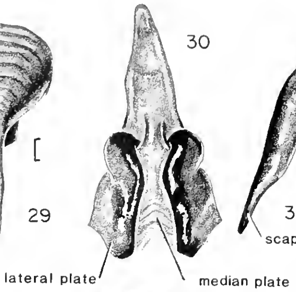
27



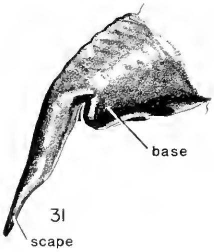
28



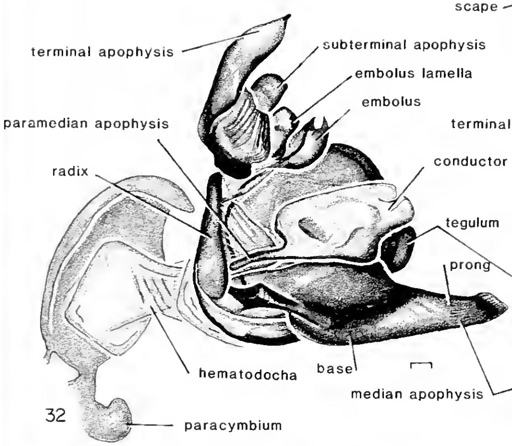
29



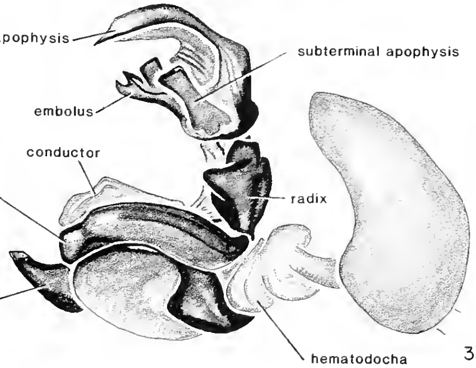
30



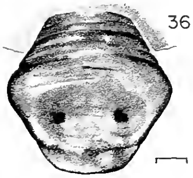
31



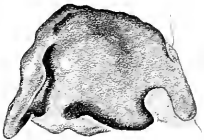
32



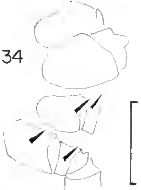
33



36



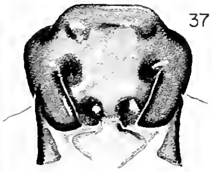
38



34

35

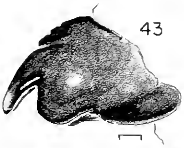
39



37

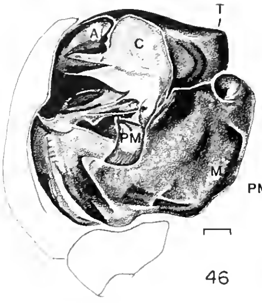
40

41

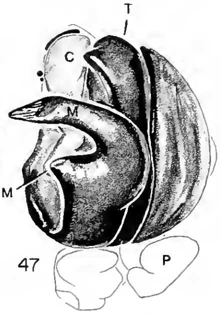


43

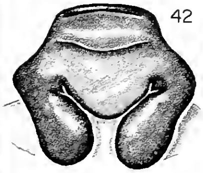
44



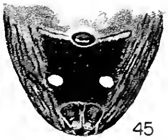
46



47



42



45

lateral eyes. Figures 41–44 were made from specimens from Sacatepequez, Guatemala, and Figures 46, 47 from the holotype of *W. sicula*.

Diagnosis. The female can be separated from that of *O. globosa* (Figs. 36–38) by the sclerotized convex median and lateral plates of the epigynum in posterior view (Fig. 42). The male is separated from others, including *O. rufa* (Figs. 69–70), by the shape of the median apophysis, and both sexes from *O. globosa* and *O. rufa* in the region by the ventral white spots on black (Fig. 45) on the abdomen.

Natural History. A female was collected in a cloud forest in Chiapas, another in live-oak foliage in Metaquesquitla, Guatemala.

Specimens Examined. MEXICO *Chiapas:* Chiapas-Oaxaca border, 21 km W Rizo del Oro, along ridge of Cerro Baul, 1,615 m, 6 Sept. 1972, ♀ (C. Mullinex, CAS). GUATEMALA *Jalapa:* Mataquesquintla, El Carrizal, 10 Aug. 1982, ♀, 7 imm. (Fend-Renkes, DU). *Sacatepequez:* Antiqua, Oct. 1965, ♀ (N. L. H. Krauss, AMNH); Antigua, 16, 17 Aug. 1947, ♂ (C., P. Vaurie, AMNH). *Quiché:* Nebaj, 9, 10 Aug. 1947, 2♀, ♂ (C., P. Vaurie, AMNH). PANAMA *Chiriquí:* El Volcán, 9–14 Aug. 1950, ♀ (A. M. Chickering, MCZ).

Ocrepeira rufa (O. P.-Cambridge), new combination

Figures 48–70; Map 4

Epeira rufa O. P.-Cambridge, 1889: 35, pl. 6, fig. 18, ♀. Female lectotype here designated from between El Petén [Depto. El Petén] and Chicoyoito [Chicoyoi, 15°23′N, 90°21′W], Guatemala, in BMNH no. 1905.4.28.2812–15, examined. Keyserling, 1892: 120, pl. 6, fig. 88, ♀.

Epeira consequa:—O. P.-Cambridge, 1889: 36.

Epeira destricta:—O. P.-Cambridge, 1889, pl. 4, fig. 14, ♀ (not male holotype, fig. 13). Illustrations to go with *Epeira consequa*.

Amamra bituberosa O. P.-Cambridge, 1889: 55, pl. 3, fig. 11, ♀. Female holotype from Costa Rica, in BMNH, examined. Keyserling, 1892: 45, pl. 2, fig. 27, ♀. NEW SYNONYMY.

Amamra gibbifera O. P.-Cambridge, 1894: 137, pl. 18, fig. 10, ♀. Two female syntypes from Guerrero, Mexico, in BMNH, examined. NEW SYNONYMY.

?*Amamra turrigera* O. P.-Cambridge, 1898: 251, pl. 31, fig. 6. Immature holotype from Chilpancingo, Guerrero State, Mexico, in BMNH, examined. NEW DOUBTFUL SYNONYMY.

Amamra clivosa O. P.-Cambridge, 1898: 270, pl. 36, figs. 1, 2, ♀, ♂. Female holotype from Amula, Guerrero State, between Tixtla and Chilapa, 6,000 ft [2,000 m], Mexico, in BMNH, examined. NEW SYNONYMY.

Wixia bituberosa:—F. P.-Cambridge, 1904: 485.

Wixia gibbifera:—F. P.-Cambridge, 1904: 882. Roewer, 1942: 882. Bonnet, 1959: 4829.

Wixia clivosa:—F. P.-Cambridge, 1904: 485, p. 46, fig. 2, ♀.

Wixia turrigera:—F. P.-Cambridge, 1904: 486, pl. 46, fig. 7, imm. Roewer, 1942: 882. Bonnet, 1959: 4830.

Wixia rufa:—F. P.-Cambridge, 1904: 486, pl. 46, fig. 5, ♀.

Aranea consequa:—F. P.-Cambridge, 1904: 518.

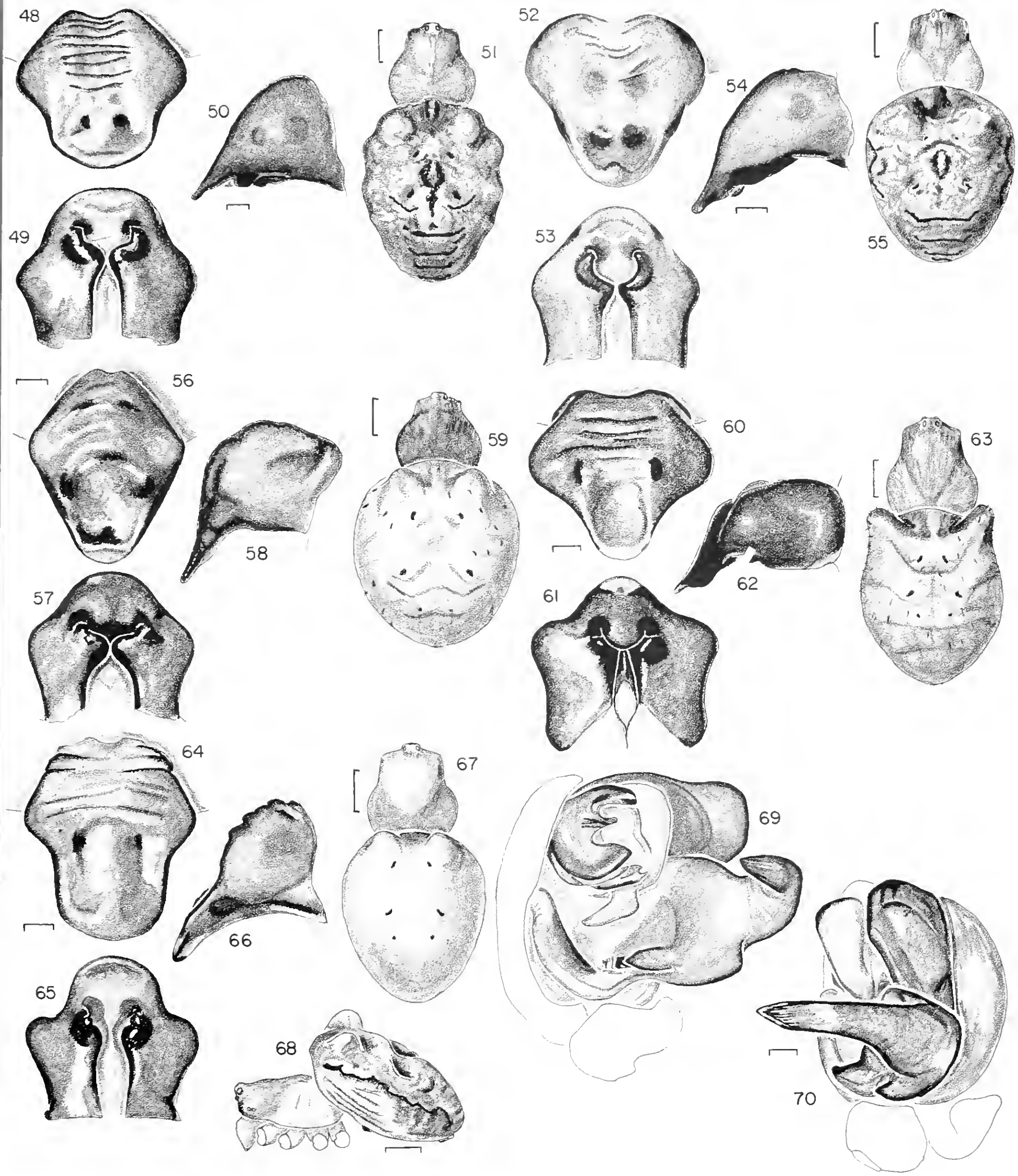
Wixia globosa:—Levi, 1976: 382, figs. 121, 122, ♂ only, not ♀.

Synonymy. The illustrations associated with *Epeira consequa* by O. P.-Cambridge (1889) are labeled *Epeira destricta*. The male illustrated by O. P.-Cambridge, 1889 as *Epeira destricta* (pl. 4, fig. 13) is the holotype of *Parawixia destricta*, but the illustration of the female is *O. rufa*. The specimen has been lost since before F. P.-Cambridge (1904).

The holotype of *Amamra turrigera* is immature, has a wide cephalic region as do other *Ocrepeira*, lacks white spots on the venter of the abdomen, and has posterior dorsal transverse bars on the abdomen as in *O. rufa;* it also has slight bulges on the sides of the abdomen as do some *O. rufa*, and the abdomen is drawn out anteriorly and projecting as in some other immatures of the genus. I assume it is an immature *O. rufa*.

F. P.-Cambridge (1904) considered *clivosa* (Figs. 56–59) and *bituberosa* (Figs. 64–67) the same species as *O. rufa* but listed them separately. In 1976 I considered the *A. clivosa* male as belonging to the female of *Wixia globosa* because of dorsal abdominal coloration. *Amamra bituberosa* (Figs. 64–67) and *A. gibbifera* (Figs. 60–63) differ in the shape of the epigynum. They may be a separate species or, much more likely, variations of *O. rufa*.

Description. Female holotype of *Epeira rufa*. Carapace dark brown, eye area light-



Figures 48–70. *Ocrepeira rufa* (O. P.-Cambridge). 48–68, female. 48–50, 52–54, 56–58, 60–62, 64–66, epigynum. 48, 52, 56, 60, 64, ventral. 49, 53, 57, 61, 65, posterior. 50, 54, 58, 62, 66, lateral. 51, 55, 59, 63, 67, dorsal. 68, lateral. 48–51, lectotype of *rufa* (Guatemala). 52–55, (Durango State, Mexico). 56–59, lectotype of *clivosa* (Guerrero State, Mexico). 60–63, syntype of *gibbifera* (Guerrero State, Mexico). 64–67, holotype of *bituberosa* (Costa Rica). 68, (Sonora State, Mexico). 69–70, male left palpus (Durango State, Mexico).

Scale lines. 1.0 mm, genitalia 0.1 mm.

est. Chelicerae orange-brown. Labium brown, endites orange-brown. Sternum orange, border brown. Coxae grayish yellow-brown; legs dark brown with indistinct rings. Dorsum of abdomen well marked with posterior transverse bars whose ends bend anteriorly, sides darker with distinct margin toward dorsum (Fig. 68); venter with white pigment covered by dark. Posterior median eyes 1.2 diameters of anterior medians, laterals 0.8 diameter. Anterior median eyes 2 diameters apart. Posterior median eyes slightly more than two diameters apart. Height of clypeus equal to 2 diameters of anterior median eyes. Abdomen (Fig. 51). Total length 6.5 mm. Carapace 3.2 mm long, 2.5 wide. First femur 3.0 mm, patella and tibia 3.8, metatarsus 2.2, tarsus 1.1. Second patella and tibia 3.5 mm, third 2.2, fourth 3.3.

Male from Encino, Durango, Mexico. Carapace orange with black setae, black clypeus, and a pair of brown patches on cephalic region. Sternum orange underlain by some white pigment. Anterior of abdomen between humps with white cardiac mark. Venter black with white on each side. Posterior median eyes same diameter as anterior medians, anterior laterals 0.6 diameter, posterior laterals 0.6. Anterior median eyes 2 diameters apart. Posterior median eyes 3 diameters apart. Ocular quadrangle wider behind than in front. Height of clypeus 1.4 diameters of the anterior median eye. Third, fourth coxae each with one macroseta. Fourth trochanter with one macroseta. Abdomen with two tubercles. Total length 5.2 mm. Carapace 2.9 mm long, 2.3 wide, 1.2 wide behind lateral eyes. First femur 2.7 mm, patella and tibia 3.4, metatarsus 1.9, tarsus 0.7. Second patella and tibia 2.7 mm, third 1.8, fourth 2.6. Abdomen about 3.1 mm long.

Note. Males and females are the most often collected species in Mexico and both sexes have similar distribution. But I am still uncertain that they belong together.

Variation. Females are quite variable in markings, shape of the abdomen (Figs. 51, 55, 59, 63, 67), and outline of the epigynum, particularly the width of the scape (Figs. 48, 52, 56, 60, 64). The seminal receptacles were examined and illustrated but no significant differences found. A female from the State of Morelos had the ocular quadrangle wider behind than in front, the clypeus equal to 1.4 diameters of the anterior median eyes, the carapace 2.3 wide, 1.4 wide behind lateral eyes. Males vary in length and thickness of median apophysis, but not in the E-shaped embolus and terminal apophysis (Fig. 69). Total length of females 6.0 to 8.2 mm, of males 4.9 to 6.2. The female and male from Durango State, Mexico, were illustrated (Figs. 52–55, 69, 70).

Diagnosis. The high clypeus and indistinct ventral markings of the abdomen are similar to those of *O. globosa* and separate both species from most others. The posterior aspect of the epigynum is similar to that of the West Indian *O. branta* and *O. serrallesi*; however, the ventral outline differs: shorter in *O. branta* (Fig. 71), longer and with a median groove in *O. serrallesi* (Figs. 78, 83–85). The male is separated from other species by the E-shaped terminal apophysis of the palpus and the shape of the median apophysis, in particular its basal, cone-shaped offset (Figs. 69, 70).

Natural History. Females were collected in pine forest in Chiapas and in oak woodland in Oaxaca.

Specimens Examined. MEXICO *Nuevo León:* Cerro Potosí, 2,400 m, 4 June 1983, ♂ (W. Maddison, MCZ). *Durango:* Encino, 27 July 1947, ♂ (W. J. Gertsch, AMNH); 16 km W El Salto, 15 July 1964, ♀ (J. E. H. M., MCZ); 10 km NE El Salto, 11 Aug. 1947, ♀ (W. J. Gertsch, AMNH). *Nayarit:* Tepic, 22 Sept. 1953, ♂ (B. Malkin, AMNH), ♀ (N. Banks, MCZ). *Jalisco:* El Molino, 10 July 1956, ♀ (R. Dreisbach, MCZ). *Veracruz:* Orizaba, 6 July 1963, ♀ (D. Bixler, MCZ). *Hidalgo:* Tenango, 5 Oct. 1947, ♀ (H. Wagner, AMNH). *Distrito Federal:* Contreras, 2,600 m, 23 July 1947, ♀ (H. Wagner, AMNH). *Puebla:* Huauchinango, 7 Oct. 1947, ♀ (H. Wagner, AMNH); nr. Villa Juarez, 26 Aug. 1946, 2♂ (J. Good-night, Bordas, AMNH). *Morelos:* Cuernavaca, Aug. 1944, ♀, July 1965, ♀ (N. L. H. Krauss, AMNH). *Oaxaca:* Monte Alban ruin, 17°02′N, 96°47′W, 5 Aug. 1983, ♂ (W. Maddison, MCZ); 27 km SW Valle Nacion, 96.4°N, 17.6°W, 24 June 1983, ♂, 2 imm. (W. Maddison, MCZ); 39 km NW Oaxaca, Hwy. 190, 1,700 m, 96°57′N, 17°17′W, 6 Aug. 1983, ♀ (W. Maddison, R. S. Anderson, MCZ). *Tabasco:* Teapa, ♂ (BMNH). *Chiapas:* Grutas de San Cristobal, 16 km SE San Cristobal, Hwy. 190, 27 July 1983, ♀ (W. Maddison, MCZ); 5 km W San Cristobal de las Casas, Hwy. 190, 2,100 m, 27–28 July 1983, ♀ (W. Maddison, R. S. Anderson, MCZ). COSTA RICA nr. San José, ♀ (Valerio, MCZ).

Ocrepeira branta new species
Figures 71–74; Map 4

Holotype. Female holotype from Blue Mountains, SW side of Main Range, 3,000–4,000 ft [900–1,200 m], Jamaica, 13 Aug. 1934 (P. J. Darlington), in MCZ. The specific name is an arbitrary combination of letters.

Description. Female holotype. Carapace reddish brown with dark gray band across the carapace (Fig. 74). Chelicerae yellowish to dark brown. Labium, endites yellowish to brown. Sternum orange, darkest on sides. Coxae yellowish; legs yellowish, ringed dusky brown. Dorsum of abdomen with white and dark marks (Fig. 74); venter black. Posterior median eyes 0.9 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 1.2 diameters apart. Posterior median eyes 2.1 diameters apart. Ocular quadrangle slightly wider than long, wider behind than in front. Height of clypeus equal to one diameter of anterior median eyes. Abdomen narrow, pointed anteriorly (Fig. 74). Total length 6.2 mm. Carapace 2.8 mm long, 2.6 wide, 1.7 wide behind lateral eyes. First femur 2.7 mm, patella and tibia 3.4, metatarsus 2.1, tarsus 0.8. Second patella and tibia 3.3 mm, third 2.1, fourth 3.1.

Diagnosis. This single specimen differs from *O. serrallesi* by the wider cephalic region, a dark band across the hairy carapace (Fig. 74), and in lacking the pair of white spots on the venter of the abdomen. The epigynum, unlike that of *O. serrallesi*, is wider than long (Figs. 71–73).

Ocrepeira potosi new species
Figures 75–77; Map 4

Holotype. Male holotype from road up to microwave tower on Cerro Potosí, 24°52′N, 100°14′W, 2,400 m, Nuevo León State, Mexico, 4 June 1983 (W. Maddison), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Male holotype. Cephalic region of carapace black; black area touches thoracic groove and has a lobe on each side of cephalic area (Fig. 77), thoracic portion orange. Chelicerae dusky orange. Labium, endites orange. Sternum yellowish underlain by some white pigment. Coxae yellowish, legs with indistinct black rings. Dorsum of abdomen spotted dark and light brown with white cardiac mark framed by black; sides with undulating black line; venter light dusky without marks. Posterior median eyes same diameter as anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.7. Anterior median eyes their diameter apart. Posterior median eyes slightly less than 2 diameters apart. Ocular quadrangle almost square, slightly wider behind than in front. Height of clypeus equal to 1.5 diameters of anterior median eyes. Palpal patella with one macroseta. Third, fourth coxae each with one macroseta. Third and fourth trochanters with one macroseta. Abdomen with a pair of humps. Total length 5.7 mm. Carapace 2.9 mm long, 2.5 wide, 1.3 wide behind lateral eyes. First femur 3.1 mm, patella and tibia 3.5, metatarsus 2.0, tarsus 1.1. Second patella and tibia 2.9 mm, third 1.9, fourth 2.8.

Note. One of the females cited as *O. rufa* may belong with this male.

Diagnosis. The shape of the median apophysis differs from that of *O. rufa* (Figs. 69, 70): the prong is longer (Figs. 75, 76) and there are two knobs on the "lower" edge, where the *O. rufa* male has an offset cone (Fig. 69).

Ocrepeira serrallesi (Bryant), new combination
Figures 78–87; Map 4

Neoscona vulgaris:—Bryant, 1940: 342; 1945: 380. Misidentification, not *Neoscona nautica* (L. Koch).

Wixia serrallesi Bryant, 1947: 90, figs. 2, 3, ♀, ♂. Male holotype and female paratype from Mona Island, West Indies, in MCZ, examined. Brignoli, 1983: 281.

Wixia pujalsi Archer, 1958: 14, figs. 31, 32, ♀. Female holotype from Chirivico [Santiago Prov.], Cuba, in AMNH, examined. Brignoli, 1983: 281. NEW SYNONYMY.

Wixia vaurieorum Archer, 1966: 131, pl. 2, fig. 10, ♀. Female holotype from Hembra, Golden Grove [?], Jamaica, in AMNH, examined. Brignoli, 1983: 281. NEW SYNONYMY.

Note. The epigyna of the types of *W. pujalsi* (Figs. 84, 86) and *W. vaurieorum* (Fig. 85) have a different outline, especially in ventral view. There are not enough specimens available to decide if this is individual or geographic variation.

Numerous localities in Jamaica have the name Golden Grove.

Description. Female paratype of *W. serrallesi* from type locality. Carapace orange-brown. Chelicerae, labium, endites brown. Sternum orange-brown underlain by white pigment. Coxae brown; legs dark brown with light orange rings. Dorsum of abdomen with black marks on gray (Fig. 81); venter black with a pair of rectangular white spots two thirds the distance between epigynum and spinnerets (Fig. 82). Posterior median eyes 0.9 diameter of anterior medians, anterior laterals 0.6 diameter, posterior 0.7. Anterior median eyes slightly less than their diameter apart. Posterior median eyes 1.2 diameters apart. Ocular quadrangle square. Height of clypeus equal to 1 diameter of anterior median eyes. Chelicerae with three teeth on anterior margin, the middle one largest; two teeth on posterior margin. Abdomen with two humps (Fig. 81). Total length 9.0 mm. Carapace 4.1 mm long, 3.6 wide, 2.1 wide behind lateral eyes. First femur 3.7 mm, patella and tibia 4.7, metatarsus 3.0, tarsus 1.1. Second patella and tibia 4.5 mm, third 2.9, fourth 4.1. Abdomen 6.7 mm high.

Male holotype of *W. serrallesi.* Color lighter than in female; sternum orange underlain by white pigment, coxae orange. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart, slightly more than 2 diameters from laterals. Posterior median eyes 2 diameters apart. Ocular quadrangle slightly narrower behind than in front. Height of clypeus equal to 0.9 diameter of anterior median eyes. Chelicerae with four teeth on anterior margin, three on posterior margin. Third, fourth coxae each with one macroseta. Third, fourth trochanters each with one macroseta. Abdomen with humps less distinct than female. Total length 6.3 mm. Carapace 3.2 mm long, 2.7 wide, 1.4 wide behind lateral eyes. First femur 3.6 mm, patella and tibia 3.7, metatarsus 2.3, tarsus 0.9. Second patella and tibia 3.7 mm, third 2.3, fourth 3.0. Abdomen 3.6 mm high.

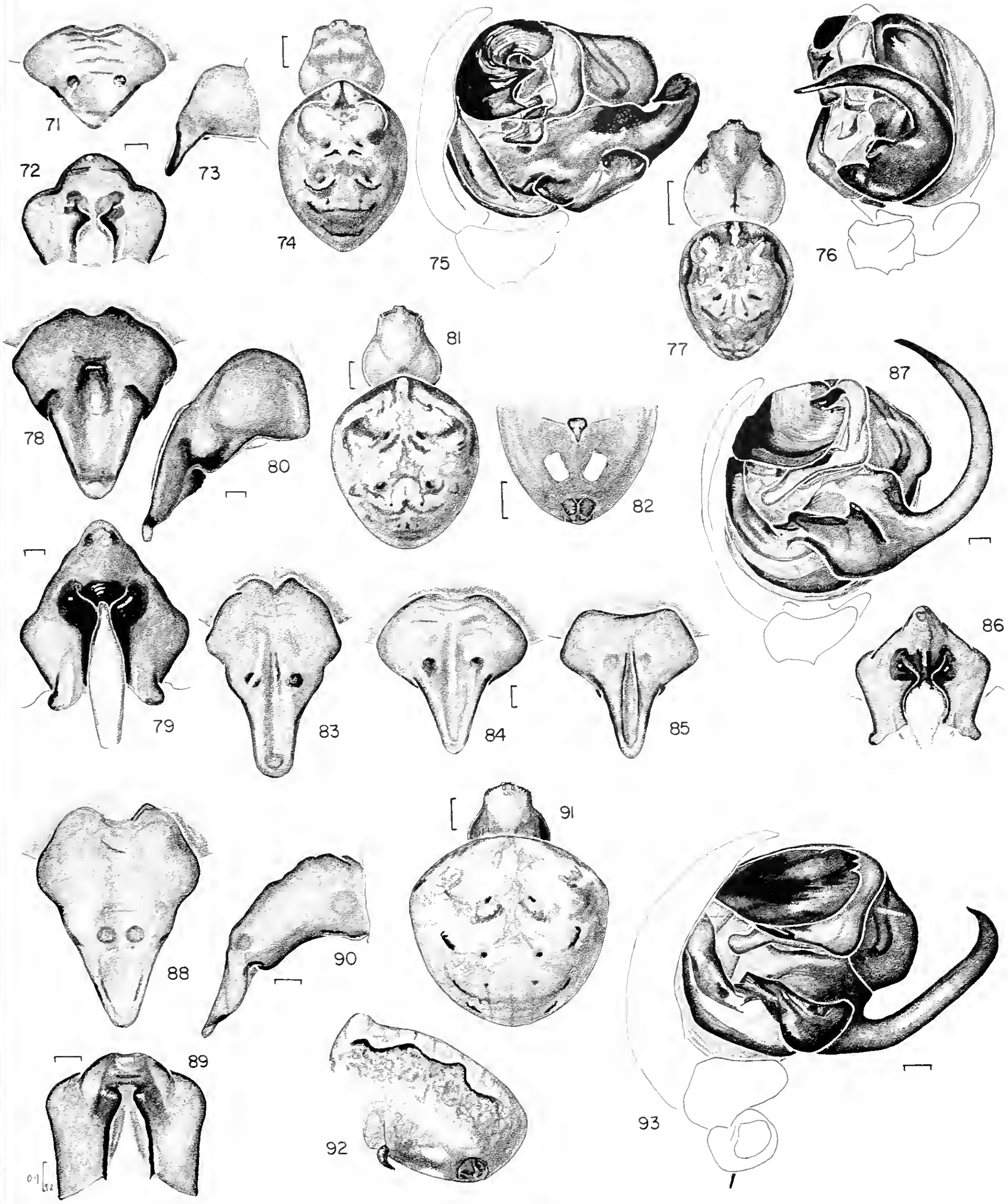
Note. Males and females were collected together.

Variation. Total length of females 5.6 to 10.3 mm, of males 4.8 to 6.4. The epigynum is quite variable in shape (Figs. 78–80, 83–86); the few males that are available differ only slightly in the shape of the terminal apophysis. It is not known if this is individual or geographic variation. Figures 78–81 were made from the paratype and Figure 87 was made from the holotype of *W. serrallesi.* Figure 84 was made from the holotype of *W. pujalsi*, Figures 85, 86 were made from that of *W. vaurieorum*, and Figure 83 was made from a specimen from Thatch Key, U. S. Virgin Islands. These illustrations show the large variation.

→

Figures 71–74. *Ocrepeira branta* n. sp., female. 71–73, epigynum. 71, ventral. 72, posterior. 73, lateral. 74, dorsal.

Figures 75–77. *O. potosi* n. sp., male. 75, 76, left palpus. 77, dorsal.



Figures 78–87. *O. serrallesi* (Bryant). 78–86, female. 78–80, 83–86, epigynum. 78, 83–85, ventral. 79, 86, posterior. 80, lateral. 81, dorsal. 82, abdomen, ventral. 87, male palpus. 78–80, 81, 87, Mona Island. 83, U.S. Virgin Islands, Thatch Key. 84, Cuba, holotype of *pujalsi*. 85, 86, Jamaica, holotype of *vaurieorum*. 87, Mona Island, holotype of *serrallesi*.

Figures 88–93. *O. redempta* (Gertsch and Mulaik). 88–92, female. 88–90, epigynum. 88, ventral. 89, posterior. 90, lateral. 91, dorsal. 92, lateral. 93, male palpus.

Scale lines. 1.0 mm, genitalia 0.1 mm.

Diagnosis. This species has been confused with *Neoscona nautica.* The posterior median eyes of *N. nautica* are on a relatively flat head and face up, while those of *Ocrepeira* are on a joint swelling, farther apart and face almost sideways (Fig. 81). *Ocrepeira serrallesi* differs from *O. redempta* and *O. branta* by the distinct rectangular white patches on the black underside of the abdomen (Fig. 82), and by the flask-shaped posterior median plate with a narrow, ventral neck (Fig. 79). The median apophysis is more slender than that of *O. redempta* and has a tooth at the widest portion of its base (Fig. 87) and a terminal apophysis as long as high.

Specimens Examined. CUBA *Cienfuegos:* Topes de Collantes, 17 July 1956, ♀ (C. P. Vaurie, AMNH). *Santiago:* Loma (Pico) de Gato, Sierra Maestra, 26–28 June 1959, 2♀ (W. M. Sanderson, AMNH); Sierra de Cobre, 900–1,200 m, 3–7 July 1936, ♀ (P. J. Darlington, MCZ). *Guantanamo:* Mts. N Imias, 900–1,200 m, 25–28 July 1936, 2♀ (P. J. Darlington, MCZ). HISPANIOLA *Dominican Republic:* Cordillera Central, La Vega, 9 Aug. 1958, ♀ (A. F. Archer, AMNH); nr. La Romana, 31 July 1935, 2♀, ♂ (Hassler, AMNH); Mt. Busú, Sierra Martín García, 300–1,300 m, 25 June 1983, ♂ (G. Flores, A. Gross, MCZ). PUERTO RICO Culebra Isl., 19 July 1965, ♂ (F. Mackenzie, AMNH); Bosque Estadual de Maricao, 23 July 1958, ♂ (A. F. Archer, AMNH); Desecheo Isl., 28 Mar. 1961, 4♀ (MCZ), 27–29 May 1965, ♀, ♂, 2 imm. (H. Heatwole, AMNH); Muertos Isl., 27–29 May 1959, 3♀ (Jordan, Martorell, AMNH), 25 June 1959, 2♂ (AMNH). U. S. VIRGIN ISLANDS Thatch Key, 12 Nov. 1966, ♀ (Univ. Puerto Rico Isl. Proj., AMNH). *St. Croix:* Christiansted, ♂ (ZMK). *St. John:* 10–12 July 1958, 6♀, 2♂ (A. F. Archer, AMNH); nr. Cinnamon and Hart Bays, 1–4 Aug. 1976, ♀ (D. E., D. N. Rosen, AMNH). BRITISH VIRGIN ISLANDS Cooper Isl., 25 July 1986, ♂ (J. Lazell, J. Bush, USNM); Little Camanoe, 2 July 1965, ♂ (Univ. Puerto Rico Isl. Proj., AMNH); Tortola, Greater Camanoe Isl., 1 July 1965, ♀ (Univ. Puerto Rico Isl. Proj., AMNH). MARTINIQUE Trois Ilets Ansemitan, 10–11 June 1960, imm. (C., P. Vaury, AMNH). GRENADA St. George's, Sept. 1967, ♀ (N. L. H. Krauss, AMNH).

Ocrepeira redempta (Gertsch and Mulaik), new combination
Figures 88–93; Map 4

Aranea redempta Gertsch and Mulaik, 1936: 18, fig. 39, ♀. Female holotype from Edinburg, Texas, in AMNH, examined.

Neoscona redempta:—Berman and Levi, 1971: 499, figs. 121–124, ♀.

Description. Female from Sonora, Mexico. Carapace orange with light colored setae, sides of thoracic region brown to black. Chelicerae orange to brown. Labium, endites brown. Sternum orange underlain by white, margin dark. Coxae orange; legs orange with dark rings. Dorsum of abdomen with white, gray, and black marks (Fig. 91); sides with undulating black line (Fig. 92); venter with a pair of light patches on gray (Fig. 92). Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes 1.2 diameters apart. Posterior median eyes 2 diameters apart. Ocular quadrangle wider behind than in front. Height of clypeus equal to 1.5 diameters of anterior median eyes. Abdomen as long as wide (Fig. 91). Total length 7.8 mm. Carapace 2.8 mm long, 2.6 wide, 1.4 wide behind lateral eyes. First femur 2.7 mm, patella and tibia 3.2, metatarsus 2.0, tarsus 0.8. Second patella and tibia 3.1 mm, third 2.0, fourth 3.0.

Male from Sonora, Mexico. Color as in female. Lateral lines on abdomen indistinct. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.5 diameter. Anterior median eyes slightly less than their diameter apart. Posterior median eyes 2 diameters apart. Ocular quadrangle wider behind than in front. Height of clypeus equal to 0.8 diameter of anterior median eyes. Third, fourth coxae each with one macroseta. Third and fourth trochanters with one macroseta. Total length 4.4 mm. Carapace 2.7 mm long, 2.3 wide, 1.2 wide behind lateral eyes. First femur 2.9 mm, patella and tibia 3.4, metatarsus 1.6, tarsus 0.8. Second patella and tibia 2.7 mm, third 1.8, fourth 2.5.

Note. Males and females were collected together.

Variation. Total length of females 5.7 to 7.8 mm, of males 4.4 to 5.0. Figures 88–92 were made from a specimen from Sonora, Figure 93 from a male from Texas.

Diagnosis. Ocrepeira redempta from Mexico and Central America can be confused with the West Indian *O. serrallesi.* The ventral white patches on the abdomen are less distinct than in the West Indian species (Fig. 92). The ventral part of the posterior median plate of the epigynum (Fig. 89) differs from that of *O. serrallesi* (Figs. 79, 86) and the median apophysis differs in that the prong is less curved and the widest part above the base has a semicircular offset (Fig. 93)

Specimens Examined. MEXICO *Sonora:* Minas Nuevas, 8 Aug. 1952, ♀, ♂ (P., C. Vaurie, AMNH); 16 km W Alamos, 19 July 1954, 2♀, ♂ (W. J. Gertsch, AMNH). *San Luis Potosí:* hotel, Covadanga, Valles, 1961, ♀ (L. Steude, AMNH). *Nayarit:* Tepic, 4 Aug. 1953, ♀ (P., C. Vaurie, AMNH). *Baja California Norte:* 24 km S Santo Domingo, 4 Oct. 1941, ♀ (E. Ross, Bohart, CAS). *Baja California Sur:* Comitán, Matorral Sarcocaule, 4 Oct. 1987, ♀ (M. L. Jiménez, MLJ); Comitán, 2 Sept. 1987, 2♂ (M. L. Jiménez, MLJ); 16 km NW La Paz, 6 Oct. 1941, ♀ (E. Ross, Bohart, CAS). GUATEMALA Ciudad Guatemala, 1,400–1,500 m, June 1981, ♀ (N. L. H. Krauss, AMNH). HONDURAS Tsecucigajo [?Tegucigalpa], 18 June, ♀ (H. Dybas, AMNH).

Ocrepeira camaca new species
Figures 94–100; Map 5

Holotype. Female holotype from Fazenda São Roque, Camacan [Camacã], Bahia State, Brazil, 2 Dec. 1977 (J. S. Santos), in MCN no. 11044. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace orange, anterior of cephalic area dusky. Chelicerae orange with a dusky reticulate pattern. Labium, endites orange. Sternum light orange. Coxae light orange, legs with indistinct dusky rings. Dorsum of abdomen with anterior edge black and with paired diagonal black marks on white (Fig. 97); venter dusky with two indistinct white patches (Fig. 98). Cephalic area of carapace unusually narrow. Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.7 diameter, posterior 0.6. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Ocular quadrangle narrower behind than in front. Height of clypeus equal to 0.8 diameter of anterior median eyes. Abdomen oval without distinct humps (Fig. 97). Total length 9.6 mm. Carapace 4.5 mm long, 4.1 wide, 1.8 wide behind lateral eyes. First femur 4.6 mm, patella and tibia 5.8, metatarsus 3.9, tarsus 1.3. Second patella and tibia 5.6 mm, third 3.3, fourth 4.9.

Male from Itamarajú, Bahia, Brazil. Color as in female but some white pigment posteriorly in cephalic area of carapace, and sternum underlain by white pigment. Legs more distinctly ringed than those of the female. Posterior median eyes same diameter as anterior medians, laterals 0.5 diameter. Anterior median eyes 0.6 diameter apart. Posterior median eyes 1.8 diameters apart. Posterior median eyes on swelling. Ocular quadrangle wider behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Palpal patella with one macroseta. Third, fourth coxae each with one macroseta. Third and fourth trochanters each with one macroseta. Abdomen oval without tubercles. Total length 5.4 mm. Carapace 3.1 mm long, 2.9 wide, 1.6 wide behind lateral eyes. First femur 3.4 mm, patella and tibia 4.2, metatarsus 2.6, tarsus 0.9. Second patella and tibia 3.9 mm, third 2.3, fourth 3.0.

Note. Males and females were collected at the same locality, and have a similar abdomen. But the eyes differ: those of the male have the posterior median eyes on a larger swelling that those of the female.

Variation. Total length of females 11.3 to 9.6 mm. The female from Curitiba has no white spots on the venter of the abdomen, has eyes on a swelling, and has the scape of the epigynum torn off. Figures 94–98 were made from the holotype, and Figures 99, 100 from a male from Itamarajú.

Diagnosis. The shape of the epigynum (Figs. 94–96) and the median apophysis of the palpus (Figs. 99, 100) resemble that of the West Indian *O. serrallesi* (Figs. 78–87), and differ from all other Brazilian species.

Records Examined. BRAZIL *Bahia:* Fazenda N. S. Neves, Itamarajú, 9 Oct. 1978, ♀, ♂ (J. S. Santos, MCN 10324, 11018). *Paraná:* Curitiba, 1945, ♀ (Gengnagel, MZSP 9647).

Ocrepeira arturi new species
Figures 101–107; Map 4

Holotype. Female holotype and one male and one immature paratype from Barro Colorado Island, Lago Gatún, Panamá Prov., Panama, May 1964 (A. M. Chickering), in MCZ. The species is named after the collector.

Description. Female holotype. Carapace orange. Chelicerae, labium, endites orange. Sternum orange, underlain by some white pigment. Coxae, legs orange. Dorsum of abdomen white, gray, and black (Fig. 104); venter black with a pair of white spots (Fig. 105). Posterior median eyes 1.1 diameters of anterior medians, anterior laterals 0.8 diameter, posterior laterals 1 diameter. Anterior median eyes 1.7 diameters apart. Posterior median eyes 2.5 diameters apart. Ocular quadrangle wider behind than in front. Height of clypeus equal to 1.7 diameters of anterior median eyes. Abdomen with an anterior median hump in addition to the anterior lateral ones, and two pairs of swellings on sides (Fig. 104). Total length 7.2 mm. Carapace 3.5 mm long, 3.2 wide, 1.8 wide behind lateral eyes. First femur 4.0 mm, patella and tibia 4.5, metatarsus 2.9, tarsus 1.1. Second patella and tibia 4.3 mm, third 2.7, fourth 3.9. Abdomen 5.5 mm long.

Male paratype. Color as in female, but legs with darker orange rings. Posterior median eyes same diameter as anterior medians, laterals 0.6 diameter. Anterior median eyes 0.7 diameter apart. Posterior median eyes two diameters apart. Ocular quadrangle slightly wider behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Third, fourth coxae each with one macroseta. Third, fourth trochanters with one macroseta. Abdomen with anterior median tubercle. Total length 6.2 mm. Carapace 3.8 mm long, 3.5 wide, 1.8 wide behind lateral eyes. First femur 4.4 mm, patella and tibia 5.1, metatarsus 2.9, tarsus 1.1. Second patella and tibia 4.7 mm, third 2.7, fourth 3.8. Abdomen 4.5 mm long.

Note. Males and females were collected together.

Diagnosis. Ocrepeira arturi differs from most *Ocrepeira* species by having an anterior median hump and humps all around the abdomen (Fig. 104). The epigynum (Figs. 101–103) can be confused with that of *O. serrallesi* (Figs. 78–86). The male palpus has differently shaped median and terminal apophyses (Figs. 106, 107) from those of *O. serrallesi* (Fig. 87).

Ocrepeira pedregal new species
Figures 108–110; Map 4

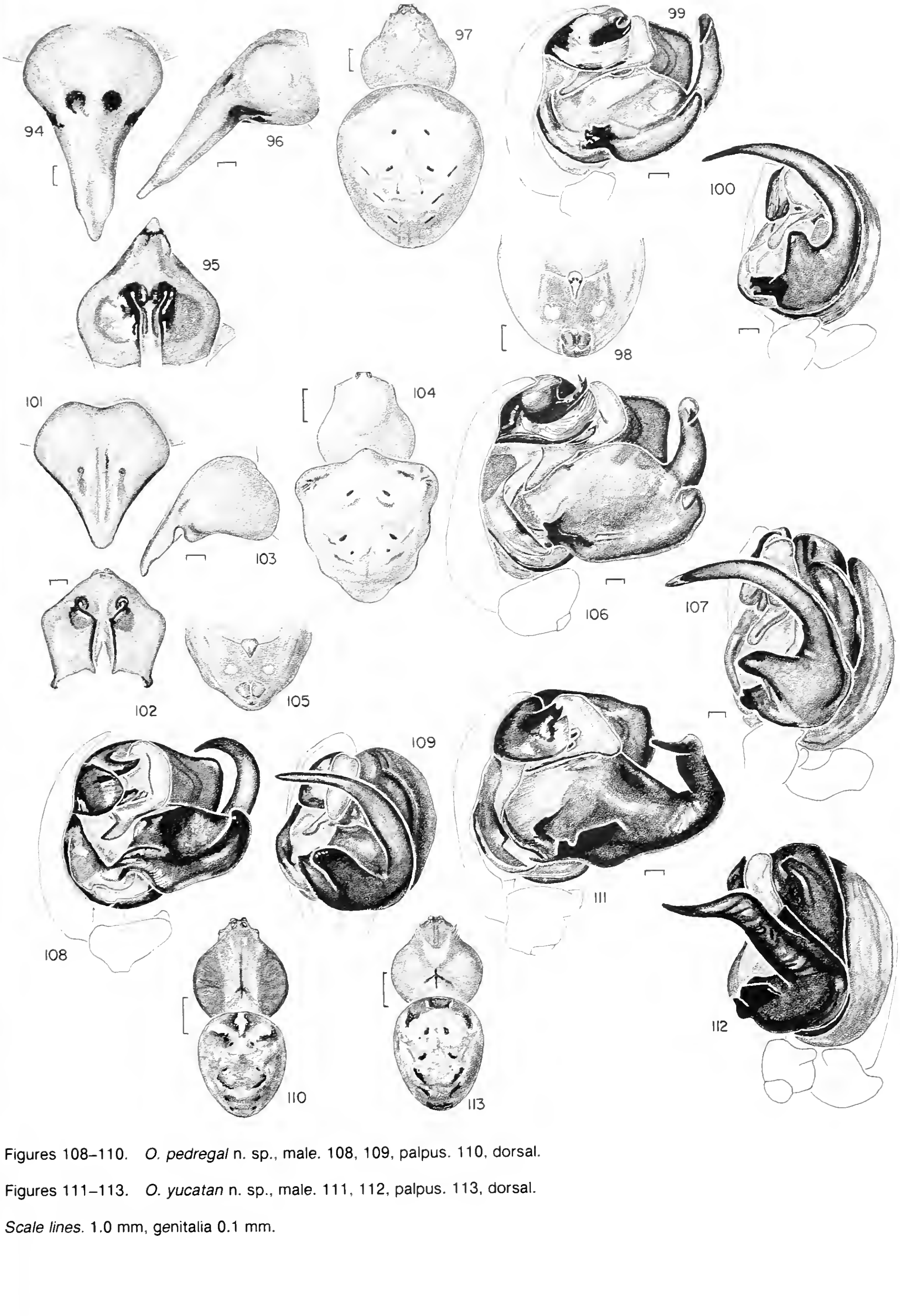
Holotype. Male holotype from Pedregal, Distríto Federal, Mexico, 8 Aug. 1947 (H. Wagner), in

---

→

Figures 94–100. *Ocrepeira camaca* n. sp. 94–97, female. 94–96, epigynum. 94, ventral. 95, posterior. 96, lateral. 97, dorsal. 98, abdomen, ventral. 99, 100, left male palpus.

Figures 101–107. *O. arturi* n. sp. 101–105, female. 101–103, epigynum. 101, ventral. 102, posterior. 103, lateral. 104, dorsal. 105, abdomen, ventral. 106, 107, male palpus.



Figures 108–110. *O. pedregal* n. sp., male. 108, 109, palpus. 110, dorsal.

Figures 111–113. *O. yucatan* n. sp., male. 111, 112, palpus. 113, dorsal.

Scale lines. 1.0 mm, genitalia 0.1 mm.

AMNH. The specific name is a noun in apposition after the type locality.

Description. Male holotype. Carapace with an orange band, band wider in front than behind, carapace brown in thoracic region. Chelicerae, labium, endites orange. Sternum orange, underlain by some white pigment. Coxae orange, legs orange-brown with indistinct darker rings. Dorsum of abdomen with white cardiac mark and black outline of a folium (Fig. 110). Venter with a white transverse rectangle between genital groove and spinnerets. Posterior median eyes 1.1 diameters of anterior medians, laterals 0.7 diameter. Anterior median eyes 1.7 diameters apart. Posterior median eyes 1.8 diameters apart. Lateral eyes their radius apart. Ocular quadrangle square. Height of clypeus equal to 1.3 diameters of anterior median eyes. Third, fourth coxae each with one macroseta. Third, fourth trochanters each with one macroseta. Abdomen with two anteriorly directed tubercles (Fig. 110). Total length 5.2 mm. Carapace 2.7 mm long, 2.3 wide, 1.2 wide behind lateral eyes. First femur 3.0 mm, patella and tibia 3.4, metatarsus 1.9, tarsus 0.7. Second patella and tibia 2.7 mm, third 1.8, fourth 2.5. Abdomen 3.1 mm long.

Variation. Total length of males 5.2 to 5.6 mm. The illustrations were made from the holotype.

Diagnosis. Ocrepeira pedregal differs from *O. yucatan*, *O. rufa*, and other males found in Mexico by the shape of the median and terminal apophyses and the knife-shaped paramedian apophysis (Figs. 108, 109).

Specimens Examined. MEXICO *Michoacan:* 16 km S Uruapan, 6 July 1985, ♂ (Woolley, Zolnerwich, DAD). NICARAGUA 5 km N Matagalpa, 15 July 1989, ♂ (R. Reinbold, JMM).

Ocrepeira yucatan new species

Figures 111–113; Map 4

Holotype. Male holotype from Piste, Yucatan, Mexico, 4–8 June 1959 (C., P. Vaurie), in AMNH. The specific name is a noun in apposition after the type locality.

Description. Male holotype. Carapace orange with white pigment in middle. Clypeus black, sides of thoracic region with some white down-like setae. Chelicerae, endites, labium dusky orange. Sternum orange underlain by some white pigment. Coxae light orange; legs light orange with black rings. Abdomen black anterior to a white line between tubercles, black outline of folium posteriorly (Fig. 113); venter with a pair of white patches on black. Posterior median eyes 0.9 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes their diameter apart. Posterior median eyes 1.8 diameters apart. Ocular quadrangle square. Height of clypeus equal to 1.2 diameters of anterior median eyes. Third, fourth coxae each with one macroseta. Third and fourth trochanters with one macroseta. Abdomen ovoid with tubercles minute (Fig. 113). Total length 5.0 mm. Carapace 3.3 mm long, 3.0 wide, 1.3 wide behind lateral eyes. First legs lost. Second patella and tibia 3.6 mm, third 2.2, fourth 3.1.

Diagnosis. Ocrepeira yucatan differs from other species by having small abdominal tubercles, light colored carapace, white patches on venter, and median apophysis with a long, distally turned "up" prong (Figs. 111, 112).

Ocrepeira incerta (Bryant), new combination

Figures 114–118; Map 4

Wixia incerta Bryant, 1936: 328, pl. 23, figs. 6, 8, ♀. Three female syntypes from Sierra del Cobre, Loma del Gato, 2,600–3,325 ft [790–1,000 m], Cuba, in MCZ, examined. Roewer, 1942: 882. Bonnet, 1959: 4829.

Description. Female syntype. Carapace orange with almost circular brown cap; area between median and lateral eyes brown. Chelicerae brown. Labium, endites yellow to brown. Sternum light yellowish with dark margin. Coxae light yellowish; legs yellowish with brown rings. Dorsum of abdomen white and black with posterior transverse bars (Fig. 117); venter dusky with a pair of large white patches anterior to spinnerets. Anterior median eyes 1.5 diameters apart, 2.5 diameters from laterals. Posterior median eyes 1.5 diameters apart, slightly more than 3 from laterals. Posterior median eyes on swelling. Ocular quadrangle square. Height of clypeus equal to 0.8 diameter of anterior median eyes. Abdomen with two large tubercles and a minute anterior median one (Fig. 117). Total length 4.3 mm. Carapace 1.8 mm long, 1.7 wide, 1.2 wide behind lateral eyes 1.2 wide. First femur 2.0 mm, patella and tibia 2.3, metatarsus 1.4, tarsus 0.6. Second patella and tibia 2.1 mm, third 1.2, fourth 1.7. Abdomen 3.1 mm high.

Variation. Total length of females 3.8 to 5.4 mm. Some specimens have a longer scape of the epigynum or have a longer abdomen than others (Fig. 118). The specimens from Pico Turquino have a dark sternum and lack dark rings on legs. Figures 114–117 were made from a syntype and the abdomen (Fig. 118) from a specimen from Pico Turquino.

Diagnosis. This species differs from all others by the triangular epigynum (in ventral view, Figs. 114, 115) and the flask-shaped outline of the median plate in posterior view (Fig. 115).

Specimens Examined. CUBA *Santiago:* Sierra del Cobre, 900–1,200 m, 3–7 July 1936, ♀ (P. J. Darlington, MCZ); Pico Turquino, 1,800 m, 16–21 June 1936, ♀ (P. J. Darlington, MCZ); S side Pico Turquino, 900–1,500 m, June 1936, ♀ (P. J. Darlington, AMNH); La Majagua, El Cardero, Pico Turquino, Mar. 1980, ♀ (G. Alayón, A. Valdés, IESC).

Ocrepeira hirsuta (Mello-Leitão), new combination
Figures 119–125; Map 5

Epeira venustula:—Keyserling, 1892: 128, pl. 6, ♀, ♂. Not *E. venustula* Keyserling, 1880, misidentification (see *O. venustula* below).

Eustala hirsuta Mello-Leitão, 1942: 400, figs. 16–18, ♂. Male holotype from Tirol, Chaco Prov., Argentina, in MLP, examined. Brignoli, 1983: 269.

Description. Female from Chaco, Paraguay. Carapace yellowish, cephalic region orange with white setae, sides of cephalic region and area between eyes dark brown; a dark brown patch on each side behind cephalic region (Fig. 122). Chelicerae dusky brown, orange proximally. Labium, endites brown. Sternum dusky with five orange patches, yellow behind labium. Coxae yellow; legs yellow, ringed dark brown. Anterior of dorsum of abdomen dark to a line between tubercles; posterior with a lyre-shaped mark (Fig. 122); venter gray with a pair of white spots (Fig. 123). Posterior median eyes 0.9 diameter of anterior medians, laterals 0.8 diameter. Anterior median eyes 1.1 diameters apart, 2.5 diameters from laterals. Posterior median eyes 1.2 diameters apart, almost 4 diameters from laterals. Ocular quadrangle narrower behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Abdomen with distinct humps (Fig. 122). Total length 6.4 mm. Carapace 3.4 mm long, 2.5 wide, 1.6 wide behind lateral eyes. First femur 2.5 mm, patella and tibia 3.2, metatarsus 2.0, tarsus 0.9. Second patella and tibia 3.1 mm, third 1.9, fourth 2.9.

Male holotype of *Eustala hirsuta.* Color as in female but dorsum of abdomen with brown chevrons. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart. Posterior median eyes slightly more than their diameter apart. Third and fourth coxae with one macroseta. Fourth trochanter with one macroseta. Abdomen oval. Total length 5.8 mm. Carapace 3.0 mm long, 2.6 wide. First femur 2.8 mm, patella and tibia 3.6, metatarsus 2.0, tarsus 0.8. Second patella and tibia 2.8 mm, third 2.1, fourth 3.0.

Note. Males and females were repeatedly collected together.

Variation. Total length of females 6.4 to 8.2 mm, of males 4.5 to 5.8. A male from Rio Grande do Sul had the ocular quadrangle narrower behind than in front, the height of the clypeus equal to the diameter of the anterior median eyes, the carapace 2.4 mm wide, 1.3 wide behind lateral eyes. Some females have the sternum colored as in *Parawixia* (Levi, 1992, fig. 6) with pairs of light colored patches.

All illustrations were made from specimens from Chaco, Paraguay.

Diagnosis. The epigynum, in ventral view, unlike that of other species, has a small lobe on each side (Fig. 119), and has a distinct constriction of the median plate in posterior view (Fig. 120). The palpus differs by the shape of the median apophysis (Figs. 124, 125).

Natural History. One female from Curitiba was observed making an orb in the grass at sunset.

Specimens Examined. BRAZIL *Paraná:* Curitiba, 3 Feb. 1988, ♀ (R. L. C. Baptista, RLCB); Rôlandia, 1948, ♀ (A. Maller, AMNH). *Rio Grande do Sul:* Guaíba, 8 Feb. 1980, ♀ (H. A. Gastal, MCN 9224); Parque Estadual de Nonoai, Nonoai, 13 Jan. 1985, ♀ (A. A. Lise, MCN 12910); São Leopoldo, 19 June 1965, 6♀, ♂ (C. Valle, MZSP 4887); Serro Claro, São Pedro do Sul, 10 Jan. 1985, 16♀, 8♂, imm. (A. A. Lise, MCN 13001). PARAGUAY *Alto Paraná:* Taguararapa, 7♀, ♂ (AMNH), 1–6 Sept. 1982, 7♀, ♂ (J. A. Kochalka, IRNP); SE Naryal [?], 18–22 Aug. 1988, ♂ (L. Peña, AMNH). *Chaco:* Parque Nacional Defensores, Misión Cué, Tribu Nueva, 1–3 Sept. 1982, 7♀, 2♂ (J. A. Kochalka, IRNP). *Itapúa:* Autidia Matiauda, 20 km NE Puerto Capitán Meza, Mar. 1984, ♂ (L. Fogarty, MCZ). ARGENTINA *Misiones:* Eldorado, Sept.–Nov. 1964, 2♀ (A. Kovacs, AMNH); Puerto Aguirre, 1943, ♀ (J. M. Siana, MACN). *Salta:* Zuviria, Dec. 1907, ♀, ♂ (E. Reimoser, MCZ). *Santa Fé:* San Javier, Feb. 1964, ♂ (M. E. Galiano, MEG).

Ocrepeira hondura new species
Figures 126–130; Map 4

Holotype. Female holotype from Bajo Hondura [10°09′N, 83°55′W], 1,200 m, San José Prov., Costa Rica, Nov. 1987 (W. Eberhard), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace orange, sides with a wide brown band broken behind posterior median eyes. Chelicerae, labium, endites brown. Sternum white with a brown rim. Anterior two pairs of coxae brown, posterior two yellowish; legs yellowish with dark rings and patches. Dorsum of abdomen with dark marks on anterior side of each tubercle, posterior with transverse dark bars (Fig. 129); venter black with a pair of white spots (Fig. 130). Posterior median eyes same diameter as anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart. Posterior median eyes 2 diameters apart. Ocular quadrangle almost square, very slightly wider behind. Height of clypeus equal to 1 diameter of anterior median eye. Abdomen with a pair of tubercles (Fig. 129). Total length 8.2 mm. Carapace 3.4 mm long, 2.7 wide, 2.0 wide behind lateral eyes. First femur 3.1 mm, patella and tibia 3.8, metatarsus 2.0, tarsus 0.9. Second patella and tibia 3.6 mm, third 2.2, fourth 3.4. Abdomen 5.7 mm long.

Diagnosis. The triangular epigynum differs from all others by the small pocket at the tip (Fig. 126) and the shape of the posterior median plate (Fig. 127).

Ocrepeira klossi new species
Figures 131–136; Map 5

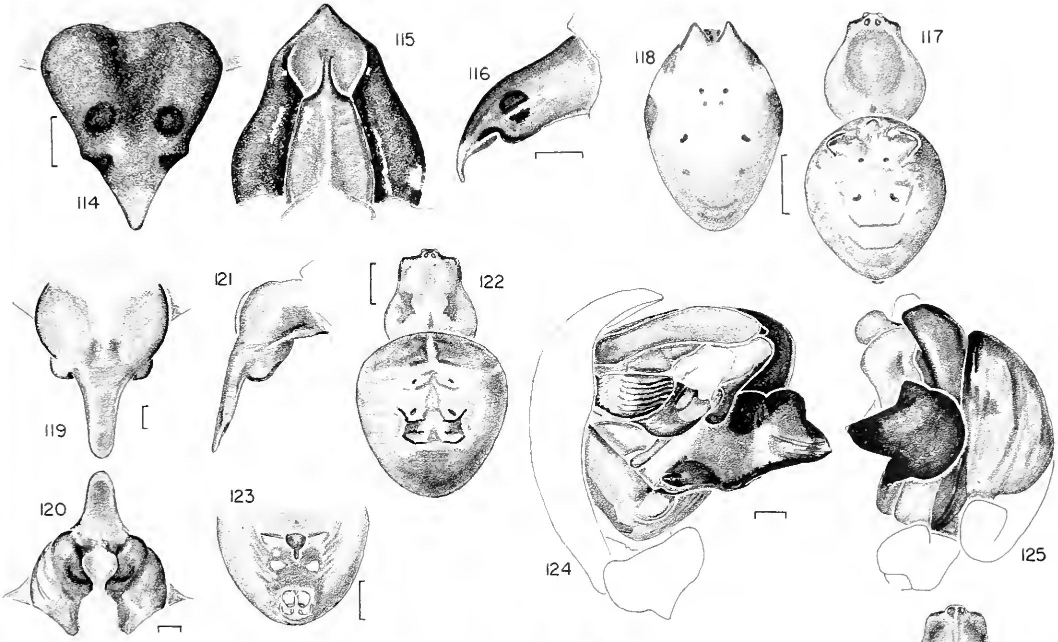
Holotype. Female holotype from Serro do Caraça, Minas Gerais State, 20°08′S, 43°30′W, Brazil, 12–23 Nov. 1961 (U. Martins, K. Lenko, R. Kloss), in MZSP no. 6710. The species is named after one of the collectors.

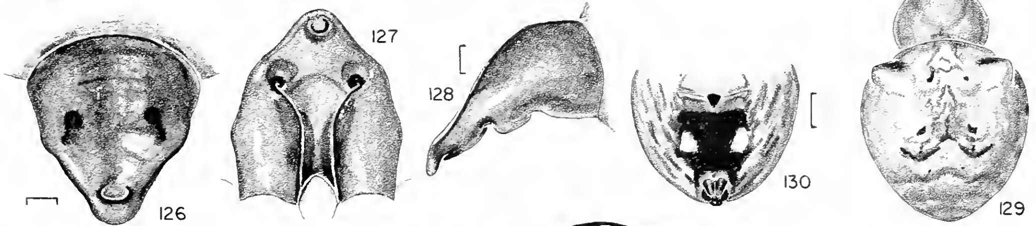
Description. Female holotype. Carapace orange. Chelicerae, labium, endites orange. Sternum orange. Coxae orange; legs orange. Dorsum of abdomen white (Fig. 134); venter without pigment except for two white pigment patches and white

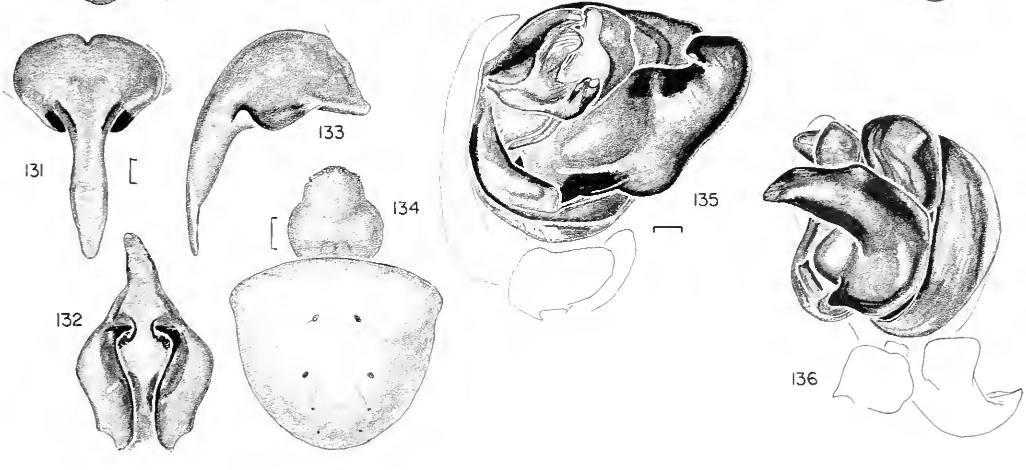
⟶

Figures 114–118. *Ocrepeira incerta* (Bryant), female. 114–116, epigynum. 114, ventral. 115, posterior. 116, lateral. 117, dorsal. 118, abdomen, dorsal.

Figures 119–125. *O. hirsuta* (Mello-Leitão). 119–123, female. 119–121, epigynum. 119, ventral. 120, posterior. 121, lateral. 122, dorsal. 123, abdomen, ventral. 124, 125, male left palpus.







Figures 126–130. *O. hondura* n. sp., female. 126–128, epigynum. 126, ventral. 127, posterior. 128, lateral. 129, dorsal. 130, abdomen, ventral.

Figures 131–136. *O. klossi* n. sp. 131–134, female. 131–133, epigynum. 131, ventral. 132, posterior. 133, lateral. 134, dorsal. 135, 136, male palpus.

Scale lines. 1.0 mm, genitalia 0.1 mm.

streaks on sides. Posterior median eyes same diameter as anterior medians, laterals 0.6 diameter. Anterior median eyes their diameter apart. Posterior median eyes 1.4 diameters apart. Ocular quadrangle almost square. Height of clypeus equal to 1 diameter of anterior median eyes. Abdomen with lateral tubercles (Fig. 134). Total length 10.0 mm. Carapace 3.7 mm long, 3.1 wide, 1.8 wide behind lateral eyes. First femur 3.4 mm, patella and tibia 4.0 , metatarsus 2.7, tarsus 1.0. Second patella and tibia 3.9 mm, third 2.5, fourth 3.6.

Male paratype. Color as in female but legs with indistinct darker rings and abdomen with anterior black with a white cardiac mark, posterior with a black outline around a dark folium. Posterior median eyes 0.9 diameter of anterior medians, laterals 0.8 diameter. Anterior median eyes 0.7 diameter apart. Posterior median eyes their diameter apart. Ocular quadrangle slightly narrower behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Third, fourth coxae each with one macroseta. Third and fourth trochanters each with one macroseta. Total length 6.0 mm. Carapace 3.3 mm long, 2.7 wide, 1.2 wide behind lateral eyes. First femur 3.4 mm, patella and tibia 3.9, metatarsus 2.3, tarsus 0.9. Second patella and tibia 3.2 mm, third 2.0, fourth 3.1.

Note. It is uncertain if male and female belong together; they were matched on account of similar size of the carapace and proximate collecting localities.

Diagnosis. The epigynum of this species has a scape that is constricted anteriorly (Fig. 131) and is relatively thick (Fig. 133). The male has a unique median apophysis with a slight swelling on its "upper" side (Fig. 136).

Paratype. BRAZIL *Minas Gerais:* Lagoa Santa, 26 Nov. 1960, ♂ (C. Araújo, Martina, MZSP 7960).

Ocrepeira mastophoroides (Mello-Leitão), new combination

Figures 137–142; Map 5

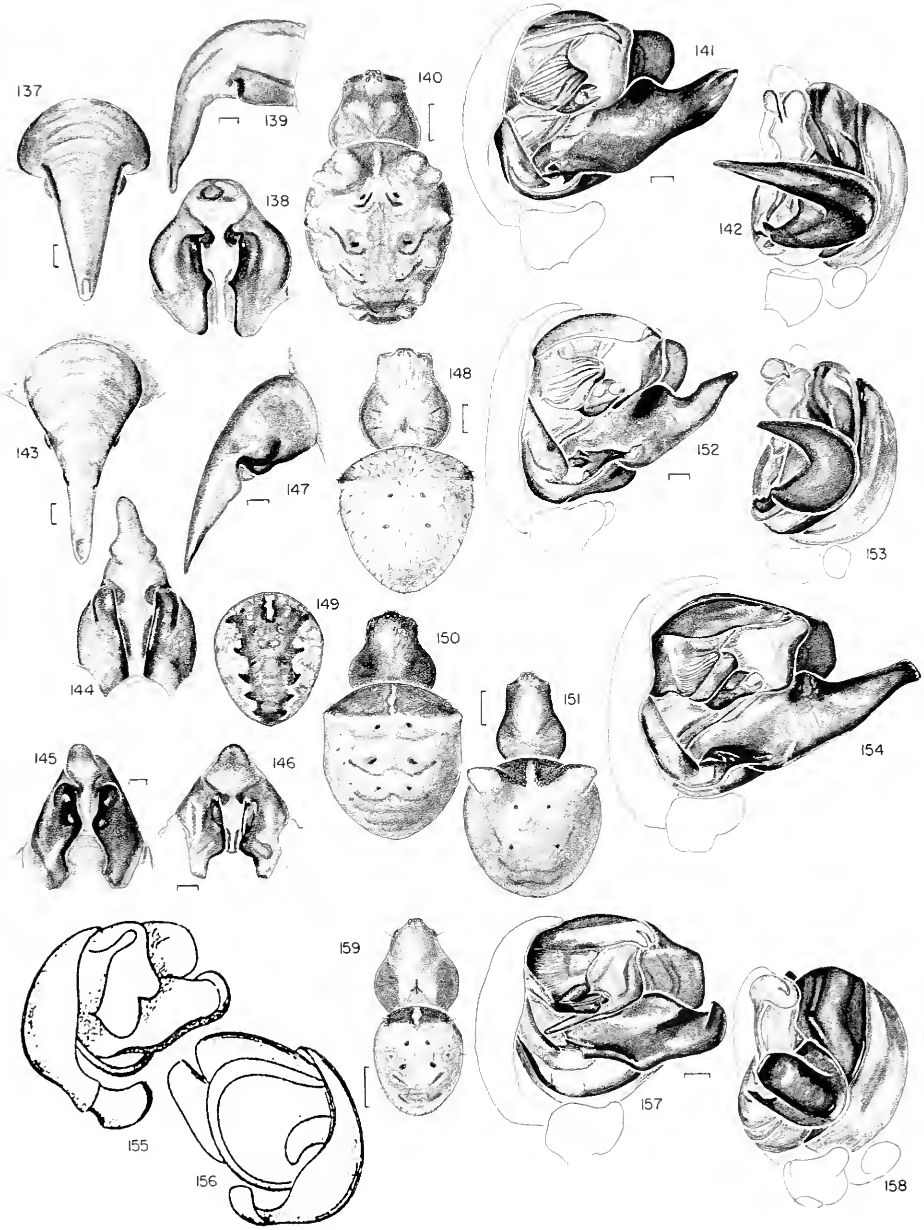
Parawixia mastophoroides Mello-Leitão, 1942: 402, figs. 23, 24, ♀. Female holotype from Quimilí, Santiago del Estero Prov., Argentina, in MLP, examined. Brignoli, 1983: 279.

Description. Female specimen from Córdoba, Argentina. Carapace orange-brown with black band across cephalic region, and clypeus black. Chelicerae dark orange. Labium, endites orange. Sternum light orange with dusky around border. Coxae light orange; legs orange, contrastingly ringed with gray to black. Dorsum of abdomen black, white, and brown (Fig. 140); venter, with white pigment between epigynum and spinnerets. Posterior median eyes same diameter as anterior medians, laterals 0.7 diameter. Anterior median eyes 1.1 diameters apart, 2.5 diameters from laterals. Posterior median eyes 2 diameters apart, 3.5 diameters from laterals. Ocular quadrangle slightly wider behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Abdomen with five pairs of tubercles, the anterior lateral double (Fig. 140). Total length 6.6 mm. Carapace 3.2 mm long, 2.3 wide, 1.6 wide behind lateral eyes. First femur 2.9 mm, patella and tibia 3.4, metatarsus 2.1, tarsus 0.9. Second patella and tibia 3.2 mm, third 2.0, fourth 3.2.

Male specimen from La Rioja Prov., Argentina. Color darker and more contrasting than in female. Sides of thorax orange, cephalic area black. Sternum with white pigment, abdomen with white cardiac mark, and venter with a pair of indistinct white spots in front of spinnerets. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 0.6 diameter apart, less than 2 diameters from laterals. Posterior median eyes 0.8 diameter apart, about 3.5 diam-

⟶

Figures 137–142. *Ocrepeira mastophoroides* (Mello-Leitão). 137–140, female. 137–139, epigynum. 137, ventral. 138, posterior. 139, lateral. 140, dorsal. 141, 142, left male palpus.



Figures 143–154. *O. venustula* (Keyserling). 143–151, females. 143–147, epigynum. 143, ventral. 144–146, posterior. 147, lateral. 148, 150, 151, dorsal. 149, abdomen, dorsal. 152–154, palpus. 143, 144, 147, 148, 152, 153, (Minas Gerais State, Brazil). 150, (Rio Grande do Sul State, Brazil). 146, 151, (Santa Catarina State, Brazil). 145, 149, 154 (Cautin Prov., Chile).

Figures 155, 156. *O. verecunda* (Keyserling), male palpus (from Keyserling, 1892).

Figures 157–159. *O. redondo* n. sp., male. 157, 158, palpus. 159, dorsal.

Scale lines. 1.0 mm, genitalia 0.1 mm.

eters from laterals. Ocular quadrangle square. Height of clypeus equals to 1.5 diameters of anterior median eyes. Third and fourth coxae with a macroseta. Fourth trochanter with one macroseta. Abdomen with tubercles as in female. Total length 5.6 mm. Carapace 2.9 mm long, 2.4 wide, 1.3 wide behind lateral eyes. First femur 3.1 mm, patella and tibia 3.6, metatarsus 2.1, tarsus 0.9. Second patella and tibia 3.1 mm, third 2.1, fourth 3.0.

Note. Males and females were matched by the shape of their abdomen.

In the Paris museum is an immature individual marked "*Ar. bergi* Simon" from Uruguay (MNHN No. 5490), a nomen nudum, a name never published.

Variation. The holotype is much larger than the specimens described here. Total length of the female 10.0 mm, carapace 4.0 mm long, 3.0 wide and first patella and tibia 4.0 mm. The illustrations were made from a female from Córdoba Prov. and from a male from La Rioja Prov., Argentina.

Diagnosis. Both males and females can be separated from all other South American species by tubercles around the abdomen (Fig. 140). The female is distinguished by the shape of the posterior median plate of the epigynum (Fig. 138) and the male by the long projecting median apophysis of the palpus (Fig. 142).

Specimens Examined. ARGENTINA *La Rioja:* Pozo de Piedra, 6 km E Chepes, 7 Jan. 1980, 2♂ (R. E. Woodruff, L. A. Stange, FSCA). *Entre Ríos*: Concepción del Uruguay, 4 Jan. 1941, ♀ (R. F. Prosen, MLP). *Córdoba:* Calamuchita, Dec. 1941, ♀ (J. M. Viana, MACN).

Ocrepeira venustula (Keyserling), new combination
Figures 29–33, 143–154; Map 5

Epeira venustula Keyserling, 1880: 308, pl. 4, fig. 11, ♀. Female holotype from Nova Friburgo [Rio de Janeiro State], Brazil, in the L. Koch collection, lost.
Aranea venustula:—Roewer, 1942: 856.
Araneus venustulus:—Bonnet, 1955: 628.

Note. The original specimen of *E. venustula* is lost. The measurements and description of Keyserling (1880) fit this common species best. However, three female, two male, and two immature specimens from Espírito Santo, Brazil, in BMNH, determined by Keyserling, and the subsequent description in Keyserling, 1892: 128, pl. 6, ♀ [?], ♂, appear to be those of *O. hirsuta* (Mello-Leitão).

Description. Female from Gonzaga, Minas Gerais, Brazil. Carapace orange with white setae on cephalic region, sides of thoracic region dusky. Chelicerae orange, distally darker. Labium, endites orange. Sternum orange with dusky marks. Coxae lighter orange; legs orange with dusky rings. Dorsum of abdomen orange with black setae, darker anterior to lateral tubercles with a light line between tubercles (Fig. 148); venter light dusky orange without marks. Posterior median eyes 0.6 diameter of anterior medians, laterals 0.5 diameter. Anterior median eyes 1.2 diameters apart. Posterior median eyes 1.2 diameters apart. Ocular quadrangle slightly narrower behind than in front. Height of clypeus equal to 1.2 diameters of anterior median eyes. Abdomen with a pair of anterior tubercles and many short setae, densest on tubercles (Fig. 148). Total length 8.5 mm. Carapace 3.8 mm long, 3.1 wide, 2.0 wide behind lateral eyes. First femur 3.2 mm, patella and tibia 4.2, metatarsus 2.8, tarsus 1.1. Second patella and tibia 3.9 mm, third 2.5, fourth 3.8.

Male from Vicosa, Minas Gerais, Brazil. Color as in female but cephalic region and sides of thoracic region darker orange than middle. Sternum orange underlain by white. Legs orange, distal articles with indistinct darker rings. Abdomen with white cardiac mark. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 1.1 diameters apart, 1.7 diameters from laterals. Posterior median eyes 1.5 diameters apart, 3.5 diameters from laterals. Ocular quadrangle slightly longer than wide and slightly narrower behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Third and fourth coxae with one macroseta. Third and fourth trochanters with one macroseta. Abdomen oval. Total length 5.2 mm. Carapace 3.1 mm long, 2.5 wide, 1.4 wide behind lateral eyes. First femur 2.7 mm, patella and tibia 3.6, metatarsus 2.0, tarsus 0.8. Second patella and tibia 3.0 mm, third 1.9, fourth 2.7.

Variation. Total length of females 6.9 to 10.8 mm, of males 5.2 to 7.2. A second male had a macroseta only on the third and fourth coxae and left fourth trochanter. Most females have a similar appearance (Fig. 148); however, a female from Santa Catarina State, Brazil, has the tubercles of the abdomen extended (Fig. 151). Some others have pointed tubercles on the abdomen and a dark folium (Figs. 146, 149 from Rio Grande do Sul). Perhaps they belong to different species. Figures 143, 144, 147, 148, 152, 153 were made from specimens from Minas Gerais State, Figures 146, 149 from Rio Grande do Sul, Figures 29–33, 145, 150, 154 from Araucaria Region, Chile.

Diagnosis. Unlike several related species the first pair of muscle scars of the abdomen are outside the anterior dark area (Figs. 148, 150, 151). The tip of the scape of the female epigynum has a slight depression (Fig. 143). There is considerable variation in the length of the scape of the epigynum.

Natural History. A female was collected in Itabapoana, Rio de Janeiro State, at night from an orb in a field (R. L. C. Baptista); in Chile specimens were collected by sweeping at dusk in a Valdivian rain forest.

Specimens Examined. BRAZIL. *Minas Gerais:* Belo Horizonte (AMNH); Carmo de Rio Clara (MNRJ); Gonzaga de Campos (MZSP); Lavras (MCZ); Minha Serinha Diamantina (AMNH); Viçosa (CUC, AMNH). *Mato Grosso do Sul:* Três Lagoas, (MZSP). *Rio de Janeiro:* Itatiaia (AMNH); Bom Jesus do Itabapoana (RLCB); Pinheiro (MNRJ). *São Paulo:* Castilho (MZSP); Emas (MZSP); Jaboticabal (MCZ, MCN); São Paulo (MZSP). *Santa Catarina:* Pinhal (AMNH). *Rio Grande do Sul:* Paso Fundo (MCN); Canela (MCN); Garruches, São Borja (MCN); Cerro Claro, São Pedro do Sul (MCN); Cidreira (MCN); Chacara Aver, Bom Jesus (MCN); Machadinho (MCN) Parque Estadual de Nonoai (MCN); Sao Leopoldo (MZSP). URUGUAY *Durazno:* Ave. de Cordoba (MHNM). Paso de los Libres [?] (CAS). ARGENTINA *Misiones:* Eldorado (AMNH); Las Flores [?] (MACN). *Chaco:* Presidente Rogue Saenz Peña (MACN). *Salta:* NE Salta (MCZ). *La Pampa:* Santa Rosa, (MACN); Realicó (MACN). *Santa Fé:* Arrufó (MCZ). *Entre Ríos:* San Felicia [? Feliciano] (MACN). *Buenos Aires:* Buenos Aires (MACN); S Las Barrancas [La Barranca] (MACN); Punta Lara (MACN). *La Rioja:* La Rioja (MACN). *Neuquén:* Piedra del Aguila (ZMK); San Martín de los Andes, Quilquihué (ZMK). *Río Negro:* (MNRJ); El Bolsón (AMNH). CHILE *Coquimbo:* 32 km E La Serena (CAS); Combarbalá, Manquehua (MCZ); Hda. Illapel (IRSNB). *Valparaiso:* Papudo (MNRJ); Quintero (AMNH) Quillota (AMNH). *Metropolitana:* Aculeo, El Patagual (AMNH); El Canelo, Maipo Canyon (AMNH); Santiago (MCZ); Malleco (AMNH). *Maule:* Río Terio (AMNH). *Bío-Bío:* Angol (CAS); Fundo Pinares (MZSP). *Araucaria:* region de Araucaría (AMNH); 30 km NE Villarica (MCZ). *Los Lagos:* Llau-llau (USNM); Valley forest, 18 km W Purranque (CAS); Osorno (AMNH); Parque Nacional Puyehue, 4.1 km E Anticura (AMNH); Pucatrihue, coast (AMNH); Chiloé, 10 km N Castro (AMNH).

Ocrepeira verecunda (Keyserling), new combination

Figures 155, 156; Map 5

Epeira verecunda Keyserling, 1865: 824, pl. 19, figs. 14–16, ♂. Male holotype from New Granada [old name of Colombia], both palpi lost in BMNH, examined; 1892: 127, pl. 6, fig. 94, ♂.

Aranea verecunda:—Roewer, 1942: 856.

Araneus verecundus:—Bonnet, 1955: 628.

Note. The male holotype lost both palpi. No other specimen was found that matches Keyserling's illustrations (Figs. 155, 156).

Description. Male holotype. Carapace orange. Sternum, legs light orange. Abdomen orange-white with a white cardiac mark; venter with a white pigment square between genital groove and spinnerets. Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes 1.5 diameters apart. Posterior median eyes 1.5 diameters apart. Ocular quadrangle slightly narrower behind than in front. Height of clypeus equal to 1.3 diameters of anterior median eyes. Third, fourth coxae each with one macroseta, both on small tubercles. Fourth trochanter with one macroseta. Abdomen with a pair of distinct dorsal, pointed tubercles. Total length 4.8 mm. Carapace 2.5 mm long, 2.1 wide, 1.2 wide behind lateral eyes. First femur 2.5 mm, patella and tibia 2.9, metatarsus 1.6, tarsus 0.8. Second patella and tibia 2.5 mm, third 1.5, fourth 2.1.

Ocrepeira redondo new species
Figures 157–159; Map 5

Holotype. Male holotype from Monteredondo, 1,200 m, Depto. Cundinamarca, Colombia, 25 Feb. 1975 (P. A. Schneble), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Male holotype. Carapace orange, sides of thoracic region dark dusky. Sternum, coxae orange. Legs dark orange, distal articles of third and fourth with indistinct darker rings. Dorsum of abdomen dusky, with white cardiac mark (Fig. 159); venter dusky without marks. Posterior median eyes same diameter as anterior medians, laterals 0.6 diameter. Anterior median eyes their diameter apart, 1.8 diameters from laterals. Posterior median eyes 1.2 diameters apart, slightly more than 2 diameters from laterals. Ocular quadrangle square. Height of clypeus equal to 1.1 diameters of anterior median eyes. Third and fourth coxae with one macroseta. Fourth trochanter with one macroseta. Total length 4.5 mm. Carapace 2.7 mm long, 2.3 wide, 1.2 wide behind lateral eyes. First femur 2.7 mm, patella and tibia 3.2, metatarsus, tarsus lost. Second patella and tibia 2.7 mm, third 1.7, fourth 2.3.

Variation. Total length of males 4.5 to 5.0 mm. The illustrations were made from the holotype.

Diagnosis. The soft terminal apophysis hangs over the conductor. The shape of the median apophysis is diagnostic (Figs. 157, 158).

Natural History. The specimen from Sierra Nevada de Santa Marta was beaten from dry banana leaves on a plantation.

Specimens Examined. COLOMBIA *Magdalena:* San Sebastian de Rabago, Sierra Nevada de Santa Marta, 2,000 m, 11–14 May 1968, ♂ (B. Malkin, AMNH).

Ocrepeira lurida (Mello-Leitão), new combination
Figures 160–166; Map 5

Wixia lurida Mello-Leitão, 1943: 106, fig. 6, ♀. Female holotype from Alta Gracia, Córdoba Prov., Argentina, in MLP, examined. Brignoli, 1983: 281.

Description. Female from Calamuchita, Córdoba Prov., Argentina. Carapace orange, eye area and clypeus dusky. Chelicerae, labium, endites orange. Sternum orange. Coxae yellowish; legs orange with black rings. Dorsum of abdomen white, dusky and with brownish black transverse bars (Fig. 163); venter dusky with a pair

⟶

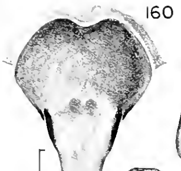
Figures 160–166. *Ocrepeira lurida* (Mello-Leitão). 160–164, female. 160–162, epigynum. 160, ventral. 161, posterior. 162, lateral. 163, dorsal. 164, abdomen, ventral. 165, 166, left male palpus.

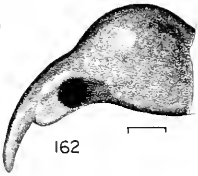
Figures 167–173. *O. willisi* n. sp. 167–171, female. 167–169, epigynum. 167, ventral. 168, posterior. 169, lateral. 170, dorsal. 171, abdomen, ventral. 172, 173, male palpus.

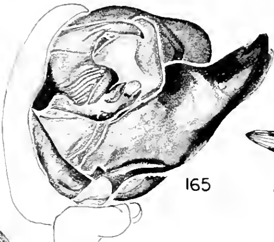
Figures 174–179. *O. tumida* (Keyserling). 174–177, female. 174–176, epigynum. 174, ventral. 175, posterior. 176, lateral. 177, dorsal. 178, 179, male palpus.

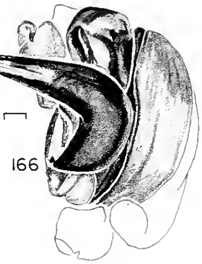
Figures 180–185. *O. malleri* n. sp. 180–183, female. 180–182, epigynum. 180, ventral. 181, posterior. 182, lateral. 183, dorsal. 184, 185, male palpus.

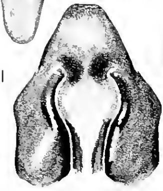
Scale lines. 1.0 mm, genitalia 0.1 mm.

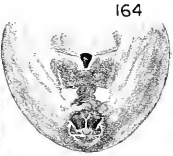

160

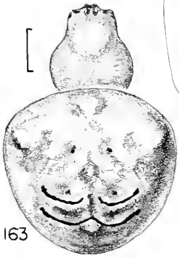

162

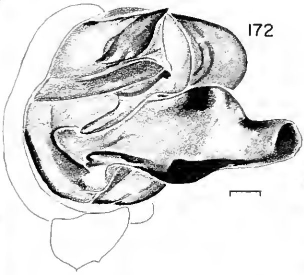

165

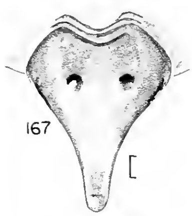

166

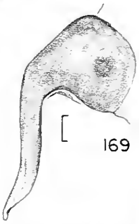

161

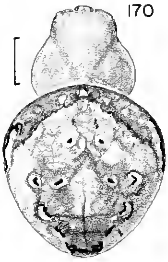

164


163

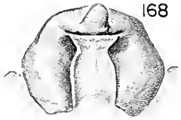

172


167

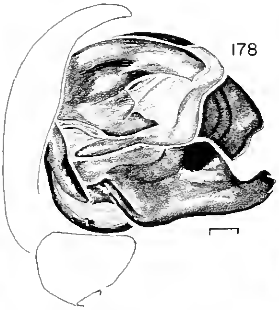

169

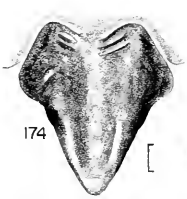

170


173


168

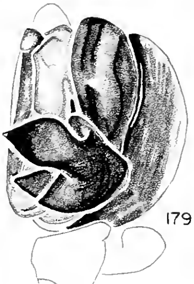

171

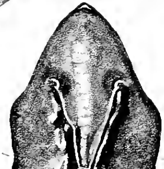

178

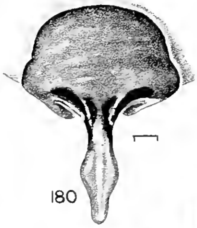

174

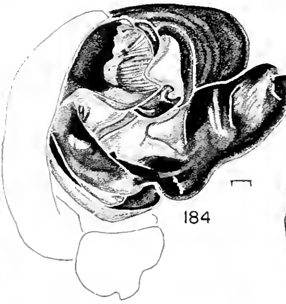

176

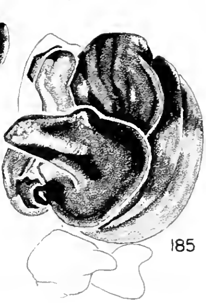

177

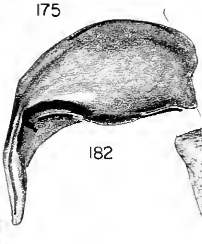

179

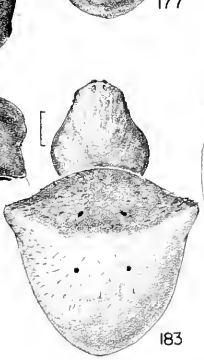

175

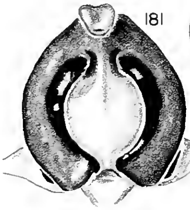

180


184


185


182


183


181

of white patches (Fig. 164). Posterior median eyes 1.2 diameters of anterior medians, laterals 0.8 diameter. Anterior median eyes their diameter apart. Posterior median eyes 1.2 diameters apart. Ocular quadrangle wider behind than in front. Height of clypeus equal to 1.2 diameters of anterior median eyes. Abdomen subspherical with a pair of humps (Fig. 163). Total length 6.0 mm. Carapace 2.5 mm long, 2.2 wide, 1.2 wide behind lateral eyes. First femur 2.7 mm, patella and tibia 2.9, metatarsus 2.6, tarsus 0.7. Second patella and tibia 2.8 mm, third 1.8, fourth 2.7.

Male from Calamuchita, Córdoba Prov., Argentina. Color as in female except venter of abdomen lighter than that of female. Posterior median eyes same diameter as anterior medians, laterals 0.6 diameter. Anterior median eyes their diameter apart. Posterior median eyes 1.3 diameters apart. Ocular quadrangle square. Height of clypeus equal to 1.2 diameters of the anterior median eyes. Third, fourth coxae each with a macroseta. Fourth trochanter with one macroseta. First, second, and fourth femurs with a ventral row of macrosetae. Second tibia thicker than first, swollen with prolateral macrosetae. Total length 5.0 mm. Carapace 2.7 mm long, 2.2 wide, 1.4 wide behind lateral eyes. First femur 2.9 mm, patella and tibia 3.5, metatarsus 1.9, tarsus 0.8. Second patella and tibia 3.0 mm, third 1.8, fourth 2.8.

Note. Two males were collected with females.

Variation. Total length of females 4.9 to 6.9 mm, of males 5.0 to 5.1. The illustrations were made from specimens of the Córdoba Prov., Argentina.

Diagnosis. The two dark spots on the flat scape of the epigynum (Fig. 160) and the vase-shaped posterior median plate (Fig. 161) separate females from *O. venustula*. The male has the terminal apophysis hanging over the conductor as in *venustula*, but is smaller and has a differently shaped median apophysis (Figs. 165, 166).

Natural History. A female was collected in Yungas forest in Argentina.

Specimens Examined. BOLIVIA *Santa Cruz:* Comarapa, 1,800 m, 14 Dec. 1984, 2♀ (L. Peña, AMNH). *Chuquisaca:* E Monteagudo, 1,600 m, 21–24 Dec. 1984, 4♀, ♂ (L. Peña, AMNH). ARGENTINA *Salta:* El Rey National Park, Pozo Verde Trail, 950 m, 10–13 Dec. 1987, ♀ (S., J. Peck, AMNH). *Córdoba:* Alta Gracia, Feb. 1934, ♀ (C. Bruch, MACN); Calamuchita, Dec. 1940, ♀, Dec. 1941, 6♀, ♂, 2 imm. (J. M. Viana, MACN). *Buenos Aires:* Sierra de la Ventana, Mar. 1939, ♀, 2♂, 3 imm. (H. Bario, MACN).

Ocrepeira willisi new species
Figures 167–173; Map 4

Holotype. Female holotype from El Volcán, Chiriquí Prov., Panama, 20 Mar. 1936 (W. J. Gertsch), in AMNH. The species is named after the collector.

Description. Female holotype. Carapace orange with light setae, cephalic region slightly darker. Clypeus dusky on each side. Chelicerae, labium, endites orange. Sternum orange, borders dark. Coxae, legs orange with darker rings. Dorsum of abdomen white and gray spotted, with dark folium and transverse bars posteriorly (Fig. 170); venter with a pair of white spots (Fig. 171). Posterior median eyes 1.1 diameters of anterior medians, anterior laterals 0.6 diameter, posterior laterals 0.8. Anterior median eyes 1.2 diameters apart. Posterior median eyes 2 diameters apart. Ocular quadrangle slightly wider behind than in front. Height of clypeus equal to 1.5 diameters of anterior median eyes. Abdomen with indistinct tubercles (Fig. 170). Total length 5.7 mm. Carapace 2.4 mm long, 2.2 wide, 1.5 wide behind lateral eyes. First femur 2.3 mm, patella and tibia 2.9, metatarsus 2.0, tarsus 0.8. Second patella and tibia 2.7 mm, third 1.6, fourth 2.5.

Male from type locality. Color as in female, except for some white pigment underneath orange of carapace. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes slightly less than their diameter apart. Posterior median eyes 2 diameters apart. Ocular quadrangle slightly wider behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Third, fourth coxae each with one macroseta. Fourth trochanter with one macroseta. Total length 4.5 mm. Carapace 2.5 mm long, 2.1 wide, 1.1 wide behind lateral eyes. First femur 2.7 mm, patella and tibia 3.1, metatarsus 1.9, tarsus 0.9. Second patella and tibia 2.7 mm, third 1.6, fourth 2.3.

Note. Males and females were collected together.

Variation. Illustrations were made from the holotype and a male collected at the type locality.

Diagnosis. The female differs from that of *O. tumida* and others by the relative "deep" position of the posterior median plate and the transverse pit behind the scape (Fig. 168). The male can be separated from the male of *O. tumida* by the shape of the median and terminal apophyses (Figs. 172, 173).

Specimens Examined. PANAMA *Chiriquí:* El Volcán, 25 Feb. 1936, 2♀, ♂, paratypes (W. J. Gertsch, AMNH). *Panamá:* Barro Colorado Isl., Lago Gatún, 12 Feb. 1936, ♀ (W. J. Gertsch, AMNH).

Ocrepeira tumida (Keyserling), new combination
Figures 174–179; Map 5

Epeira tumida Keyserling, 1865: 808, pl. 18, fig. 18, figs. 6–8, ♀. Female lectotype here designated, and one paralectotype (belonging to another species) from New Granada [old name for Colombia], in BMNH no. 1890.7.1.4675, examined; (not *Acrosoma tumida* Taczanowski, which has been placed in *Araneus* by later authors).

Wixia tumida:—Keyserling, 1892: 48, pl. 2, fig. 39, ♀. Roewer, 1942: 882. Bonnet, 1959: 4830.

Description. Female specimen from Ecuador. Carapace dark brown with long white setae. Chelicerae dark brown. Labium brown. Endites, sternum, coxae orange-brown; legs dark brown. Dorsum of abdomen light with some tiny dark dots, anterior dark (Fig. 177); venter black without marks. Posterior median eyes 1.3 diameters of anterior medians, laterals 0.8 diameter. Anterior median eyes 1.1 diameters apart. Posterior median eyes 1.4 diameters apart. Ocular quadrangle wider behind than in front. Posterior median eyes on a swelling. Height of clypeus equal to 1.2 diameters of anterior median eye. Abdomen with a pair of humps facing anteriorly (Fig. 177). Total length 6.8 mm. Carapace 3.1 mm long, 2.4 wide, 1.8 wide behind lateral eyes. First femur 2.7 mm, patella and tibia 3.4, metatarsus 2.1, tarsus 0.8. Second patella and tibia 3.4 mm, third 2.1, fourth 2.9.

Male from Ecuador in poorly preserved condition. Carapace dark orange, sternum underlain by white pigment, legs ringed. Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes 0.8 diameter apart. Posterior median eyes 1.3 diameters apart. Ocular quadrangle wider behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Third, fourth coxae each with one macroseta. Fourth trochanter with one macroseta. Abdomen with humps facing anteriorly. Total length 4.5 mm. Carapace 2.7 mm long, 2.1 wide, 1.3 wide behind lateral eyes. First femur 2.5 mm, patella and tibia 3.0, metatarsus 1.8, tarsus 0.7. Second patella and tibia 2.7 mm, third 1.8, fourth 2.5.

Note. A male and a female were collected together and both have the forward-facing abdominal humps.

Variation. The lectotype has similar measurements to the specimen described. It differs in coloration: the anterior of the abdomen is brown bordered by white, and the transverse line between the tubercles is broken by a light cardiac mark. Behind the line most of the abdomen is light with a rectangular gray mark. The venter of the abdomen has a white square between epigynum and spinnerets. The humps are farther apart than the illustrated specimen (Fig. 177) and face laterally. The epigynum differs in ventral view by having less of a groove on the scape, and a greater depression anteriorly on the base. In posterior view, the median plate is slightly narrower, the laterals are wider, and the scape has no ridge ventrally; it is flat. Figures 174 to 179 were made from specimens from Ecuador.

Diagnosis. Both the holotype and the specimen described have the first and second patella-tibia of equal length. The epigynum has a longitudinal groove in ventral view (Fig. 174) and the median plate has a keel in posterior view (Fig. 175). The prong of the median apophysis, unlike that of other males, is wide just below its tip and slightly flattened (Figs. 178, 179).

Specimens Examined. ECUADOR *Tungurahua:* Baños, Falls of Agoyan, 1,500 m, 12 May 1939, ♀, 2♂ (W. Clarke-Macintyre, AMNH).

Ocrepeira malleri new species
Figures 180–185; Map 5

Holotype. Female holotype from Pinhal, Santa Catarina State, Brazil, Dec. 1947 (A. Maller), in AMNH. The species is named after the collector.

Description. Female holotype. Carapace orange-brown with white and dark setae. Chelicerae, labium, endites dark orange. Sternum, coxae dark orange; legs orange-brown. Dorsum of abdomen light gray, anterior black between tubercles, dark area includes anterior pair of muscle scars (Fig. 183); venter dusky orange-gray, without marks. Posterior median eyes 1.1 diameters of anterior medians, laterals 0.7 diameter. Anterior median eyes 1.2 diameters apart. Posterior median eyes 2 diameters apart. Laterals almost their diameter apart. Ocular quadrangle very slightly wider behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Abdomen as in Figure 183. Total length 8.8 mm. Carapace 3.9 mm long, 3.3 wide, 1.8 wide behind lateral eyes. First femur 3.5 mm, patella and tibia 4.2, metatarsus 2.7, tarsus 1.1. Second patella and tibia 3.9 mm, third 2.4, fourth 3.5.

Male from Pinhal, Santa Catarina, Brazil. Color as in female but sternum underlain by white; anterior dark area of abdomen divided by white cardiac mark and does not include anterior muscle scars. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes their diameter apart, 1.7 diameters from laterals. Posterior median eyes 1.5 diameters apart, 3 diameters from laterals. Ocular quadrangle slightly narrower behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Third and fourth coxae with one macroseta. Third and fourth trochanters with one macroseta. Total length 7.0 mm. Carapace 3.7 mm long, 3.1 wide, 1.4 wide behind lateral eyes. First femur 3.8 mm, patella and tibia 4.2, metatarsus 2.6, tarsus 1.0. Second patella and tibia 3.4 mm, third 2.3, fourth 3.2.

Note. Males and females were matched because they were collected at the same locality and both lack ventral markings.

Variation. The scape of the epigynum of two females is broken off leaving a short pointed stump. Total length of females 8.8 to 9.0 mm, of males 5.7 to 9.0. Illustrations were made from the female holotype and a male from the type locality.

Diagnosis. Of all females in which the anterior abdominal dark area includes the first muscle scars, *O. malleri* is distinguished by the distinct shape of the scape, which is widened above its tip (Fig. 180) and the circular posterior median plate (Fig. 181). Males can be separated from others by the short terminal apophysis and the shape of the median apophysis (Figs. 184, 185), which shows a slight hump on its "upper" face (Fig. 185).

Specimens Examined. BRAZIL *Rio de Janeiro:* Petrópolis, Dec. 1945, 850 m, ♀ (H. Sick, AMNH). *Paraná:* Rio Negro, ♂ (MNRJ); Rôlandia, ♂ (A. Maller, AMNH). *Santa Catarina:* Pinhal, Dec. 1947, 2♀, Jan. 1948, 6♀, ♂ paratypes (all A. Maller, AMNH).

Ocrepeira galianoae new species
Figures 186–191; Map 5

Holotype. Female holotype from General Belgrano, Misiones Prov., Argentina, Dec. 1972 (M. E. Galiano), in MACN no. 8915. The species is named after colleague M. E. Galiano, the collector.

Description. Female holotype. Carapace orange-brown with hair-like setae. Chelicerae orange, distally darker. Labium, endites brown. Sternum brown with median light line. Coxae light orange; legs orange-brown, distal articles with indistinct darker ring. Dorsum of abdomen grayish orange-brown, darker anterior to a line between tubercles, dark area including first pair of muscle scars (Fig. 189); venter dusky orange-brown. Posterior median eyes same diameter as anterior medians, laterals 0.5 diameter. Anterior median eyes their diameter apart. Posterior median eyes 1.8 diameters apart. Ocular quadrangle square. Height of clypeus equal to 1 diameter of anterior median eyes. Leg 2 longer than 4. Abdomen as in Figure 189. Total length 8.5 mm. Carapace 3.5 mm long, 2.9 wide, 1.7 wide behind lateral eyes. First femur 3.5 mm, patella and tibia 4.1, metatarsus 2.7, tarsus 0.9. Second patella and tibia 3.9 mm, third 2.5, fourth 3.6.

Male from Vacaria, Rio Grande do Sul, Brazil. Color as in female, except for white pigment spots under sternum and a white cardiac mark dividing dark area of abdomen; dark area not covering anterior muscle scars. Posterior median eyes 0.9 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 1.1 diameters apart, 2 diameters from laterals. Posterior median eyes 1.2 diameters apart, 2.5 diameters from laterals. Ocular quadrangle slightly narrower behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Third and fourth coxae each with one macroseta. Fourth trochanter with one macroseta. Total length 6.0 mm. Carapace 3.2 mm long, 2.7 wide, 1.3 wide behind lateral eyes. First femur 3.1 mm, patella and tibia 3.8, metatarsus 2.1, tarsus 0.8. Second patella and tibia 3.0 mm, third 2.1, fourth 2.8.

Note. Males and females were collected together. Both sexes have an indistinct pair of white, ventral patches.

Variation. Total length of females 6.3 to 10.2 mm, of males 5.6 to 7.3. The scape of the epigynum is of variable length. Some specimens have a pair of indistinct, ventral white patches. Figures 186–189 were made from the holotype; Figures 190, 191 were made from a male from Vacaria, Rio Grande do Sul.

Diagnosis. The base of the female epigynum, unlike that of *O. fiebrigi* and *O. gima*, is longer than wide in posterior view (Fig. 187); the male differs from others by the long, pointed terminal apophysis and the shape of the median apophysis, which has a tubercle on the "upper" face below the tip of the prong (Figs. 190, 191).

Natural History. A female was collected in an orb web at night, 2 m above the ground on a tree in Paraná State, Brazil.

Specimens Examined. BRAZIL *São Paulo:* Boracéia, 5 Feb. 1960, ♀ (F. Lane, MZSP 3860); Fazenda Intervales, 15 km E Guapiara, 700 m, Feb. 1990, 2♀ (W. Eberhard, MCZ). *Paraná:* Curitiba, 5 Feb. 1988, ♀ (R. C. L. Baptista, MZSP 13170); Rio Negro, ♂ (MNRJ). *Santa Catarina:* Pinhal, Dec. 1947, 2♀, Jan. 1948, ♀; May 1948, ♀; Dec. 1948, 2♀, ♂ (A. Maller, AMNH). *Rio Grande do Sul:* Parque Estadual de Nonoai, Nonoai, 14 Jan. 1985, 3♀ (A. A. Lise, MCN 12811); Pelotas, 2 Mar. 1964, ♀, ♂ (C. M. Biezanko, MCZ); Machadinho, 8–14 Feb. 1989, ♀ (A. B. Bonaldo, MCN 18191); Sobradinho, 10 Jan. 1985, 5♀, 4♂ (A. A. Lise, MCN 12889); Canela, 26 Dec. 1974, 4♀, ♂, imm. (A. A. Lise, MCN 02445); Santa Maria, 2 Nov. 1985, 6♀, 2♂ (A. D. Brescovit, MCN 14592, 14593); São Francisco de Paula, 4♀ (MNRJ); Vacaria, 14 Jan. 1974, ♂ (A. A. Lise, MCN 00309a). ARGENTINA *Misiones:* Cataratas de Iguazú, 5 Sept. 1963, ♂ paratype (M. E. Galiano, MEG); General Belgrano, Dec. 1972, ♂ paratype (M. E. Galiano, MEG). *Corrientes:* Colón, Dec. 1975, ♂ (M. E. Galiano, MEG). *Buenos Aires:* Boulogne, Oct. 1938, ♀ (R. F. Prosen, MLP); Glew, 1969, ♀ (D. Carpintero, MACN). *Neuquén:* Parque Nacional Lanin, Pucará, Feb. 1963, ♀ (S. Schajovskoy, MACN).

Ocrepeira fiebrigi (Dahl), new combination
Figures 192–199; Map 5

Aranea fiebrigi Dahl, 1906: 735. Syntypes: two females, eight males, two immatures from Paraguay [no locality], in ZMB, examined. Roewer, 1942: 842.
Araneus fiebrigi:—Bonnet, 1955: 502.

Description. Female syntype. Carapace orange. Chelicerae, labium, endites orange. Sternum orange. Coxae orange; legs light orange, with indistinct darker rings. Dorsum of abdomen brownish, anterior darker and covering anterior pair of muscle scars as in Figure 189; venter with pair of white patches (Fig. 197). Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Ocular quadrangle square. Height of clypeus equal to 1 diameter of anterior median eyes. Abdomen as in Figure 197. Total length 9.7 mm. Carapace 4.7 mm long, 4.0 wide, 2.7 wide behind lateral eyes. First femur 4.0 mm, patella and tibia 5.2, metatarsus 3.1, tarsus 1.1. Second patella and tibia 4.9 mm, third 3.2, fourth 4.7.

Male syntype. Color as in female but with white cardiac mark on abdomen. Posterior median eyes same diameter as anterior medians, laterals 0.6 diameter. Anterior median eyes 0.6 diameter apart. Posterior median eyes their diameter apart. Ocular quadrangle square. Height of clypeus equal to 1 diameter of anterior median eyes. First coxa with hook and small posterodorsal tubercle. Third and fourth coxae and trochanters each with one short macroseta. Abdomen oval. Total length 7.7 mm. Carapace 4.2 mm long, 3.3 wide, 1.5 wide behind lateral eyes. First femur 4.5 mm, patella and tibia 5.1, metatarsus 3.1, tarsus 1.1. Second patella and tibia 4.0 mm, third 2.9, fourth 3.9.

Note. Males and females were collected together.

Variation. Total length of females 8.0 to 10.1 mm, of males 6.7 to 8.2. Most females have the scape of the epigynum torn off (Figs. 194–196). The posterior median plate of the epigynum is longer in some individuals than in the one illustrated. Some males lack a macroseta on the third coxa. Description and figures were made from syntypes. However, the description of the ocular square, height of clypeus, and width of carapace behind lateral eyes was made from a female from São Paulo State and a male from Rio Grande do Sul State. Figures 191, 192, 193 were made from a female from Paraguay.

Diagnosis. Only *O. gima* also has a laterally flattened epigynal scape. *Ocrepeira fiebrigi* can be separated from *O. gima* by the trapezoid shape of the posterior median plate (Fig. 195). The male can be separated from others by the sclerotized conductor, the short terminal apophysis, and a keel on the "upper" face of the prong of the median apophysis (Figs. 198, 199).

Natural History. Specimens were collected as they hung from a thread at night, another specimen was in an orb web in Chaco Dept., Paraguay.

Specimens Examined. BRAZIL *Pará:* Belém, ♀ (C. F. Baker, MCZ). *Goias:* Jataí, Fazenda Cachoeirinha, ♀ (Exped. Dept Zool., MZSP 9560). *Mato Grosso:* Chapada dos Guimaraes, Nov. 1963, ♀ (M. Alvar-

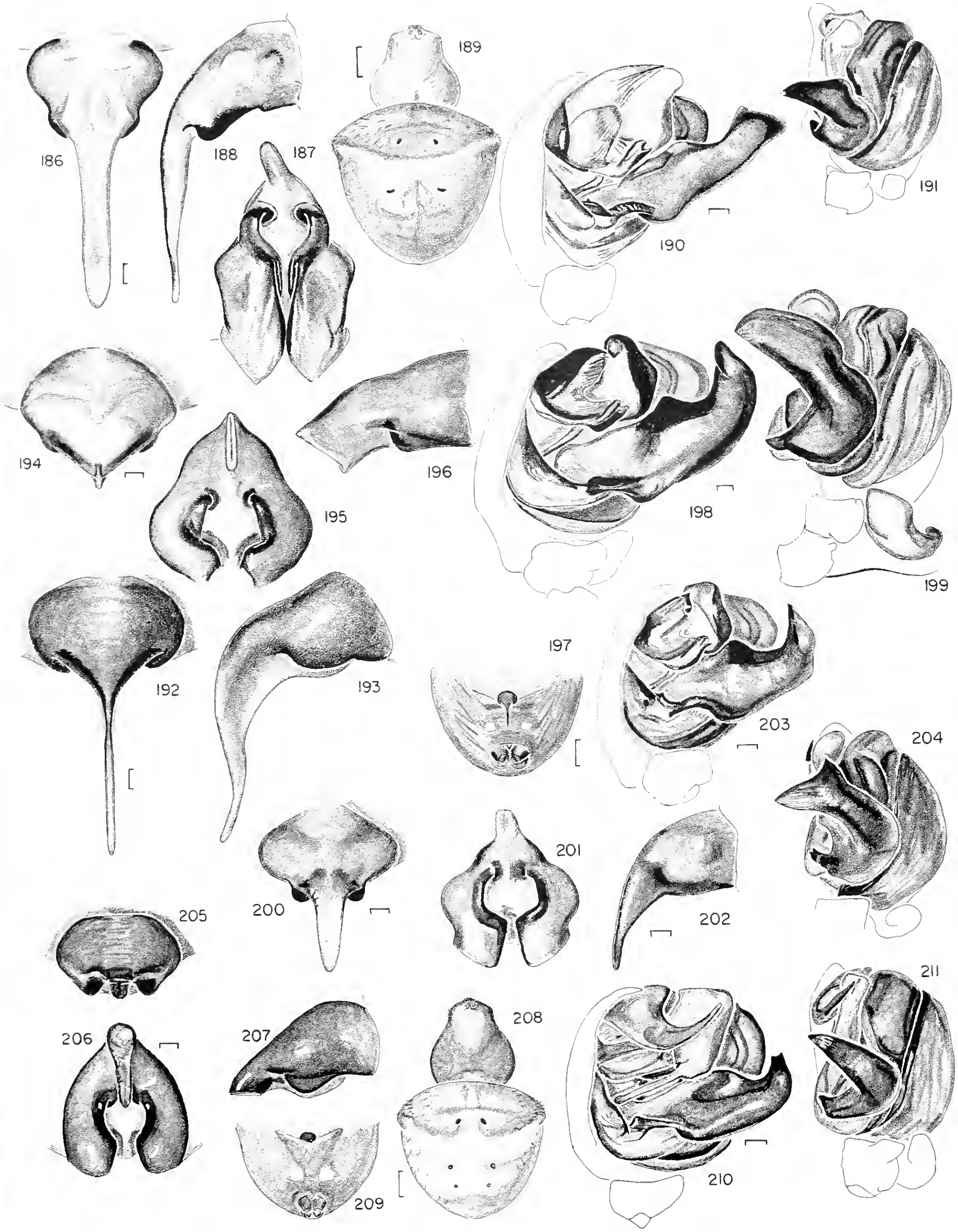
---

⟶

Figures 186–191. *Ocrepeira galianoae* n. sp. 186–189, female. 186–188, epigynum. 186, ventral. 187, posterior. 188, lateral. 189, dorsal. 190, 191, left male palpus.

Figures 192–199. *O. fiebrigi* (Dahl). 192–198, female. 192–196, epigynum. 192, 194, ventral. 195, posterior. 193, 196, lateral. 194–196, scape torn off. 197, abdomen, ventral. 198, 199, male palpus.

Figures 200–204. *O. molle* n. sp. 200–202, female epigynum. 200, ventral. 201, posterior. 202, lateral. 203, 204, male palpus.



Figures 205–211. *O. gima* n. sp. 205–209, female. 205–207, epigynum. 205, ventral. 206, posterior. 207, lateral. 208, dorsal. 209, abdomen, ventral. 210, 211, male palpus.

Scale lines. 1.0 mm, genitalia 0.1 mm.

enga, AMNH); Cuiabá, Nov. 1963, 2♀ (M. Alvarenga, AMNH). *São Paulo:* Estrada Santa Amaro, Engo. Marcilac, km 48, 15 Jan. 1961, ♀ (F. Werner, MZSP). *Rio Grande do Sul:* Garruchos, S Borja, 10 Dec. 1975, 6♀, 3♂, 11 imm. (A. A. Lise, MCN 3223). PARAGUAY *Chaco:* Parque Nacional Defensores del Chaco, Cerro León, 18–27 Nov. 1984, 3♀, 4♂ (J. A. Kochalka, IRNP).

Ocrepeira molle new species

Figures 200–204; Map 5

Holotype. Female holotype from Horco Molle, Tucumán Prov., Argentina, Nov. 1965 (A. Bachmann), in Galiano Coll., MACN no. 8916. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace orange, cephalic region dusky with white setae. Chelicerae, labium, endites dusky orange. Sternum dark orange with white pigment. Coxae light orange; legs dark orange with darker rings, more distinct ventrally. Dorsum of abdomen gray, the anterior dark area includes anterior muscle scars (as in Figure 189); venter with tiny white pigment spots, dusky between epigynum and spinnerets. Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes 1.3 diameters apart. Posterior median eyes 1.5 diameters apart. Ocular quadrangle very slightly wider behind than in front. The height of the clypeus equal to 1.2 diameters of anterior median eyes. Total length 8.2 mm. Carapace 3.5 mm long, 2.8 wide, 1.8 wide behind lateral eyes. First femur 3.2 mm, patella and tibia 3.8, metatarsus 2.7, tarsus 0.9. Second patella and tibia 3.6 mm, third 2.3, fourth 3.4.

Male from Argentina. Color as in female but dorsum of abdomen with a white cardiac mark dividing dark area and dark areas not covering anterior pair of muscle scars. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 0.8 diameter apart. Posterior median eyes 1.4 diameters apart. Ocular quadrangle wider behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Third, fourth coxae each with one macroseta. Fourth trochanter with one macroseta. Total length 5.0 mm. Carapace 2.7 mm long, 2.3 wide, 1.3 wide behind lateral eyes. First femur 2.8 mm, patella and tibia 3.3, metatarsus 1.8, tarsus 0.8. Second patella and tibia 2.6 mm, third 1.7, fourth 2.5.

Variation. Total length of females 8.2 to 8.5 mm. The illustrations were made from the holotype.

Diagnosis. In ventral view (Fig. 200), the epigynum can be confused with that of *O. hirsuta* (Fig. 119), in posterior view (Fig. 201) with that of *O. fiebrigi* (Fig. 195). In lateral view, the tip of the median apophysis has the silhouette resembling a mouse head (Fig. 204).

Natural History. Specimens were collected by sweeping in the Yungas forest in Argentina.

Specimens Examined. BOLIVIA *Santa Cruz:* Santa Rosa, N Mataral, 1,100 m, 14–15 Dec. 1984, 4♀, ♂ (L. Peña, AMNH). *Chuquisaca:* E Monteagudo, 1,600 m, 21–24 Dec. 1984, 2♀, 2♂ (L. Peña, AMNH). ARGENTINA *Salta:* El Rey National Park, Pozo Verde Trail, 950 m, 10–13 Dec. 1987, 3♂ (S., J. Peck, AMNH).

Ocrepeira gima new species

Figures 205–211; Map 5

Holotype. Female holotype, male paratype from Chapada dos Guimarães, Mato Grosso State, Brazil, Nov. 1963 (M. Alvarenga), in AMNH. The specific name is an arbitrary combination of letters.

Description. Female holotype. Carapace orange with many short white setae. Chelicerae, labium, endites orange. Sternum orange with some darker streaks. Coxae, legs orange. Anterior of dorsum of abdomen dark, dark area enclosing first pair of muscle scars, posterior with faint transverse bands (Fig. 208); venter gray with a pair of white patches (Fig. 209). Posterior median eyes same diameter as anterior medians, laterals 0.7 diameter. Anterior median eyes 0.9 diameter apart. Posterior median eyes 1.3 diameters apart. Ocular quadrangle slightly wider than long, wider behind than in front. Height of clypeus equal to 1.3 diameters of anterior median eyes. Posterior median eyes on swelling. Abdomen as in Figure 208. Total length 9.5 mm. Carapace 4.0 mm long, 3.4 wide, 1.8 wide behind lateral eyes. First femur 3.9 mm, patella and tibia 4.6, metatarsus 2.9, tarsus 1.1. Second patella and tibia 4.3 mm, third 2.8, fourth 4.1.

Male paratype. Color as in female, but with white pigment under orange sternum, legs with dark rings, and anterior dark area of abdomen between tubercles not enclosing anterior muscle scars. Posterior median eyes 0.9 diameter of anterior medians, laterals 0.5 diameter. Anterior median eyes 0.8 diameter apart. Posterior median eyes 1.4 diameters apart. Ocular quadrangle slightly longer than wide, narrower behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Third, fourth coxae each with one macroseta. Third and fourth trochanters each with one macroseta. Total length 5.2 mm. Carapace 2.9 mm long, 2.4 wide, 1.2 wide behind lateral eyes. First femur 3.1 mm, patella and tibia 3.2, metatarsus 2.0, tarsus 0.8. Second patella and tibia 2.9 mm, third 2.0, fourth 2.7.

Note. Males and females were collected at the same locality.

Variation. Total length of females 9.5 to 10.5 mm. Illustrations were made from the holotype and the paratype from the type locality.

Diagnosis. This species resembles *O. lurida* (Figs. 160–166) and is distinguished from it by the laterally flattened scape (or scar of the torn scape), and by the curved shape of the terminal apophysis of the palpus (Fig. 210).

Specimens Examined. BRAZIL *Mato Grosso:* Rio Xingu, Pôsto Jacaré, Nov. 1961, ♀ (M. Alvarenga, F. Werner, AMNH); Jaciara, Nov. 1963, ♀ (M. Alvarenga, AMNH).

Ocrepeira pinhal new species
Figures 212–215; Map 5

Holotype. Female holotype from Pinhal, Santa Catarina State, Brazil, Dec. 1948 (A. Maller), in AMNH. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace orange-brown with dark and white hairs. Chelicerae orange-brown. Labium, endites brown. Sternum orange, darker on sides. Coxae orange with brown margins; legs dark orange with darker rings. Dorsum of abdomen white to brown with two black transverse bars posteriorly (Fig. 215); venter dusky. Posterior median eyes same diameter as anterior medians, laterals 0.7 diameter. Anterior median eyes 1 diameter apart. Posterior median eyes 2 diameters apart. Ocular quadrangle wider behind than in front. Height of clypeus equal to 1.2 diameters of anterior median eyes. Abdomen oval with two round humps facing anteriorly (Fig. 215). Total length 8.0 mm. Carapace 3.2 mm long, 2.7 wide, 1.7 wide behind lateral eyes. First femur 3.1 mm, patella and tibia 3.5, metatarsus 2.4, tarsus 0.9. Second patella and tibia 3.4 mm, third 2.1, fourth 3.2.

Variation. Total length of females 7.0 to 8.5 mm. The paratypes have a pair of white patches on the venter of the abdomen. The illustration was made from the holotype.

Diagnosis. The shape of the ventral face of the epigynum (Fig. 212) differs from that of other species and, unlike most others, the lateral plates touch in the midline in posterior view (Fig. 213).

Specimens Examined. BRAZIL *Santa Catarina:* Pinhal, Dec. 1947, 2♀, Jan. 1948 4♀, Dec. 1948–Jan. 1950, 2♀ paratypes (A. Maller, AMNH). *Rio Grande do Sul:* Garruchos, São Borja, 9 Dec. 1975, ♀ (A. A. Lise, MCN 3272).

Ocrepeira maltana new species
Figures 216–217; Map 6

Holotype. Male holotype and one male paratype from Machupicchu, above ruins, 2,600–2,800 m, Depto. Cuzco, Peru, 1–5 July 1964 (B. Malkin), in AMNH. The specific name is an arbitrary combination of letters.

Description. Male holotype. Carapace reddish brown. Chelicerae dark brown, distally lighter. Labium, endites brown. Sternum brown, posterior lighter. Coxae dark orange. Legs red-brown with black rings. Dorsum of abdomen with anterior dark area covering the first pair of muscle scars, posterior with dark folium (Fig. 217); venter black. Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Ocular quadrangle slightly narrower behind than in front. Height of clypeus equal to 1.1 diameters of anterior median eyes. Fourth coxa with one macroseta without tubercle. Total length 3.8 mm. Carapace 2.1 mm long, 1.6 wide, 0.9 wide behind lateral eyes. First femur 2.7 mm, patella and tibia 2.9, metatarsus 1.8, tarsus 0.7. Second patella and tibia 2.4 mm, third 1.3, fourth 1.7.

Diagnosis. Unlike that of other species of the genus, this male resembles that of *Alpaida* species by having the tip of the paramedian apophysis covered by the cymbium, by having the axis of the radix at an almost right angle to the margin of the cymbium, by the long curved embolus, and by the shape of the median apophysis (Fig. 216). Also the tooth on the endite is opposed by a tooth on the palpal trochanter. However, the coloration of the abdomen and the pointed tip of the paramedian apophysis, hidden by the cymbium, place this male in *Ocrepeira*.

Ocrepeira bispinosa (Mello-Leitão), new combination

Figures 218–223; Map 5

Carepalxis bispinosus Mello-Leitão, 1945: 173. Immature holotype and one smaller imm. paratype from Monjolinho, Corumbá, Goiás State, Brazil, in MZSP, examined. Brignoli, 1983: 264.

Wixia bicornuta Mello-Leitão, 1949: 19, fig. 11, imm. Immature holotype from confluence of Rio Culuene and Rio Xingu, Mato Grosso State, Brazil, in MNRJ, examined. Brignoli, 1983: 281. NEW SYNONYMY.

Synonymy. Since the types of both *C. bispinosus* and *W. bicornuta* are immature, the synonymy remains uncertain.

Description. Female from Santa Rita do Araguaia, Goiás, Brazil. Carapace orange, cephalic region darkest. Chelicerae orange with a dark patch. Labium, endites dark orange. Sternum orange. Coxae orange; legs orange with indistinct dark rings. Dorsum of abdomen with gray and black patches, no distinct marks (Fig. 221); venter dusky orange. Posterior median eyes same diameter as anterior medians, laterals 0.6 diameter. Anterior median eyes 0.9 diameter apart. Posterior median eyes 1.7 diameters apart. Ocular quadrangle wider than long, wider behind than in front. Height of clypeus equal to 1.2 diameters of anterior median eyes. Abdomen with a pair of pointed tubercles close together (Fig. 221). Total length 8.5 mm. Carapace 3.4 mm long, 3.1 wide, 2.0 wide behind lateral eyes. First femur 3.4 mm, patella and tibia 4.0, metatarsus 2.7, tarsus 0.9. Second patella and tibia 3.7 mm, third 2.5, fourth 3.4.

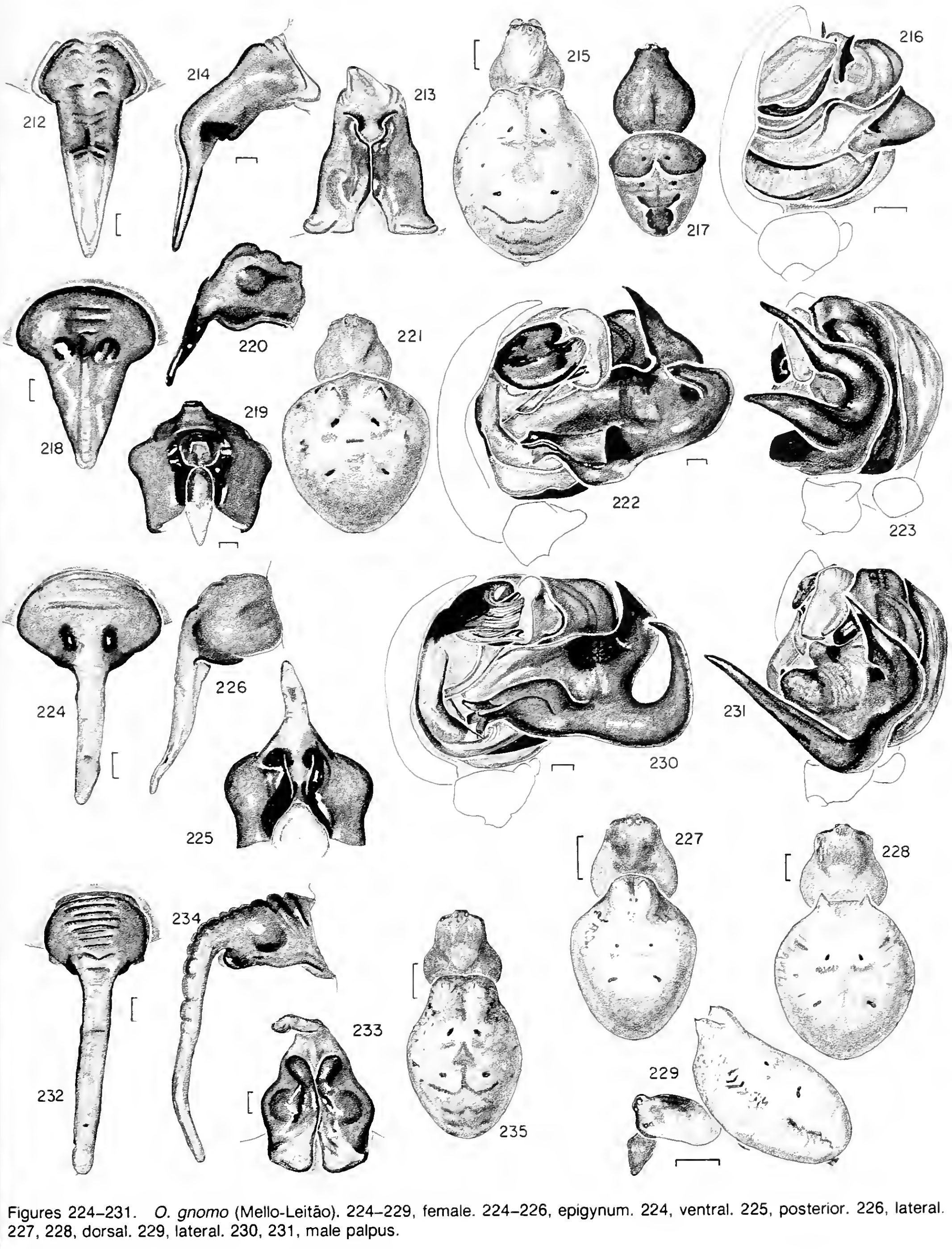
Male from Chapada dos Guimaraes, Mato Grosso, Brazil. Coloration as in female. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 0.9 diameter apart. Posterior median eyes 2 diameters apart on a swelling. Ocular quadrangle wider behind than in front. Height of clypeus equal to 1.4 diameters of anterior median eyes. Fourth coxa with one macroseta. Fourth trochanter with one macroseta. Abdomen with two anterior spine-shaped tubercles as in *O. gnomo*, each with a sclerotized cap. Total length 4.8 mm. Carapace 2.9 mm long, 2.9 wide, 1.5 wide behind lateral eyes. First femur 2.9 mm, patella and tibia 3.7, metatarsus 2.3, tarsus 1.1.

⟶

Figures 212–215. *Ocrepeira pinhal* n. sp., female. 212–214, epigynum. 212, ventral. 213, posterior. 214, lateral. 215, dorsal.

Figures 216–217. *O. maltana* n. sp., male. 216, left palpus. 217, dorsal.

Figures 218–223. *O. bispinosa* (Mello-Leitão). 218–221, female. 218–220, epigynum. 218, ventral. 219, posterior. 220, lateral. 221, dorsal. 222, 223, male palpus.



Figures 224–231. *O. gnomo* (Mello-Leitão). 224–229, female. 224–226, epigynum. 224, ventral. 225, posterior. 226, lateral. 227, 228, dorsal. 229, lateral. 230, 231, male palpus.

Figures 232–235. *O. lisei* n. sp., female. 232–234, epigynum. 232, ventral. 233, posterior. 234, lateral. 235, dorsal.

Scale lines. 1.0 mm, genitalia 0.1 mm.

Second patella and tibia 3.1 mm, third 2.0, fourth 2.7.

Note. Males and females were matched because they have similar-shaped tubercles with a sclerotized cap on the abdomen. The upper prong of the left median apophysis of the palpus is broken, and the outline was drawn from the mirror image of the right (Fig. 223).

Variation. Total length of males 4.8 to 5.7 mm. Figures were made from the only two adults available.

Diagnosis. Ocrepeira bispinosa has a wider scape (Fig. 218) than does *O. gnomo* (Fig. 224), and the median apophysis of the male palpus has a "vertical" keel in its widest portion (Fig. 222), absent in the male of *O. gnomo* (Fig. 230).

Specimens Examined. BRAZIL *Mato Grosso:* Chapada dos Guimarães, 18 Nov. 1983, ♂ (M. Hoffmann, MCN 11986). *Goiás:* Santa Rita do Araguaia, Dec. 1963, ♀ (M. Alvarenga, AMNH).

Ocrepeira gnomo (Mello-Leitão), new combination
Figures 224–231; Map 5

Wixia gnomo Mello-Leitão, 1943: 195, fig. 25, imm. Immature male holotype from Rio Grande do Sul, Brazil, in MNRJ, examined. Brignoli, 1983: 281.

Description. Female from Montenegro, Rio Grande do Sul, Brazil. Carapace orange, cephalic region darkest, clypeus dark. Chelicerae brown with a yellow patch. Labium, endites brown. Sternum light orange underlain by white pigment spots and edge dark. Coxae light orange; legs orange with brown rings. Dorsum of abdomen white with black and gray spots (Figs. 227, 228); venter dusky. Cephalic region very wide (Figs. 227, 228). Posterior median eyes 1.1 diameters of anterior medians, laterals 0.6 diameter. Anterior median eyes their diameter apart. Posterior median eyes 1.2 diameters apart. Posterior median eyes on swelling, facing forward and to sides. Ocular quadrangle wider behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Abdomen with projecting tubercles (Figs. 227–229). Total length 5.4 mm. Carapace 2.3 mm long, 2.1 wide, 1.4 wide behind lateral eyes. First femur 2.1 mm, patella and tibia 2.7, metatarsus 1.7, tarsus 0.7. Second patella and tibia 2.4 mm, third 1.5, fourth 2.1. Abdomen 4.9 mm long.

Male from Santo Amaro, São Paulo, Brazil. Carapace orange, sides of cephalic region and area between median and lateral eyes brown. Chelicerae brown. Labium, endites orange. Sternum orange underlain by white pigment. Coxae orange; legs orange with indistinctly bordered dark rings. Dorsum of abdomen gray and white spotted, venter gray. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 0.7 diameter apart, 1.5 diameters from laterals. Posterior median eyes 1.5 diameters apart. Ocular quadrangle square. Height of clypeus equal to 1.1 diameters of anterior median eyes. Fourth coxa with one macroseta. Fourth trochanter with one macroseta. Abdomen oval with two anterior tubercles. Total length 5.3 mm. Carapace 2.8 mm long, 2.5 wide, 1.3 wide behind lateral eyes. First femur 2.7 mm, patella and tibia 3.4, metatarsus 2.0, tarsus 0.9. Second patella and tibia 2.7 mm, third 1.7, fourth 2.5.

Note. Males and females were collected together.

Variation. Total length of females 5.0 to 5.8 mm, of males 4.1 to 5.2. The anterior tubercles of the abdomen are pointed (Fig. 228) or swollen humps (Fig. 227), and proximal to each other pointing forward. One individual has the pedicel inserted on the posterior half of the abdomen. The females illustrated (Figs. 224–229) were made from two individuals from Rio Grande do Sul: Figures 224–227, 229 from the first, 228 from the second. The male illustrated came from Engo. Marcilac, São Paulo State.

Diagnosis. Females differ from those of *O. bispinosa* by the narrow scape with parallel sides, from those of *O. lisei* (Fig. 233) by the larger posterior median plate (Fig. 225). The male differs from that of *O.*

bispinosa (Fig. 222) by having two "horizontal" keels above the base of the median apophysis (Fig. 230).

Specimens Examined. BRAZIL *São Paulo:* Engo. Marcilac, Santo Amaro, 16–17 Dec. 1966, ♂ (P. de Biasi, MZSP 5400a); Honto Florestal [?], Dec. 1943, ♀, ♂ (F. Lane, MZSP 4549). *Paraná:* Curitiba, Nov. 1938, ♂ (F. S. Pereira, MZSP 7566). *Rio Grande do Sul:* Campo Bom, 28 Nov. 1979, ♀ (C. J. Becker, MCN 8778); Carazinho, 10 Nov. 1979, ♀ (H. Bischoff, MCN 8680); Montenegro, 1 Dec. 1977, ♀ (H, A. Gestal, MCN 7476); Triunfo, 20 Oct. 1947, ♀ (T. Arigony, MCN 6907).

Ocrepeira lisei new species
Figures 232–235; Map 5

Holotype. Female holotype from Canela, Rio Grande do Sul State, Brazil, 26 Dec. 1974 (A. A. Lise), in MCN no. 10569. The species is named after the collector.

Description. Female holotype. Carapace orange-brown, cephalic region and sides of thoracic region darker. Chelicerae distally dark brown. Labium, endites brown. Sternum orange-brown, lightest in center. Coxae orange-brown; legs orange-brown with darker patches. Dorsum of abdomen whitish with dark spots and posterior transverse bars (Fig. 235); venter black. Posterior median eyes 1.2 diameters of anterior medians, laterals 0.7 diameter. Anterior median eyes 1.2 diameters apart. Posterior median eyes 1.5 diameters apart. Posterior median eyes on swelling and facing laterally. Ocular quadrangle wider behind than in front. Lateral eyes separated by their diameter. Height of clypeus equal to 1.2 diameters of anterior median eyes. Abdomen with pair of anterior-facing tubercles (Fig. 235). Total length 6.6 mm. Carapace 2.8 mm long, 2.3 wide, 1.5 wide behind lateral eyes. First femur 2.4 mm, patella and tibia 3.0, metatarsus 1.8, tarsus 0.7. Second patella and tibia 2.7 mm, third 1.7, fourth 2.7. Abdomen 6.5 mm long.

Variation. Total length of females 5.2 to 7.7 mm. The illustration was made from the holotype.

Diagnosis. Ocrepeira lisei differs from *O. gnomo* (Fig. 225) by having the lateral plates overlapping in posterior view of the epigynum (Fig. 233), and from *O. pinhal* (Fig. 212) by a scape with parallel sides (Fig. 232).

Specimens Examined. BRAZIL *Rio de Janeiro:* Petrópolis, Dec. 1945, ♀ (H. Sick, AMNH); Mar. 1946, ♀ (H. Sick, AMNH). *Santa Catarina:* Pinhal, Dec. 1947, 2♀, Jan. 1948, 3♀ (A. Maller, AMNH). *Rio Grande do Sul:* Bagé, 23 Oct. 1981, ♀ (A. A. Lise, MCN 9964); Porto Alegre, ♀ (P. Buck, MNRJ).

Ocrepeira gulielmi new species
Figures 236–242; Map 5

Holotype. Female holotype, paratypes: two females and four males from La Planada, 7 km S of Choconés, Depto. Nariño, Colombia, July 1986 (W. Eberhard), in MCZ. The species is named after colleague William Eberhard, the collector.

Description. Female holotype. Carapace light orange, cephalic region dusky with light setae. Chelicerae dusky orange. Labium, endites orange. Sternum, coxae light orange. Legs light orange, distal articles dusky. Anterior of dorsum of abdomen dark, posterior with five pairs of black spots emphasized by light rings (Fig. 239); venter black with a pair of white bands (Fig. 240). Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes their diameter apart, 1.3 diameters from laterals. Posterior median eyes their diameter apart, 2.5 diameters from laterals. Posterior median eyes on a swelling. Ocular quadrangle slightly narrower behind than in front. Height of clypeus equal to 0.8 diameter of anterior median eyes. Abdomen with indistinct humps (Fig. 239). Total length 5.0 mm. Carapace 2.3 mm long, 1.7 wide, 1.0 wide behind lateral eyes. First femur 2.3 mm, patella and tibia 2.9, metatarsus 1.9, tarsus 0.9. Second patella and tibia 2.1 mm, third 1.3, fourth 1.7.

Male paratype from type locality. Color as in female, but legs faintly ringed. Posterior median eyes same diameter as anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart, their diameter from laterals. Posterior median eyes 0.8 diameter apart, 1.8 diameters from laterals. Posterior median eyes on slight swelling. Ocular quadrangle square, slightly narrower behind than in front. Fourth coxa with a macroseta on a tubercle. Right fourth trochanter with a macroseta, none on left. Total length 3.8 mm. Carapace 2.1 mm long, 1.7 wide, 0.8 wide behind lateral eyes. First femur 2.5 mm, patella and tibia 2.8, metatarsus 1.6, tarsus 0.7. Second patella and tibia 2.3 mm, third 1.1, fourth 1.9.

Note. Males and females were collected together and have similar markings on the abdomen.

Variation. The male described had a macroseta on the right trochanter but not on the left; none of the others had a fourth trochanter macroseta. Total length of females 4.5 to 5.6 mm, of males 3.6 to 3.8. The illustrations were made from the holotype and from a male from the type locality.

Diagnosis. Unlike that of other species the female scape has a swelling above its tip (Fig. 236). As in *O. atuncela* (Fig. 254) the posterior median plate has parallel sides (Fig. 237) but differs by a deep groove on each side of its base (Figs. 237, 238). The male differs from that of *O. steineri* (Fig. 240) by the shape of the base of the median apophysis (Fig. 241).

Specimens Examined. COLOMBIA *Nariño:* La Planada, 1,800 m, 7 km S Chocones, July 1986, ♀, 3♂ paratypes (W. Eberhard, MCZ). ECUADOR *Pichincha:* Río Faisanes, 15 km NE La Palma, 1,380 m, 17 Feb. 1979, 2♀ (L. Burnham, MCZ).

Ocrepeira steineri new species
Figures 243–248; Map 5

Holotype. Female holotype, female and male paratypes from Cerro de la Neblina, 1,690 m, Territ. Feder. Amazonas, Venezuela, 12 Feb. 1985 (W. E. Steiner), in USNM. The species is named after the collector.

Description. Female holotype. Carapace dark orange with white setae, sides of thoracic region lightest. Chelicerae orange, distally brown. Labium, endites brown. Sternum orange, borders darker. Coxae dusky orange; legs orange with indistinct dark rings. Dorsum of abdomen white, gray, and with black caps on humps and black transverse bars posteriorly (Fig. 246); venter black. Posterior median eyes 1.2 diameters of anterior medians, laterals 0.8 diameter. Anterior median eyes their diameter apart. Posterior median eyes 1.3 diameters apart. Lateral eyes their diameter apart. Posterior median eyes on swelling. Ocular quadrangle wider behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Abdomen with tips of humps facing anteriorly (Fig. 246). Total length 4.8 mm. Carapace 2.5 mm long, 1.9 wide, 1.2 wide behind lateral eyes. First femur 2.3 mm, patella and tibia 2.7, metatarsus 1.8, tarsus 0.8. Second patella and tibia 2.4 mm, third 1.4, fourth 2.2.

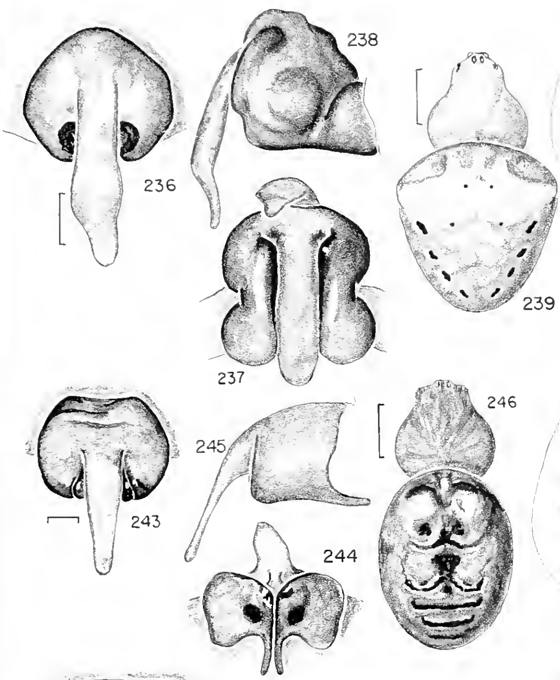
Male paratype. Color as in female except without the transverse bars on the abdomen; in its place there is a black folium. Posterior median eyes 1.2 diameters of anterior medians, laterals 0.8 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Ocular quadrangle wider behind than in

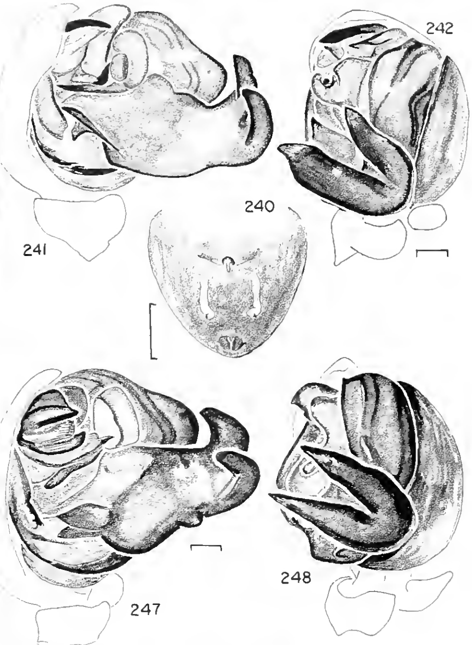
⟶

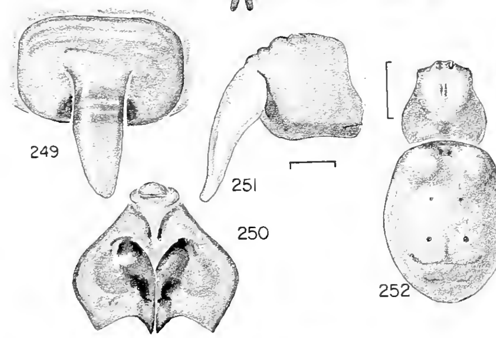
Figures 236–242. *Ocrepeira gulielmi* n. sp. 236–240, female. 236–238, epigynum. 236, ventral. 237, posterior. 238, lateral. 239, dorsal. 240, abdomen, ventral. 241, 242, left male palpus.

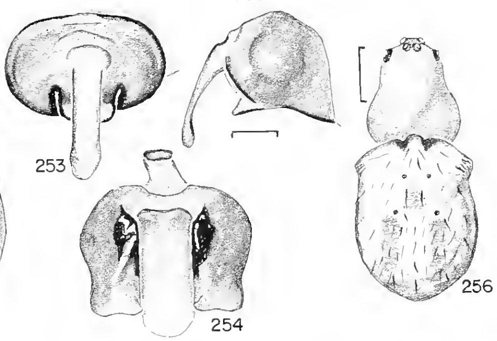
Figures 243–248. *O. steineri* n. sp. 243–246, female. 243–245, epigynum. 243, ventral. 244, posterior. 245, lateral. 246, dorsal. 247, 248, male palpus.

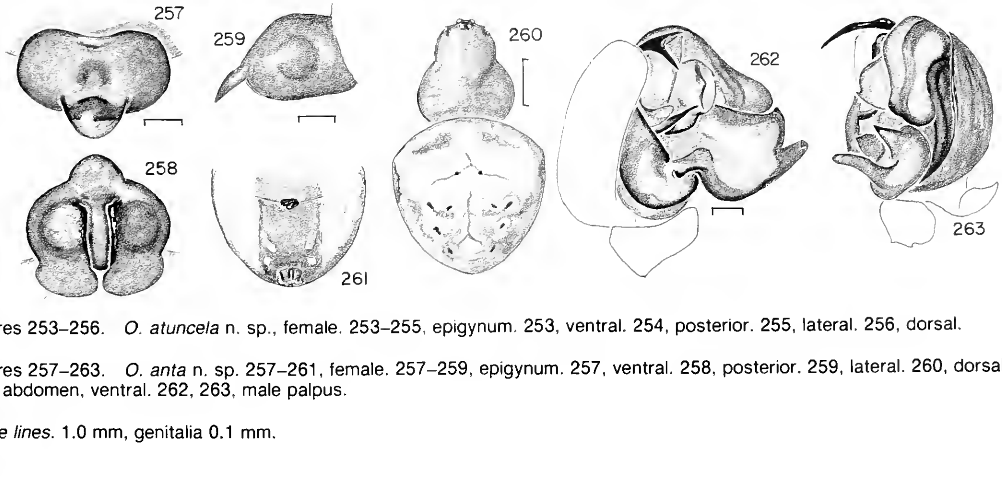
Figures 249–252. *O. macaiba* n. sp., female. 249–251, epigynum. 249, ventral. 250, posterior. 251, lateral. 252, dorsal.











Figures 253–256. *O. atuncela* n. sp., female. 253–255, epigynum. 253, ventral. 254, posterior. 255, lateral. 256, dorsal.

Figures 257–263. *O. anta* n. sp. 257–261, female. 257–259, epigynum. 257, ventral. 258, posterior. 259, lateral. 260, dorsal. 261, abdomen, ventral. 262, 263, male palpus.

Scale lines. 1.0 mm, genitalia 0.1 mm.

front. Height of clypeus equal to 1 diameter of anterior median eyes. Fourth coxa with one macroseta. Fourth trochanter with one macroseta. Abdomen as in female but smaller. Total length 4.0 mm. Carapace 2.5 mm long, 2.0 wide, 0.9 wide behind lateral eyes. First femur 2.9 mm, patella and tibia 3.2, metatarsus 1.8, tarsus 0.7. Second patella and tibia 2.8 mm, third 1.7, fourth 2.3.

Note. The male was collected with the female.

Diagnosis. The female is separated from others by the lack of posterior median plate, and by the lateral plates with dorsal projection (Fig. 244). The base of the male's median apophysis (Fig. 247) is shaped differently from that of *O. gulielmi* (Fig. 241).

Ocrepeira macaiba new species
Figures 249–252; Map 5

Holotype. Female holotype from Fazenda Canao, Macaíba, Rio Grande do Norte, Brazil, 15 Sept. 1951 (M. Alvarenga), in MZSP no. 5383. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace light orange, darkest on sides of thoracic region. Chelicerae, labium, endites orange. Sternum orange. Coxae, legs light orange. Dorsum of abdomen white with some dusky transverse bars posteriorly (Fig. 252); venter dusky with a pair of white spots in front of spinnerets, darkest anteriorly above pedicel. Posterior median eyes 1.3 diameters of anterior medians, laterals 0.9 diameter. Anterior median eyes 1.2 diameters apart. Posterior median eyes 1.5 diameters apart. Posterior median eyes on a swelling. Ocular quadrangle wider behind than in front. Height of clypeus equal to 1.2 diameters of anterior median eyes. Abdomen as in Figure 252. Total length 4.3 mm. Carapace 2.1 mm long, 1.8 wide, 1.1 wide behind lateral eyes. First femur 2.1 mm, patella and tibia 2.3, metatarsus 1.5, tarsus 0.6. Second patella and tibia 2.2 mm, third 1.4, fourth 2.0.

Diagnosis. Ocrepeira macaiba differs from *O. steineri* (Fig. 244) in the shape of the lateral plates of the epigynum (Fig. 250).

Ocrepeira atuncela new species
Plate 1; Figures 253–256; Map 5

Holotype. Female from above Atuncela, 1,800 m, cloud forest, Depto. Valle, Colombia, 15 Mar. 1969 (W. Eberhard, no. 173p), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace, chelicerae, labium, endites yellowish. Sternum yellowish. Coxae, legs yellowish, distally darker. Dorsum of abdomen light yellow with anterior dark marks, and with two indistinct longitudinal dusky bands (Fig. 256); venter with a black square between epigynum and spinnerets. Posterior median eyes same diameter as anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Lateral eyes 0.3 diameter apart. Posterior median eyes on swelling. Ocular quadrangle slightly narrower behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Abdomen shield-shaped with scattered long setae (Fig. 256). Total length 4.8 mm. Carapace 2.4 mm long, 1.9 wide, 1.1 wide behind lateral eyes. First legs lost. Second patella and tibia 2.7 mm, third 1.6, fourth 2.6.

Diagnosis. The epigynum of this female (Figs. 254, 255) differs from that of *O. gulielmi* by lacking the deep groove on the side of the base (Figs. 237, 238). The abdomen is differently marked and shaped (Fig. 256).

Natural History. Plate 1 illustrates the orb web.

Ocrepeira anta new species
Figures 257–263; Map 5

Holotype. Female holotype and male paratype from Alto de Minas, 30 km S of Medellin, 2,700 m, Depto. Antioquia, Colombia, 27 Aug. 1963 (P. B. Schneble), in MCZ. The specific name is an arbitrary combination of letters.

Description. Female holotype. Carapace, chelicerae, labium, endites yellowish. Sternum yellow. Legs yellowish. Dorsum of abdomen white with pairs of dark spots, each surrounded by a light ring (Fig. 260); venter dusky with a pair of white spots (Fig. 261). Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes 1.2 diameters apart. Posterior median eyes their diameter apart. Ocular quadrangle narrower behind than in front. Height of clypeus equal to 1.1 diameters of anterior median eyes. Abdomen with indistinct humps (Fig. 260). Total length 5.5 mm. Carapace 2.5 mm long, 2.1 wide, 1.1 wide behind lateral eyes. First femur 2.5 mm, patella and tibia 2.9, metatarsus 2.0, tarsus 0.8. Second patella and tibia 2.7 mm, third 1.5, fourth lost.

Male paratype. Color as in female. Posterior median eyes 0.9 diameter of anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.6. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Ocular quadrangle slightly longer than wide, slightly narrower behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Fourth coxa with one macroseta. Fourth trochanter with one macroseta. Total length 4.2 mm. Carapace 2.0 mm long, 1.6 wide, 0.9 wide behind lateral eyes. First femur 2.3 mm, patella and tibia 2.7, metatarsus 1.7, tarsus 0.7. Second patella and tibia 2.2 mm, third 1.3, fourth 1.9.

Note. Males and females were collected together.

Variation. Total length of females 5.2 to 5.5 mm. Illustrations were made from the holotype and from the male collected with it.

Diagnosis. The female differs from that of other species by the narrow, sclerotized median plate of the epigynum (Fig. 258) and the short semicircular scape (Fig. 257). The male differs by the shape of the terminal and median apophyses (Figs. 262, 263).

Specimens Examined. COLOMBIA *Antioquia:* Guarne, 2,000 m, July–Aug. 1976, 2♀ (P. Schneble, MCZ).

Ocrepeira barbara new species
Figures 264–268; Map 6

Holotype. Female holotype from "El Abiseo", Río Montecristo campsite, La Playa, Parque Nacional Río Abiseo, Depto. San Martín, Peru, 19 Aug. 1987 (B. Roth), in MUSM. The specific name is a noun in apposition after the collector.

Description. Female holotype. Carapace light orange with short, white setae, darkest in eye region. Chelicerae, labium, endites light orange. Sternum orange, dusky around border. Coxae, legs dusky orange. Dorsum of abdomen with dark mark between tubercles, posterior with pairs of black streaks and indistinct transverse darker bands (Fig. 267); venter with a pair of white spots posteriorly (Fig. 268). Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes 0.9 diameter apart. Posterior median eyes 0.9 diameter apart. Posterior median eyes on swelling. Ocular quadrangle square. Height of clypeus equal to 1.3 diameters of anterior median eyes. Abdomen with small humps (Fig. 267). Total length 8.2 mm. Carapace 3.6 mm long, 2.8 wide, 1.7 wide behind lateral eyes. First femur 3.6 mm, patella and tibia 4.7, metatarsus 3.1, tarsus 1.3. Second patella and tibia 4.2 mm, third 2.6, fourth 3.7.

Variation. Total length of females 5.8 to 8.2 mm. The specimen from Pumamarca lacks the white spots on the underside. The illustrations were made from the holotype.

Diagnosis. The female differs from others by the drop-shaped scape of the epigynum (Fig. 264) and by the median divisions of the posterior median plate (Fig. 265).

Specimen Examined. PERU *Junín:* Pumamarca, ♀ (K. Jelski, J. Sztolcman, PAN).

Ocrepeira macintyrei new species
Figures 269–271; Map 6

Holotype. Male holotypes from Baños, 2,200–2,500 m, Tungurahua Prov., Ecuador, Apr. 1939 (W. C. Macintyre), in MCZ. The species is named after the collector.

Description. Male holotype. Carapace orange, anterior of cephalic region and anterior of sides of thoracic region darker. Chelicerae, labium, endites orange. Sternum orange with dusky margin. Coxae orange; legs orange with brown rings. Abdomen with white cardiac mark, a black outline of folium, darker inside of folium than outside; venter gray with a pair of round white spots. Posterior median eyes same diameter as anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart. Posterior median eyes 0.8 diameter apart. Ocular quadrangle longer than wide, narrower behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Fourth coxa with one macroseta on tubercle. Fourth trochanter with one macroseta. Abdomen with anterior lateral tubercles (Fig. 271). Total length 6.2 mm. Carapace 3.3 mm long, 2.7 wide, 1.4 wide behind lateral eyes. First femur 3.8 mm, patella and tibia 4.3, metatarsus 2.7, tarsus 1.3. Second patella and tibia 3.6 mm, third 2.1, fourth 3.1.

Diagnosis. The sickle-shaped terminal apophysis and the swelling at the base of the median apophysis (Fig. 269) separate *O. macintyrei* from other species.

Ocrepeira tungurahua new species
Figures 272–277; Map 6

Holotype. Female holotype, one female and one male paratype from Tungurahua, 2,600 m, Tungurahua Prov., Ecuador, 6 May 1939 (W. Clarke-Macintyre), in AMNH. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace dark orange, with darker streaks, darkest at lateral eyes. Chelicerae, labium, endites dark orange. Sternum dark orange. Coxae, legs orange. Dorsum of abdomen orange-white with pairs of dark spots, the posteriormost pair connected by a transverse line (Fig. 275); venter dusky with indistinct pair of white longitudinal lines. Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes their diameter apart. Posterior median eyes 0.7 diameter apart. Ocular quadrangle slightly narrower behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Abdomen as in Figure 275. Total length 6.4 mm. Carapace 2.7 mm long, 2.3 wide, 1.4 wide behind lateral eyes. First femur 3.0 mm, patella and tibia 3.8, metatarsus 2.1, tarsus 1.1. Second patella and tibia 3.3 mm, third 1.9 , fourth 2.9.

Male paratype from type locality. Color as in female but legs with faintly darker rings. Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes 0.7 diameter apart. Posterior median eyes their diameter apart. Ocular quadrangle narrower behind than in front. Height of clypeus equal to 0.8 diameter of anterior median eyes. Fourth coxa with one macroseta on a tubercle. Fourth trochanter with one macroseta. Total length 5.4 mm. Carapace 2.4 mm long, 2.1 wide, 1.1 wide behind lateral eyes. First femur 2.9 mm, patella and tibia 3.2, metatarsus 2.0, tarsus 0.9. Second patella and tibia 2.9 mm, third 1.6, fourth 2.3.

⟶

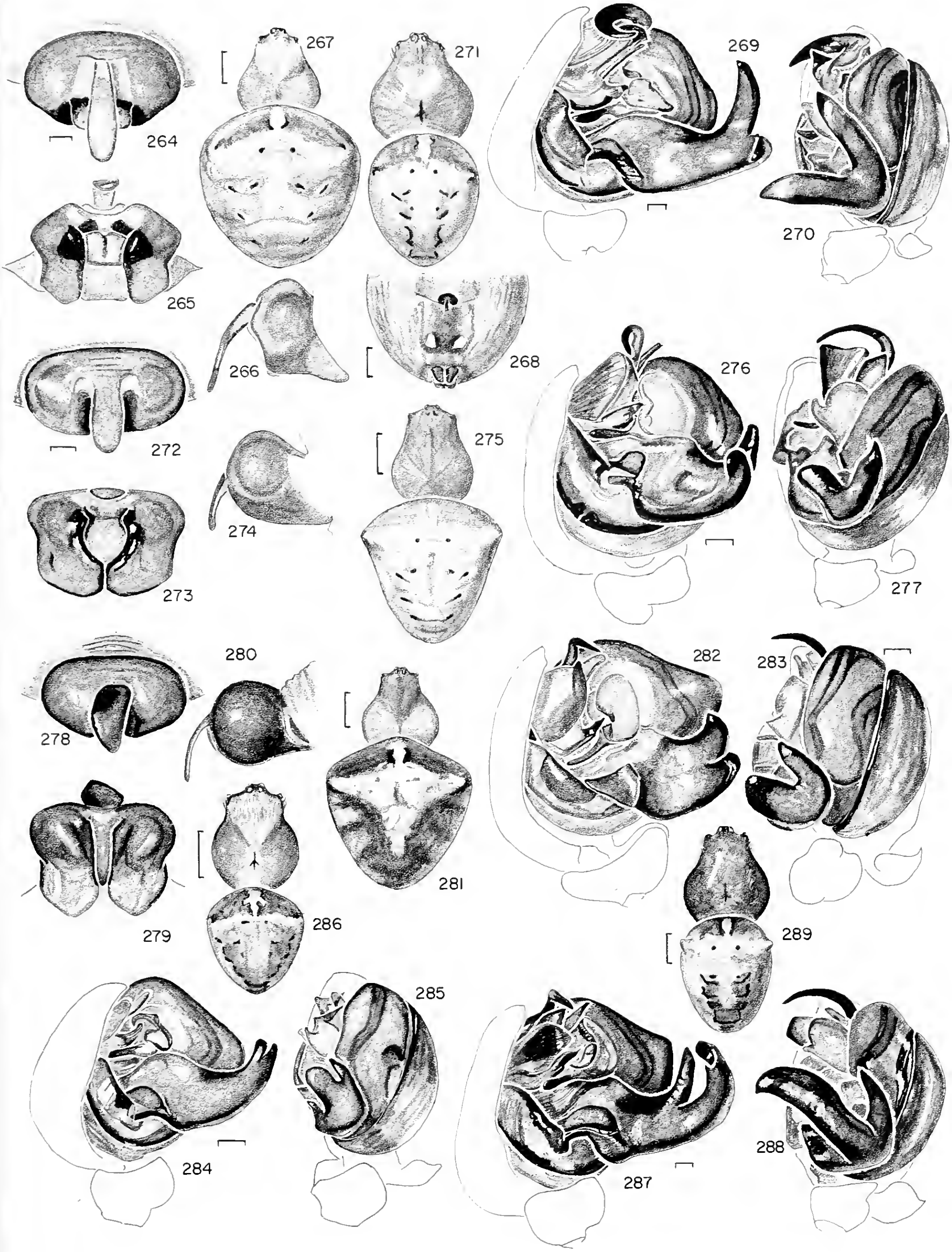
Figures 264–268. *Ocrepeira barbara* n. sp., female. 264–266, epigynum. 264, ventral. 265, posterior. 266, lateral. 267, dorsal. 268, abdomen, ventral.

Figures 269–271. *O. macintyrei* n. sp., male. 269, 270, male left palpus. 271, dorsal.

Figures 272–277. *O. tungurahua* n. sp. 272–275, female. 272–274, epigynum. 272, ventral. 273, posterior. 274, lateral. 275, dorsal. 276, 277, male palpus.

Figures 278–283. *O. valderramai* n. sp. 278–281, female. 278–280, epigynum. 278, ventral. 279, posterior. 280, lateral. 281, dorsal. 282, 283, male palpus.

Figures 284–286. *O. jamora* n. sp., male. 284, 285, palpus. 286, dorsal.



Figures 287–289. *O. pista* n. sp., male. 287, 288, palpus. 289, dorsal.

Scale lines. 1.0 mm, genitalia 0.1 mm.

Note. The male was collected with the female.

Diagnosis. The female differs from that of *O. barbara* by the circular shape of the posterior median plate (Fig. 273); the male differs from that of other species by the loop of the terminal apophysis and the shape of the base of the median apophysis (Fig. 276).

Ocrepeira valderramai new species
Figures 278–283; Map 6

Holotype. Male holotype with immature female on web in vegetation, from Paramo de Chingaza, Monteredondo, 3,100 m, Depto. Cundinamarca, Colombia, 20 July 1986 (C. Valderrama), in MCZ. The species is named after the collector.

Description. Female from Paramo de Monteserrate. Carapace brownish black with sides of thoracic region yellowish. Chelicerae, labium, endites dark brown. Sternum dark brown, lighter in center. Coxae yellowish; legs yellowish with brown rings and patches. Dorsum of abdomen with black marks and a white triangle (Fig. 281); venter black with a pair of white spots. Posterior median eyes 1.2 diameters of anterior medians, laterals 0.8 diameter. Anterior median eyes their diameter apart. Posterior median eyes 0.9 diameter apart. Ocular quadrangle slightly narrower behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Abdomen with a pair of lateral humps (Fig. 281). Total length 7.0 mm. Carapace 2.9 mm long, 2.3 wide, 1.3 wide behind lateral eyes. First femur 3.1 mm, patella and tibia 3.8, metatarsus 2.5, tarsus 1.1. Second patella and tibia 3.4 mm, third 2.1, fourth 3.0.

Male holotype. Color darker than in female. Carapace with paired dark streaks. Abdomen with a dark, dorsal folium. Posterior median eyes 1.2 diameters of anterior medians, anterior laterals 1.2 diameters, posterior laterals 1 diameter. Anterior median eyes their diameter apart. Posterior median eyes 0.8 diameter apart. Posterior median eyes on a swelling. Ocular quadrangle narrower behind than in front. Height of clypeus equal to 0.9 diameter of anterior median eyes. Fourth coxa with one macroseta. Fourth trochanter without macroseta. Total length 5.0 mm. Carapace 2.7 mm long, 2.3 wide, 1.1 wide behind lateral eyes. First femur 3.1 mm, patella and tibia 3.9, metatarsus 2.5, tarsus 1.1. Second patella and tibia 3.1 mm, third 1.9, fourth 2.6.

Note. The male and the females were collected from the same locality.

Variation. The epigynum of the paratype illustrated is asymmetrical (Fig. 278). A penultimate female, just before the molt, had an oval scape narrow at both ends, the posterior median plate slightly wider and shorter than the one illustrated. Total length of males 5.0 to 5.2 mm. The illustrations were made from the male holotype and from a female from Paramo de Monserrate.

Diagnosis. The female differs from others with a narrow posterior median plate, *O. anta* (Figs. 257–259) and *O. planada* (Figs. 290–292), by the shape of the epigynal scape in ventral view (Fig. 278) and lateral view (Fig. 280). The male differs from those of *O. pista* (Figs. 287, 288) and *O. tungurahua* (Figs. 276, 277) by the raised triangular sculpturing of the base of the median apophysis (Fig. 282).

Natural History. One specimen was hanging in vegetation in a cloud forest, others in orb webs between flowers and leaves of *Espeletia grandiflora*.

Specimens Examined. COLOMBIA *Cundinamarca:* Paramo de Monserrate, 7.5 km NE Bogotá, in natural vegetation, 04°15′N, 74°01′W, 13 Sept. 1986, ♀ (H. Sturm, MCZ); Paramo de Chingaza, 3,400 m, 04°31′N, 73°45′W, 14 Apr. 1986, imm., 15 Apr. 1986, ♀ paratype, 22 Mar. 1987, 2 imm., 3,100 m, 23 Mar. 1987, ♂ paratype (all C. Valderrama, CV, MCZ).

Ocrepeira jamora new species
Figures 284–286; Map 6

Holotype. Male holotype from Cerro Tinajillas, 3,100 m, S of Cuenca, Azuay Prov., Ecuador (L. Peña), in MCZ. The specific name is an arbitrary combination of letters.

Description. Male holotype. Carapace orange with white setae, anterior of cephalic region and sides of thoracic region darkest. Chelicerae, labium, endites dark orange. Sternum orange-brown. Coxae, legs orange with darker rings. Abdomen with white cardiac mark and brown outline of folium (Fig. 286); venter gray with a pair of white patches. Posterior median eyes 1.3 diameters of anterior medians, laterals 0.8 diameter. Anterior median eyes their diameter apart. Posterior median eyes 0.8 diameter apart. Ocular quadrangle slightly narrower behind than in front. Height of clypeus equal to 0.8 diameter of anterior median eyes. Fourth coxa with one macroseta on a tubercle. Fourth trochanter without macroseta. Total length 5.0 mm. Carapace 2.5 mm long, 2.0 wide, 1.3 wide behind lateral eyes. First femur 3.0 mm, patella and tibia 3.4, metatarsus 1.9, tarsus 0.8. Second patella and tibia 2.8 mm, third 1.7, fourth 2.3.

Note. Illustrations were made from the holotype.

Diagnosis. Ocrepeira jamora differs from other male *Ocrepeira* by the shape of the terminal and median apophyses (Figs. 284, 285).

Specimen Examined. ECUADOR *Tungurahua:* Tungurahua, 2,600 m, 6 June 1939, ♂ (W. Clarke-Macintyre, AMNH).

Ocrepeira pista new species
Figures 287–289; Map 6

Holotype. Male holotype and one male paratype from Machupicchu, above ruins, 2,600–2,800 m, Depto. Cuzco, Peru, 1–5 July 1964, beaten from vegetation, (B. Malkin), in AMNH. The specific name is an arbitrary combination of letters.

Description. Male holotype. Carapace reddish brown, sides of thoracic region black with some white setae. Chelicerae dark brown. Labium, endites, sternum dark orange. Legs dark orange with darker patches. Dorsum of abdomen with white cardiac spot and dark folium (Fig. 289); venter black with a pair of contrasting white spots. Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Ocular quadrangle slightly narrower behind than in front. Height of clypeus equal to 1.1 diameters of anterior median eyes. Fourth coxa with one macroseta on a tubercle. Total length 6.7 mm. Carapace 3.9 mm long, 3.0 wide, 1.5 wide behind lateral eyes. First femur 3.9 mm, patella and tibia 4.7, metatarsus 2.8, tarsus 1.3. Second patella and tibia 4.0 mm, third 2.6, fourth 3.6.

Diagnosis. Ocrepeira pista differs from the male of *O. valderramai* by the large lower prong of the median apophysis and the semicircular offset near its base (Figs. 287, 288).

Ocrepeira planada new species
Figures 290–296; Map 6

Holotype. Female from La Planada, 1,800 m, 7 km S of Choconés, Depto. Nariño, Colombia, July 1986 (W. Eberhard, 3358), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace orange, posterior of cephalic region dusky, darkest between median and lateral eyes. Chelicerae light orange. Labium, endites orange. Sternum dusky orange. Coxae orange; legs with darker and lighter rings and patches. Dorsum of abdomen with folium and white cardiac mark (Fig. 293); venter dusky with a pair of white spots (Fig. 294). Posterior median eyes 0.9 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes their diameter apart, 2 diameters from laterals. Posterior median eyes their diameter apart, 3.5 diameters from laterals. Ocular quadrangle slightly longer than wide, narrower behind than in front. Height of clypeus equal to 0.7 diameter of anterior median eyes. Abdomen with a pair of humps (Fig. 293). Total length 9.2 mm. Carapace 3.9 mm long, 3.1 wide, 1.7 wide behind lateral eyes. First femur 3.8 mm, patella and tibia 4.8, metatarsus 3.3, tarsus 1.3. Second patella and tibia 4.4 mm, third 2.7, fourth 4.2.

Male from Río Calima, Valle, Colombia.

Color as in female. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 0.8 diameter apart, 1.5 from laterals. Posterior median eyes their diameter apart, 3.5 from laterals. Ocular quadrangle narrower behind than in front. Height of clypeus equal to 0.6 diameter of anterior median eyes. Fourth coxa with large posterior tubercle bearing a macroseta. Abdomen as in female. Total length 6.8 mm. Carapace 4.4 mm long, 3.5 wide, 1.7 wide behind lateral eyes. First femur 4.7 mm, patella and tibia 5.5, metatarsus 3.1, tarsus 1.3. Second patella and tibia 4.6 mm, third 2.8, fourth 3.7.

Note. Males and females were matched because of similar markings.

Variation. Total length of females 6.5 to 10.2 mm, of males 5.9 to 6.8. Illustrations were made from the female holotype and a male from the type locality.

Diagnosis. Females can be separated from others with a narrow median posterior plate (Fig. 291) by the long scape having parallel sides and an attachment near the anterior of the base of the epigynum (Figs. 290–292). The male can be separated by the distinctly shaped terminal and median apophyses (Figs. 295, 296).

Specimens Examined. COLOMBIA *Cundinamarca:* road Fusagasuga to Anolaima, 2,800 m, 2 Sept. 1969, ♀ (P., B. Wygodzinsky, AMNH). *Valle:* Río Calima, nr. Lago Calima, 1,400 m, June 1976, ♂ (W. Eberhard, MCZ). *Nariño:* La Planada, 1,800 m, 7 km S Chocones, July 1986, 5♀, ♂ paratypes (W. Eberhard, 3347, MCZ). ECUADOR *Pichincha:* Quebrada La Plata, 2.1 km E Tandapi, 1,550 m, [00°25′N, 78°47′W], 3 Feb. 1979, ♀ (L. Burnham, MCZ). *Napo:* 6.5 km S Baeza, 1,810 m, Feb. 1979, ♀ (L. Burnham, MCZ). Río Yocuchiqui [?], W slope of Andes, ♀ (MCZ).

Ocrepeira ituango new species
Figures 297–301; Map 6

Holotype. Female holotype from Municipio de Ituango, 1,450 m, Depto. Antioquia, Colombia, 26 May 1989 (M. A. Serna), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace orange, cephalic region with a black circular patch, black between median and lateral eyes. Chelicerae dark brown. Labium, endites dark brown. Sternum dark brown. Coxae orange with dark patches; legs orange with dark rings. Dorsum of abdomen damaged, with white cardiac mark (Fig. 300); venter black with a pair of white spots (Fig. 301). Posterior median eyes 0.7 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 0.8 diameter apart, 2.8 diameters from laterals. Posterior median eyes 0.8 diameter apart, 4.5 diameters from laterals. Ocular quadrangle slightly narrower behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Abdomen as in Figure 300. Total length 10.4 mm. Carapace 4.0 mm long, 3.5 wide, 1.9 wide

→

Figures 290–296. *Ocrepeira planada* n. sp. 290–294, female. 290–292, epigynum. 290, ventral. 291, posterior. 292, lateral. 293, dorsal. 294, abdomen, ventral. 295, 296, left male palpus.

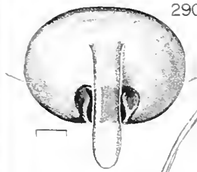
Figures 297–301. *O. ituango* n. sp., female. 297–299, epigynum. 297, ventral. 298, posterior. 299, lateral. 300, dorsal. 301, abdomen, ventral.

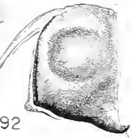
Figures 302–307. *O. saladito* n. sp. 302–305, female. 302–304, epigynum. 302, ventral. 303, posterior. 304, lateral. 305, dorsal. 306, 307, male palpus.

Figures 308–314. *O. cuy* n. sp. 308–312, female. 308–310, epigynum. 308, ventral. 309, posterior. 310, lateral. 311, dorsal. 312, abdomen, ventral. 313, 314, male palpus.

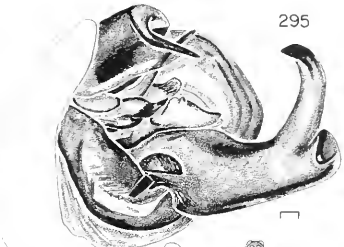
Figures 315–320. *O. abiseo* n. sp. 315–318, female. 315–317, epigynum. 315, ventral. 316, posterior. 317, lateral. 318, dorsal. 319, 320, male palpus.

Scale lines. 1.0 mm, genitalia 0.1 mm.

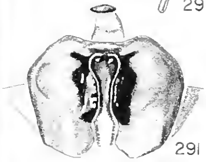

290


292


293

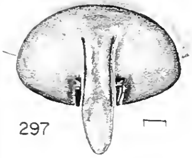

295

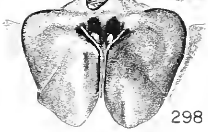

296

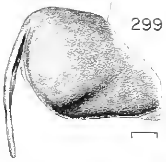

291

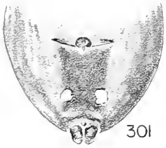

294

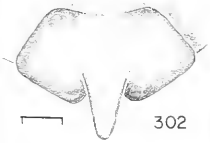

300

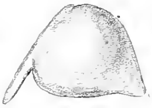

297

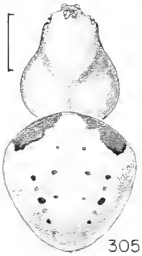

298

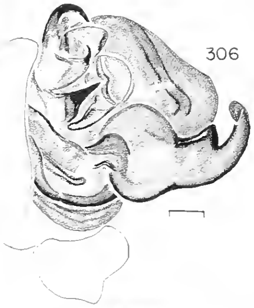

299

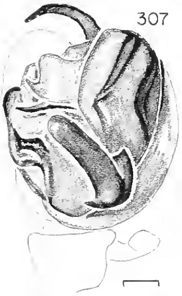

301

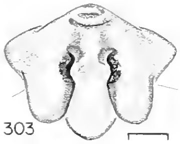

302

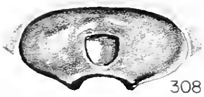

304


305

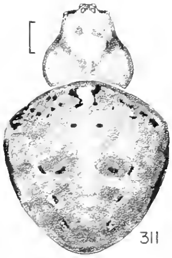

306

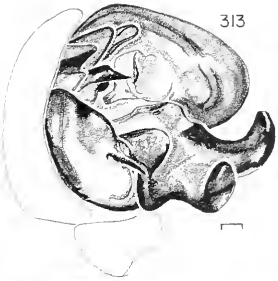

307


303

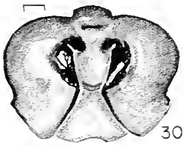

308


310


311


313


314

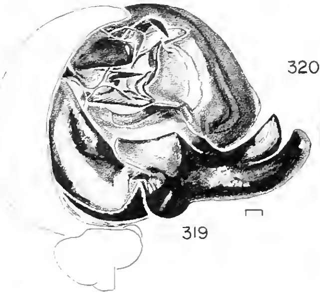

309


312

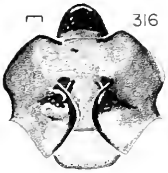

315


317


318


319


320


316

behind lateral eyes. First femur 4.3 mm, patella and tibia 5.4, metatarsus 3.5, tarsus 1.3. Second patella and tibia 5.0 mm, third 3.1, fourth 4.6.

Diagnosis. The female can be separated from *O. planada* (Figs. 290–292) by the posterior lateral plates of the epigynum which touch each other (Fig. 298).

Ocrepeira saladito new species
Figures 302–307; Map 6

Holotype. Female from near Saladito, 1,800 m, Depto. Valle, Colombia, Jan. 1977, (W. Eberhard, 1139), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace, chelicerae, labium, endites yellowish. Sternum yellowish. Coxae, legs yellowish with indistinct dusky rings. Dorsum of abdomen with anterior of each side black and posteriorly six pairs of spots highlighted by white rings, alternating black and red, first pair black, last pair red (Fig. 305); venter dusky, black in median area. Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes 1.3 diameters apart. Posterior median eyes 1.1 diameters apart. Laterals separated by half their diameter. Ocular quadrangle slightly narrower behind than in front. Height of clypeus equal to 1 diameter of the anterior median eyes. Abdomen as in Figure 305. Total length 4.7 mm. Carapace 2.3 mm long, 1.7 wide, 1.1 wide behind lateral eyes. First femur 2.5 mm, patella and tibia 2.8, metatarsus 1.8, tarsus 0.9. Second patella and tibia 2.4 mm, third 1.3, fourth 2.0.

Male from type locality. Color and markings as in female. Posterior median eyes same diameter as anterior medians, laterals 0.6 diameter. Anterior median eyes their diameter apart, 1.2 diameters from laterals. Posterior median eyes their diameter apart, 2 diameters from laterals. Ocular quadrangle square. Height of clypeus equal to 1 diameter of anterior median eyes. Fourth coxa with one macroseta. Fourth trochanter with one macroseta. Abdomen as in female. Total length 4.2 mm. Carapace 2.1 mm long, 1.7 wide, 0.8 wide behind lateral eyes. First femur 2.7 mm, patella and tibia 3.0, metatarsus 1.8, tarsus 0.8. Second patella and tibia 2.2 mm, third 1.3, fourth 1.7.

Note. Males and females came from the same locality and have similar distinctive markings on the abdomen.

Variation. The second female has the base of the epigynum more oval; the scape has parallel sides. Total length of males 4.0 to 4.2 mm.

Diagnosis. The female differs from others by the wide posterior median plate (Fig. 303), the male by the shape of the terminal and median apophyses (Figs. 306, 307)

Paratypes. COLOMBIA *Valle:* above Saladito, 1,800 m, 1975, ♀, 1979, ♂ (W. Eberhard, MCZ).

Ocrepeira cuy new species
Figures 308–314; Map 6

Holotype. Male holotype and female paratype from Pampa del Cuy, montane forest, Parque Nacional Abiseo, 3,550 m, Depto. San Martín, Peru, 5–12 Mar. 1988 (D. Silva D.), in MUSM. The specific name is a noun in apposition after the type locality.

Description. Female paratype collected with male. Carapace orange-yellow, with a dark patch on each side and long white setae above lateral eyes; clypeus dark. Chelicerae dark brown. Labium, endites brown. Sternum orange in center, dark all around. Coxae yellowish; legs yellowish with brown rings and black patches. Dorsum of abdomen with dark spot on each tubercle and paired dark streaks posteriorly (Fig. 311); venter with a pair of white marks (Fig. 312). Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes their diameter apart. Posterior median eyes slightly more than their diameter apart. Posterior median eyes on swelling. Ocular quadrangle slightly longer than wide. Height of clypeus equal to 1 diameter of anterior median eyes. Abdomen as in Figure 311. Total length 8.0 mm. Carapace 3.4 mm long, 2.9 wide, 1.6 wide behind lateral eyes. First femur 3.4 mm, patella and tibia 4.3, metatarsus 2.7, tarsus 0.9. Second patella and tibia 3.7 mm, third 2.3, fourth 3.2.

Male holotype. Color as in female. Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes their diameter apart. Posterior median eyes their diameter apart. Posterior median eyes on swelling. Ocular quadrangle square. Height of clypeus equal to 0.9 diameter of anterior median eyes. Fourth coxa with one macroseta. Fourth trochanter without macroseta. Total length 6.2 mm. Carapace 3.2 mm long, 2.7 wide, 1.3 wide behind lateral eyes. First femur 3.7 mm, patella and tibia 4.0, metatarsus 2.6, tarsus 1.0. Second patella and tibia 3.1 mm, third 1.9, fourth 2.7.

Note. Males and females were collected together.

Variation. Total length of females 8.0 to 8.3 mm, of males 5.9 to 6.2. The illustrations were made from the male holotype and a female paratype.

Diagnosis. The female has a smaller scape (Fig. 308) than the very similar *O. abiseo* (Fig. 315). The male differs from *O. abiseo* (Figs. 319, 320) by having both prongs of the median apophysis about the same length (Figs. 313, 314).

Paratypes. All from type locality: 8 Mar. 1988, 5♀, 2 Mar. 1988, ♂ (all D. Silva D., MUSM).

Ocrepeira abiseo new species
Figures 315–321; Map 6

Holotype. Male holotype, four female paratypes, from Parque Nacional Abiseo, Puerta del Monte, 3,300 m, Depto. San Martín, Peru, 4 Mar. 1988 (D. Silva D., A. Salirrosas), in MUSM. The specific name is a noun in apposition after the type locality.

Description. Female paratype collected with male. Carapace orange, with a dark patch on each side, posterior of cephalic region, sides of cephalic and thoracic region dark, white hair-like setae behind lateral eyes. Chelicerae dark brown with median light patch. Labium black, endites brown to orange. Sternum orange in middle, each side dark brown. Coxae yellowish with brown patches; legs yellowish with dark brown rings and patches. Dorsum of abdomen with white cardiac mark and with folium outline posteriorly (Fig. 318); venter with pair of light patches posteriorly. Posterior median eyes 0.9 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes their diameter apart. Posterior median eyes 0.8 diameter apart. Ocular quadrangle narrower behind than in front. Posterior median eyes on slight swelling. Height of clypeus equal to 1.2 diameters of anterior median eyes. Abdomen with pair of humps (Fig. 318). Total length 10.2 mm. Carapace 4.2 mm long, 3.4 wide, 1.8 wide behind lateral eyes. First femur 4.4 mm, patella and tibia 5.2, metatarsus 3.3, tarsus 1.3. Second patella and tibia 4.8 mm, third 2.9, fourth 4.2.

Male holotype. Color as in female, but legs light orange. Posterior median eyes same diameter as anterior medians, anterior laterals 0.8 diameter, posterior laterals 0.6. Anterior median eyes 0.8 diameter apart, 1.5 diameters from laterals. Posterior median eyes 0.7 diameter apart. Ocular quadrangle narrower behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Fourth coxa with one macroseta on a tubercle. Fourth trochanter without macroseta. Abdomen with pair of tubercles. Total length 8.2 mm. Carapace 4.4 mm long, 3.6 wide, 1.8 wide behind lateral eyes. First femur 4.3 mm, patella and tibia 5.4, metatarsus 3.5, tarsus 1.3. Second patella and tibia 4.5 mm, third 2.7, fourth 3.7.

Note. Males and females were collected together.

Variation. Total length of females 8.1 to 10.8 mm, of males 6.1 to 8.2. The scape of the epigynum (when present) is variable in shape; it is torn off from most individuals. The illustrations were made from the male holotype and the female collected with it.

Diagnosis. Females can be confused with those of *O. cuy* (Figs. 308–310) and *O. tinajillas* (Figs. 322–324); they differ by having a larger scape (Fig. 315) than that of *O. cuy* and a shorter scape (Fig. 317) than that of *O. tinajillas* (Fig. 324). The male differs from that of *A. cuy* (Figs. 313, 314) by having one prong of the median apophysis longer than the other (Figs. 319–321) and from *O. tinajillas* (Figs. 327, 328) by the differently shaped tegulum and median apophysis (Figs. 319, 320).

Natural History. The collecting sites were montane forest.

Specimens Examined. PERU *San Martín:* Parque Nacional Abiseo, Puerta del Monte, 3,300 m, 4 Mar. 1988, 5♀ paratypes, 13 Mar. 1988, 8♀, 2♂ paratypes, 14 Mar. 1988, ♀ paratype (D. Silva D., A. Salirrosas, MUSM); Pampa del Cuy, 3,550 m, 5–12 Mar. 1988 , 2♀, ♂ (D. Silva D., MUSM).

Ocrepeira tinajillas new species

Figures 322–328; Map 6

Holotype. Female holotype and male paratype and one immature from Cerro Tinajillas, 3,100 m, S of Cuenca, Azuay Prov., Ecuador, 18–21 Mar. 1965 (L. Peña), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace orange. Chelicerae orange. Labium, endites brown. Sternum orange, brown around border. Coxae orange and brown; legs orange with brown rings. Dorsum of abdomen with a dark sickle-shaped area anteriorly between tubercles and a small posterior folium (Fig. 325); venter dusky with a pair of white spots (Fig. 326). Eyes subequal. Anterior median eyes 1.2 diameters apart. Posterior median eyes their diameter apart. Ocular quadrangle narrower behind than in front. Height of clypeus equal to 1.2 diameters of anterior median eyes. Abdomen subspherical, with widely separated humps (Fig. 325). Total length 8.2 mm. Carapace 3.7 mm long, 2.8 wide, 1.8 wide behind lateral eyes. First femur 3.6 mm, patella and tibia 4.7, metatarsus 3.1, tarsus 1.3. Second patella and tibia 4.2 mm, third 2.5, fourth 3.8.

Male paratype. Color as in female, but abdomen with a white cardiac mark and pairs of dark patches posteriorly. Posterior median eyes 1.2 diameters of anterior medians, anterior laterals 0.9 diameter, posterior laterals 0.8. Anterior median eyes 1.2 diameters apart. Posterior median eyes their diameter apart. Ocular quadrangle narrower behind than in front. Height of clypeus equal to 1.2 diameters of anterior median eyes. Fourth coxa with one macroseta on a tubercle. Fourth trochanter without macroseta. Total length 6.4 mm. Carapace 3.8 mm long, 3.1 wide, 1.5 wide behind lateral eyes. First femur 3.9 mm, patella and tibia 4.7, metatarsus 2.7, tarsus 1.1. Second patella and tibia 3.8 mm, third 2.4, fourth 3.4.

Note. The male was collected with the female.

Variation. Total length of females 6.2 to 8.7 mm, of males 4.5 to 6.4. The scape of the second female's epigynum has parallel sides and is distally rounded; also the embolus and the conductor of the second male are of slightly different shape. The illustrations were made from the female holotype and the male paratype collected with it.

Diagnosis. The epigynum of *O. tinajillas* (Figs. 322–324) has a longer scape than that of *O. cuy* (Fig. 310) and *O. abiseo* (Fig. 317). The male has differently shaped tegulum and terminal apophysis (Figs. 327, 328) from those of *O. abiseo* (Figs. 319, 321).

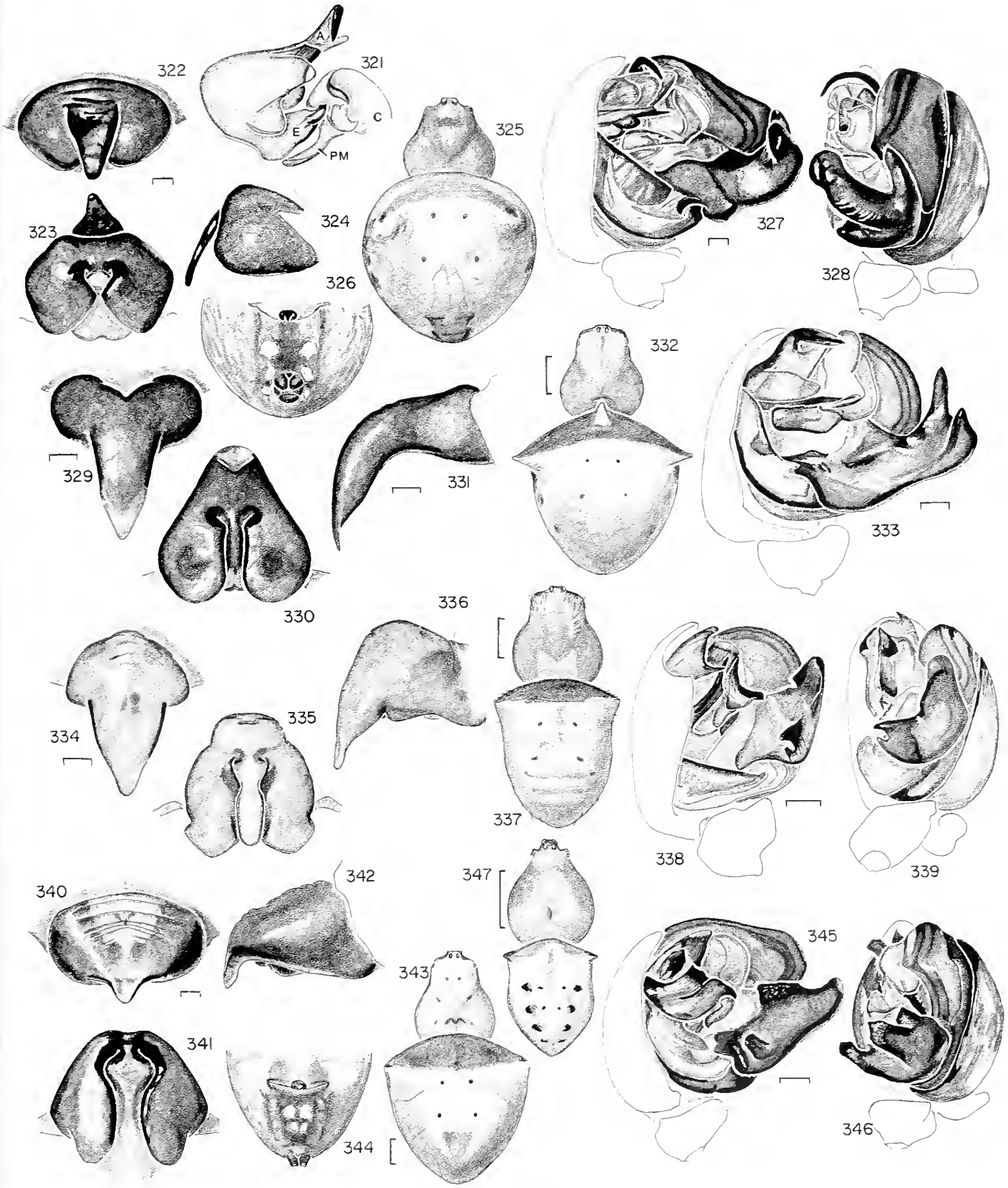
Specimens Examined. COLOMBIA *Valle*: Arriba de Saladito, 1973, ♂ (W.

⟶

Figure 321. *Ocrepeira abiseo* n. sp., male palpus; embolus (E), terminal apophysis (A), conductor (C), and paramedian apophysis (PM).

Figures 322–328. *O. tinajillas* n. sp. 322–326, female. 322–324, epigynum. 322, ventral. 323, posterior. 324, lateral. 325, dorsal. 326, abdomen, ventral. 327, 328, left male palpus.

Figures 329–333. *O. darlingtoni* (Bryant). 329–332, female. 329–331, epigynum. 329, ventral. 330, posterior. 331, lateral. 332, dorsal. 333, male palpus.



Figures 334–339. *O. magdalena* n. sp. 334–337, female. 334–336, epigynum. 334, ventral. 335, posterior. 336, lateral. 337, dorsal. 338, 339, male palpus.

Figures 340–344. *O. lapeza* n. sp., female. 340–342, epigynum. 340, ventral. 341, posterior. 342, lateral. 343, dorsal. 344, abdomen, ventral.

Figures 345–347. *O. aragua* n. sp., male. 345, 346, palpus. 347, dorsal.

Scale lines. 1.0 mm, genitalia 0.1 mm.

Eberhard, MCZ). ECUADOR *Loja:* Zamora, 1,800–2,200 m, 28 Oct. 1977, ♀ (L. Peña, AMNH).

Ocrepeira darlingtoni (Bryant), new combination
Figures 329–333; Map 6

Parawixia darlingtoni Bryant, 1945: 382, figs. 14, 16 (not 21), ♂. Male holotype (not female allotype) from Villa Altagracia, Dominican Republic, Hispaniola, in MCZ. Brignoli, 1983: 278.
Wixia darlingtoni Levi, 1992: 8.

Note. The female allotype of *Parawixia darlingtoni* is the holotype of *Aculepeira visite* Levi, 1991a: 307.

Description. Female from Valle de Polo, Dominican Republic. Carapace orange, eye region darkest. Chelicerae orange, distally darker. Labium, endites orange. Sternum light orange with brown border. Coxae light orange; legs indistinctly ringed with light orange. Dorsum of abdomen with white anterior median tubercle, dark anterior to a line between lateral tubercles (Fig. 332); venter with a pair of light patches separated by their diameter. Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes their diameter apart. Posterior median eyes 1.3 diameters apart. Ocular quadrangle narrower behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Abdomen with anterior median tubercle [posterior of abdomen damaged] (Fig. 332). Total length 6.5 mm. Carapace 2.7 mm long, 2.1 wide, 1.4 wide behind posterior lateral eyes. First femur 2.7 mm, patella and tibia 3.5, metatarsus 2.1, tarsus 0.9. Second patella and tibia 3.2 mm, third 1.8, fourth 2.7.

Male holotype. Color as in female except thoracic region darker than cephalic region. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart. Posterior median eyes 1.3 diameters apart. Ocular quadrangle narrower behind than in front. Height of clypeus equal to slightly less than 1 diameter of anterior median eyes. Fourth coxa with one macroseta. Fourth trochanter with one macroseta. Second femur with a ventral row of macrosetae; the most proximal one longer than diameter of femur and on a tubercle. Abdomen without anterior median tubercle. Total length 4.4 mm. Carapace 2.2 mm long, 1.8 wide, 1.0 wide behind lateral eyes. First femur 2.7 mm, patella and tibia 3.1, metatarsus 1.9, tarsus 0.9. Second patella and tibia 2.5 mm, third 1.5, fourth 2.1.

Note. Males and females were collected together. The male from Haiti had an additional macroseta on the third coxa and the carapace had symmetrical radiating dark bands originating from thoracic area.

Variation. Total length of females 4.6 to 6.5 mm, of males 4.4 to 4.5. The female from La Ciénaga had rounded lateral tubercles and some additional pairs of rounded humps on sides. The specimen from near Banano had a more slender epigynum and lacked the median anterior tubercle on the abdomen. Illustrations were made from the male holotype and a female from Valle de Polo.

Diagnosis. The female is contrastingly colored with an anterior median tubercle on the abdomen (Fig. 332) and the epigynum, unlike other species, has a strong glossy, curved scape (Figs. 329–331); the male differs from others by the distinct terminal and median apophyses (Fig. 333).

Specimens Examined. DOMINICAN REPUBLIC *Barahona:* Valle de Polo, 700–850 m, 18 Aug. 1935, ♀, 2♂, imm. (W. G. Hassler, AMNH). *La Vega:* La Ciénaga, along Arroyo Frío, 19°04′N, 70°51′W, 8 Jan. 1986, ♀ (S. Larcher, F. Mora, C. Domínguez, USNM). *Pedernales:* La Aguita, 1 km W antes de Cruce del Banana, 14 Aug. 1991 (K. Guerrero, D. Matusik, MNSD). HAITI 40 km from Aux Cayes, 600–900 m, 29 Aug. 1935, ♂ (W. G. Hassler, AMNH).

Ocrepeira magdalena new species
Figures 334–339; Map 6

Holotype. Female holotype from San Pedro, 1,200 m, Sierra Nevada de Santa Marta, Depto. Magdalena, Colombia, 16 May 1975 (J. A. Kochalka), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace yellowish, darker on cephalic area and sides of thorax, cephalic region with white setae. Chelicerae yellowish, distally darker. Labium, endites dusky. Sternum orange. Coxae yellow; legs yellow with dark rings. Dorsum of abdomen black anteriorly, posterior light with indistinct transverse bars (Fig. 337); sides dark dusky; venter light dusky. Posterior median eyes same diameter as anterior medians, laterals 0.7 diameter. Anterior median eyes 1.3 diameters apart. Posterior median eyes 1.4 diameters apart. Laterals separated by about 0.4 diameter. Ocular quadrangle, wider than long, wider behind than in front. Posterior median eyes on swelling facing anterolaterally. Height of clypeus equal to 1.3 diameters of anterior median eyes. Abdomen shield-shaped (Fig. 337). Total length 5.7 mm. Carapace 3.0 mm long, 2.5 wide, 1.6 wide behind lateral eyes 1.6. First legs lost. Second patella and tibia 3.2 mm, third 2.0, fourth 3.0.

Male paratype. Color as in female except carapace darker orange, with white setae and scales in cephalic region, and legs without rings but distally darker. Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.7. Anterior median eyes 1.2 diameters apart. Posterior median eyes 1.5 diameters apart. Ocular quadrangle narrower behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Third, fourth coxae without macroseta. Abdomen as in female. Total length 3.4 mm. Carapace 2.0 mm long, 1.5 wide, 0.8 wide behind lateral eyes 0.8 wide. First femur 2.9 mm, patella and tibia 3.1, metatarsus 1.7, tarsus 0.6. Second patella and tibia 2.6 mm, third 0.3, fourth 1.7.

Note. Males and females were matched because they came from the same locality and have similarly shaped abdomens.

Diagnosis. The female differs from that of *O. darlingtoni* (Figs. 329–331) by having a wider scape of the epigynum (Fig. 334) with a sharper curve in lateral view (Fig. 336), the male differs from all other species by having a median apophysis "higher" than long (Figs. 338, 339).

Paratype. From type locality, 19 May 1975, ♂ (J. A. Kochalka, MCZ).

Ocrepeira lapeza new species
Plate 1; Figures 340–344; Map 6

Holotype. Female holotype from Hacienda Mozambique, 500 m, 15 km SW of Puerto Lopez, Depto. Meta, Colombia (W. Eberhard, 1491), in MCZ. The specific name is an arbitrary combination of letters.

Description. Female holotype. Carapace orange, dusky between median and lateral eyes, and with paired dusky spots. Chelicerae, labium, endites orange. Sternum dark orange with three pairs of lighter patches. Coxae orange with dusky patches; legs orange, only fourth with dark rings. Dorsum of abdomen black anteriorly with a median brown mark posteriorly (Fig. 343); venter black with two pairs of white spots and a white patch on each side of booklungs (Fig. 344). Posterior median eyes same diameter as anterior medians, laterals 0.9 diameter. Anterior median eyes their diameter apart, 2.5 diameters from laterals. Posterior median eyes their diameter apart, 4 diameters from laterals. Ocular quadrangle narrower behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Abdomen as in Figure 343. Total length 9.0 mm. Carapace 4.1 mm long, 3.0 wide, 1.8 wide behind lateral eyes. First femur 4.2 mm, patella and tibia 5.2, metatarsus 3.1, tarsus 1.2. Second patella and tibia 4.5 mm, third 2.7, fourth 4.6.

Note. The abdomen of the holotype is damaged and separate from the cephalothorax. The carapace has the spots (Fig. 343), and the sternum the pattern of a *Parawixia* species (Levi, 1992, fig. 6). The parts probably belong together.

Diagnosis. The female differs from others by having a minute scape and two dark spots in ventral view (Fig. 340).

Natural History. Plate 1 illustrates the orb web of *O. lapeza*.

Ocrepeira aragua new species
Figures 345–347; Map 6

Holotype. Male holotype from Rancho Grande, near Maracay, Est. Aragua, Venezuela, 14–31 Mar. 1946, in AMNH. The specific name is a noun in apposition after the type locality.

Description. Male holotype. Carapace orange, sides of thoracic region darker. Chelicerae, labium, endites orange. Sternum light orange. Legs orange. Dorsum of abdomen with paired black spots forming outline of a folium (Fig. 347). Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.8. Anterior median eyes 0.9 diameter apart. Posterior median eyes their diameter apart. Ocular quadrangle narrower behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Fourth coxa with one macroseta. Fourth trochanter with one macroseta. Abdomen with distinct lateral tubercles (Fig. 347). Total length 3.2 mm. Carapace 1.9 mm long, 1.6 wide, 0.9 wide behind lateral eyes. First femur 2.3 mm, patella and tibia 2.5, metatarsus 1.7, tarsus 0.7. Second patella and tibia 2.1 mm, third 1.1, fourth 1.8.

Diagnosis. The male differs from others in the projection on the "lower" edge of the widest area of the median apophysis (Figs. 345, 346).

Ocrepeira maraca new species
Figures 348–353; Map 6

Holotype. Female holotype from Estação Ecológica de Maracá, Ilha de Maracá, Rio Uraricoera, Roraima Territ., Brazil, 25 July 1987 (L. P. Albuquerque), in MCN no. 19282. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace orange, cephalic region darkest. Chelicerae, labium, endites orange. Sternum orange. Coxae orange; legs orange. Dorsum of abdomen white, anterior black (Fig. 351); venter light dusky. Posterior median eyes same diameter as anterior medians, laterals 0.7 diameter. Anterior median eyes 0.8 diameter apart. Posterior median eyes 0.8 diameter apart on only slight swelling. Ocular quadrangle narrower behind than in front. Height of clypeus equal to 0.6 diameter of anterior median eye. Abdomen shield-shaped (Fig. 351). Total length 7.0 mm. Carapace 3.1 mm long, 2.5 wide, 1.5 wide behind lateral eyes. First femur 3.2 mm, patella and tibia 4.0, metatarsus 2.5, tarsus 1.0. Second patella and tibia 3.7 mm, third 2.0, fourth 3.1.

Male paratype from type locality. Color lighter than in female. Dorsum of abdomen framed by black, sides black grading ventrally into dusky venter. Posterior median eyes 0.9 diameter of anterior medians, anterior laterals 0.7 diameter. Anterior median eyes their diameter apart. Posterior median eyes 1.1 diameters apart and each on a swelling. Ocular quadrangle narrower behind than in front. Height of clypeus equal to 0.8 diameter of anterior median eyes. Third, fourth coxae each with one long macroseta. Fourth trochanter with one macroseta. Total length 4.7 mm. Carapace 2.5 mm long, 1.9 wide, 0.9 wide behind lateral eyes. First femur 2.7 mm, patella and tibia 3.2, metatarsus 1.7, tarsus 0.8. Second patella and tibia 2.6 mm, third 1.5, fourth 2.1.

Note. Males and females were collected together. The epigynum appears as if the

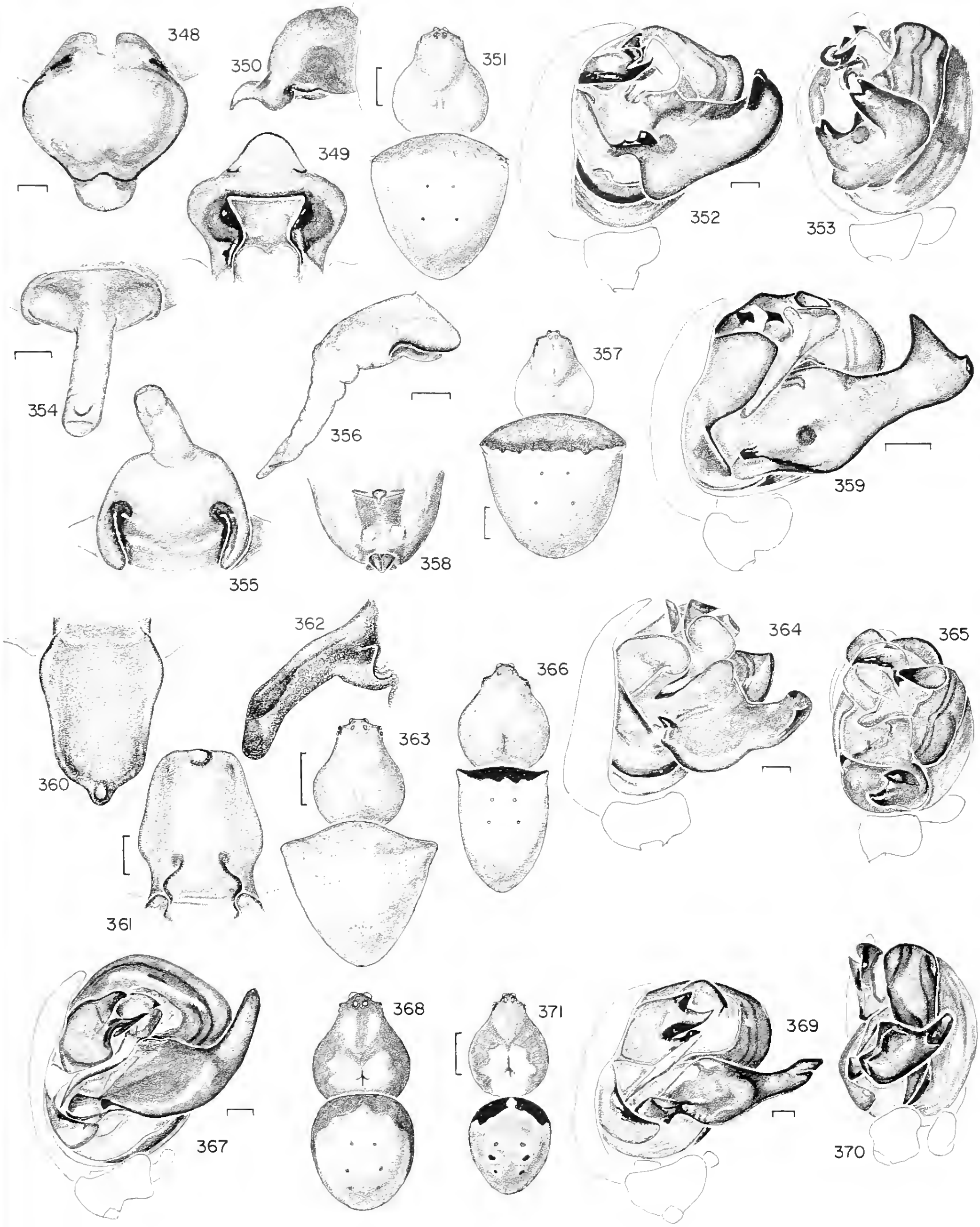
---

→

Figures 348–353. *Ocrepeira maraca* n. sp. 348–351, female. 348–350, epigynum. 348, ventral. 349, posterior. 350, lateral. 351, dorsal. 352, 353, left male palpus.

Figures 354–359. *O. yaelae* n. sp. 354–358, female. 354–356, epigynum. 354, ventral. 355, posterior. 356, lateral. 357, dorsal. 358, abdomen, ventral. 359, male palpus.

Figures 360–363. *O. duocypha* (Chamberlin), female. 360–362, epigynum. 360, ventral. 361, posterior. 362, lateral. 363, dorsal.



Figures 364–366. *O. jacara* n. sp., male. 364, 365, palpus. 366, dorsal.

Figures 367, 368. *O. comaina* n. sp., male. 367, palpus. 368, dorsal.

Figures 369–371. *O. heredia* n. sp., male. 369, 370, palpus. 371, dorsal.

Scale lines. 1.0 mm, genitalia 0.1 mm.

tip of the lobe might break when mating, but none were torn.

Variation. Total length of females 5.8 to 9.0 mm, of males 3.9 to 4.7. Illustrations were made from specimens from Terr. Roraima.

Diagnosis. The posterior median eyes of this species, unlike those of most *Ocrepeira* species, face dorsally (Fig. 351). The short round scape or lobe of the epigynum, with a dark, curved line at its base (Figs. 348, 350), and the "deep" position of the posterior median plate (Fig. 349) readily separate females from those of other species. The male has only a small terminal apophysis and two teeth at the base of the median apophysis (Figs. 352, 353).

Specimens Examined. VENEZUELA *Carabobo:* San Esteban, 26 Jan. 1940, ♂ (P. Andruze, AMNH). COLOMBIA *César:* La Jagua, 15 km S Becerril, 20–21 July 1968, 2♀, 2 imm. (B. Malkin, AMNH). BRAZIL *Roraima:* Estac. Ecol. Maracá, 29. Mar. 1987, ♂ paratype (M. E. L. de Souza, INPA). *Amazonas:* Maués, 1 Aug. 1983, ♀ (L. P. Alberquerque, INPA); Manaus, Reserva Ducke, Aug. 1971, ♀ (M. E. Galiano, MEG). *Pará:* Fazenda Velha, Belém, July 1970, ♀ (M. E. Galiano, MEG); Jacaré-Acanga, Dec. 1968, 3♀, ♂ (M. Alvarenga, AMNH). *Mato Grosso:* 260 km N Xavantina, 12°49'S, 51°46'W, 400 m, Feb.–Apr. 1969, 2♂ (Xavantina-Cachimbo Exped., MCZ).

Ocrepeira yaelae new species
Figures 354–359; Map 6

Holotype. Male holotype and female paratype from Río Palenque, 47 km SW of Santo Domingo de los Colorados, road to Quevedo, 150 m, Pichincha Prov., Ecuador, 14 Mar. 1982 (Y. D. Lubin, YDL-378), in MCZ. The species is named after collector and colleague Yael Lubin.

Description. Female paratype from Via Puerto Quito. Carapace orange, darker anteriorly; clypeus with dark dusky transverse band. Chelicerae, labium, endites dusky orange. Sternum dusky orange. Coxae, legs dusky orange. Dorsum of abdomen white, anterior black (Fig. 357); sides black, sharply bordered toward dorsum, grading into dusky venter. Venter with two indistinct white patches (Fig. 358). Posterior median eyes same diameter as anterior medians, anterior laterals 0.7 diameter, posterior laterals 0.6. Anterior median eyes 0.8 diameter apart. Posterior median eyes their diameter apart. Lateral eyes separated by 0.4 diameter of posterior laterals. Posterior median eyes on very slight swelling. Ocular quadrangle square. Height of clypeus equal to 0.6 diameter of anterior median eyes. Abdomen shield-shaped (Fig. 357). Total length 7.0 mm. Carapace 2.8 mm long, 2.4 wide, 1.4 wide behind lateral eyes. First femur 2.9 mm, patella and tibia 3.5, metatarsus 2.2, tarsus 0.9. Second patella and tibia 3.4 mm, third 1.9, fourth 2.7. Abdomen 4.9 mm long.

Male paratype from Pedro Vicente Maldonado. Coloration as in female but carapace with elongate dusky patch on each side of thoracic region, reddish around swollen posterior median eyes. Abdomen with white cardiac mark in center of dark area anterior to and between tubercles, posteriorly with four pairs of streaks outlining a folium. Posterior median eyes 0.9 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart, slightly more than 1 diameter from laterals. Posterior median eyes 0.8 diameter apart, slightly more than 2 diameters from laterals. Posterior median eyes on slight swelling facing sides. Third coxa with small macroseta, fourth with macroseta on a tubercle. Fourth trochanter without macroseta. Total length 3.9 mm. Carapace 2.0 mm long, 1.5 wide, 0.8 wide behind lateral eyes. First femur 2.2 mm, patella and tibia 2.5, metatarsus 1.5, tarsus 0.7. Second patella and tibia 2.1 mm, third 1.3, fourth 1.8.

Note. Males and females were collected together.

Variation. The male holotype, not the paratype described, has a macroseta on the fourth trochanter. Total length of females 4.8 to 7.0 mm, of males 3.6 to 3.9. Figures 354–358 were prepared from the paratype from Via Puerto Quito, Figure 359 was made from the paratype from Pedro Vicente Maldonado.

Diagnosis. The female differs from many *Ocrepeira* females by having the posterior median eyes face dorsally (Fig. 357), and from all by the weakly sclerotized epigynum having a scape with parallel sides (Fig. 354) and having a very wide posterior median plate framed by small lateral plates (Fig. 355). The male differs from all others by the very distinctive shape of the median apophysis, with a dark round spot on its widest area (Fig. 359).

Natural History. A female was found at night in an asymmetrical vertical orb, 20 cm below hub, 10 cm above; the male holotype was on the periphery of the web. The habitat was dense, old, very wet second-growth rain forest understory (Y. Lubin, personal communication). Female paratypes from Tinalandia were hand-collected, the male was collected as a result of beating vegetation.

Specimens Examined. ECUADOR *Pichincha:* 4 km NE of Pedro Vicente Maldonado, km 113 on road from Quito to Puerto Quito, ENDESA Compartamento Madereiro, 0°05′N, 79°07′W, 9–12 July, 1988, ♂ (W. Maddison, MCZ 88-014); Tinalandia, 12 km E Santo Domingo de los Colorados, 750 m, 11–17 May 1986, ♀, ♂, 5 imm. (G. B. Edwards, FSCA); Via Puerto Quito, km 113, 31 Oct. 1984, ♀ (L. Avilés, MECN). *Bolívar:* Balzapampa, 700–900 m, May 1938, ♀ (W. Clarke-Macintyre, AMNH). *Loja:* betw. Celica and Alamor, 1,100–2,200 m, 16–17 Aug. 1977, ♀ (L. Peña, AMNH).

Ocrepeira duocypha (Chamberlin), new combination
Figures 360–363; Map 6

Araneus duocyphus Chamberlin, 1916: 256, pl. 18, figs. 8–10, ♀. Female holotype from Huadquina, 5,000 ft [1,500 m], Depto. Cuzco, Peru, in MCZ, examined. Bonnet, 1955: 469.
Aranea duocypha:—Roewer, 1942: 841.

Description. Female holotype. Carapace orange. Chelicerae, labium, endites orange. Sternum orange. Legs orange with faint longitudinal darker lines. Dorsum of abdomen orange-white, anterior to a line between tubercles are dark stipples (Fig. 363); venter light, without marks. Eyes small, subequal. Anterior median eyes 1.8 diameters apart, 1.8 diameters from laterals. Posterior median eyes 1.7 diameters apart, 2.1 diameters from laterals. Ocular quadrangle square, posterior median eyes on swellings (Fig. 363). Height of clypeus equal to 1 diameter of anterior median eyes. Abdomen with pointed tubercles (Fig. 363). Total length 4.3 mm. Carapace 2.0 mm long, 1.7 wide, 0.9 wide behind lateral eyes. First femur 2.5 mm, patella and tibia 2.8, metatarsus 1.5, tarsus 0.6. Second patella and tibia 2.7 mm, third 1.4, fourth 1.9.

Diagnosis. The large flat scape of the epigynum (Figs. 360–362) separates this species from all other *Ocrepeira*. The epigynum resembles that of *Alpaida banos* Levi from Ecuador.

Ocrepeira jacara new species
Figures 364–366; Map 6

Holotype. Male holotype from Fazenda Jacaranda, Itamarajú, Bahia State, Brazil, 9 Dec. 1977 (J. S. Santos), in MCN no. 11122. The specific name is an arbitrary combination of letters.

Description. Male holotype. Carapace, chelicerae, labium, endites, sternum, legs orange. Abdomen, white dorsally with anterior black (Fig. 366), venter gray. Posterior median eyes 0.5 diameter of anterior medians, laterals 0.4 diameter. Anterior median eyes 0.6 diameter apart. Posterior median eyes their diameter apart and on swelling. Ocular quadrangle narrower behind than in front. Height of clypeus equal to 0.6 diameter of anterior median eyes. Third, fourth coxae each with one macroseta. Fourth trochanter with one macroseta. Abdomen shield-shaped (Fig. 366). Total length 3.8 mm. Carapace 2.4 mm long, 1.8 wide, 0.9 wide behind lateral eyes. First femur 2.7 mm, patella and tibia 2.9, metatarsus 1.9, tarsus 0.6. Second patella and tibia 2.5 mm, third 1.5, fourth 2.0. Abdomen 2.1 mm long.

Note. The male is in poor condition, the palpi are transparent as if the specimen had once been dry.

Variation. Total length of males 3.8 to 4.4. Figures were made from the holotype, and soft parts may be slightly deformed because of its poor condition.

Diagnosis. As is the case for *O. yaelae* (Fig. 359), the radix of the palpus has a large sclerotized lobe (Fig. 364). The shape of the median apophysis and the presence of a tooth on its base (Figs. 364, 365) distinguish the species from *O. yaelae* (Fig. 359).

Specimen Examined. BRAZIL *São Paulo:* Estrada Santa Amaro, Engo. Marcilac, km 48, 15 Jan. 1961, ♂ (F. Werner, MZSP 7964).

Ocrepeira comaina new species
Figures 367, 368; Map 6

Holotype. Male holotype and male paratype from Alto Río Comaina, 04°27'S, 78°13'W, Puesto de Vigilancia 22, "Falso Paquisha," 850–1,150 m, Depto. Amazonas, Peru, 21 Oct.–3 Nov. 1987 (D. Silva D.), in MUSM. The specific name is a noun in apposition after the type locality.

Description. Male holotype. Cephalic region with dusky marks on light orange; sides of carapace with dusky marks. Sternum light orange, legs light orange with indistinct darker rings. Abdomen white dorsally, sides black (Fig. 368); venter light dusky. Posterior median eyes 0.7 diameter of anterior medians, anterior laterals 0.5 diameter, posterior laterals 0.5. Anterior median eyes 0.7 diameter apart, 0.3 diameter from laterals. Posterior median eyes 0.8 diameter apart, 1.6 diameters from laterals. Posterior median eyes not on swelling, facing dorsally. Ocular quadrangle narrower behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Third, fourth coxae each with one macroseta. Fourth trochanter with one macroseta. Abdomen oval without humps (Fig. 368). Total length 4.2 mm. Carapace 2.2 mm long, 1.9 wide, 0.8 wide behind lateral eyes. First femur 2.2 mm, patella and tibia 2.7, metatarsus 1.7, tarsus 0.7. Second patella and tibia 2.4 mm, third 1.4, fourth 2.0.

Diagnosis. The terminal apophysis, unlike that of *O. albopunctata* (Fig. 377) is a small, simple thorn (Fig. 367). The base of the median apophysis (Fig. 367) lacks the sculpturing present in *O. herrera* (Fig. 391) and *O. covillei* (Fig. 402).

Ocrepeira heredia new species
Figures 369–371; Map 6

Holotype. Male holotype from 1 km N of Montaña Azul, 1,500 m, cloud forest, Heredia Prov., Costa Rica, 7–8 May 1987 (D. Ubick), in CAS. The specific name is a noun in apposition after the type locality.

Description. Male holotype. Carapace yellowish, cephalic region and sides of thoracic region darker. Chelicerae yellowish, proximally dusky. Labium, endites, sternum yellowish. Legs yellowish with indistinct darker rings. Anterior of dorsum of abdomen black, divided by a white cardiac mark; posterior white with paired dark spots having light rings (Fig. 371); venter dusky with a pair of white patches. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 0.5 diameter apart. Posterior median eyes 0.8 diameter apart. Ocular quadrangle narrower behind than in front. Posterior median eyes on slight swelling. Height of clypeus equal to 0.3 diameter of anterior median eyes. Third, fourth coxae each with one macroseta. Fourth trochanter with one macroseta on left side only. Abdomen without distinct humps (Fig. 371). Total length 4.8 mm. Carapace 2.5 mm long, 2.1 wide, 1.0 wide behind lateral eyes. First femur 3.2 mm, patella and tibia 3.7, metatarsus 2.5, tarsus 1.0. Second patella and tibia 3.0 mm, third 1.8, fourth 2.7.

Diagnosis. Ocrepeira heredia male differs from the male *O. comaina* (Fig. 367), *O. herrera* (Fig. 391), and *O. covillei* (Fig. 402), which also lack distinct humps on the abdomen, by the shape of the median apophysis, whose prong has two tips with a notch in between (Figs. 369, 370).

Ocrepeira albopunctata (Taczanowski), new combination
Figures 372–379; Map 6

Tricantha albopunctata Taczanowski, 1879: 123, pl. 2, fig. 36, ♂. Male holotype and 2 imm. paratypes from Amable María, Depto. Junín, Peru, in PAN, examined.

Araneus albopunctatus:—Simon, 1895: 817. Bonnet, 1955: 426.

Aranea albopunctata:—Roewer, 1942: 837.

Singa essequibensis:—Mello-Leitão, 1948: 17. Probably erroneous determination.

Araneus trigonellus di Caporiacco, 1954: 107, fig. 26, ♀. Female holotype from Charvein, French Guiana, in MZUF, examined. Brignoli, 1983: 263. NEW SYNONYMY.

Synonymy. Tricantha Simon, the original genus of *albopunctata* is a theridiid with the type species *T. tricornis* Simon, 1864, and a subjective synonym of *Phoroncidia* (Levi and Levi, 1962). A specimen in the British Museum, collected by Hingston, labeled *Singa essequibensis* (Hingston) by Mello-Leitão, is *O. albopunctata*. But Hingston's (1932) description of *Epeira essequibensis* from Essequibo River, Guyana, with the type lost, is unrecognizable: "greyish-brown with distinct black spot in center of dorsum and two sinuous brown lines that start at the shoulders and converge toward the apex which they almost reach, ventral surface greyish-brown with a short median white longitudinal band. Total length 7 mm." The light median area of the venter of the abdomen suggests that it may have been a *Eustala*. The *Araneus trigonellus* holotype is a female in poor condition and has a relatively narrow cephalic region (examined in 1973). One opening of its epigynum is covered by a scale from the male palpus.

Description. Female from Pasco, Peru. Carapace orange. Chelicerae, labium, endites orange. Sternum orange. Coxae, legs orange. Dorsum of abdomen with anterior black, posterior white (Fig. 376); sides of venter black, sharply bordered toward dorsum, white but ventrally grading into gray and black. Posterior median eyes same diameter as anterior medians, anterior laterals 0.9 diameter, posterior laterals 0.8. Anterior median eyes 1.1 diameters apart. Posterior median eyes 1.1 diameters apart. Posterior median eyes on very slight swelling facing anterolaterally (Fig. 376). Ocular quadrangle slightly longer than wide. Height of clypeus equal to 1 diameter of anterior median eyes. Abdomen shield-shaped (Fig. 376). Total length 7.5 mm. Carapace 3.9 mm long, 3.0 wide, 1.8 wide behind posterior median eyes. First femur 3.7 mm, patella and tibia 4.5, metatarsus 3.1, tarsus 1.3. Second patella and tibia 4.4 mm, third 2.4, fourth 3.4.

Male holotype of *T. albopunctata*. Coloration as in female. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes their diameter apart, slightly more than 2 diameters from laterals. Posterior median eyes 1.2 diameters apart, 3 diameters from laterals. Posterior median eyes on slight swelling facing sideways. Third coxa with small macroseta, fourth with strong macroseta. Total length 4.2 mm. Carapace 2.6 mm long, 1.9 wide. First femur 2.7 mm, patella and tibia 3.0, metatarsus 1.8, tarsus 0.9. Second patella and tibia 2.3 mm, third 1.4, fourth 2.0.

Note. Males and females were collected in the same area in Mato Grosso, Brazil. Virgin males have the large scale in the palpus attached to the base of the embolus (Fig. 379), which is found in the epigynum of mated females (Fig. 373).

Variation. Taczanowski (1879, pl. 2, fig. 36) illustrates the abdomen; it is handcolored green. The radix of the male palpus has a large projection that supports the scale at the base of the embolus (Fig. 379). The scale is absent in mated males (Fig. 377). Some males lack the macroseta on coxae and trochanters entirely. Others have them on the fourth trochanter and coxa, the one on the coxa being on a tubercle. The conductor is much smaller and the paramedian apophysis wider in some individuals than in the specimen illustrated (Fig. 377) which, except for the scale, is similar to the holotype. Total length of females 7.0 to 10.0 mm, of males 3.0 to 4.7. The holotype of *T. albopunctata* is a virgin male. Illustrations (Figs. 372–374, 376) were made from specimens from Depto. Pasco, Peru; Figure 375 was made from a female from Mato Grosso State, Brazil, Figure 377 from Mato Grosso, Figure 378 from Depto. Madre de Dios, Peru, and Figure 379 from a male from Amazonas State, Brazil.

Diagnosis. The female is separated from *O. viejo* (Fig. 380) by the anterior attachment of the scape on the base of the epigynum (Figs. 372, 375). The male differs from *O. viejo* (Figs. 385, 386) by the shape of the terminal apophysis and the distal tip of the median apophysis, which is wide and has two points (Figs. 377, 378).

Natural History. Two males from Mato Grosso, Brazil, were collected, one in a gallery forest, the other in campo-grassland. The female from Juanjui, Peru, was collected at night.

Specimens Examined. GUYANA Moraballi Riv., Essequibo Riv., 15 mi. above Bartica, ♀ (R. W. G. Hingston, BMNH); "[?] Brazil, Kartabo" (Kartabu Point, Mazaruni-Potaro Prov.), 06°23'N, 58°41'W, Apr. 1924, ♀ (W. Beebe, AMNH). PERU *San Martín:* Juanjui, 350 m, 16–24 Aug. 1978, ♀ (D. Silva D., MUSM). *Huánuco:* Monzon Valley, Tingo María, 20 Nov. 1954, ♀ (E. I. Schlinger, E. S. Ross, CAS). *Pasco:* Quebrada Chispa, NW Iscozacin, 345 m, Huancabamba, 10°10'S, 75°15'W, 29 Oct. 1986, 2♀ (D. Silva D., MUSM). *Cuzco:* Paltaybamba [Paltaypampa], 2 imm. paratypes (K. Jelski, J. Sztolcman, PAN). *Madre de Dios:* Iberia, 30 Apr. 1947, ♂ (J. C. Pallister, AMNH). BRAZIL *Amazonas:* Manaus, Reserva Ducke, Aug. 1971, ♂ (M. E. Galiano, MEG). *Rondônia:* Madeira-Mamoré, railway camp, 1911, ♀ (W. M. Mann, MCZ); Fazenda Rancho Grande, NE Caculandia, Dec. 1990, ♂ (G. B. Edwards, FSCA). *Mato Grosso:* 260 km N Xavantina, 12°39'S, 51°46'W, 400 m, Feb.–Apr. 1969, 2♂ (Xavant.-Cachimbo Exped., MCZ); Barra dos Bugres, Nov. 1938, ♀, ♂ (A. Cerrutti, MNRJ).

Ocrepeira viejo new species
Figures 380–386; Map 6

Holotype. Female holotype and male paratype from La Selva, 4 km SE of Puerto Viejo, Heredia Prov., Costa Rica, from wasp trap nest, 20 Sept. 1981 (R. E. Coville, AR07), in MCZ. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace, chelicerae, labium, endites, sternum, coxae, legs orange. Dorsum of abdomen white framed by black (Fig. 384); black sides fading ventrally into colorless venter. Posterior median eyes same diameter as anterior medians, anterior laterals 0.7 diameter, posterior 0.8. Anterior median eyes 1.2 diameters apart. Posterior median eyes 1.3 diameters apart. Ocular quadrangle square. Height of clypeus equal to 1 diameter of anterior median eyes. Abdomen shield-shaped (Fig. 384). Total length 5.0

⟶

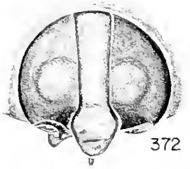
Figures 372–379. *Ocrepeira albopunctata* (Taczanowski). 372–376, female. 372–375, epigynum. 372, 375, ventral. 373, posterior. 374, lateral. 376, dorsal. 377–379, male. 377, 378, left male palpus. 379, embolus, terminal apophysis (A), conductor (C), radix (R), paramedian apophysis (PM), and scale to be transferred to epigynum (SC).

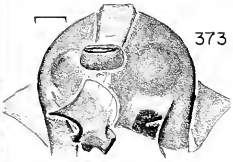
Figures 380–386. *O. viejo* n. sp. 380–383, female. 380–382, epigynum. 380, ventral. 381, 383, posterior. 382, lateral. 383, with scale from male palpus. 384, dorsal. 385, 386, male palpus.

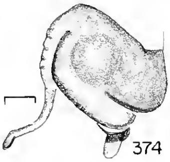
Figures 387–391. *O. herrera* n. sp. 387–390, female. 387–389, epigynum. 387, ventral. 388, posterior. 389, lateral. 390, dorsal. 391, male palpus.

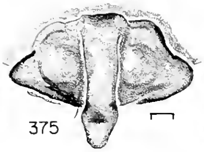
Figures 392–402. *O. covillei* n. sp. 392–401, female. 392–398, epigynum. 392, 395, 397, ventral. 393, 396, 398, posterior. 399, dorsal. 400, abdomen, dorsal. 401, abdomen, ventral. 402, male palpus.

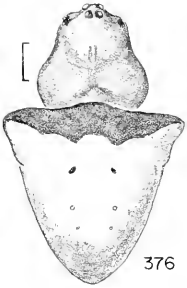
Scale lines. 1.0 mm, genitalia 0.1 mm.

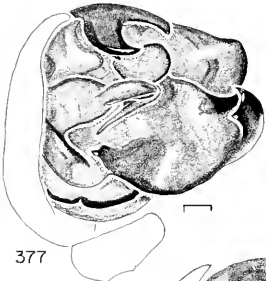

372

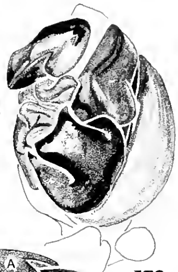

373

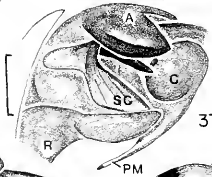

374

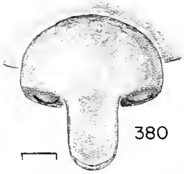

375

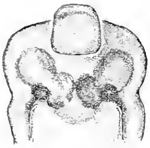

376

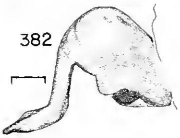

377

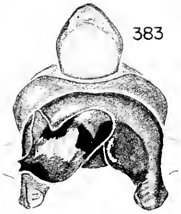

378

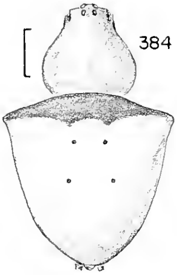

379

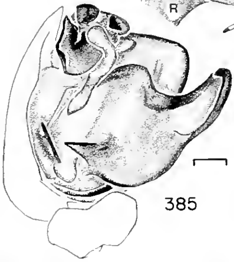

380


381

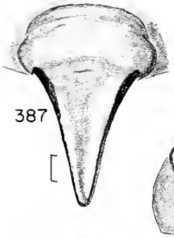

382


383

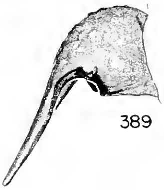

384

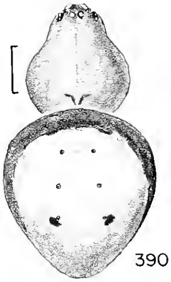

385

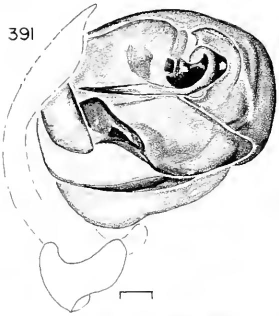

386

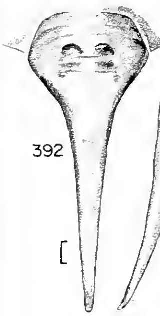

387


388

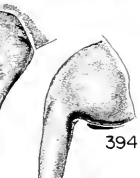

389

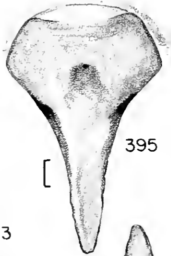

390

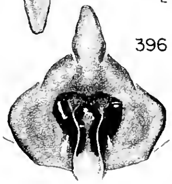

391

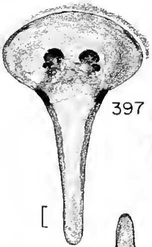

392

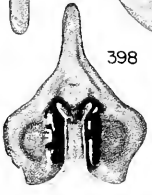

393

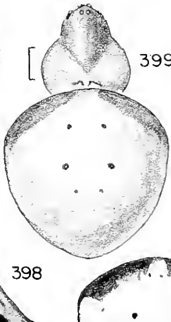

394


395


396

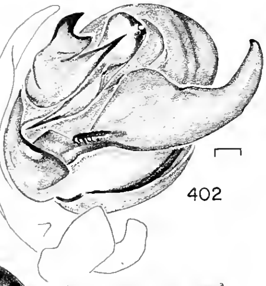

397


398


399


400


401


402

mm. Carapace 2.7 mm long, 2.1 wide, 1.4 wide behind lateral eyes. First femur 2.9 mm, patella and tibia 3.4, metatarsus 2.2, tarsus 0.9. Second patella and tibia 3.2 mm, third 1.9, fourth 2.7. Abdomen 3.8 mm long.

Male paratype from Costa Rica. Color as in female. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes their diameter apart. Posterior median eyes 1.1 diameters apart. Ocular quadrangle wider in front than behind. Height of clypeus equal to 1 diameter of anterior median eyes. Fourth coxa with one macroseta. Fourth trochanter with one macroseta on right only. Abdomen as in female. Total length 3.9 mm. Carapace 2.1 mm long, 1.4 wide, 0.8 wide behind lateral eyes. First femur 2.2 mm, patella and tibia 2.5, metatarsus 1.5, tarsus 0.7. Second patella and tibia 2.0 mm, third 0.5, fourth 1.5.

Note. Males and females were collected together. Figures 380–382, 384 were made from the holotype, Figures 385, 386 from the male collected with the holotype, Figure 383 was made from a female from near Iquitos, Peru.

Variation. Total length of females 5.0 to 7.7 mm, of males 3.2 to 3.9. Females from Panama and some others have in posterior view of the epigynum a slight transverse lip dorsal to the scape and ventral to the dark areas, and a depression between this lip and the scape (Fig. 383). A male from Panama has no macroseta on the coxae and one small macroseta on each fourth trochanter.

Diagnosis. The species has a relatively narrow cephalic area, but the posterior median eyes are on a slight swelling. *Ocrepeira viejo* differs from *O. albopunctata* (Figs. 372, 374) by having its scape attached to the posterior of the base of the epigynum (Figs. 380, 382). The male differs from *O. albopunctata* (Figs. 377, 378) in the different shape of the terminal apophysis and the narrow prong of the median apophysis which also has a flat conical offset at its base (Figs. 385, 386).

Natural History. A female from Costa Rica came from foliage in a wet tropical forest, another from Panama from a canopy.

Specimens Examined. COSTA RICA *Limón:* 5.5 km E Guápiles, 200 m, 9 May 1987, ♀ (D. Ubick, DU). PANAMA *Colón:* Fort Davis, Aug. 1936, ♂ (A. M. Chickering, MCZ). *Panamá:* Forest Reserve, Aug. 1936, ♀ (A. M. Chickering, MCZ); Barro Colorado Island, Lago Gatún, July 1936, ♀ (A. M. Chickering, AMNH); Pipeline Road, 12 July 1976, ♀ (G. Montgomery, Y. Lubin, JAK). VENEZUELA *Carabobo:* San Esteban, 26 Jan. 1940, ♀ (P. Andruze, AMNH). *Sucre:* Caripito,15 Aug. 1968, ♀ (J. M. Osorio, FSCA). COLOMBIA *Santander:* Río Opón, Jan. 1947, ♀ (L. Richter, AMNH). *Nariño:* Barbacoas, 20 Mar. 1974, ♂ (W. Eberhard, MCZ); La Planada, 7 km S Chocones, 1,800 m, July 1986, ♂ (W. Eberhard, MCZ). PERU *Loreto:* Explorama Inn, 40 km NE Iquitos, 19–21 July 1989 (H. V. Weems, FSCA). *Junín:* Utcuyacu, 8–26 Feb. 1948, ♀ (F. Woytkowski, AMNH).

Ocrepeira herrera new species
Figures 387–391; Map 6

Holotype. Female holotype from Genaro Herrera, 04°55'S, 73°45'W, Río Ucayali, 100 m, Depto. Loreto, Peru, 24 Aug. 1988, (D. Silva D.), in MUSM. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace orange, eye region darkest. Chelicerae, labium, endites orange. Sternum orange. Coxae, legs orange. Dorsum of abdomen white, framed by black and containing a pair of black spots (Fig. 390); venter dusky. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.5 diameter. Anterior median eyes 0.7 diameter apart, 0.8 diameter from laterals. Posterior median eyes 0.8 diameter apart, 2 diameters from laterals. Posterior median eyes facing up, not on swelling. Ocular quadrangle wider than long, narrower behind than in front. Height of clypeus equal to 0.5 diameter of anterior median eyes. Abdomen oval (Fig. 390). Total length

5.5 mm. Carapace 2.7 mm long, 2.2 wide, 1.0 wide behind lateral eyes. First femur 2.7 mm, patella and tibia 3.5, metatarsus 2.3, tarsus 1.0. Second patella and tibia 3.1 mm, third 2.0, fourth 2.7.

Male paratype. Coloration as in female but carapace orange with four black streaks radiating anteriorly from thoracic groove, cephalic region and sides of head dusky, sides of thoracic region with dusky patches. Legs with dusky rings on distal articles. Dorsum of abdomen greenish white with black anterior and sides, and two tiny black spots in middle. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.5 diameter. Anterior median eyes 0.8 diameter apart, 0.5 diameter from laterals. Posterior median eyes their diameter apart, 2 diameters from laterals. Ocular quadrangle narrower behind than in front. Height of clypeus equal to 0.3 diameter of anterior median eyes. Third and fourth coxae each with one macroseta. Fourth trochanter with one macroseta. Total length 4.4 mm. Carapace 2.3 mm long, 1.9 wide, 0.8 wide behind lateral eyes. First femur 2.2 mm, patella and tibia 2.7, metatarsus 1.8, tarsus 0.7. Second patella and tibia 2.5 mm, third 1.3, fourth 2.0.

Note. Male and female were matched because both have posterior median eyes facing up and both may have a similar pair of black spots on the oval abdomen.

Variation. Total length of females 5.2 to 6. 4 mm. Several females lack the black spots on the abdomen. Illustrations were prepared from the female holotype and a male from Depto. Pasco, Peru.

Diagnosis. The female differs from that of most other species by having the posterior median eyes facing dorsally and an oval abdomen (Fig. 390). It differs from all by the triangular, rugose posterior median plate of the epigynum (Fig. 388). The male has only a lobe as terminal apophysis and, unlike *O. comaina* (Fig. 367), a short median apophysis (Fig. 391).

Specimens Examined. ECUADOR *Napo:* Pompeya, Río Napo, May 1965, ♀ (L. Peña, MCZ). PERU *Loreto:* Iquitos, May 1920, ♀ (H. S. Parrish, MCZ). *Huánuco:* Huallaga Valley, Feb.–Apr. 1954, ♀ (F. Woytkowski, CAS). *Pasco:* Río Chispa, 345 m, NW of Iscozacin, 30–31 Oct. 1986, ♂ (D. Silva D., MUSM). *Madre de Dios:* Zona Reservada Tambopata, 14 May 1988, ♀, 15 May 1988, ♀ (D. Silva D., MUSM); Zona Reservada Pakitza, 11°58′S, 71°18′W, 6 Oct. 1989, ♀ (J. Coddington, D. Silva D., MUSM); Reservada Cuzco Amazonica, 15 km NE Puerto Maldonado, 12°33′S, 69°03′W, 22 June 1989, ♀ (D. Silva D., MUSM).

Ocrepeira covillei new species
Figures 392–402; Map 6

Holotype. Female holotype, two male paratypes from La Selva, 4 km SE Puerto Viejo, Heredia Prov., Costa Rica, 24 June 1980, from wasp nest (R. Coville, AR 01), in MCZ. The species is named after the collector.

Description. Female holotype. Carapace orange, cephalic region darker orange. Chelicerae, labium, endites dark orange. Sternum, coxae orange; legs dark orange. Dorsum of abdomen white, black anterolaterally (Fig. 399); venter dusky with a pair of white spots side by side (Fig. 401). Posterior median eyes same diameter as anterior medians, laterals 0.8 diameter. Anterior median eyes 0.9 diameter apart. Posterior median eyes 0.8 diameter apart. Laterals 0.4 diameter apart. Posterior median eyes without swelling, facing dorsally (Fig. 399). Ocular quadrangle square, slightly narrower behind than in front. Abdomen subspherical without humps (Fig. 399). Total length 8.0 mm. Carapace 3.2 mm long, 2.8 wide, 1.4 wide behind posterior median eyes. First femur 3.4 mm, patella and tibia 4.2, metatarsus 2.8, tarsus 1.0. Second patella and tibia 3.9 mm, third 2.4, fourth 3.5.

Male paratype collected with holotype. Color as in female but carapace orange with sides of thoracic region having darker patches. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes 0.7 diameter apart. Posterior median eyes 0.7

diameter apart. Ocular quadrangle almost square, slightly narrower behind than in front. Height of clypeus equal to 0.8 diameter of anterior median eyes. Sternum with four macrosetae in center. Third and fourth coxae each with one macroseta. Fourth trochanter with one short macroseta. Abdomen oval without humps. Total length 6.4 mm. Carapace 3.1 mm long, 2.5 wide, 1.1 wide behind lateral eyes. First femur 2.7 mm, patella and tibia 3.4, metatarsus 2.2, tarsus 0.9. Second patella and tibia 3.0 mm, third 2.0, fourth 2.8.

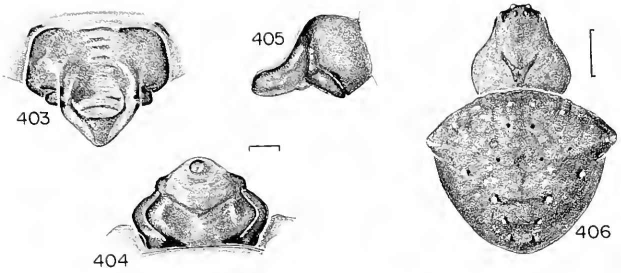
Variation. There is considerable variation and I first considered the specimens listed here to belong to several species. Specimens from Monterrico, Peru, have the ocular quadrangle narrower behind than in the holotype. The length and the width of the scape of the epigynum are variable (Figs. 392–398). One male lacks a macroseta on the third coxa on one side. Some males lack the macrosetae on the sternum. Total length of females 6.2 to 9.0 mm, of males 4.4 to 6.4. The illustrations (Figs. 392–394, 399, 401) were made from the holotype, Figures 395, 396 from a female from the Depto. Junín, Peru, Figures 397, 398 from Depto. Loreto, Peru, Figure 400 was made from a female from Amazonas State, Brazil, and Figure 402 from a male collected with the holotype.

Diagnosis. This species, unlike most, has a spherical abdomen, and the posterior median eyes face dorsally (Fig. 399). Females differ from other species by the shape of the scape and the narrow posterior median plate of the epigynum (Figs. 392–398) and from males by the shape of the terminal apophysis and the pointed tip of the median apophysis prong (Fig. 402).

Natural History. Most specimens were collected from wasp nests or wasp traps and others came from a rain forest.

Paratypes. COSTA RICA *Heredia:* La Selva nr. Puerto Viejo, Feb. 1981, ♂, Feb. 1986, ♂, June 1982, ♀ (W. Eberhard, TL32-1, MCZ), 20 June 1980, ♀, ♂ (R. Coville AR 05, MCZ); Feb. 1960, ♀ (W. Eberhard, 3235, MCZ).

Specimens Examined. TRINIDAD *St. George:* Simla, Arima Valley, 244 m, 27 June–3 July 1978, ♀ (B. Camilla, H. V. Weems, FSCA). GUYANA Kurupukari Riv., Essequibo Riv., 1 Oct. 1937, ♀ (Hassler, AMNH). SURINAM Paramaribo, Aug. 1967, ♀ (V. Doesburg, AMNH). COLOMBIA *Boyaca:* Río Upia, 850–950 m, Nov., Dec. 1945, ♀ (AMNH). *Meta:* Puerto Lleras, Lomalinda, 13 Sept. 1986, ♀ (B. T. Carroll, MCZ). ECUADOR 7♀ (von Hagen, AMNH). PERU *Loreto:* Chanchamayo Valley, 2♀ (W. Weyrauch, AMNH); Parque Nac. Pacaya Samiria, 04°39'S, 74°21'W, 12 Aug. 1989, ♀ (S. Silva D., MUSM); Estiron, Río Ampiyacu, 13 Nov.–9 Dec., ♀ (B. Malkin, AMNH); Iquitos ♀ (MCZ); Parinari Canyon, Río Samiria, Nov. 1912, ♀ (Bluntschli, AMNH). *Huánuco:* Tingo María, Apr. 1940, ♀ (W. Weyrauch, AMNH); 8 km W Las Palmas, 5 Oct. 1954, ♀ (E. S. Ross, E. I. Schlinger, CAS). *Pasco:* Huancabamba, Quebrada Castillo, NW Iscozacin, 345 m, 10°10'S, 75°15'W, 8♀ (D. Silva D., MUSM). *Junín:* Amable María, ♀ (K. Jelski, PAN). *Ayacucho:* Monterrico, E Huanta, on Río San Miguel, 12°28'S, 73°54'W, (K. Jelski, J. Sztolcman, PAN). *Madre de Dios:* Reserva Cuzco Amazonico, 12°33'S, 69°23'W, 15–17 June, 1989, 8♀ (D. Silva D., MUSM); Río Tambopata Reserve, 30 km SW Puerto Maldonado, Nov. 1982, ♀ (E. S. Ross, CAS), 18 June 1987, ♂, 17–25 July 1987, 3♀, 11–29 May 1988, 4♀, ♂, 2 imm. (D. Silva D., MUSM); Zona Reservada de Manu, Puesto de Vigilancia Pakitza, 11°58'S, 71°18'W, 26 Sept. 1987, 2♀ (J. Coddington, D.Silva D., MUSM), 9 Oct. 1987, 2♂ (D. Silva D., J. Coddington, USNM), 27 Nov. 1987, ♀ (J. Bohorquez, MUSM). BRAZIL *Roraima:* Estação Ecológica de Maracá, Ilha de Maracá, Rio Uraricoera, 29 Mar. 1987, ♂ (A. A. Lise, INPA). *Amazonas:* Rio Autás, Santa Amelia, 9 Sept. 1914, ♀ (A. Roman, NRMS); Manaus, Igapó Tarumá Mirim, 3 Oct. 1987, ♀, 11 Mar. 1988, ♀ (H. Höfer, INPA); Manaus, Reserva Ducke, 11 Apr. 1973, ♀ (L. P. Albuquerque, MCN, 19290); Manaus, Reserva Campina, 7 Dec. 1973,



Figures 403–406. *Ocrepeira sorota* n. sp., female. 403–405, epigynum. 403, ventral. 404, posterior. 405, lateral. 406, dorsal. *Scale lines.* 1.0 mm, genitalia 0.1 mm.

♀ (L. P. Albuquerque, MCN); Fazenda Esteio, Manaus, 11 Dec. 1985, ♂ (B. C. Klein, MCN 20052); Tabatinga, Aug. 1984, ♀ (A. Cerrutti, MNRJ). *Mato Grosso:* Utiariti, Nov. 1966, ♂ (F. Lenko, MZSP 5616). *Bahia:* Fazenda N. S. Das Neves, Itamarajú, 9 Oct. 1987, ♂ (J. S. Santos, MCN 11011); Fazenda Almada, Uruçuca, 27 Nov. 1977, ♂ (J. S. Santos, MCN 20052). BOLIVIA *La Paz:* Miguillas, 1,800 m, Irupana to Circuata, 2–3 Dec. 1984, ♂ (L. Peña, AMNH).

Ocrepeira sorota new species
Figures 403–406; Map 6

Holotype. Female holotype from Sorota, 2,800 m, Depto. La Paz, Bolivia, 11–14 Nov. 1984 (L. E. Peña), in AMNH. The specific name is a noun in apposition after the type locality.

Description. Female holotype. Carapace orange-brown, cephalic region gray to black. Chelicerae, labium, endites orange. Sternum orange. Coxae light orange; legs with femora orange, distally black, distal articles black; third femora with a black ring. Dorsum of abdomen black with irregular white spots and posteriorly paired white spots (Fig. 406); venter whitish gray, sides black. Eyes subequal. Anterior median eyes 1.3 diameters apart. Posterior median eyes 1.2 diameters apart. Ocular quadrangle slightly narrower behind than in front. Height of clypeus equal to 1 diameter of anterior median eyes. Abdomen as in Figure 406. Total length 5.5 mm. Carapace 2.7 mm long, 2.1 wide, 1.1 wide behind lateral eyes. First femur 3.1 mm, patella and tibia 3.4, metatarsus 2.1, tarsus 0.7. Second patella and tibia 3.2 mm, third 1.7, fourth 2.4.

Diagnosis. Ocrepeira sorota differs from all others by its black coloration (Fig. 406) and the unusual epigynum, having a median lobe with a lip and the posterior median plate raised above the lateral plates (Fig. 404).

LITERATURE CITED

ARCHER, A. F. 1958. Studies in the orbweaving spiders (Argiopidae) 4. American Museum Novitates, **1922:** 1–21.

———. 1966. Nuevos argiopidos de las Antillas. Caribbean Journal of Science, **5:** 129–133.

BERMAN, J. D., AND H. W. LEVI. 1971. The orbweaver genus *Neoscona* in North America (Araneae: Araneidae). Bulletin of the Museum of Comparative Zoology, **141**(8): 465–500.

BONNET, P. 1955. Bibliographia Araneorum. Toulouse, **2** (1): 1–918.

———. 1956. Bibliographia Araneorum. Toulouse, **2** (2): 919–1925.

———. 1959. Bibliographia Araneorum. Toulouse, **2** (5): 4231–5058.

BRIGNOLI, P. 1983. A Catalogue of the Araneae Described Between 1940 and 1981. Manchester: Manchester University Press, 755 pp.

BRYANT, E. B. 1936. Descriptions of some new species of Cuban spiders. Memorias de la Sociedad

Cubana de Historia Natural "Felipe Poey," **10**(5): 325–332.

———. 1940. Cuban spiders in the Museum of Comparative Zoology. Bulletin of the Museum of Comparative Zoology, **86:** 247–554.

———. 1945. The Argiopidae of Hispaniola. Bulletin of the Museum of Comparative Zoology, **95**(4): 357–418.

———. 1947. A list of spiders from Mona Island, with descriptions of new and little known species. Psyche, **54:** 86–99.

CAMARGO, H. F. DE A. 1950. Contribuição ao estudo das aranhas Brasileiras (Arachnida-Araneae). Papéis Avulsos do Departamento do Zoologia, São Paulo, **9**(15): 223–248.

CAMBRIDGE, F. P.-. 1904. Arachnida, Araneidea and Opiliones. **2:** 465–545. *In* Biologia Centrali-Americana, Zoologia, London.

CAMBRIDGE, O. P.-. 1882. On new genera and species of Araneidea. Proceedings of the Zoological Society of London, **1882:** 423–442.

———. 1889. Arachnida-Araneida. **1:** 1–56. *In* Biologia Centrali-Americana, Zoologia, London.

———. 1893. Arachnida-Araneida. **1:** 105–120. *In* Biologia Centrali-Americana, Zoologia, London.

———. 1894. Arachnida-Araneida. **1:** 121–144. *In* Biologia Centrali-Americana, Zoologia, London.

———. 1898. Arachnida-Araneida. **1:** 233–288. *In* Biologia Centrali-Americana, Zoologia, London.

CAPORIACCO, L. DI. 1954. Araignées de la Guyane Française du Muséum d'Histoire Naturelle de Paris. Commentationes, Pontificia Academia Scientiarum, **16:** 45–193.

CHAMBERLIN, R. V. 1916. Results of the Yale Peruvian Expedition of 1911. The Arachnida. Bulletin of the Museum of Comparative Zoology, **60**(6): 175–299.

CRANE, J. 1948. Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part I. Systematics and life histories in *Corythalia*. Zoologica, Scientific Contributions of the New York Zoological Society, **33**(1): 1–38.

DAHL, F. 1906. Symbiose, Kommensalismus, Parasitismus. Naturwissenschaftliche Wochenschrift, 21, (N. F.) **5**(46): 734–735.

EBERHARD, W. 1986. Effects of orb-web geometry on prey interception and retention, pp. 70–100. *In* W. Shear (ed.), Spiders: Webs, Behavior, and Evolution, Stanford University Press.

GERTSCH, W. J., AND S. MULAIK. 1936. Diagnoses of new southern spiders. American Museum Novitates, **851:** 1–21.

GRASSHOFF, M. 1968. Morphologische Kriterien als Ausdruck von Artgrenzen bei Radnetzspinnen der Subfamilie Araneinae (Arachnida: Araneae: Araneidae). Abhandlungen der senckenbergischen naturforschenden Gesellschaft, **516:** 1–100.

HARROD, J. C., H. W. LEVI, AND L. B. LEIBENSPERGER. 1991. (For 1990.) The Neotropical orbweavers of the genus *Larinia* (Araneae: Araneidae). Psyche, **97:** 241–265.

HINGSTON, R. W. G. 1932. A Naturalist in the Guiana Forest. London: Longmans, Green & Co., 384 pp.

HODGES, E. R. S. (EDITOR). 1988. The Guild Handbook of Scientific Illustration. New York: Van Nostrand Reinhold, 575 pp.

INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE. 1985. London: International Trust on Zoological Nomenclature, 338 pp.

KASTON, B. J. 1948. Spiders of Connecticut. Connecticut Geological and Natural History Survey, **70:** 1–874.

KEYSERLING, E. 1865. Beiträge zur Kenntniss der Orbitelae Latrl. Verhandlungen der k. k. zoologischen und botanischen Gesellschaft in Wien, **15:** 799–856.

———. 1880. Neue Spinnen aus Amerika. Verhandlungen der k. k. zoologischen und botanischen Gesellschaft in Wien, **29:** 293–350.

———. 1892–1893. Die Spinnen Amerikas, Epeiridae. Nürnberg, **4:** 1–377.

KRANTZ, G. W. 1970. A Manual of Acarology. Corvallis: Oregon State University Book Store, 335 pp.

KRAUS, O. 1955. Spinnen aus El Salvador (Arachnoida, Araneae). Abhandlungen der senckenbergischen naturforschenden Gesellschaft, **493:** 1–112.

LEVI, H. W. 1964. Nineteenth century South American Araneology. Papéis Avulsos do Departamento de Zoologia, São Paulo, **16:** 9–19.

———. 1968. The spider genera *Gea* and *Argiope* in America (Araneae: Araneidae). Bulletin of the Museum of Comparative Zoology, **136**(9): 319–352.

———. 1971. (For 1970.) The *Ravilla* group of the orbweaver genus *Eriophora* in North America (Araneae: Araneidae). Psyche, **77**(3): 280–302.

———. 1976. The orb-weaver genera *Verrucosa*, *Acanthepeira*, *Wagneriana*, *Acacesia*, *Wixia*, *Scoloderus*, and *Alpaida* north of Mexico (Araneae: Araneidae). Bulletin of the Museum of Comparative Zoology, **147**(8): 351–391.

———. 1985. The spiny orb-weaver genera *Micrathena* and *Chaetacis* (Araneae: Araneidae). Bulletin of the Museum of Comparative Zoology, **150**(8): 429–618.

———. 1986. The orb-weaver genus *Witica* (Araneae: Araneidae). Psyche, **93**(1–2): 35–46.

———. 1988. The Neotropical orb-weaving spiders of the genus *Alpaida* (Araneae: Araneidae). Bulletin of the Museum of Comparative Zoology, **151**(7): 365–487.

———. 1989. The Neotropical orb-weaver genera *Epeiroides*, *Bertrana* and *Amazonepeira* (Araneae: Araneidae). Psyche, **96:** 75–99.

———. 1991a. The Neotropical and Mexican species of the orb-weaver genera *Araneus*, *Dubiepeira*, and *Aculepeira* (Araneae: Araneidae). Bulletin of the Museum of Comparative Zoology, **152**(4): 167–315.

———. 1991b. The Neotropical orb-weaver genera *Edricus* and *Wagneriana* (Araneae: Araneidae).

Bulletin of the Museum of Comparative Zoology, **152**(6): 363–415.

———. 1992. Spiders of the orb-weaver genus *Parawixia* in America (Araneae: Araneidae). Bulletin of the Museum of Comparative Zoology, **153**(1): 1–45.

Levi, H. W., and L. R. Levi. 1962. The genera of the spider family Theridiidae. Bulletin of the Museum of Comparative Zoology, **127:** 1–100.

Marx, G. 1883. Araneina. *In* L. O. Howard, A list of the invertebrate fauna of South Carolina, Charleston, pp. 21–26.

Mayr, E. 1969. Principles of Systematic Zoology. New York: McGraw Hill Book Co., 428 pp.

Mayr, E., and P. Ashcroft. 1991. Principles of Systematic Zoology, 2nd edition. New York: McGraw Hill Book Co., 475 pp.

Mello-Leitão, C. 1939. Some new Argiopid spiders of British Guiana taken by Mr. C. W. Richards from the nests of solitary wasps. Annaes da Academia brasileira de Sciencias, Rio de Janeiro, **11**(2): 105–112.

———. 1940. Aranhas do Espírito Santo coligidas per Mario Rosa, em 1936 e 1937. Arquivos de Zoologia do Estado de São Paulo, **2**(5): 199–214.

———. 1941. Arañas de la provincia de Santa Fé collectadas por el Profesor Birabén. Revista del Museo de La Plata, (Nueva Serie) Zoología, **2:** 199–225.

———. 1942. Arañas del Chaco y Santiago del Estero. Revista del Museo de La Plata, (Nueva Serie) Zoología, **2:** 381–426.

———. 1943. Arañas nuevas de Mendoza, La Rioja y Córdoba colectadas por el Profesor Max Birabén. Revista del Museo de La Plata, (Nueva Serie) Zoología, **3**(20): 101–121.

———. 1945. Arañas de Misiones, Corrientes y Entre Ríos. Revista del Museo de La Plata, (Nueva Serie) Zoología, **4:** 213–302.

———. 1948. Contribuição ao conhecimento da Fauna Araneológica da Guianas. Anais da Academia Brasileira de Ciencias, **20:** 151–196.

———. 1949. Aranhas da Foz do Koluene. Boletim do Museu Nacional, Rio de Janeiro, (Nova Sére) Zoología, **92:** 1–17.

Neave, S. A. 1939–1975. Nomenclator Zoologicus. Zoological Society of London, vols. 1–7.

Opell, B. 1983. Non-glare material for positioning specimens during study. Journal of Arachnology, **11**(3): 449.

Paynter, R. A. et al. 1975–1991. Ornithological Gazetteer. Bird Department, Museum of Comparative Zoology, 12 vols.

Petrunkevitch, A. 1925. Arachnida from Panama. Transactions of the Connecticut Academy of Arts and Sciences, **27:** 51–248.

Roewer, C. Fr. 1942. Katalog der Araneae von 1758 bis 1940. Bremen, **1:** 1–1040.

Schenkel, E. 1953. Bericht über einige Spinnentiere aus Venezuela. Verhandlungen der naturforschenden Gesellschaft in Basel, **64:** 1–57.

Selander, R. B, and P. Vaurie. 1962. A gazetteer to accompany the "Insecta" volumes of the "Biologia Centrali-Americana". American Museum Novitates, **2099:** 1–70.

Simon, E. 1895. Histoire Naturelle des Araignées. 2nd. edit., Paris, **1:** 761–1084.

———. 1897. Viaggio del Dott. A. Borelli nella Republica Argentina e nel Paraguay. XXII. Liste des Arachnides. Bollettino dei Musei de Zoologia ed Anatomia Comparata della R. Università di Torino, **12**(270): 1–8.

Soares, B. A. M., and H. F. de Almeida Camargo. 1948. Aranhas coligidas per la Fundação Brasil-Central (Arachnida–Araneae). Boletim do Museu Paraense E. Goeldi, **10:** 355–409.

Stowe, M. 1978. Observations of two nocturnal orbweavers that build specialized webs: *Scoloderus cordatus* and *Wixia ectypa*. Journal of Arachnology, **6**(2): 141–146.

Taczanowski, L. 1879. Les Aranéides du Pérou central. Horae Societatis Entomologicae Rossicae. St.-Petersburg, **15:** 102–136.

Tullgren, A. 1905. Araneida from the Swedish Expedition through the Gran Chaco and the Cordilleras. Arkiv för zoologi, Stockholm, **2**(19): 1–81.

Walckenaer, C. A. 1841. Histoire Naturelle des Insectes Aptères. Librairie Encyclopédique de Roret. Paris, **2:** 1–548.

Zweifel, F. W. 1988. A Handbook of Biological Illustration. Chicago: University of Chicago Press, 137 pp.

INDEX

Valid names are printed in italics. Page numbers refer to main references, starred page numbers to illustrations.

(US ISSN 0027-4100)

Bulletin OF THE
Museum of
Comparative
Zoology

Systematics of the Holarctic Beetle Subgenus *Bracteon* and Related *Bembidion* (Coleoptera: Carabidae)

DAVID R. MADDISON

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 153, NUMBER 3
12 JULY 1993

(US ISSN 0027-4100)

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

Breviora 1952–
Bulletin 1863–
Memoirs 1865–1938
Johnsonia, Department of Mollusks, 1941–1974
Occasional Papers on Mollusks, 1945–

SPECIAL PUBLICATIONS.

1. Whittington, H. B., and W. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. 192 pp.
2. Turner, R. D., 1966. A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia). 265 pp.
3. Sprinkle, J., 1973. Morphology and Evolution of Blastozoan Echinoderms. 284 pp.
4. Eaton, R. J., 1974. A Flora of Concord from Thoreau's Time to the Present Day. 236 pp.
5. Rhodin, A. G. J., and K. Miyata (eds.), 1983. Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams. 725 pp.
6. Angelo, R., 1990. Concord Area Trees and Shrubs. 118 pp.

Other Publications.

Bigelow, H. B., and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprinted 1964.

Brues, C. T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects. (*Bulletin of the M.C.Z.*, Vol. 108.) Reprinted 1971.

Creighton, W. S., 1950. The Ants of North America. Reprinted 1966.

Lyman, C. P., and A. R. Dawe (eds.), 1960. Proceedings of the First International Symposium on Natural Mammalian Hibernation. (*Bulletin of the M.C.Z.*, Vol. 124.)

Ornithological Gazetteers of the Neotropics (1975–).

Peters' Check-list of Birds of the World, vols. 1–16.

Proceedings of the New England Zoological Club 1899–1947. (Complete sets only.)

Proceedings of the Boston Society of Natural History.

Price list and catalog of MCZ publications may be obtained from Publications Office, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A.

This publication has been printed on acid-free permanent paper stock.

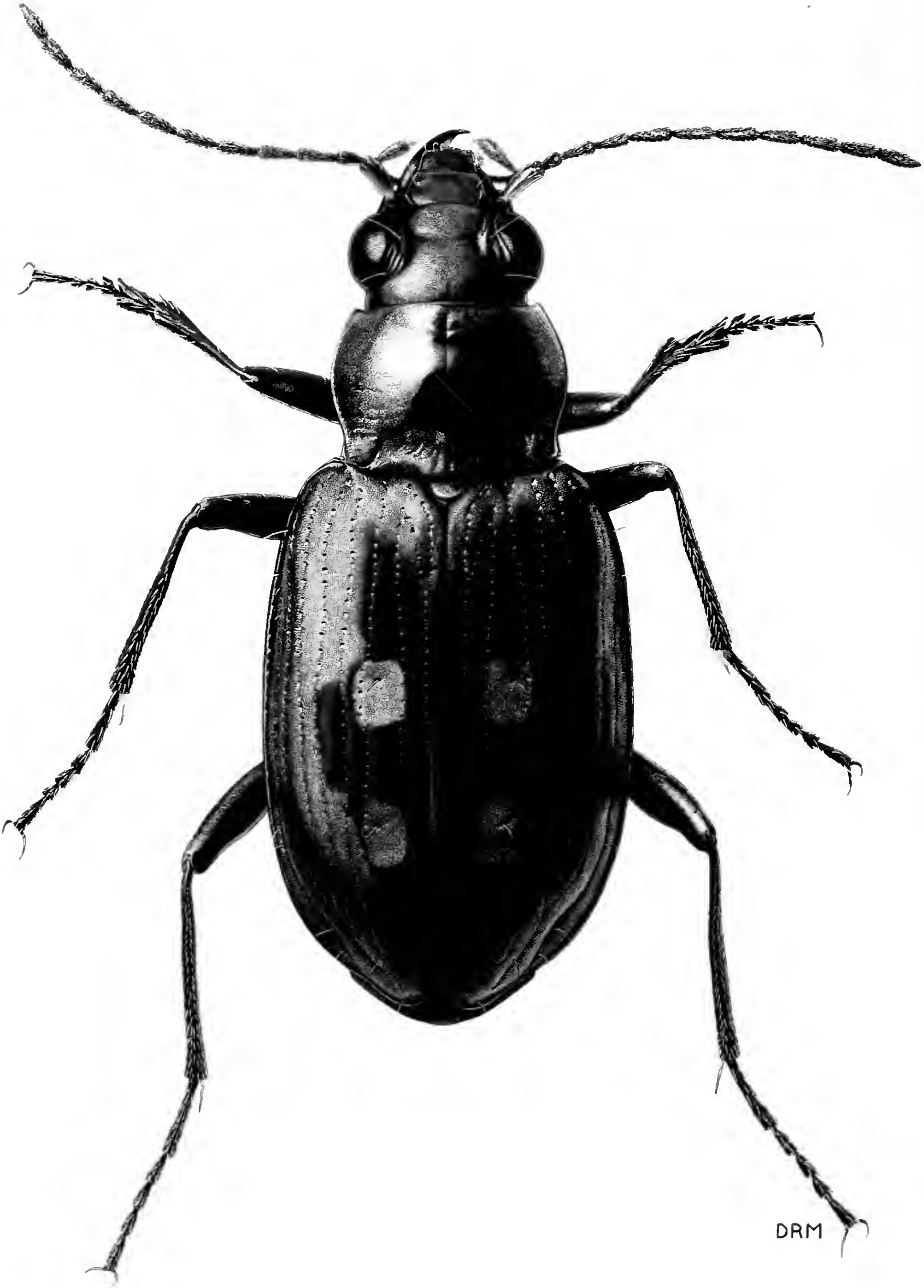


Figure 1. *Bembidion* (*Bracteon*) *alaskense* Lindroth, adult male, Killik River, Alaska. Length about 5.2 mm.

SYSTEMATICS OF THE HOLARCTIC BEETLE SUBGENUS *BRACTEON* AND RELATED *BEMBIDION* (COLEOPTERA: CARABIDAE)

DAVID R. MADDISON[1]

TABLE OF CONTENTS

---

[1] Department of Entomology, University of Alberta, Edmonton, Alberta T6G 2E3, Canada. Present address: Department of Entomology, University of Arizona, Tucson, AZ 85721.

Bull. Mus. Comp. Zool., 153(3): 143–299, July, 1993

ABSTRACT. A review of the Holarctic subgenus *Bracteon* Bedel (=*Chrysobracteon* Netolitzky) of the genus *Bembidion* Latreille reveals seventeen valid species (six Palearctic, eight Nearctic, and three Holarctic). The names *B. colvillense* Lindroth and *B. alaskense* Lindroth are newly synonymized, as are *B. uenoshiba* Jedlička and *B. stenoderum* Bates. *B. levettei carrianum* Casey is resurrected as a northern and eastern subspecies of *B. levettei* Casey, while the subspecies *B. inaequale opaciceps* Casey is no longer recognized.

On the basis of a detailed study of structure of adults and larvae, *Bracteon* is grouped with the subgenera *Odontium* LeConte (synonym: *Cylindrobracteon* Netolitzky) and *Ochthedromus* LeConte to form the *Odontium* subgeneric group. *Ochthedromus* and *Odontium* are briefly characterized; within *Ochthedromus*, an eastern form of *B. bifossulatum* LeConte is recognized as *B. bifossulatum cheyennense* Casey.

For adults, keys are provided to subgenera of the *Odontium* subgeneric group, and for species of *Bracteon*. For known first instar larvae, a key is provided to species of the *Odontium* subgeneric group.

States of 85 characters are described for *Bracteon*, nineteen additional species of the *Odontium* subgeneric group, nineteen other *Bembidion* species, and *Asaphidion alaskanum* Wickham. Adult structural characters, including male and female genitalia, as well as larval and chromosomal characters are studied. Some phylogenetic relationships within *Odontium*, *Ochthedromus*, and *Pseudoperyphus* Hatch are proposed using these characters; the traits also serve as evidence for the phylogenetic analysis within *Bracteon*.

A phylogeny of *Bracteon* is inferred, using both traditional (non-numerical) and algorithmic (numerical) parsimony analysis. I conclude, tentatively, that *Bracteon* is monophyletic. Contradictory evidence suggests that three species related to *B. argenteolum* are actually more closely related to a group of *Odontium* species including *B. aenulum* and *B. fusiforme* than they are to other *Bracteon*. In addition, *B. balli* and *B. foveum* may not belong with the remainder of *Bracteon*.

Almost all of the larval evolution within the group is clustered within one clade, whereas external traits of adults and genitalic features exhibit more uniform change throughout *Bracteon*. A possible correlation between female ovipositor length and size of eggbursters in larvae is noted.

Widespread dispersal and resulting sympatry of these lowland beetle taxa obscures past vicariant events. This, combined with the lack of resolution in the inferred phylogeny, creates difficulty in inferring past biogeographic events. A brief discussion of historical geographic movements of lineages is presented.

INTRODUCTION

On bare sand beaches of northern lakes and rivers, small carabid beetles, whose intricately microsculptured surfaces reflect silver and gold, scamper in the bright sunlight of warmer days. These silver-spotted beach beetles are members of *Bracteon*, a Holarctic subgenus of the large and worldwide genus *Bembidion*.

The first of seventeen known *Bracteon* species to receive a name was *Bembidion velox*, described by Carl von Linné in 1761. Since then, nearly sixty formal names have been applied to members of *Bracteon*. The Palearctic fauna was first comprehensively studied by Netolitzky (1940, 1942, 1943) and Lindroth (1940). Lindroth's later (1962, 1963, 1965) examination of world *Bracteon* included the first review of all known Nearctic species; his work forms the foundation for present worldwide studies of the subgenus.

Netolitzky and Lindroth provided descriptions of external adult structure and male genitalia of the species of *Bracteon* that they recognized. For the most part, I confirm their conclusions on delineation of extant species, and expand their study of character systems to include female genitalia and chromosomes. In addition, I extend Andersen's (1966) work on Palearctic *Bracteon* larvae, describing larvae of all eleven Nearctic species.

This character analysis serves not only to help delimit species, and provide aids for their identification, but also to supply the evidence for the primary purpose of this work: the study of evolution of members of the subgenus.

A necessary background for such investigations is the placement of *Bracteon* into its phylogenetic context; that is, a deciphering of relationships of the subgenus to other carabids. I have therefore examined the cladistic structure of the near-relatives of *Bracteon*. I present results of this preliminary work, discussing the relationships of some of the species of *Odontium* and *Ochthedromus*, groups closely related to

Bracteon. I include a redescription of the genus *Bembidion*, and notes on the subgenera related most closely to *Bracteon*, belonging to the *Odontium* subgeneric group.

The thrust of my work is the relationships of species. Present patterns within extant species, such as geographic variation, are treated only superficially. The short discussion of biogeography of the group is restricted to historical movements of lineages.

An extensive character analysis forms the core of this paper, along with a detailed examination of the phylogeny and character evolution of *Bracteon*. Separate nonnumerical and numerical analyses are presented and compared.

MATERIALS AND METHODS

Specimens Studied

About 10,100 adult, 550 first instar, 60 second instar, and 30 third instar larval specimens of Recent *Bracteon* were examined routinely; a smaller sample of specimens was studied in greater detail. Sample sizes are given for most of the data presented (Table 3). Two Pleistocene and 12 Miocene fragments were also available. About 500 Recent adults and 70 larvae of other subgenera of *Bembidion*, and of related genera, were studied as well.

Acronyms of collections from which specimens were borrowed are listed below. Also included are addresses and names of the curatorial staff with whom I corresponded. Acronyms are used throughout the text.

AMNH	Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024, U.S.A. (L. H. Herman)
AMor	A. and A. V. Morgan, Department of Biology, University of Waterloo, Waterloo, Ontario N2L 3G1, Canada
BCPM	British Columbia Provincial Museum, Parliament Buildings, Victoria, British Columbia V8V 1X4, Canada (R. A. Cannings)
BHar	Brian Harrison, #405-16 Lakewood Drive, Vancouver, British Columbia, Canada
BJCa	B. F. and J. L. Carr, 24 Dalrymple Green NW, Calgary, Alberta T3A 1Y2, Canada
BMNH	British Museum (Natural History), Cromwell Road, London SW7 5BD, England (N. E. Stork)
CAS	Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A. (D. H. Kavanaugh)
CNC	Canadian National Collections of Insects, Arachnids and Nematodes, Biosystematics Research Institute, Research Branch, Ottawa, Ontario K1A 0C6, Canada (A. Smetana)
CUIC	Cornell University Insect Collections, Department of Entomology, Cornell University, Ithaca, New York 14853, U.S.A. (Q. D. Wheeler)
DEUN	University of Nebraska State Museum, Research and Systematics Collections, W-436 Nebraska Hall, Lincoln, Nebraska 68588, U.S.A. (B. C. Ratcliffe)
DHKa	David H. Kavanaugh, Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A.
DRMa	David R. Maddison, Department of Entomology, University of Arizona, Tucson, Arizona 85721, U.S.A.
FMNH	Field Museum of Natural History, Roosevelt Rd. and Lake

	Shore Dr., Chicago, Illinois 60605, U.S.A. (J. Keethley and J. S. Ashe)
GDND	Geology Department, North Dakota State University, Fargo, North Dakota 58105, U.S.A. (D. P. Schwert)
HNHM	Hungarian Natural History Museum, H-1088 Budapest, Baross u.13., Hungary (Z. Kaszab)
ICCM	Carnegie Museum of Natural History, Section of Entomology, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213, U.S.A. (G. Ekis and R. Davidson)
ISAs	I. S. Askevold, Entomology and Biological Control, Florida A & M University, Tallahassee, Florida 32307, U.S.A.
JHAc	J. H. Acorn, Department of Entomology, University of Alberta, Edmonton, Alberta T6G 2E3, Canada
JKLi	J. K. Liebherr, Department of Entomology, Cornell University, Ithaca, New York 14853, U.S.A.
JVMa	J. V. Matthews, Jr., Terrain Sciences Division, Geological Survey of Canada, Ottawa, Ontario K1A 0E8, Canada
KUSM	Snow Entomological Museum, University of Kansas, Lawrence, Kansas 66044, U.S.A. (P. D. Ashlock)
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A. (A. F. Newton, Jr.)
MNHP	Entomologie, Muséum National d'Histoire Naturelle, 45 Rue Buffon, 75005 Paris, France (H. Perrin)
OSUC	Department of Entomology, Ohio State University, Columbus, Ohio 43210, U.S.A. (C. A. Triplehorn)
OSUO	Oregon Systematic Entomology Laboratory, Department of Entomology, Oregon State University, Corvallis, Oregon 97331, U.S.A. (G. L. Peters)
ROM	Department of Entomology, Royal Ontario Museum, 100 Queens Park, Toronto, Ontario M5S 2C6, Canada (G. B. Wiggins)
SAEl	Scott A. Elias, Instaar, Box 450, University of Colorado, Boulder, Colorado 80309, U.S.A.
SMNH	Saskatchewan Museum of Natural History, Wascana Park, Regina, Saskatchewan S4P 3V7, Canada (R. R. Hooper)
TBau	Thomas Bauer collection, Universität Regensburg, Zoologisches Institut, Universitätstrasse 31, D-8400 Regensburg, Germany
UASM	Department of Entomology, University of Alberta, Edmonton, Alberta T6G 2E3, Canada (G. E. Ball and D. Shpeley)
UBC	Spencer Entomological Museum, Department of Zoology, University of British Columbia, Vancouver, British Columbia V6T 2A9, Canada (S. G. Cannings)
UCB	California Insect Survey, Division of Entomology and Parasitology, University of California, Berkeley, California 94720, U.S.A. (J. K. Liebherr and J. A. Chemsak)
UMHF	Division of Entomology, Zoological Museum, University of Helsinki, N. Järnvägsgatan 13, SF-00100 Helsinki 10, Finland (H. Silfverberg)
UMSP	Department of Entomology, Fisheries, and Wildlife, University of Minnesota, St. Paul, Minnesota 55101, U.S.A. (P. J. Clausen)

UMMZ	The University of Michigan, Museum of Zoology, Division of Insects, Ann Arbor, Michigan 48109, U.S.A. (B. M. O'Connor)
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A. (T. L. Erwin and W. N. Mathis)
UWLW	Entomological Museum, University of Wyoming, Laramie, Wyoming 83070, U.S.A. (R. J. Lavigne)
ZIL	Zoological Institute, Academy of Sciences of Russia, 199164, St. Petersburg, Russia (O. L. Kryzhanovskij)
ZMLS	Museum of Zoology and Entomology, Lund University, Helgonavägen 3, S-223 62 Lund, Sweden (R. Danielsson)
ZMUM	Zoological Museum, Moscow Lomonosov State University, Herzen Street 6, Moscow K-9, Russia (N. Nikitsky)

Collecting *Bracteon*

On cloudy, cool days, *Bracteon* adults were found in cracks and burrows in sandy banks of river, creek, lake, and ocean shores. They were forced onto the surface by flooding the banks with water, and then were collected by hand; larvae were also occasionally captured by this method. On sunny and warm days, however, the beetles were active on the surface and flew if disturbed. They were caught with a net. Most adults were killed with ethyl acetate.

Most larvae were obtained using a modification of the techniques of J. Andersen and D. J. Larson (pers. comm., 1981). Adult females and males were kept in clear plastic boxes half-filled with damp, uncontaminated sand, and fed moistened pieces of Purina Puppy Chow® or Safeway Complete and Balanced Cat Food®, which were changed daily. Freshly killed insects and spiders were added on occasion. First instar larvae appeared in the sand one to eight weeks later. Some were raised to later instars on the same diet. Larvae were killed in boiling water and stored in Barber's solution or 70% ethanol. All described larvae were raised *ex ovo*.

Specimen Preparation and Examination

Wild M5® and Leitz Model RS® stereo dissecting microscopes were used to study external structures of dried adults. Permanent microscope slides were made of one or two adults of each species (except *B. semenovi* Lindroth and *B. conicolle* Motschulsky). These specimens were disarticulated and cleared, using hot 10% KOH to remove soft tissue and warm 1:1, 95% ethanol:30% hydrogen peroxide solution to reduce pigmentation, before being mounted in Euparal®. Cleared adults, genitalia, and larvae were examined using a Leitz SM-Lux® brightfield microscope at 100× or 400×. Some structures were examined with a Cambridge Stereoscan 250® Scanning Electron Microscope.

Preparation procedures for study of some characters are described in more detail below.

Genitalia

Most studied genitalia were dissected out of water-softened adults, placed in hot 5–10% KOH (aq.) for ten minutes to remove soft tissue, and then transferred via distilled water and 95% ethanol into the observation medium. Membranous portions of female genitalia were stained with chlorazol black in 70% ethanol. I examined the majority of genitalia in glycerin, except for those illustrated by line drawings, which were mounted in either Euparal® or cedarwood oil.

Some internal sacs of dried males were everted by suction (using a technique suggested by K. W. Cooper and H. Goulet, pers. comm.) after water softening and hot KOH treatment. The suction device consisted of a syringe with a thin plastic tube in place of a needle. At the end of the plastic tube was a glass capillary tube, drawn so that the internal diameter at its tip was slightly greater than the width of a *Bracteon* aedeagus. By placing this capillary tube over the apex of the aedeagus, but not over the parameres, suction could be applied to the median lobe without the whole genitalia being sucked into the syringe. The internal sac was carefully sucked out in water or weak acetic acid, then transferred to 70% ethanol for storage. The internal sacs invariably collapsed slightly after the pressure was relieved.

Most everted sacs studied were prepared by a superior technique, requiring live specimens, suggested by T. L. Erwin (pers. comm.). A live adult male was held between fingers under a dissecting scope, and gently squeezed until the genitalia and then the internal sac popped out. While being careful to maintain pressure, I grasped the specimen with a pair of forceps, and held it in boiling water for a few seconds. It was then released, and allowed to cook for about 20 seconds, the contents of the internal sac thus getting hard-boiled. The beetle was then placed in 70% ethanol for storage, or through 95% ethanol and amyl acetate in preparation for critical-point drying and SEM study. The female genitalia illustrated in Figures 185–187 were prepared by the same forced-eversion technique.

Larvae

Permanent microscope slides of cleared larvae were made by a technique similar to Goulet's (1977, 1983:226). Specimens were transferred from water through a graded series of KOH solutions into 5% KOH (aq.), which was heated to a gentle boil. After internal tissues cleared, larvae were cooled and taken through a graded series of solutions from 5% KOH down to distilled water then up to 95% ethanol; specimens were transferred with a wide-mouthed eyedropper. Larvae were placed in a weak (about 5%) solution of Euparal® in 95% ethanol, and eventually became impregnated with the mounting medium as the ethanol evaporated. To speed evaporation and prevent unwanted precipitation of Euparal, the weak Euparal solution with larvae was placed in open glass vials on a low-heat hotplate, with an electric fan close by blowing air over the vial tops. After impregnation, the larvae were mounted on slides.

Chromosomes

For most examined species, hypothesized counts and sex-chromosome systems are based on observations of male meiosis as well as male and female mitosis of Feulgen-stained squash preparations. Male and female mitoses were not observed in *B. levettei levettei*, and females of *B. lorquinii* were not studied cytogenetically. For details of the method used, see D. Maddison (1985b).

Measurements

The following measurements of adults and larvae were made using an eyepiece reticle on Wild M5® or Leitz SM-Lux® microscopes.

ADULTS:

Hl	length of head, along midline, from apex of clypeus to posterior margin of left eye
Pl	length of pronotum along midline
Pwm	maximum width of pronotum in front of hind angles
El	length of elytra, from tip of scutellum to apex
SBL	standardized body length, SBL = Hl+Pl+El

LARVAE:

LFl	length of frontale of larval head along midline
LCl	length of coronal suture
LHl	head length = LFl + LCl
LHw	width of head behind posterior stemmata

Standardized body length (SBL) is used as a measurement of overall length that is not subject to the effects of varied membrane foldings or body positions. However, there are two "standardized body length" definitions within carabid literature, because of two definitions of head length or Hl. Ball (1972) defines Hl as "straight-line distance from base of mandible to posterior margin of compound eye, on left side of head," whereas Kavanaugh (1979) treats head length as "length of head, measured along midline from apical margin of clypeus to a point opposite posterior margin of eye." Whitehead (1972), and Erwin and Kavanaugh (1981) use head length measures equivalent to Kavanaugh's. I use Kavanaugh's definition, as it is closer to the "apparent" length of the head from the neck to the apex of normally resting mandibles, and thus SBL is closer to apparent body length.

Illustrations

All drawings of beetle parts were made with a Wild M5® or Leitz SM-Lux® microscope, using a *camera lucida*, except for Figure 1, for which photographic slides were used to aid in reproducing proportions. Scanning electron micrographs were produced using a Cambridge Stereoscan 250® Scanning Electron Microscope. Photographs of cleared structures were taken with a Carl Zeiss Ultraphot II®.

Terms

The diacritical mark (!) indicates I examined the specimens being discussed.

For most structures of adults, I use terms employed by Ball and Shpeley (1983). I use "stria" in the sense of Cooper (1990). Nomenclature of elytral setae, genitalia, and larval sensilla posed some special problems, which will now be discussed. A few other terms are defined in the section "Character states in *Bracteon*," or as required in the text.

Erwin and Kavanaugh's (1981) nomenclature of setae of bembidiine elytra is used for the most part. However, within *Bracteon* there is considerably more variation in number and position of elytral setae than in most bembidiine species, making it difficult to identify homologous setae. For example, in most bembidiines, the umbilical series is constantly segregated into a humeral set of four setae (eo1 to eo4), and a subapical set of four to five setae (eo5 to eo9, Fig. 4). Within *Bracteon*, the umbilical series varies. In most specimens, two setae are present in the position of eo5 and eo6, but they occasionally number one or three. In some species, there are no umbilical setae between eo4 and eo5. In others, additional setae are present (Fig. 4), of various numbers, with as many as five setae between eo4 and eo5 on one elytron (as in the holotype of *B. semenovi*). I do not give these additional setae names (although "eo4.2," "eo4.4," and so on, could be used). I designate as eo4 the fourth most anterior umbilical seta, and eo5 and eo6 as the most posterior two setae in the position of Erwin and Kavanaugh's (1981) eo5 and eo6. The names of pre-eo4 and post-eo5 setae follow from these designations (Fig. 4).

Lindroth (1940) developed a nomenclature for male internal sac structures of several Old World species of *Bembidion*. Among species of a subgenus, Lindroth used the same name to denote homologous features. But between subgenera, no such homology is implied. Thus his "Ch1" for *Bracteon* specimens is undoubtedly not homologous to the "Ch1" of *Philochthus*. Erwin and Kavanaugh (1981) use names taken mostly from Lindroth (1940) for their treatment of the *Bembidion wickhami* (=*B. carlhi*, see Erwin [1984]) and *B. erasum* groups; indeed, the internal sac sclerites they name are probably homologous to homonymous structures shown by Lindroth (1940) for *Philochthus*. From my meager investigation of the male genitalia of *Bembidion*, I cannot determine the nature of homologies between sclerites named by Erwin and Kavanaugh and those seen in *Bracteon*. Because of this, I avoid Lindroth's and Erwin and Kavanaugh's letter and number codes, and use instead descriptive names (Figs. 99–102). These are discussed in more detail later, in the characterization of *Bracteon*.

Names of parts of beetle spermathecae vary from author to author, so that discussion of structure of these organs becomes difficult. I have chosen to follow Howden (1976) and Gordon (1985) in calling the basal bulb, near the attachment of the spermathecal duct, the nodulus; the area of attachment of the spermathecal gland, the ramus; the portion protruding beyond the ramus, the cornu (Fig. 165).

Notation of most larval sensilla follows that proposed by Bousquet and Goulet (1984). Their system works very well for *Bracteon;* that is, the sensilla of *Bracteon* larvae are for the most part in about the same positions as figured by Bousquet and Goulet (1984). I have encountered two difficulties in using their nomenclature. First, they name only setae and flat, circular sensilla of the exterior surface (their "pores"). Their system does not include hypopharyngeal sensilla, nor most sensilla on the apical articles of the maxillary palp, galea, and labial palp, and apical two antennomeres. While this is a limitation of their system, it does not diminish the excellent foundation they provided. The second difficulty is in the division of the names into two groups, one (a two-letter uppercase sclerite or organ code as well as an arabic number) for setae, and the other (a two-letter uppercase sclerite or organ code as well as a lowercase letter) for "pores." This division is based not on study of function, nor detailed electron microscope study of structure, but rather on appearance under a light microscope. Most of the "setae" in their system are probably trichoid sensilla, and most of the "pores" are probably chordotonal organs, but there are exceptions. For example, the "pore" FR_f (Figs. 194, 204) is most likely a contact chemoreceptor. Bousquet and Goulet's (1984) nomenclature may need to be revised, but for now I will use it; however, I will avoid the word "pore" for any small sensillum.

Names of Taxa

Numerous names given to members of *Bracteon* have primary types deposited in collections in Europe. I have examined few of these, and instead rely on Lindroth's (1962, 1963) interpretation of types and names. As his concepts of the species of *Bracteon* were almost identical to mine (only a few of our placements of specimens differ), I doubt that reexamination of the types he studied is crucial at present. However, Lindroth (1962, 1963) did not consider some early (pre-1961) names, as he thought they were described as mere aberrations, and did not study types of these names. Some of these were originally described as varieties, and are available names (International Code of Zoological Nomenclature [ICZN], Third edition, Article 45[g]). I list all of these names, including those clearly of infrasubspecific rank, and note those I consider unavailable. As well, primary types of some *Bracteon* names where thought by Lindroth to be lost. I make no effort to locate these types, nor to designate neotypes. Work in European museums is necessary before this can be accomplished.

For primary types that I have seen, I provide a description of the labels present with the specimen.

Publication dates of most *Bracteon* names are not controversial, except for those described by Netolitzky (1940, 1942). Lindroth (1962, 1963) considered Netolitzky (1940) to constitute a valid publication, and thus treated the names *Litoreobracteon*, *Argyrobracteon*, etc., as being published in 1940; he viewed the 1942 paper as a republication. Erwin and Sims (1984) as well as Netolitzky himself (1942) appear to consider the 1940 paper as unpublished, and state the publication date of those names as 1942. Apparently only reprints of the 1940 paper were issued (Lindroth, 1962:18, and Netolitzky, 1942: 29). If those reprints were distributed, then the paper does constitute a valid publication (ICZN, Third edition, Article 8). A search of North American libraries by the University of Alberta discovered not one copy; a search by Lund University of major western European libraries came up with similarly negative results (L. Cederholm, pers. comm.). However, the work was publicly distributed, at least to some extent, as a library in Chernovsti, Ukraine, possesses a copy (L. Cederholm, pers. comm.), and as Aleš Smetana (Ottawa) possesses a copy (Y. Bousquet, pers. comm.). I will therefore consider the work to constitute a valid publication.

Systematic Procedures

Methods used for inferring species limits are described later, in the section on "Species of *Bracteon*" under "Species and Subspecies Recognition." Techniques used to infer the phylogeny and biogeography of *Bracteon* and its relatives are discussed in the sections about phylogenetic and biogeographic analysis of *Bracteon*. Although the results of phylogeny reconstruction are used as part of the foundation for the supraspecific classification that follows, I defer discussion of the phylogeny reconstruction until the classification is presented and the species are described.

CHARACTERIZATION OF SUPRASPECIFIC TAXA

Genus *Bembidion*

Bembidion Latreille, 1802:82. (Type species *Carabus quadriguttatus* Fabricius, 1775:248 [=*B. quadrimaculatum* Linné, 1761:211], designated by Jeannel [1941:475].) (Generic synonymies given by Erwin and Sims, 1984.)

Notes on the type species

The originally included nominal species are *B. biguttatum* (Fabricius) and *B. quadriguttatum* (Fabricius) (Latreille, 1802), and thus one of these nominal species must serve as the type species of the genus (ICZN, Third edition, Article 69). Andrewes's (1935) designation of *B. quadrimaculatum* is therefore invalid. As he did not explicitly state that he considered *B. quadriguttatum* Fabricius to be a synonym of *B. quadrimaculatum* Linné (as is now believed [Jeannel, 1941; Lindroth, 1974a]), his designation does not constitute a fixation of the former as type species (ICZN, Third edition, Article 69[a][v]). Jeannel's (1941) statements do, however, constitute a valid designation, which is ironic considering his preference for *B. biguttatum* as the type (Jeannel [1941:475–476, footnote]). The recognition of *B. quadriguttatum* rather than *B. quadrimaculatum* as the type should not alter existing nomenclature so long as they are considered synonymous or are considered to belong to the same subgenus.

Species included

I follow Netolitzky (1942, 1943), Lindroth (1963, 1976, 1980), and Erwin and Kavanaugh (1981) in treating *Bembidion* as a very large genus with perhaps more than a thousand species, including almost all members of the subtribe Bembidiina. I conservatively follow Erwin (1972) and Lindroth (1963, 1976, 1980) in excluding from *Bembidion* members of *Asaphidion* Gosiz, *Phrypeus* Casey, *Bembidarenas* Erwin, and *Zecillenus* Lindroth; all other Bembidiina are included within the genus.

In contrast, Jeannel (1941) split *Bembidion* into numerous genera (17 in the French fauna alone), and several European systematists have followed suit (for example, Jeanne, 1971, and other titles in the same series; Antoine, 1955). Perrault (1981) has recently adopted an intermediate position; he splits *Bembidion* into ten genera world-wide. Unfortunately, rigorous phylogenetic studies of the lineages within bembidiines have yet to be performed, and as a result the cladistic structure of the subtribe Bembidiina as a whole is unclear. If future world-wide studies reveal distinct major lineages, it may prove best to divide *Bembidion* into a few smaller genera, as Erwin (1974) has done for tachyines. However, until *Bembidion* is better known, I think it best to retain the broad generic concept and avoid fragmentation into poorly resolved groups.

Papers dealing extensively with systematics of *Bembidion* on a local or global scale include Andrewes (1935), Antoine (1955), Basilewsky (1968, 1972), Casey (1918, 1924), Darlington (1959, 1962), Erwin (1982, 1984), Erwin and Kavanaugh (1981), Hayward (1897, 1901), Jeannel (1941, 1962), Jedlička (1961, 1965a), Kirschenhofer (1984), Kryzhanovskij (1983), Larochelle (1977), Lindroth (1940, 1945, 1954, 1955, 1962, 1963, 1965, 1974a, 1976, 1980), Müller (1918, 1926–1927), Netolitzky (1914a, 1927, 1940, 1942, 1943), Pawlowski (1974), Perrault (1981, 1982), and Schuler (1959).

Evidence for the monophyly (or lack thereof) of *Bembidion* is discussed under "The Phylogenetic Context of *Bracteon*"; here I give only a characterization of members of the genus. This is difficult, if not impossible, to do well at present, in part because of the large number of species in the taxon, but also because of the lack of knowledge of most members of *Bembidion*. I have gleaned information in the following diagnoses and description from Andrewes (1935), Netolitzky (1942, 1943), Lindroth (1940, 1963, 1976, 1980), Erwin (1982), Erwin and Kavanaugh (1981), Erwin and Sims (1984), from other cited sources, and from personal observations.

Diagnostic combination

Adults small to medium carabids. Members sharing with other Bembidiini narrow, subconical apical palpomere, lack of dorsal paraorbital groove, separation (in most species) of interval 9 setae into humeral set and apical set. Distinguished from other Bembidiini by possession of lacinia without dorso-apical setae; glossal sclerite bisetose; paraglossal lobes short to moderate in length; clypeus bisetose; elytra with striae represented as grooves, or rows of punctures, or effaced, sutural stria present, but short; recurrent elytral groove absent; seta eo9 lacking; uniperforate procoxal cavities; protibia truncate, not apically notched; protarsomere 1 of male with two rows of transversely apically dilated adhesive setae; internal sac of male aedeagus with brush sclerite.

First instar larva sharing with other Bembidiini egg bursters consisting of denticulate microsculpture on parietale or frontale, single-clawed tarsi, unarticulated urogomphi, which are fused to tergum nine. In addition, setae of dorsal surface generally distally tapered; if not tapered, then bluntly tipped, *not* tipped by two to six projections; seta PR_{13}, ME_{14}, and TE_{11} generally present, abdominal hypopleurites lacking setae; seta TA_1 in proximal one-third of tarsus; coronal suture relatively long ($LCl/LHl = 0.09–0.22$), not shorter than length of antennomere 1; mandible with cutting edge not denticulate (except slightly so in the two *B. umbratum* examined); galeomere 2 relatively short, less than 1.5 times as long as first article.

The subtribe Bembidiina contains four genera in addition to *Bembidion: Asaphidion, Phrypeus, Bembidarenas,* and *Zecillenus*. Adults of *Asaphidion* (Holarctic) differ from *Bembidion* in lacking visible elytral striae, possessing pubescent pronota and elytra, having 6 to 8 setae on the apex of the glossal sclerite (as opposed to the pair found in *Bembidion*), and having protarsomere 1 of males with small adhesive setae generally distributed, not arranged in two rows (Figs. 87, 89). Adults of *Phrypeus* (western North America) differ in lacking a brush sclerite on the internal sac of male genitalia. Adults of *Bembidarenas* (southern South America) can be distinguished from *Bembidion* by the presence of two pairs of clypeal setae, presence of 6 to 8 glossal setae, lack of a brush sclerite on the internal sac of male genitalia, and symmetrical parameres. Adults of *Zecillenus* (New Zealand) are distinct from *Bembidion* in lacking a brush sclerite on the internal sac of the male genitalia, in possessing a pronounced subapical elytral sinuation, and in having the basilateral pronotal seta far in front of hind angle (although this latter state is characteristic of several *Bembidion* species from Saint Helena [Basilewsky, 1972]).

Bembidion larvae are difficult to distinguish from those of related genera. Among Bembidiini other than *Bembidion*, larvae are known of only a few Tachyina (Cerruti, 1939; van Emden, 1942; Erwin, 1975; Gardner, 1938; Kirk, 1972; Perris, 1862; Stebbing, 1914; Thompson, 1979; Xambeau, 1894) and *Asaphidion* (Bauer, 1971; Boldori, 1939; Bøving, 1911; van Emden, 1942; Larsson, 1939; Raynaud, 1976a; my observations). The known tachyine larvae have seta TA_1 near or distal to middle of tarsus, in contrast to the more proximally placed TA_1 of *Bembidion*, the tachyine galeomere 2 is relatively long (about two times length of first), and the coronal suture is relatively short (shorter than antennomere 1) (van Emden, 1942; Hůrka, 1978). More differences may become apparent once tachyine larvae are studied in greater detail; sensillar characters are for the most part unexamined.

Many of the characters used by van Emden (1942) to distinguish *Bembidion* from *Asaphidion* do not hold for all species (Andersen, 1966; Hůrka, 1978). The single character considered by van Emden (1942), Andersen (1966), and Hůrka (1978) to separate the genera consistently is the size and number of the egg bursters: *Asaphidion* first instar larvae reportedly have a few large tooth-like spikes on the frontale in contrast to the numerous smaller denticles of *Bembidion* specimens. However, this character is inconstant. The microsculpture on the frontale of *Bembidion* ranges from absent (*B. carinula* Chaudoir, *B. aenulum* Hayward, and others), to low and multipointed (many species, including *B. foveum* Motschulsky, *B. bowditchii* LeConte, and others), to numerous small denticles (many species, including several *Bracteon* species), to a few large teeth (*B. interventor* Lindroth and *B. obtusum* Serville). Denticulate microsculpture is also present on the parietale, near the coronal suture, of all *Bembidion* first instars I have studied, reaching its most extreme form in *B. carinula* (Figs. 228, 234). This parietal microsculpture, as well as any found on the frontale, probably serves an egg-bursting function. First instars of both *Asaphidion flavipes* Linné and *A. alaskanum* Wickham have large frontale teeth *and* prominent denticles on the parietale (Boldori, 1939; van Emden, 1942: fig. 64; Bauer, 1971:158,159; my observations), a condition virtually identical to that found in *B. interventor* and *B. obtusum*. Other characters must thus be sought.

At least four characters can be used to distinguish first instar larvae of all 33 *Bembidion* species I have examined (those characterized in Tables 2, 4, and 5) from the one first instar *Asaphidion alaskanum* at my disposal. The *A. alaskanum* larva has: sensilla MX_{11} and MX_{12} relatively long (longer than a quarter the width of the palpomere to which they are attached; very much shorter in *Bembidion*); setae PR_{13}, ME_{14}, and TE_{11} each replaced by a patch of two to four short, thick setae; abdominal hypopleurites with one seta each (absent in *Bembidion*); most large dorsal setae not distally tapered (Fig. 225), instead tipped by a frequently crown-like arrangement of two to six projections (Fig. 195). Apically dilated and crowned setae are present as well in all instars of *A. flavipes* (Boldori, 1939; Bauer, 1971:fig. 4; personal observations), but apparently not in *A. yukonense* first instars (one specimen in the CNC, raised *ex ovo* by Henri Goulet, examined). I cannot yet judge the uniformity of *Asaphidion* with respect to the first three characters. The diagnosis of *Bembidion* larvae given above is thus tentative.

Description

In the following description of *Bembidion*, I include a number of previously unstudied characters. Chief among these are characters of sensilla. Setation has long been used for taxonomic characters within carabids, but the smaller sensilla of adults have generally been neglected. There is a wealth of small receptors on the surface of carabid adults, particularly on the head (for example, see the studies on antennal sensilla by Juberthie and Massoud [1977] and Daley and Ryan [1979]). The number, position, and types of these sensilla should provide numerous characters for phylogenetic analyses. Goulet (1983), Bousquet and Goulet (1984), and Landry and Bousquet (1984) have already shown the usefulness of some sensilla of larvae for inferring phylogeny, and the same may apply to other larval sensilla and sensilla of adults. I do not by any means attempt to fully describe the sensilla of *Bembidion* specimens, nor exhaust the supply of other characters. Instead, I discuss only some of those characters that appear, based upon previous work and a preliminary examination of cleared specimens of several carabid tribes, to be potentially useful for studies of carabid phylogeny.

Adult. Adults small to medium (about 2 to 9 mm in length), generally slender, in many species with relatively narrow forebody.

Color varied, many species dark, concolorous, many others with spotted elytra, or generally pale. Appendages pale yellow to black. Most species have a metallic reflection.

Microsculpture of dorsal surface varied, ranging from close-set transverse lines, giving the surface an iridescent reflection, to granulate isodiametric sculpticells, to absent.

Two supraorbital setae. Antennomeres 3 through 11 pubescent throughout length. Clypeus with one seta near each lateral margin. Labrum with six setae dorsally near apex, more numerous shorter ones ventrally; numerous sensilla of various sorts clothe the surface of the epipharynx; with one cluster of presumed chemoreceptors in a sclerotized patch on either side of epipharyngeal hump (Figs. 24, 37). Mandible with one seta in each well-developed scrobe; basomedial brush short, not extended far apically along inner surface of mandible; numerous small sensilla, with three large sensilla on dorsal surface (visible as small open circles in Figs. 25 and 28): these may be large chordotonal organs. Digitiform sensilla (Zacharuk *et al.*, 1977; Honomichl, 1980; Guse and Honomichl, 1980; Honomichl and Guse, 1981) arranged in one row near base of last maxillary palp article; tip of maxillary palp with several kinds of sensilla (Fig. 38); three centrally convergent rows of what are probably contact chemoreceptors flanked by a few small clusters of minute sensilla and a few larger possible plate-like organs (observed: *B. balli* Lindroth, *B. foveum*, *B. carinula*, and *B. umbratum* LeConte); palpomere 3 pubescent. Stipes with two long and several shorter setae in most species. Lacinia without dorso-apical setae; dorsal surface with only one to three setal rows (Figs. 42, 43, 46–48). Galea tip with three or four sensillar types, arranged as in Figure 41 (only studied in *B. foveum*). Terminal labial palpomere without digitiform sensilla, apical sensilla similar in type, but different in distribution to those of maxillary palps (Fig. 39); palpomere 2 with two to five setae on anterior margin. Glossal sclerite with two long subapical setae. One pair of setae on the mentum and 2–5 pairs of setae on the submentum. Pronotum generally with one midlateral and one basilateral seta on each side. Generally two discal setae on elytral interval 3, although *B. quinqestriatum* Gyllenhal has one, *B. laterale* Samouelle four, and a number of species have three setae (Lindroth, 1976); occasionally on other intervals as well (especially 5 and 7); elytra not pubescent; basal setiferous pore puncture (ed1) present, as well as one or two preapical discal setae (ed6 and ed7); umbilical series of setae (in interval 9, adjacent to stria 8) in most species separated into a humeral set (eo1 through eo4) and a subapical set (eo5 through eo8); eo9 lacking (*B. foveum*, *B. argenteolum* Ahrens, *B. semenovi*, and *B. punctatostriatum* Say generally have extra setae between eo4 and eo5; *B. planatum* LeConte generally has an extra seta between eo6 and eo7; members of subgenus *Euperyphus* Jeannel generally have one extra seta in the humeral set). Procoxa without setae, mesocoxa bi- or tri-setose, metacoxa trisetose on ventral surface; pro- and mesotrochanters unisetose; metatrochanter with one ventral seta in addition to several short dorso-basal setae; protarsomere 4 in both sexes of most species with ventroapical projection with four setae, the two central of which are generally apically flattened (projection and setae are lacking in *Asaphidion*, *Phrypeus*, and *Zecillenus*); male with adhesive squamo-setae (Stork, 1980), apically dilated transversely, present in two rows on protarsomere 1, and in one to two rows on protarsomere 2. Males with two major setae on sternum seven, females with four. (In this and following descriptions, sensilla of genitalia will be described elsewhere, in the sections "Male genitalia" and "Female genitalia.")

Head prognathous, with frontal furrows variously developed, from shallow to deeply incised. Eyes generally moderate to large, and convex, although small in a few subgenera (*Amerizus* Chaudoir, *Tiruka* Andrewes, etc.). Antenna in most species slender, articles subcylindrical, slightly flattened. Clypeus with frontoclypeal suture impressed. Labrum as in Figure 24, subrectangular, with front margin entire. Mandibles (Figs. 25, 28–30) falcate; terebral margin thin and cutting, with many regularly spaced pore canals extended to mesal margin (Fig. 31); ventral groove with brush of clumped microtrichia (Figs. 29c, 30c, 32, 33); right mandible generally with distinct anterior and posterior retinacular teeth, terebral tooth, premolar, and molar; left mandible with short retinacular ridge, and distinct premolar and molar; molars on both mandibles thin, only slightly sclerotized, sharply pointed (Figs. 32, 33). Maxilla (Fig. 26) with small, subulate, subconical palpomere 4; galeomeres subequal in length (articles fused in *B.* (*Amerizus*) *wingatei* Bland); galeomere 2 with groove for reception of lacinia; lacinia in most species generalized, without microsculpture. Labium (Fig. 27) with palpomere 3 small, subulate, subconical; paraglossal lobes thin (but not nearly as thin as those of trechines), rounded; short to moderate in length; with short microtrichia; glossal sclerite broad and flat. Mentum with single tooth; epilobes usually distinct; pits of mentum absent. Mentum and submentum distinct, except in members of *Ocys* Stephens.

Prothorax with closed, uniperforate coxal cavities. Pronotal shape varied, from cordate to subcircular to trapezoidal. Mesothorax broadly connected to prothorax, with conjunct-confluent coxal cavities. Scutellum visible externally, moderate in size. Metathorax with disjunct-lobate, confluent coxal cavities.

Elytron generally with nine punctate striae, in many species effaced laterally or posteriorly; sutural stria short; recurrent groove absent, although apex of stria 5 sulcate in some species; subapical plica present (most species, Fig. 67) or absent (*B. aenulum* Hayward and *B.* sp. nr. *aenulum*, Fig. 65); if present, then as typical for carabids, a simple, curved ridge on the undersurface of the elytron below setae eo7 and eo8, in most species merged with the elytral margin.

Metathoracic wing present, full, or variously reduced; if well-developed, then wedge cell a thin triangle or absent (Fig. 74); oblongulum cell elongate.

Legs long and slender in most adults. Groove in coxa for reception of metafemur restricted to posterior margin of coxa. Protibia anisochaetous, with distinct antennal cleaner ("Grade B" [Hlavac, 1971]). Protarsus with first two to three articles slightly expanded in male, with apico-lateral projections. Unguitractor plate present, plate-like. Tarsal claws simple, untoothed.

Abdomen with wing-folding spicule patches on first and sixth abdominal sterna, as well as front of seventh.

Male genitalia with styliform parameres (Figs. 180, 181), the right smaller than the left; parameres with 1 to 5 apical setae; ring sclerite as in Figure 182. Basal bulb of median lobe with most of right wall lacking; internal sac with brush sclerite (Figs. 99–102, 107) (except in a few species of subgenera *Antiperyphanes* Jeannel and *Chilioperyphus* Jeannel [Jeannel, 1962]), often with numerous other sclerites; flagellum often present, of varied shapes. Right and left testes equally developed.

Female genitalia with sclerotized spermatheca (except in the subgenera *Synechostictus* Motschulsky, *Amerizus*, *Tiru-*

ka, Pseudolimnaeum Kraatz [Perrault, 1981]), connected to bursa copulatrix by spermathecal duct; duct in many species with a sclerotized base, called the sclerotized vaginal plate (in coccinellids, a similar structure is referred to as the infundibulum [Gordon, 1985]); spermathecal gland present, with subbasal portion enlarged and annulated; spermatheca lying in right side of abdomen (Fig. 145; Schuler, 1960; Erwin and Kavanaugh, 1981; Perrault, 1981). Two stylomeres, second spatulate; first stylomere (S1) asetose or setose; second stylomere (S2) with zero to five or more dorsolateral ensiform and one dorsomedial ensiform setae, in addition to two nematoid setae and several furrow peg sensilla in sensory furrow, and numerous scattered chordotonal organs. Seven to ten ovarioles per ovary (Robertson, 1961).

Nervous system with first abdominal ganglion fused to last thoracic ganglion; second through seventh abdominal ganglia fused together (Ali, 1967; I have confirmed this as well for one *B. lorquinii* Chaudoir female). Proventriculus (Figs. 188, 189) with four similar, inwardly directed lobes, each lobe with patch of stout, posteriorly directed scales at anterior end, and a tubercle-studded sclerotized lobe at posterior end; in between is a membranous region of posteriorly directed microtrichia; the exact pattern varies considerably between species (observed in *B. carinula*, *B. levettei* Casey, *B. harpaloides* Serville, and *B. wingatei*). Six oval or circular rectal sclerites, arranged in one circle around circumference of rectum (Fig. 183; observed in several *Bracteon* species, as well as *B. coxendix* Say, *B. confusum* Hayward, *B. chalceum* Dejean, *B. aeneicolle* LeConte, and *B. viridicolle* La Ferté). Prothoracic muscle M15 three-parted, with M15b connected to M15c (Baehr, 1979; see that paper for further description of prothoracic musculature). Origin of muscle M3 of female abdomen at caudal end of tergum VIII (Bils, 1976; see that paper for more information about female abdominal musculature).

Pygidial defense glands (Fig. 184) paired, consisting of a long secretory duct, large, ovoid reservoir, and a pleated exit tube exiting laterally in membranous dorsum anterior to ninth and tenth tergum. Defense secretion consisting of aliphadic ketones, higher saturated acids, and aromatic aldehydes, secreted by oozing (Schildknecht *et al.*, 1968; Moore, 1979).

Chromosomes about 24 in number (male $2n = 22+XY$ in most species); sex chromosome system XY/XX or XO/XX (Smith, 1960; Rožek, 1981; Serrano, 1981a, 1981b, 1984; D. Maddison, 1985b). Male meiosis achiasmate, lacking a typical diplotene stage (Serrano, 1981c; personal observations).

Egg. Essentially unknown; only a brief description of *B. confusum* eggs exists (Silvey, 1935).

Larva. Larva generalized, without striking modifications. The following description is based on examination of 35 species in my collection as well as the brief published descriptions of *Bembidion* larvae (Andersen, 1966; Bauer, 1975; Bøving, 1911; van Emden, 1942; Jeannel, 1941; Larsson, 1941, 1968; Kirk, 1972; Lindroth, 1955, 1980; Netolitzky, 1926; Raynaud, 1976b, 1977; Rey, 1887; Rye, 1908; Schaum, 1859; Schiødte, 1867; Silvey, 1935; Smrz, 1979; Thompson, 1979; Uéno, 1955). The description applies to first instar larvae; details about second and third instars are given later.

Size. LHw = 240–605 μm, LHl = 240–570 μm.

Microsculpture denticulate on parietale near coronal suture, probably serving an egg-bursting function (Figs. 226–231). Frontale posteriorly with microsculpture absent, or low, multitoothed combs, or consisting of numerous or few small denticles, or a few large denticles (Figs. 226–231); frontal microsculpture probably also serves an egg-bursting function.

Number and position of setae and chordotonal organs ("pores") are as inferred by Bousquet and Goulet (1984) to be ancestral carabid state, except as noted below. Frontale with extra small sensillum (Fig. 205) between or near FR_8 and FR_9; this sensillum is present in many carabids, including *Opisthius*, *Elaphrus*, *Gehringia*, *Patrobus*, *Pterostichus*, *Platynus*, and *Harpalus* larvae, and perhaps should be added to the hypothesized ancestral complement. Antenna (Fig. 201) with sensorial appendage prominent and basally constricted. Chordotonal organ MX_c of maxilla (Fig. 203) equidistant from MX_2 and MX_3; setal group gMX with only one to two rows of setae; MX_{11} and MX_{12} very small, conical (similar to FR_f, Fig. 204). Digitiform sensilla on maxillary palpomere 4 arranged in one subapical row around circumference of article (Fig. 206); apical sensilla of palpomere as in Figure 206. Galea with four apical sensilla (Fig. 207), in same pattern as found in *Nebria* (Spence and Sutcliffe, 1982). Labium (Fig. 202) with LA_5 on glossal projection, which is therefore quadrisetose (Fig. 209); digitiform sensilla arranged irregularly laterally on apical palpomere near base (Fig. 208); apical sensilla as in Figure 208. Many long setae covered with short projections emerge from the mouth cavity over the labium (Fig. 202), similar to setae found in *Omophron* (Landry and Bousquet, 1984) and many other carabids (my observations). Chordotonal organs PR_h, PR_i, and PR_j absent from pronotum. Mesothorax with chordotonal organs ME_d and ME_e absent. Metathorax lacking seta ES_1. Legs with seta FE_2 shorter and thinner than other setae on femur. Abdomen with TE_b absent from all segments; seta TE_3, TE_4, TE_5 present on first segment; TE_5 and one of TE_3 or TE_4 absent from all other segments. First abdominal sternum with ST_5 absent; all sterna without setae on hypopleurites.

Head (Figs. 194, 210–217, 219–224) with postorbital groove shallow or absent, occipital groove shallow. Nasale varied, denticulate (Figs. 192, 193, 238). Six stemmata on each side (apparently absent in *B. obtusum*). Mandible (Figs. 198–200) with single retinacular tooth, and penicillus; mesal margin not denticulate anterior to retinacular tooth (except slightly denticulate in the two *B. umbratum* examined). Maxilla as in Figure 203, without remnant of lacinia; palp with three articles, none subdivided. Galeomere 2 narrow, elongate, 1 to 1.5 times length of galeomere 1. Labium as in Figure 202, palp with two articles, none subdivided; palpomere 2 elongate and narrow.

Prothorax and metathorax lacking spiracles; spiracles present on mesothorax.

Leg with only one claw.

First through eighth abdominal segments with spiracles. Urogomphus not articulated, fused to ninth tergum.

Second and third instar larvae with characters of first instar, but with setae more numerous on most body sclerites. Body sparsely covered with very short setae, in addition to the more evident, long setae. Stipes with three or four setae on outer margin. Egg bursters absent. Cervical groove more prominent than in first instars, head less constricted basally (Fig. 218). Antennae and maxillae more elongate than in first instars.

Pupa. Unknown, except for a brief published description for *B. confusum* (Silvey, 1935).

Subgenera and subgeneric groups of *Bembidion*

The genus *Bembidion* is divided into a large number of subgenera or species groups. Only a few attempts have been made to join these subgeneric taxa into more inclusive natural groups. Netolitzky (1942, 1943) recognized several divisions within *Bembidion*. Species with an angulate humeral margin (including *Bracteon*) were separated from those with an evenly prolonged or absent margin; in the latter group he proposed two major series, divided between species with ed3 and ed5 attached to stria 3 (the "*Peryphus*-Reihe"), and those with ed3 and ed5 in interval 3, unattached to a stria (the "*Notaphus*-Reihe"). Jeannel (1941) divided *Bembidion* more finely, into six phylogenetic series: the *Ocys*, *Cillenus*, *Notaphus*, *Bem-*

bidion, *Peryphus*, and *Odontium* series. The *Odontium* series contains four taxa, ranked by Jeannel as genera, namely *Phyla*, *Metallina*, *Hydrium*, and *Odontium*, linked by common possession of angulate humeral margin. His genus *Odontium* includes a number of subgenera, among them *Bracteon*, that appear closely related. I include his genus *Odontium* within *Bembidion*, and call it the "*Odontium* subgeneric group." The group comprises three subgenera from the northern hemisphere. Possibly related to it are the subgenera *Microserrullula* and *Pseudoperyphus*, which I will now briefly discuss.

Subgenus *Microserrullula* Netolitzky

Serrula Netolitzky, 1910:209 (not Mörch 1853).
Microserrullula Netolitzky, 1921:185. (Type species *Bembidion aegyptiacum* Dejean, designated by Jeannel, 1941:540.)

Darlington (1959) suggested that the Oriental-Ethiopian subgenus *Microserrullula* may be related to *Odontium*. *Microserrullula* contains about thirteen species, ranging from Laos and India north into the Caucasus, west into Africa, and as far south as Madagascar (Andrewes, 1935; Netolitzky, 1942; Schuler, 1959; Basilewsky, 1968). Members of the subgenus are characterized by a number of features, including: possession of serrulate elytral margin; prominent suborbital ridge; broad pronotal base; very long flagellum of male genitalia; long, multiply coiled spermathecal duct. Judging by the apparent uniqueness of these features within the bembidiines, they are probably derived traits.

In general appearance, *Microserrullula* specimens greatly resemble members of *Odontium*, especially with the prominent and angulate shoulder margin, large size, broad pronotum, and full elytral striae. However, I cannot clearly interpret these characters phylogenetically; genitalic character states in *Pseudoperyphus* that suggest relationship with the *Odontium* group are not present in *Microserrullula*, but the states of *Microserrullula* may simply be autapomorphies. Proper placement of the subgenus awaits more detailed study, especially of first instar larvae. *Microserrullula* may belong in this group, but I will exclude it from subsequent analyses because of the uncertainty.

Subgenus *Pseudoperyphus* Hatch

Pseudoperyphus Hatch, 1950:100. (Type species *Bembidion chalceum* Dejean, by original designation.)
Bracteomimus Lindroth, 1955:49. (Type species *Bembidion chalceum* Dejean, by original designation.)

Subgenus *Pseudoperyphus* Hatch may be closely related to the *Odontium* subgeneric group. It contains at least six North American species (*B. chalceum* Dejean, *B. antiquum* Dejean, *B. honestum* Say, *B. integrum* Casey, *B. rufotinctum* Chaudoir, and one undescribed species, herein called *B.* "*sp. 17*") (D. Maddison, in preparation). Adults differ from the *Odontium* subgeneric-group by lack of an angulate humeral margin, and by possession of an exceptionally thick ventral margin of the right lobe of the central sclerite complex of the internal sac of the male genitalia. The first stylomeres of females have numerous (eight or more) long setae (as long or longer than those of *B. stenoderum* Bates, see Fig. 152), a state I have seen elsewhere only in *B. (Hirmoplataphus) concolor* Kirby. First instar larvae lack a frontal spot pattern and have a relatively unconstricted neck. Members are found on rocky shorelines. In spite of these differences, the construction of the male internal sac and spermatheca are essentially identical to those of *Bracteon* and its relatives, and some relationship may be indicated. I will discuss *Pseudoperyphus* further in my phylogenetic analyses.

The *Odontium* Subgeneric Group

Members of the *Odontium* subgeneric group are generally large *Bembidion* (SBL = 3.3 to 7.1 mm, generally over 4.5 mm), inhabiting sand or silt shores of creeks, rivers, and lakes. Internal sac of male genitalia strikingly uniform in pattern, consisting of large dorsal plate, central sclerite complex with right lobe and long flagellum, and relatively small ventral sclerite patch of two basins, as in Figures 112–128. In females, S1 is setose, without sclerotized plate at base of spermathecal duct. The humeral margin is angulate; stria 5 is not apically sulcate, with the adjacent outer interval not ridged; elytra unspotted by pigment. Larvae generally have a three-spotted frontale (Figs. 215, 216, 219), with posterior part of the wide head constricted, and short coronal suture (for the *Odontium* subgeneric group, LCl/LHl = 0.09–0.20 [excluding *B. aenulum*, 0.09–0.16], mean = 0.12 [n = 16 species, 42 specimens]; for other *Bembidion*, LCl/LHl = 0.15–0.22, mean = 0.18 [n = 16 species, 20 specimens]).

Two apparent clades within this group are generally considered distinct subgenera: *Bracteon*, with 17 species; *Ochthedromus*, with two species. The remainder of the subgeneric group is placed within subgenus *Odontium;* some authors remove from *Odontium* a collection of species including *B. striatum* (Fabricius) and *B. bowditchii* (for example, Lindroth, 1963), but I prefer to follow Jeannel (1941), and not recognize the distinction. I also include within *Odontium* the members of *Cylindrobracteon* Netolitzky, following Kryzhanovskij (1983). I will discuss these decisions further under the account of subgenus *Odontium*.

New subgeneric names could be proposed for clades such as the *B. confusum* + *B. arizonae* + *B. sculpturatum* group, but this is quite unnecessary at present and would only add unneeded names to the literature. I will not radically alter existing subgeneric classification; such changes await more detailed study of the group.

KEY TO ADULTS OF THE *ODONTIUM* SUBGENERIC GROUP

1. Setae in elytral interval 3 surrounded by a distinct, dull patch, which has deeper microsculpture lines and is therefore more granulate than the rest of the elytron .... *Bracteon*

1′. Elytral interval 3 with more uniform microsculpture 2

2(1′). Setae ed3 and ed5 in elytral interval 3 in large foveae; pronotal base markedly constricted; submentum with more than eight long setae .... *Ochthedromus*

2′. Elytral intervals lacking foveae, or, if foveae present (*B. foraminosum* Sturm), then pronotum less constricted (similar to Fig. 6); submentum with six or less long setae .... *Odontium*

Subgenus *Ochthedromus* LeConte

Ochthedromus LeConte, 1848:453. (Type species *Bembidion americanum* Dejean, designated by Lindroth [1963].)

Adults of *Ochthedromus* can be distinguished by the following combination of characters: protruding eyes; submentum with transverse row of about 10 long setae, suborbital setae especially long; pronotum with constricted base, and markedly rounded sides; humeral margin angulate; elytra with foveae at bases of ed3 and ed5; punctures of striae small; male internal sac with markedly sclerotized strip inward of ostium: a similar sclerotized strip occurs in some other *Odontium* subgeneric group members, but in *Ochthedromus* specimens the strip has a papillate appearance, as if composed of numerous minute beads. Larva known of *B. bifossulatum cheyennense* Casey; with three-spotted frontale; other characters listed in Table 5.

Lindroth (1963) considered *Ochthedromus* as consisting of two species, *B. bifossulatum* LeConte and *B. americanum* Dejean. My studies indicate that *B. bifossulatum* consists of two distinct forms, separable on the basis of the mentum teeth and male genitalia. As they are important for my discussions of *Bracteon* phylogeny, a clarification of their nomenclature is warranted. The western form has a rounded, somewhat-trapezoidal, laterally ridged mentum tooth, with distinct epilobes (Fig. 58); the ostial sclerotized strip in the male internal sac is abruptly bent. The eastern form has a rectangular, truncate, bulbous mentum tooth, with somewhat indistinct epilobes (Fig. 57); males have a more gently curved ostial sclerotized strip. In the material at hand, the two forms appear allopatric. However, I have not studied much material, and further study may reveal sympatry with or without evidence of gene flow. I am uncertain as to whether to consider them separate species or subspecies; nonetheless, distinct names are warranted, and herein I will treat them as subspecies. The types of three names belong to the western form (*B. bifossulatum* LeConte, 1851 [holotype female, MCZ!], *B. regestum* Casey, 1918 [lectotype male, USNM!], and *B. ferreum* Casey, 1924 [lectotype female, USNM!]), with *B. bifossulatum* LeConte being the valid name. The types of three names belong to the eastern form (*B. cheyennense* Casey, 1918 [lectotype male, USNM!], *B. sufflatum* Casey, 1918 [lectotype male, USNM!], and *B. nuperum* Casey, 1918 [holotype male, USNM!]); I herewith choose *B. bifossulatum cheyennense* Casey as the valid name.

Taxa included in *Ochthedromus:*

B. bifossulatum bifossulatum LeConte, 1851:186. (CA, ID, BC) !

B. bifossulatum cheyennense Casey, 1918:15. (AZ, CO, WY, AB, SA, and eastward) !

B. americanum Dejean, 1831:87. (U.S.A., Canada) !

Subgenus *Odontium* LeConte

Odontium LeConte, 1848:452. (Type species *Bembidion coxendix* Say, designated by Jeannel [1941].)

Cylindrobracteon Netolitzky, 1940:159. (Type species *Bembidion fusiforme* Netolitzky, by original designation.)

Adult *Odontium* can be distinguished by the following combination of characters: with characters of the *Odontium* subgeneric group; silver spots lacking; elytra around ed3 and ed5 generally without foveae; if foveae present, then submentum with six or less long setae.

Odontium is often split into two or three subgenera, but the distinction between them seems rather slight. The *B. striatum* group has been removed because of the wide interval 9 (as wide as 8), and the shallow stria 8 in front half of the elytron (Lindroth, 1963:242), and mouthpart structure (Netolitzky, 1942:49). The elytral characters, however, are not at all clear, with several species (for example, *B. robusticolle* Hayward, *B. carinatum* [LeConte], and *B. durangoense* Bates) showing intermediate states. Figure 2 illustrates the lack of two distinct groups in the *Odontium* complex based on the relative widths of intervals 8 and 9. As well, mouthpart structure is more uniform across the group than supposed by Netolitzky: only *B. confusum*, *B. sculpturatum*, and *B. arizonae* have distinctive mandibles and laciniae. Four or five East Asian species are occasionally distinguished as a separate subgenus, *Cylindrobracteon*. The only known distinctive character of the group is the fusiform body, with pronota that are trapezodial, with broad base (extended outward to humeral angles), nearly straight margins, and protruding, almost-divergent front angles. As well, the midlateral pronotal seta is absent, and the humeral margin is long, but these latter traits are shared with a number of *Odontium* (s. str.) species. The North American species *B. aenulum* and *B.* sp. nr. *aenulum* are two such species, and their pronota are somewhat intermediate between those of *Cylindrobracteon* and other *Odontium* (s. str.). Following Kryzhanovskij (1983), I do not consider *Cylindrobracteon* distinctive enough to warrant subgeneric status. Until *Odontium* is better understood phylogenetically, I will treat the species as belonging to one subgenus.

Odontium comprises all species of the *Odontium* subgeneric group other than *Ochthedromus* and *Bracteon*. It is likely that it is paraphyletic, with *Ochthedromus* or *Bracteon* derived from it. I hesitate splitting it into monophyletic units until its parts are better known.

North American and western Palearctic members of the subgenus appear well understood (except for one undescribed species in southern U.S.A.), but material from the eastern Palearctic region is in need of study.

Note that "*Bembidion bowditchi*" is an incorrect subsequent spelling of *Bembidion bowditchii* LeConte (see ICZN, Third edition, Article 33[d]).

Taxa included in *Odontium:*
(for some synonyms, see Lindroth [1963], Erwin [1984], and Morita [1987])

B. bowditchii LeConte, 1878:451. (WY, ID, WA, BC) !
B. foraminosum Sturm, 1825:183. (Europe) !
B. striatum (Fabricius), 1792:179. (Palearctic) !
B. suturale Motschulsky, 1850:16 (Caucasus)
B. persimile Morawitz, 1862:225. (Japan, northeastern China) !
B. gebieni Netolitzky, 1928:168. (China)
B. japonicum Jedlička, 1961:311. (Japan)
B. soederbomi Jedlička, 1965b:203. (Mongolia)
B. robusticolle Hayward, 1897:50. (U.S.A.) !
B. coxendix Say, 1823a:151. (U.S.A., Canada) !
B. carinatum (LeConte), 1851:186. (CA, AZ) !
B. sculpturatum (Motschulsky), 1859:132. (CA, NV, WA) !
B. confusum Hayward, 1897:52. (U.S.A., Canada) !
B. arizonae Lindroth, 1962:246. (AZ, Mexico) !
B. durangoense Bates, 1891:263. (AZ, Mexico) !
B. aenulum Hayward, 1901:156. (IW, NK) !
B. sp. nr. *aenulum* (MS, MO) !
B. aeneipes Bates, 1883:276. (Japan, China) !
B. fusiforme Netolitzky, 1914b:168. (Formosa, Japan) !
B. subfusum Darlington, 1959:335. (Philippines) !
B. chloropus Bates, 1883:277. (Japan) !
B. suensoni Kirschenhofer, 1984:58. (Korea)

Subgenus *Bracteon* Bedel

Bembidion sensu LeConte, 1848, not Latreille, 1802.
Bracteon Bedel, 1879:27. (Type species *Bembidion litorale* [Olivier], designated by Bedel [1881].)
Chrysobracteon Netolitzky, 1914a:166. (Type species *Bembidion velox* [Linné], designated by Netolitzky [1940].)
Parabracteon Notman, 1929:157. (Type species *Bembidion tuberculatum* Notman [=*B. carinula* Chaudoir], by monotypy.)
Litoreobracteon Netolitzky, 1940:160. (Type species *Bembidion litorale* [Olivier], by original designation.)
Argyrobracteon Netolitzky, 1940:162. (Type species *Bembidion argenteolum* Ahrens, by original designation.)
Conicibracteon Netolitzky, 1940:162. (Type species *Bembidion stenoderum* Bates, by original designation.)
Stylobracteon Netolitzky, 1940:163. (Type species *Bembidion baikaloussuricum* Netolitzky [=*B. conicolle* Motschulsky], by original designation.)
Foveobracteon Netolitzky, 1940:164. (Type species *Bembidion foveum* Motschulsky, by original designation.)

Notes about synonymy

The name *Chrysobracteon* Netolitzky has traditionally been applied to this group, with the name *Bracteon* Bedel referring to *B. striatum* and its relatives (see, for example, Netolitzky, 1942 and Lindroth, 1963). However, as Bousquet and Larochelle (in press) note, the type species of *Bracteon* is *B. litorale* (as designated by Bedel [1881:xxiii]), not *B. striatum*. Thus, *Bracteon* must be applied to *B. litorale* and its relatives, with *B. striatum* falling within the subgenus *Odontium* LeConte.

Andrewes (1935), Lindroth (1963), Erwin and Kavanaugh (1981), and Erwin (1982) avoid use of subgeneric names, and use instead more informal species-group names for groupings within *Bembidion*. If this practice were followed for *Bracteon*, it could be referred to as the *B. inaequale*-group, as Lindroth (1962) did for the Nearctic fauna, or, perhaps more appropriately for the world fauna, the *B. litorale*-group.

Characterization of *Bracteon*

Adult Diagnostic Combination. Most easily recognized by possession of two "silver spots" on each elytron, that is, with a distinct patch of granulate microsculpture surrounding ed3 and ed5 (Figs. 5–23, 61). Most species have as well dark, shiny patches of weaker microsculpture on the elytral disc; these are termed "mirrors" (Figs. 7–23). Other character states as for *Odontium* subgeneric group.

Adult Description. **Size**. Relatively large *Bembidion*, SBL = 4.4–7.1 mm. **Color**. Body black or piceous, unspotted by pigment (although variation in microsculpture and metallic sheen produces a spotted pattern). Generally with metallic reflection (except in some black, presumably old and worn specimens), ranging in color from reddish, to coppery, golden, aeneous, green, blue-green, or bright blue. At least some parts of appendages paler, either testaceous, rufotestaceous, or rufous. **Microsculpture**. For the most part isodiametric on dorsal surface, although slightly transverse in some *B. hesperium* Casey. **Sensilla**. Basilateral seta of prothorax at hind angle. Setae ed3 and ed5 in third interval, not attached to stria; ed4 absent; eo1 generally far in front of eo2–eo4. Protarsomere 4 with ventroapical setae present, narrowly or widely separated. **Thorax**. Pronotum with tubercle between basilateral fovea and side margin. Elytral striae punctatostriate, including 8 and 9; striae 2 and 3 generally deepened and with larger punctures around silver spots (most extreme in *B. hesperium*); stria 8 more shallowly impressed anteriorly than 7, interval 8 relatively wide (Fig. 2). Elytral margin angulate at humerus; humeral margin reaching striae 4 to 6. **Male genitalia**. Internal sac with large dorsal plate; with central sclerite complex consisting of right and left lobes, both moderate to large, as well as a short to medium-length flagellum; with a ventral sclerite patch of two basins separated by a ridge (Fig. 99). Parameres with a varied number of setae, but generally trisetose (for example, of the 102 parameres of *B. lapponicum* studied, 62 had three apical setae, and 37 had four). **Female genitalia**. Spermatheca sclerotized, with a distinct ringed cornu; cornu without prominent apical indentation (Figs. 165–179). Spermathecal duct relatively short, with only a few turns and coils, not multiply coiled (Fig. 145). Sclerotized plate at base of spermathecal duct absent. Female basal stylomere (S1) setose (except in *B. carinula*, members of which have a few minute peg-like sensilla in place of setae). **Chromosomes**. Male 2n = 20+XY or 22+XY or 34+XY; chromosomes of normal size for *Bembidion* (autosomes 1.2–2.5 μm), submetacentric or metacentric (D. Maddison, 1985b:fig. 1; Nettman, 1986).

Larval Diagnostic Combination. Not yet distinguishable as a group from members of subgenera *Odontium* and *Ochthedromus;* the description below applies equally well to the known *Bracteon, Odontium,* and *Ochthedromus* larvae.

The larval instars can be distinguished by the following key:

1. Parietale with denticulate microsculpture near coronal suture (Figs. 226 to 231). Stipes with two setae on outer margin .... first instar
1′. Parietale with microsculpture near coronal suture consisting of shallow meshes or scales, not denticulate. Stipes with three setae on outer margin. Cervical groove prominent 2
2(1′). Head capsule narrower (LHw = 510–750 μm); stipes of maxilla relatively short and wide (length/width = 2.50–3.05) .... second instar
2′. Head capsule wider (LHw = 630–1040 μm); stipes of maxilla relatively long and thin (length/width = 3.22–3.89) .... third instar

First Instar Description. **Size**. LHw = 330–505 μm, LHl = 255–390 μm. **Color**. Frontale generally with one central dark spot, and one elongate dark patch on either side of the posterior portion of the frontale (Fig. 215); parietale in several species with dark patch on each side posteriorly near coronal suture (Fig. 215). Some species (*B. balli, B. foveum*) with these patches partly masked by generally dark ground color; others (*B. argenteolum, B. alaskense* Lindroth, *B. carinula,* and *B. lapponicum*) without distinct patches, having only diffusely darker head center or uniformly dark head. **Microsculpture**. Frontale without a row of a few large denticles; with or without a posterolateral patch of small denticles or multitoothed combs. Parietale with smooth patch mostly lacking microsculpture between FR_4, FR_7, FR_8 and the frontal suture (with a few denticles in *B. punctatostriatum*); generally with denticulate microsculpture laterally. **Head**. Head capsule constricted posteriorly; coronal suture short (LCl/LHl mean = 0.127, n = 11 species, 35 specimens).

Second Instar Description. As for *Bembidion*, plus: Stipes with three setae on outer margin.

Species included

Bracteon includes 17 known species, ranging throughout the temperate, cold-temperate, and subarctic regions of the northern hemisphere. Delimitation, identification, and description of these species are dealt with later, in the section "Species of *Bracteon*."

One Chilean *Bembidion* species, *B. chlorostictum* Reed (1874), was included in the subgenus by Csiki (1928). Reed (1874), Netolitzky (1931), and Lindroth (1962) considered the Chilean species to be unrelated to *Bracteon* as elytral interval 8 merges with 9 posteriorly as in subgenus *Notaphus* and related *Bembidion*, in contrast to the presumably primitively separated intervals 8 and 9 of *Bracteon*. However, *B. chlorostictum* shares with *Bracteon* "discoloured shining streaks on the third elytral interstice" (Reed, 1874); that is, shallowly microsculptured mirrors. Reichardt (1977) maintains *B. chlorostictum* within *Bracteon*, citing Jeannel (1962) as an authority for this action. As Perrault (1981:245) notes, Reichardt was in error in attributing to Jeannel (1962) the return of *B. chlorostictum* to *Bracteon*, as the species was not mentioned in Jeannel's work. Indeed, Jeannel (1962:536) states, "Quant aux séries phylétiques d'*Ocys*, de *Cillenus*, de *Bembidium*, d'*Odontium*, d'*Asaphidion* définies dans la Faune de France, elles n'ont aucun représentant dans l'hémisphère austral," indicating that he does not believe *Bracteon* (a taxon he includes within *Odontium*) occurs in South America. I could not locate type material of *B. chlorostictum*. D. H. Kavanaugh informs me (pers. comm., 1984) that no authentic *B. chlorostictum* specimens could be found in the Reed collection at the California Academy of Sciences. I have thus not seen specimens that I can definitely assign to *B. chlorostictum* Reed, nor to my knowledge has any recent carabidologist, but I suspect, as does Perrault (1981), that *B. chlorostictum* is related (if not identical) to *B. (Notaphiellus) cupreostriatum* Germain. I have examined two unidentified species of *Notaphiellus* (MCZ!), both from Chile. They possess distinct *mirror* patches around ed3 and ed5 (not silver spots); the elytra are a patchwork of mirrors and more deeply microsculptured areas. The male genitalia of the one specimen I studied is clearly "notaphoid," with a large, doubled, scaled ventral sclerite patch; the form of the internal sac structures is very similar to some North American *Notaphus* such as *B. graphicum* Casey. *B. chlorostictum* Reed is therefore probably also of notaphoid stock, and not a *Bracteon*.

Natural history

Bracteon are shoreline insects, spending most of their lives on vegetationless or sparsely vegetated beaches. In general, they occur on sandy substrates, which may or may not contain fine-grain silts and clays. This uniformity of broad habitat requirements allows rich *Bracteon* communities along some watercourses: I have found six species (*B. balli*, *B. foveum*, *B. carinula*, *B. lapponicum*, *B. punctatostriatum*, *B. levettei carrianum*) in company of related *B. coxendix* and *B. bifossulatum cheyennense* on the barren shores of the North Saskatchewan River near Paynton, Saskatchewan (Fig. 190), and occurrence of four or five species together is not uncommon (Lindroth, 1962; my observations). Most shores inhabited by *Bracteon* have at least two species. The means by which these ecologically and phylogenetically similar species coexist in an apparently uniform habitat is uncertain, but a closer examination of the animals and their habitats reveals a greater ecological diversity than is at first evident.

Lindroth (1945) and Andersen (1970) have shown that each European species prefers slightly different habitat substrates. On several beaches in North America, adults of different species were generally found in different microhabitats (my observations). Along the North Saskatchewan River near Paynton, for example, *B. foveum* is commonest around the clay-mixed banks of backwater pools (but many specimens are found along the river shore); *B. balli* and *B. lapponicum* on wet sand close to the river shore; *B. levettei carrianum* on wet sand along the river shore and backwater pool shores; *B. carinula* on sand, including the dry, wind-blown sand of the upper banks as well as along the river shore; *B. punctatostriatum* only on hot, dry sand more than 10 m from the river. These patterns appear to hold throughout the range of each species, but the North American species have not been studied in detail; my data are based on passing observations, lacking careful measurements. I have not collected most of the other species extensively enough to discover microhabitat preferences, but ranges of two other species are nonetheless quite clear: *B. inaequale* is found on clay-mixed sand, usually with a sparse cover of vegetation, around shores of creeks, rivers, and lakes; *B. zephyrum* is almost restricted to wind-blown sand beaches of the Pacific Ocean.

Behavioral observations of *Bracteon* are notably scarce. Andersen (1978) studied tunneling of several species, and showed that adults of *B. argenteolum* dig prodigiously into sand, *B. velox* and *B. lapponicum* extensively but to a lesser extent, and *B. litorale* rarely. Andersen (1978) also conducted substrate preference tests on *B. argenteolum*, *B. lapponicum*, and *B. litorale*, finding that *B. argenteolum* prefers finer dry sand to coarser dry sand, and *B. litorale* dry silt to dry sand. This is more or less consistent with the natural substrates of these beetles.

Bracteon adults are predacious: besides occasional reports of adults feeding upon various arthropods (Gersdorf, 1937; my observations), I have noted, in the course of dissecting numerous specimens of most *Bracteon* species, recta filled with pieces of arthropod cuticle. The full course of their diet is unknown.

Bracteon adults are generally active during the day, especially under bright summer sunshine, but they are at least occasionally nocturnal (against Larochelle, 1975). On the shores of the North Saskatchewan River at Deer Creek Bridge in Saskatchewan, a large number (123) of adults were collected between 21:30 and 22:30, 0.5 to 1.5 hours after sunset on a warm, moonless, September night. The adults were active on the surface, and several were feeding on dead insects, including nematocerous flies. A similar observation was made at the same locality on a cool, July night. That this is a general phenomenon has yet to be demonstrated.

Bracteon overwinter as adults, and breed in the late spring and early summer. There are three larval instars, and pupation presumably occurs in mid to late summer. Teneral adults appear in the late summer and fall.

I have observed adults of all eleven North American species in flight; among strictly Palearctic species, members of *B. argenteolum*, *B. velox*, and *B. litorale* have been observed flying (Lindroth, 1945). On warm, sunny days they are very active fliers, and will take to the wing quickly if approached, rather as do *Cicindela* adults.

Character states of *Bracteon*

Variation in many characters was seen within *Bracteon*. Some of this variety was useful in delimiting species, some for reconstructing phylogeny; some appeared useful for neither. In this section I introduce some of the character systems studied, describe some of the variation observed, and include tips for examination. I also comment briefly on characters that show potential for future research, but which I have only superficially examined. If, during the course of using this paper, some question arises concerning a character that cannot be answered by the cited figures or descriptions, this section should be consulted.

Color. The metallic hues of the body of *Bracteon* specimens as seen under diffuse light are relatively distinct, and need no introduction. I rarely use them in formulating my systematic conclusions, in good part because of the large amount of within-taxon variation. I include them for the value they have in aiding identification of some species.

Appendage color is less variable within species, but it can be more difficult to determine the color of an appendage as it would be in its pristine state, because of grease darkening the paler regions of the appendage. Specimens to be examined should be as clean as possible.

Microsculpture. The most striking features of the microsculpture of a *Bracteon* are silver spots on elytra of all species, and mirrors on elytra of some. These features are clearly studied under diffuse light on clean specimens.

Distinct silver spots are only found around discal setae ed3 and ed5 of the elytra, although indistinct silvery spots are present on the pronota of specimens of *B. inaequale* and some other related species. The number of silver spots, while generally two per elytron, varies to a considerable extent in some populations of *Bracteon*. For example, in a series of 94 specimens of *B. lapponicum* from Old Crow River, northern Yukon territory, Canada (DRMa, UASM), 36 (or 19.1%) of the 188 elytra had three setiferous silver spots; four had one silver spot, one had four silver spots, while the remaining 147 elytra had two silver spots.

The difference visible between silver spots, mirrors, and other portions is often due to differences in the metallic hue of these regions, in addition to the depth of the microsculpture lines. As well, silver spots are depressed within the elytra, and mirrors are generally raised, further enhancing the distinctiveness of each region. For example, the depressed silver spots of *B. zephyrum* are silvery-gray or blue-green, the raised mirrors generally dark coppery red or purplish, and the surrounding elytral surface has a green or blue-green reflection. On their own, the microsculpture differences are not always striking (see, for example, the scanning electron micrograph of Fig. 61). In some species, especially shiny *B. semenovi*, *B. punctatostriatum*, and *B. stenoderum*, the mirrors and silver spots are not nearly so distinctive, because of the general reduction of microsculpture on these animals. The extent of mirrors on these beetles can best be observed in the more deeply microsculptured females.

Some species (especially *B. argenteolum*, *B. alaskense*, *B. carinula*, and *B. punctatostriatum*) exhibit a great variation in overall microsculpture depth, with specimens ranging from shiny to dull. As a result, the absolute depth of microsculpture of mirrors and silver spots varies from specimen to specimen, so that some individuals may have shiny mirrors (or silver spots), while others have quite dull mirrors (or silver spots). Thus, mirrors and silver spots must be defined by *relative* microsculpture depth, not absolute depth; the pattern within an elytron of relative microsculpture depth is more or less constant within a species.

Some generally shiny specimens, lacking areas that would be deemed mirrors on the basis of markedly shallower microsculpture, nonetheless have central patches of a distinct metallic color in regions that would typically contain microsculpture mirrors. For example, while the shiny elytra of the *B. semenovi* holotype lack distinctly shinier patches, intervals 3 to 5 are darker, having a coppery tint lacking on the outer intervals; I consider this tint to delimit faint mirrors, homologous to the more distinct mirrors of other species.

The extent and distribution of mirrors provide some of the best characters for species delimitation and identification. When present, mirrors occur on interval 3, surrounding the silver spots. There may also be mirrors on intervals 1 through 5 near the center of the elytra, as well as on the anterior portions of the same intervals, or the posterior portions of intervals 6 and 7. In general, mirrors on intervals 3, 5, and

7 are more prominent than those on other intervals. Figures 7 to 23 illustrate some of the variation in mirror extent and position.

Sensilla. I investigated only a few adult sensillar characters, all setal.

One such character is suborbital setation. The head laterally beneath the eyes is either barren of setae (for example, in *B. punctatostriatum*, Fig. 60), or has a number of setae, ranging from relatively dense and long (*B. lapponicum* and others, Fig. 59), to shorter and sparser. The distinction between these states is not clear-cut, and as I have not quantified states, this character is relatively prone to errors in interpretation.

Protarsomere 4 of both sexes of most species of *Bembidion* possess ventrally an apical set of four setae, the two inner of which are thin, almost transparent, dorsoventrally flattened, and laterally expanded (Fig. 96a). The bases of these setae are generally close-set, almost touching in the midline. However, three *Bracteon* species have relatively cylindrical setae, with one of these species, *B. alaskense*, having their bases widely separated (Fig. 92).

Several sensillar characters showed variation within *Bembidion:* number of setae on the anterior margin of the labial palpomere 2; number of setae of submentum; tarsomere 5 setation; profemur setation; metafemur setation. These might provide evidence in future studies about *Bembidion* relationships.

Head. There is a wealth of mouthpart characters showing variation within *Bracteon*, but I have been able to examine only a few of them. Mandibles vary in overall shape, in microsculpture (especially of the terebral/premolar region [Figs. 32–34]), in distinctiveness of premolars (compare Figs. 32 and 33), and in size of pores dorsally and mesally near the dorsal condyle (Figs. 35–36). My preliminary study of these characters revealed extensive infraspecific variation within most of them, and I did not pursue them. Laciniae vary in width from narrow (Fig. 46) to robust and wide (Fig. 48). The shape varies in addition to simple width: some specimens have more definitely curved apices, or subapical indentations (Figs. 43, 44), or subapical ridges (Fig. 44); these characters warrant further study.

The shape of the mentum tooth has been used by Netolitzky (1942) and others as a character for *Bracteon* taxonomy. Netolitzky (1927,1942:33–34) cautions against overestimation of the value of the mentum tooth as a systematic character; however, he does use it to separate his "subgenera" *Litoreobracteon*, *Argyrobracteon*, etc. Lindroth (1962:1) disagrees with this use, claiming that the mentum tooth is too infraspecifically variable: "for instance, the two male paratypes of *carrianum* Csy. (=*levettei* Csy.), both from St. Albert, Alberta, and with identical penis, have a quite different mentum tooth, triangular in one, practically parallel-sided in the other specimen." While there is some variation in shape of the mentum tooth within *Bracteon* species, the variation I have seen is slight, and I consider it a stable enough character to be taxonomically useful. Even within *B. levettei* the mentum tooth is constant. I have examined the two paratypes of *B. carrianum* (USNM!) mentioned by Lindroth, and found them both to have the bulbous, parallel-sided mentum teeth characteristic of other members of *B. levettei*. Figures 49–56 illustrate some of mentum tooth shapes found in *Bracteon*.

Elytra. Two elytral characters not carefully studied herein but which should be investigated are: interval 3 width; anterior protrusion of humerus (protruding in *B. punctatostriatum*, *B. inaequale*, and to a lesser extent in some other taxa).

Metathoracic Wings. Two wing characters of potential future use are: pigmentation of metathoracic wing veins; shape of plica vein, whether sharply or gently curved.

Legs. Both sexes of many bembidiines and trechines have an apical projection bearing four setae ventrally on protarsomere 4; the length of this projection varies between species, and is essentially absent in *B. alaskense*, *B. argenteolum*, and *B. punctatostriatum*. Under a light microscope, however, the length of such a projection can be difficult to determine accurately. My observations of this structure therefore provide only uncertain evidence about relationship.

Claw shape, male protarsomere 1 and 2 shape, and protibial apices also show interspecific variation, but I have not studied these in great detail.

Male Genitalia. Because of the importance of male genitalia as a source of characters for species identification and phylogenetic analysis, I will describe their complicated structure in some detail.

Bracteon aedeagi at rest consist of a sclerotized outer tube and a membranous internal sac, containing several sclerites, folded in an inverted position within the tube (Fig. 99). The internal sac is attached to the tube dorsally near the apex, at the *ostium* (Lindroth, 1957b); this is the entrance into the internal sac from the exterior. During copulation the internal sac everts through the ostium; everted sacs are shown in Figures 101 to 103. I will first describe the internal sac as it sits in a rested, inverted position, beginning at the ostium. Many of the features are illustrated in Figures 99 to 102.

At the ostium the left and right external walls of the aedeagus extend inward. The ostial cavity formed by these two walls is bounded anteriorly where they join (Fig. 99, "anterior edge of ostial cavity"). The natures of the microtrichia and scales in the "ostial microtrichial patch" associated with this edge provide good characters for species identification. These microtrichia or scales occasionally extend upward, forming a *dorsal field* on the outer wall of the aedeagus. The walls of the ostial cavity are membranous anteriorly and posteriorly, but centrally they are sclerotized in a roughly triangular patch called the *ostial flag* (Lindroth, 1940).

A pathway into the internal sac is shown by the arrow in Figure 99. The ostial cavity ends ventrally as the two enclosing membranes fold together to the right and continue on the right side of the cavity upward to near the dorsal surface; anteriorly they extend upward to the *dorsal plate*. Nearer the ostium, they are folded again to the right, and extend back down toward the venter. This simple pattern is complicated in some species by additional folds or membranous lobes. Anteriorly, near the sclerite complexes, membrane structure is much more complex, and I have not yet resolved the folding pattern.

There are two sclerite complexes on the internal sac. The largest, and the one to which the sperm duct connects, is the *central sclerite complex* (CSC, Figs. 99–102). It is partly enclosed by the dorsal plate. The left lobe of the CSC consists of two closely adjacent domes, from the rightmost of which a flange is extended down and merged with the right lobe. The right lobe often has a bulge dorsally on its left side; as the ventral edge of this bulge is heavily sclerotized, a dark line or ridge is visible on the lobe in lateral view in some species. The lobe is often sculptured: *B. lapponicum* usually has triangular scales and longitudinal striations, *B. inaequale* has a rugose surface, whereas *B. balli* and *B. foveum* usually are quite smooth. However, there seems to be a great deal of intraspecific variation, and I have not used this character in my analysis. Similar variation is also seen in microsculpture present on the left CSC lobe.

Apically from these lobes a complicated grooved spike (*flagellum*) projects; it is species-specific in form (Figs. 99–102, 109, 110, 129–144). It is presumably the conductor of sperm, and may enter the spermathecal duct during copulation (Schuler, 1960). As the flagellum is partly surrounded by a scaly *flagellar sheath*, it can be very difficult to see in inverted position. The flagellar sheath is most prominent among *Bracteon* species in the *B. argenteolum*-subgroup, *B. stenoderum*, *B. hesperium*, *B. lorquinii*, and the *B. inaequale*-subgroup. In Figures 112 to 128, I have emphasized the flagellum beyond its normal visibility, and I present in Figures 129 to 144 drawings of isolated CSCs including flagella. The flagella provide excellent characters for species identification in *Bracteon* and other *Bembidion;* if all other identification aids fail, I recommend dissecting out a CSC and comparing the isolated flagellum with Figures 129 to 144.

From the baso-dorsal portion of the flagellum a heavily sclerotized wrinkled structure (Lindroth's "*ribbon brush,*" "*brush sclerite,*" or "BW") arises and passes on the right side of the CSC down toward the venter, where it joins the *ventral sclerite patch* (VSP). This latter complex is quite varied within the subgenus, and is one of the most useful genitalic features for specimen identification. In *Bracteon,* it consists of two basins, connected by a dorsal ridge; the posterior basin extends distally into a wrinkled sclerotized patch.

Everted internal sacs clearly show lobes and surface sculpture of the membrane. SEM views of the membranes reveal a surprising complexity and diversity of microsculpture, with striking within-specimen (Figs. 103–106) and between species variation. I have not had time to study lobes or microsculpture in detail, but they seem to me to be some of the most, if not the most, fruitful areas for future *Bembidion* studies.

Female Genitalia. Female genitalia vary considerably from species to species, as well as within species. Some characters, such as length of stylomere 2, were seen to be fairly constant within most species. Many other characters, such as the number of dorsolateral ensiform setae, show more variation within species. Most aspects of spermathecal shape are quite varied within some species, but there are consistent differences between them. I figure the spermatheca of most species (Figs. 165–179), as some useful information is contained therein. Spermathecal shape should prove more useful in other subgenera and for studies of subgeneric delimitation and relationships.

Characters that have interesting patterns of variation, and which might prove useful in future research, include the form of sternum VIII, shape and setation of the valvifers (sternum IX), spermathecal duct coiling and turn pattern, and stylomere 1 structure. I have also not studied bursa copulatrix shape, although Erwin and Kavanaugh (1981) found it useful in their work on the *B. erasum* group.

Chromosomes. Chromosomes of all North American taxa of *Bracteon* have been investigated, as well as the Palearctic *B. litorale* (Nettman, 1986). Members of *Bracteon* are relatively constant in chromosome number, although there is some variation. Autosomes differ little in length. The only striking variation in form is found in Y chromosomes: all species have a Y equal in size to the autosomes, or only slightly smaller, except *B. alaskense* and *B. carinula,* which have Y chromosomes less than two-thirds the length of the smallest autosomes. Karyotypes and other details of these species' chromosomes, as well as localities of capture of specimens examined, are presented elsewhere (D. Maddison, 1985b).

Larva. The most obvious differences between first instar larvae of *Bracteon* species are in color, especially of the head. Closer examination, however, reveals numerous other differences, mostly in sculpture and setation. This observation matches that of Goulet (1983) on elaphrine larvae, on which he found many systematically useful microsculptural and sensillar characters. In *Bracteon,* variation among species was noted in microsculpture of the frontale, parietale, mandibles, and pronotum of first instars. The presence, length, and form of setae of the head capsule, thoracic nota, abdominal terga, and abdominal sternum IX also provided useful characters. For identification purposes, setal width and length are best characterized by comparison to nearby setae; thus I do not give absolute measurements. For example, I state that seta FR_3 of most *Bracteon* is basally less than one-third the width of the nearby FR_2, but the absolute basal widths have not been measured.

One of the few microsculptural characters I have investigated is frontal microsculpture. Most *Bracteon* have a patch of microsculpture posteriorly and laterally on the frontale, in the position of the postero-lateral dark spots on Figure 215. Descriptions of type of frontal microsculpture (whether or not multitoothed combs are present; character 64 of Table 2) are restricted to the anterior half of this patch, and characterization of extent of frontal microsculpture (character 63) applies only to the posterior half of the patch.

I have not carefully studied nasale structure; while there is much infraspecific variation, in good part due to wear, there are some differences between species. Urogomphus length varies between species, and is also worth further examination.

SPECIES OF *BRACTEON*

Species and Subspecies Recognition

Species concepts

The diversity of opinion about the meaning of "species" has lead to a voluminous literature. The definition one chooses to adopt, is, for the most part, dependent on what one wants to do with the resulting taxa. Different biologists may choose to divide organisms into species in different ways, each choosing a definition that is best suited for their fields. As a phylogeneticist, I adopt a species concept similar to that of the evolutionary species concept of Simpson (1961:153) and Wiley (1978, 1981), basically a rephrasing in phylogenetic terms of the Biological Species Concept (Mayr, 1940; Dobzhansky, 1937; Coyne, Orr, and Futuyma, 1988).

If we are to explain the origin of diversity of form, then we must use the "vehicles" of evolution (lineages) in our theories, if our theories are to be both explanatory and simple. For dioecious organisms, a species, as I use the term, is a portion of a lineage of a phylogeny, with a lineage being (somewhat vaguely) defined as a set of organisms cohesively linked by breeding ties, which is distinct from other such sets. In the genealogical nexus of organisms, the boundaries of species occur where the anastomizing lines within species are replaced by the gaps between lineages.

In dealing with fossils, the starting and the ending points of this portion are not easily decided. However, as the fossil record of *Bracteon* is inadequate, consisting of only a few Miocene and Pleistocene fragments, this is not a concern. To use a phrase from R. C. Fox, my specimens come from the "thin veneer of the present." Among Recent organisms a species consists of a time-transect of a lineage.

Lineages (and thus species as I use the term) are genealogical, and therefore some of the same sorts of evidence can be used for delimiting them as for subsequent inferences regarding their interrelationships, but here the pattern being sought is not simply one of sets of dichotomizing lineages, but also of anastomozing lines. We might detect anastomosing lines by at least two methods: by detecting discordant apomorphies indicating past joining of two once-independent lines (Wanntorp, 1983; Nelson, 1983), or by more-direct evidence of reproductive cohesion. Within one small monophyletic group, one kind of "more-direct evidence" might be repeated discovery of one form of male microsympatrically with just one form of female, in addition to some observed matings between the types. Similarly, we can detect lack of anastomosis between two forms by maintenance of distinctiveness in the face of sympatry. If in the area of sympatry there is a lack of the phenotypes expected if there were gene flow between the forms, then gene flow is probably absent or minimal, and the forms are maintaining their genealogical distinction.

Using morphological and geographic data, the boundaries of a species can be inferred by observation of a set of individual organisms possessing a unique combination of (ancestral or derived) character states. The character states might be structural, behavioral, or ecologic. Additional evidence may be provided in the form of directly observed matings between members of the set, or distinctiveness of sympatric forms. If the forms are allopatric or parapatric, the evidence may not be as clear. While no gene flow may be present at this exact moment between currently allopatric forms, the forms may have been genealogically connected very recently. Morphological distinctiveness is used as the clue: if two allopatric forms differ as much as two sympatric forms, they are judged to be long-established lineages and separate species; otherwise they are treated as subspecies.

Species delimitation within *Bracteon*

I will not present in detail my reasoning for my recognition of each of 17 species within *Bracteon*. Any two forms each with their own unique character combination, occuring sympatrically, are judged to be separate species. Suffice it to say that 17 forms maintain their distinctiveness where they occur sympatrically (Table 1). Geographically separated forms that show intermediate regions of intermediate specimens are considered as belonging to one species (eastern and western forms of *B. inaequale* are the clearest examples of this). Other parapatric or allopatric forms are judged on the basis of similarity. If the forms are very similar, only consistently differing in one or a few characters, I have recognized them as belonging to the same species (for example, *B. levettei levettei* and *B. levettei carrianum* Casey, the Lake Baikal and Alaskan *B. alaskense*, southern Nearctic and northern *B. lapponicum*). If, however, the forms differ by at least the same magnitude as do sympatric species, they are construed as distinct species (for example, *B. litorale* and *B. levettei*, *B. velox* and *B. carinula*). This judgement is admittedly rather subjective; if any errors have been made, they are probably more errors in lumping than errors in splitting.

The phylogenetic analysis (presented later in the chapter "Phylogeny of *Bracteon*") indicated the monophyly of 10 of the 17 *Bracteon* species: *B. foveum*, *B. alaskense*, *B. semenovi*, *B. stenoderum*, *B. carinula*, *B. lapponicum*, *B. punctatostriatum*, *B. hesperium*, *B. zephyrum*, and *B. inaequale;* the phylesis of the other seven species was not apparent. Note, however, that paraphyly or polyphyly of most species could not be detected by the methods I used (in order to do that, I would have needed to treat each specimen individually, an impractical task!).

One form which may be shown to be paraphyletic is *B. levettei;* I could not demonstrate that *B. levettei levettei* plus *B. levettei carrianum* constitute a monophyletic group. If future work shows *B. levettei* to be paraphyletic, and collections from the Alberta foothills indicate a lack of recent gene flow between the montane *B. levettei levettei* and the lowland *B. levettei carrianum*, then I would favor splitting of the taxon into two separate species. However, in the face of ignorance, I prefer to be conservative, following Lindroth (1963) in retaining montane and lowland specimens within one species.

Subspecies concepts

A subspecies is a phenetically distinct and geographically cohesive portion of a species, that is not connected to other such units by extensive geographic clines (such clines, if they do exist, are short and steep). Subspecies are units of convenience, recognized because they are worthy of discussion in comparative work. I recognize subspecies in only one *Bracteon* (*B. levettei*), although further work may reveal the value of similarly dividing at least *B. alaskense*, *B. lapponicum*, and *B. inaequale*.

Checklist of extant *Bracteon* taxa

B. balli Lindroth
B. foveum Motschulsky
B. argenteolum Ahrens
B. alaskense Lindroth
B. semenovi Lindroth
B. stenoderum Bates
B. carinula Chaudoir
B. velox (Linné)
B. lapponicum Zetterstedt
B. punctatostriatum Say
B. hesperium Casey

B. lorquinii Chaudoir
B. zephyrum Fall
B. levettei Casey
  B. levettei levettei Casey
  B. levettei carrianum Casey
B. inaequale Say
B. litorale (Olivier)
B. conicolle Motschulsky

Key to Adults of *Bracteon*

To identify specimens of adult *Bracteon*, the key below should be consulted, as well as additional information provided in the account of each species. The figures (especially of habitus [Figs. 5–23] and male genitalia [Figs. 112–128]) may prove especially helpful.

1. Distinct smooth patches ("mirrors") on elytra, at least on interval 3 surrounding silver spots, or elytra generally smooth and shiny (Figs. 7–23) 3

1′. Distinct elytral mirrors lacking, interval 3 between silver spots dull (Figs. 5, 6) 2

2(1′). Pronotum small in comparison to the long elytra (El/Pwm = 2.44–2.60). Male protarsomere 1 relatively large (Fig. 76) *B. foveum* Motschulsky

2′. Pronotum and elytra of typical proportions (El/Pwm = 2.25–2.35). Male protarsomere 1 of normal size (Fig. 75) *B. balli* Lindroth

3(1). Intervals 6 or 7 with mirrors as or nearly as distinct as interval 3 mirrors, at or near level of silver spots (Figs. 17–23) 13

3′. Outer elytral intervals lacking distinct mirrors, more or less uniform in luster 4

4(3′). Midlateral seta of pronotum present (if the seta has broken off accidently, then its former presence is indicated by a pore puncture in the lateral margin) 5

4′. Midlateral seta of pronotum absent 8

5(4). Large (SBL generally more than 6.2 mm) and shiny, with wide body (Fig. 11). Prothorax wide at base, with sides little sinuate. Mentum tooth large, bulbous, rectangular, without distinct epilobes (Fig. 52) *B. punctatostriatum* Say

5′. Smaller (SBL generally less than 6.2 mm) and in most specimens duller. Body proportions more normal, not atypically wide (Figs. 12–14). Prothorax more constricted near base. Mentum tooth smaller, flatter, triangular or trapezoidal, epilobes distinct (Fig. 7) 6

6(5′). Pronotum with distinct, long carina inside hind angles near base; carina extended to basal edge of pronotum (Figs. 12, 70) *B. carinula* Chaudoir

6′. Basilateral carina, if present, thin, oblique, and short, not extended to basal edge of pronotum 7

7(6′). Third elytral interval wide, 1.7–2.6 times as wide as second. Pronotum flatter, with flaring hind angles. (Holarctic.) *B. lapponicum* Zetterstedt

7′. Third elytral interval narrower, 1.4–1.6 times as wide as second. Pronotum more convex, hind angles less prominent. (Palearctic.) *B. velox* (Linné)

8(4′). Small (SBL = 4.4–5.4 mm) specimen, elytra narrowing apically, striae deeply impressed; legs mostly pale, rufous. Generally with two setae in neighborhood of ed7. (Japan and neighboring mainland.) *B. stenoderum* Bates

8′. Generally larger, with wider elytra and less fusiform shape. Generally with one seta at ed7 9

9(8′). Shoulder margin longer (as in Figs. 68, 70, 71), reaching or nearly reaching stria 5. Aedeagi as in Figures 114 and 115; female S2s exceptionally long (Figs. 150, 151). (Palearctic region and Alaska.) 10

9′. Shoulder margin shorter (as in Fig. 69), reaching at most just beyond stria 6. Aedeagi as in Figures 121 and 122; female S2s of normal length (Figs. 157, 158). (Western North America south of Alaska.) 12

10(9). Legs pale rufous. Dorsal surface of body shiny, with inconspicuous mirrors and silver spots. Interval 3 narrow (Fig. 9) *B. semenovi* Lindroth

10′. Legs darker, at least apex of femur as well as tibia and tarsus infuscated. Duller, with mirrors and silver spots in most specimens more distinct. Interval 3 wider (Figs. 7, 8) 11

11(10′). Duller, elytra in most specimens distinctly duller than pronotum. ed3 and ed5 near center of silver spots. Extra setae between eo4 and eo5 generally absent. Protarsomere 4 ventroapical setae widely separated (Fig. 92) *B. alaskense* Lindroth

11′. Dorsal surface, including elytra, shinier. ed3 and ed5 at or near anterior edge of silver spots. Extra setae between eo4 and eo5 generally present. Protarsomere 4 ventroapical setae narrowly separated (Fig. 93) *B. argenteolum* Ahrens

12(9′). Small (SBL = 4.7–5.8 mm). Very shiny and dark. Microsculpture in shinier areas of elytral disc consisting of transversely stretched sculpticells, at least in males. Femora generally with basal half rufous .... *B. hesperium* Casey

12′. Larger (SBL = 5.3–6.8 mm). Duller and brighter. Elytral microsculpture isodiametric throughout. Femora entirely piceous or black .... *B. lorquinii* Chaudoir

13(3). Mentum tooth rectangular, bulbous, epilobes indistinct. (Nearctic.) 14

13′. Mentum tooth flatter, not bulbous, epilobes distinct 15

14(13). Mirrors on intervals 6 and 7 more or less isolated from mirrors on inner intervals, and present near level of posterior silver spot (Figs. 22, 23) .... *B. inaequale* Say

14′. Outer elytral mirrors broadly connected to inner mirrors; outer mirrors closer to anterior silver spots. (Figs. 20, 21) .... *B. levettei* Casey

15(13′). Lateral margins of pronotum wide, flared into protrudent front angles (Fig. 19). (Pacific coastal beaches of North America.) .... *B. zephyrum* Fall

15′. Pronotal margins narrower (Figs. 17, 18). (Palearctic.) 16

16(15′). Pronotum flatter with sides at most slightly sinuate; midlateral seta absent; ed3 and ed5 generally at anterior edge of silver spots .... *B. conicolle* Motschulsky

16′. Pronotum more convex, sides more rounded; midlateral seta present or absent; ed3 and ed5 generally closer to center of silver spots .... *B. litorale* (Olivier)

KEY TO FIRST INSTAR LARVAE OF THE *ODONTIUM* SUBGENERIC-GROUP

In the following key I have included first instar larvae of all eleven North American *Bracteon* species; I have omitted *B. argenteolum* and *B. litorale*, the larvae of which were described by Andersen (1966), as I have not seen specimens. I have also incorporated all other known larvae of the *Odontium* subgeneric-group, as these cannot yet be separated as a group from those of *Bracteon*.

1. Parietale each with 2–6 large, tooth-like egg bursters in a cluster on each side near coronal suture (Figs. 228, 234); setae PR_{13}, ME_{14}, TE_{11} short (Fig. 250) .... *B. carinula* Chaudoir

1′. Parietale each with more numerous, smaller denticles (Figs. 226–227, 229–233, 235); if egg bursters large, then not set in a small cluster; setae PR_{13}, ME_{14}, TE_{11} relatively long (Figs. 240, 248) 2

2(1′). Setae ME_2 and TE_6 small (Figs. 246, 254) 3

2′. Setae ME_2 and TE_6 relatively long (Figs. 245, 252) 5

3(2). Head capsule dark; pronotum with faint traces of microsculpture; seta PR_{10} present and long .... *B. lapponicum* Zetterstedt

3′. Head capsule pale with five dark spots; pronotum with distinct microtubercles; PR_{10} absent or small 4

4(3′). Seta EP_1 of abdominal segments 2–6 long, greater than one-third the length of EP_2; FR_3 thin, less than one-third the width of FR_2; PR_{10} present, short; setal groups gPR and gME absent; TE_α absent; pronotum with microsculpture lacking between the two PR_{14}s .... *B. (Ochthedromus) bifossulatum cheyennense* Casey

4′. Seta EP_1 very short, less than one-fifth length of EP_2; FR_3 thick, basally greater than one-half width of FR_2; PR_{10} absent, replaced by setal group gPR; gME and TE_α present; pronotum with microsculpture present between the PR_{14}s .... *B. punctatostriatum* Say

5(2′). Small (head capsule width 275 µm); head only slightly constricted posteriorly (Fig. 223), with long coronal suture (LCl/LHl = 0.196); frontale lacking microsculpture, with faint midlateral dark spots; parietale with large, widely separated egg bursters .... *B. (Odontium) aenulum* Hayward

5′. Larger (head capsule width 330 µm or more); head more definitely constricted posteriorly (Figs. 210–217, 219, 220), with shorter coronal suture (LCl/LHl < 0.165); frontale generally with posterior-lateral microsculpture (lacking only in *B. alaskense*), with or without dark spots; parietale with smaller denticles 6

6(5′). Frontale lacking microsculpture posteriorly, parietal microsculpture consisting of long, thin denticles (Figs. 227, 233); head capsule wide (LHw > 490 µm, LHw/LHl = 1.35–1.47) .... *B. alaskense* Lindroth

6′. Frontale with multipointed or singly pointed microsculpture, parietale with smaller denticles (Figs. 226, 231, 232); head capsule narrow (LHw < 470 µm, generally < 420 µm, LHw/LHl = 0.99–1.37) 7

7(6′). Head capsule more or less uniformly dark 8

7′. Head capsule mostly pale, or pale with three dark spots upon the frontale and generally one on each parietal side 9

8(7). Seta TE_{11} thin, blunt, parallel-sided; much narrower than TE_{10} .... *B. foveum* Motschulsky
8′. Seta TE_{11} tapered, about as thick basally as TE_{10} .... *B . balli* Lindroth
9(7′). Anterior two-thirds of posterior-lateral microsculpture patch of frontale consisting of relatively large, single denticles; nasale blunt (Fig. 193) 10
9′. Posterior-lateral microsculpture mostly multitoothed combs; where single denticles, these are relatively small; nasale generally more sharply pointed (Fig. 192) 11
10(9). Microsculpture of parietale near coronal suture absent or very sparse .... *B. hesperium* Casey
10′. Microsculpture of parietale near coronal suture more extensive and prominent .... *B. lorquinii* Chaudoir + *B. inaequale*-subgroup
11(9′). Pronotum with microsculpture (small tubercles) between PR_8, PR_9, and PR_{10} ... 12
11′. Pronotum lacking microsculpture .... *B. (Odontium) bowditchii* LeConte + *B. (O.) foraminosum* Sturm
12(11). Mandible long, markedly curved (Fig. 200) .... *B. (Odontium) coxendix* Say
12′. Mandible shorter, less curved (similar to mandible of Fig. 199) .... *B. (Odontium) confusum* Hayward

Accounts of Species of *Bracteon*

The arrangement of *Bracteon* below matches that of the inferred phylogeny of the group, presented in the section "Phylogeny of *Bracteon*." I include within *Bracteon* two subgroups, the *B. argenteolum*-subgroup and the *B. inaequale*-subgroup, together containing seven of the 17 species. The *B. argenteolum*-subgroup contains *B. argenteolum*, *B. alaskense*, and *B. semenovi;* see the section "Comparison with related species" under *B. argenteolum* for a discussion of this subgroup. The *B. inaequale*-subgroup, defined by extensive elytral mirrors, straight CSC flagella, 10 pairs of autosomal chromosomes, and similar larvae, includes *B. levettei*, *B. inaequale*, *B. litorale*, and *B. conicolle*. The other ten species are not arranged in subgroups.

Bembidion balli Lindroth

Bembidion balli Lindroth, 1962:15. HOLOTYPE male examined, in CNC, labeled: "McMurray, Alta. VIII.11.53 George E. Ball / Holotypus balli Lth. [red label, in Lindroth's handwriting] / HOLOTYPE CNC No 8375 [red label]." Type locality Fort McMurray, Alberta.

Derivation of Specific Epithet. Patronym given by C. H. Lindroth to honor his friend and fellow carabidologist, George E. Ball.

Characteristics of Adult. (Figs. 5, 35, 40, 49, 62, 68, 75, 96, 98, 99–102, 109, 112, 129, 147, 148, 165, 184, 186.)

Diagnostic combination. Body proportions as in Figure 5; distinct elytral mirrors lacking; pronotum lacking long basilateral carina; male protarsomere 1 of normal size (Fig. 75); male aedeagus with flagellum long and ventrally curved (Fig. 129), apical boundaries of the two basins of the VSP well separated in left lateral view (Fig. 112).

Comparisons with related species. Difficult to distinguish from specimens of *B. foveum*. *B. balli* members are smaller, with broader prothoraces and shorter, more convex elytra (compare Fig. 5 of *B. balli* with Fig. 6 of *B. foveum*). For *B. balli*, El/PWm = 2.25–2.35 (n = 7); for *B. foveum*, El/PWm = 2.44–2.60 (n = 9). *B. balli* generally more golden in color. Microsculpture of most specimens more deeply engraved, surface therefore duller, especially on forebody; microsculpture around anterior discal seta of elytron (ed3) irregularly disrupted in most specimens (Fig. 62), as opposed to the more smoothly circular pit in *B. foveum* (Fig. 63). In *B. foveum*, an extra seta is generally present on the elytra between eo4 and eo5, lacking in *B. balli*. Pores on surface of mandibles just mesal of dorsal condyle (Fig. 35) much narrower than those of *B. foveum* (Fig. 36); confirmed in four specimens of each species. As well, front angles of pronotum somewhat less protruded in *B. balli*, and humeral margin generally longer and more angulate. Males of *B. balli* can be distinguished by the considerably smaller basal protarsomeres (Fig. 75). Most external characters require experience to interpret, and, until this is gained, I recommend examination of the male aedeagus for more certain identification. Aedeagus thinner, less curved than in *B. foveum*, with narrower apex; right lobe of CSC generally less protruded in *B. balli;* apical boundaries of the two basins of the ventral sclerite patch of *B. balli* more widely separated in left lateral view; flagellum much longer, thinner, more curved in *B. balli*.

B. balli are occasionally confused with dark, unmetallic specimens of *B. carinula* lacking distinct mirrors (apparently through wear); however, *B. balli* adults do not have a long basilateral carina confluent with the pronotal base.

Description. See Table 2 for character states. Additional traits follow. SBL = 4.8–5.8 mm. Dorsal surface bronze or gray-bronze, silver spots blue, bronze, or aeneous. Appendages for the most part piceous, except for the venter of antennomere 1, the pro- and mesotrochanters, and the base and venters of femora, which are testaceous; antennomeres 2 through 4 and tibiae paler ventrally in some specimens. Silver spots inconspicuous, not or only slightly depressed below rest of interval; elytra lacking mirrors, although interval 3 in some specimens slightly darker between silver spots, giving the illusion of very faint mirrors. Sides of pronotum sinuate, greatest width at or slightly before middle. Elytral striae slightly to moderately impressed; interval 3 not or only slightly wider than 2. Spermatheca as in Figure 165, ramus lobe in many specimens longer; cornus long, slightly curved, dorso-basal bulb curved, short. No posterior lobe at base of spermathecal duct. Stylomeres as in Figure 148.

Characteristics of First Instar Larva. (Figs. 191, 196, 210, 240, 242, 245, 248, 252, 255, 257.)

Diagnostic combination. Head capsule dark (Fig. 210), with faint trace of three-spotted frontal pattern; parietale with slightly darker patch in front of PA_4 and PA_7; parietal denticles small; ME_2 and TE_6 long; TE_{11} tapered, basally thick, as thick as TE_{10} (Fig. 248); abdominal segment VIII with EP_1 less than one-half width of EP_2.

Comparisons with related species. From the very similar *B. foveum*, distinguished by thick, tapered setae TE_{11} of the abdominal terga. As well, mandible of *B. balli* with only one or two denticles near seta MN_1, in contrast to the more numerous denticles of *B. foveum;* setae FR_1 and FR_3 shorter than those of *B. foveum*.

From the other *Bembidion* with dark larval head capsules, *B. lapponicum*, distinguished by many traits, including the smaller parietal denticles; narrow setae FR_1, FR_3, and segment VIII EP_1; long setae ME_2 and TE_6; absence of setae ST_2 on abdominal sternum IX.

Description. See Table 2 for character states. Additional traits follow. LHw = 400–415 μm, LHl = 360–380 μm, LCl/LHl = 0.132–0.147. Four specimens measured.

Characteristics of Second Instar Larva. (Fig. 258.)

Description. LHw = 540–595 μm (n = 2). Frontale without extra setae near FR_3, and lacking microsculpture posteriorly. Head and pronotum with accessory microsetae clearly over three times longer than wide. Microsculpture absent centrally on pronotum. Urogomphus with seven long setae.

Specimens Examined. I have seen 259 adults, 29 first instars, and 5 second instars from the following collections: AMNH, BMNH, CAS, CNC, CUIC, DRMa, HNHM, ICCM, MCZ, SMNH, UASM, USNM, ZIL, ZMLS.

Geographic Distribution. Found only in west-central Saskatchewan and at the type locality of Fort McMurray, Alberta (Fig. 261). The report of *B. balli* from Churchill, Manitoba (Elias, 1984), is based on a series of *B. carinula* adults (SAEl!).

Geographic Variation. None noted over the small known range.

Habitat. Known only from rivers, on barren beaches composed mainly of sand.

Phylogenetic Relationships. I place *B. balli* as the sister group of *B. foveum* (Figs. 292, 293).

Bembidion foveum Motschulsky

Bembidium foveum Motschulsky, 1845:271. LECTOTYPE male, designated by Lafer (1975), in ZMUM, not seen. Type locality L. Baikal, Russia.

Bembidion bryanti Carr, 1932:191 (not *B. bryanti* Andrewes, 1921:249). HOLOTYPE male examined, in CNC, labeled: "Norman, N.W.T. Sept.23.1929 Owen Bryant / Mackenzie River 1929 Trip. Lot Owen Bryant 23 / above San Sault Rapids 70 mi Norman [handwritten] / HOLOTYPE Bembidion bryanti Carr No 3435 [red label] / Holotype Bembidion bryanti Carr ex coll. F. S. Carr [red label] / SLIDE No. 2102 [green label] / Bembidion foveum Mtsch Det. Lindroth, 1961." Type locality Mackenzie River, 70 miles below Fort Norman, above Sans Sault Rapids.

Bembidion beringi Netolitzky, 1940:164. HOLOTYPE male examined by Lindroth (1962), in Swedish Riksmuseum, Stockholm. Type locality Petropavlovsk, Kamchatka, Russia.

Bembidion grahami Hatch, 1951:114. HOLOTYPE male examined, in OSUO, labeled: "Findlay Forks B.C. 22/6 1930 Coll. R. Graham [partly handwritten] / Bembidion (Chrysobracteon) foveum Mots. M. Hatch 1969 / bryanti Carr (Prob = Siberian species) Det. Lindroth, 1958 / TYPE Bembidion (Chrysobracteon) grahami 1950 - M. Hatch [red label, handwritten]." Type locality Findlay Forks, British Columbia, Canada.

Derivation of Specific Epithet. From the Latin *fovea,* meaning "pit," referring to the elytral silver spots.

Characteristics of Adult. (Figs. 6, 24–27, 29–32, 36, 37–39, 41, 63, 69, 76, 113, 130, 149, 166, 183.)

Diagnostic combination. Body proportions as in Figure 6; distinct elytral mirrors lacking; pronotum lacking long basilateral carina, with midlateral seta; male protarsomere I exceptionally large (Fig. 76); flagellum of male aedeagus relatively short and thick (Fig. 130); apical boundaries of two basins of VSP narrowly separated in left lateral view (Fig. 113).

Comparisons with related species. Similar to *B. balli;* many specimens difficult to identify with certainty using external characters. For a discussion of differences between the species, see account of *B. balli.*

Description. See Table 2 for character states. Additional traits follow. SBL = 5.5–6.5 mm. Dorsal surface grayish, in many specimens with bronze or aeneous tint; silver spots bronze, greenish, or bluish. Appendages colored as in *B. balli* but slightly darker, pale areas a bit more rufous. Disc of pronotum diffusely shinier. Elytral mirrors absent, although in some specimens the inner intervals are slightly shinier; silver spots in many specimens slightly more depressed into elytra than in *B. balli.* Sides of pronotum sinuate; greatest width generally further forward than in *B. balli,* before middle. Elytral striae shallow to moderately impressed; interval 3 only slightly wider than 2. Spermatheca as in Figure 166, similar to that of *B. balli.* No posterior lobe at base of spermathecal duct. Stylomeres as in Figure 149.

Characteristics of First Instar Larva. (Figs. 199, 201–203, 205, 211, 226, 232, 238, 249.)

Diagnostic combination. Head capsule dark, with faint trace of three-spotted frontal pattern; parietal denticles small; ME$_2$ and TE$_6$ long; TE$_{11}$ parallel-sided, bluntly tipped, basally thin, less than one-half width of TE$_{10}$ (Fig. 249); abdominal segment VIII with EP$_1$ less than one-half width of EP$_2$.

Comparisons with related species. Very similar to larva of *B. balli;* best distinguished by the thin, blunt, parallel-sided setae TE$_{11}$ of the abdominal terga; a few more characters are mentioned under the account of *B. balli.*

From *B. lapponicum,* distinguished by the smaller parietal denticles; narrow setae FR$_1$, FR$_3$, TE$_{11}$, and segment VIII EP$_1$; long setae ME$_2$ and TE$_6$; absence of setae ST$_2$ on abdominal sternum IX.

Description. See Table 2 for character states. Additional traits follow. LHw = 460–465 μm, LHl = 410–415 μm, LCl/LHl = 0.135–0.146. Two specimens measured.

Specimens Examined. I have seen 645 adults and 17 first instars from the following collections: AMNH, BJCa, BMNH, CAS, CNC, CUIC, DHKa, DRMa, HNHM, ICCM, JKLi, MCZ, OSUO, ROM, SMNH, UASM, UBC, UMHF, USNM, ZMLS.

Geographic Distribution. A Holarctic species (Fig. 262). In the Palearctic, from northeasternmost Europe, across the width of northern Asia to Kamtchatka. In North America (Fig. 262b), from Alaska east to Churchill, Manitoba, and south to central Saskatchewan.

Geographic Variation. No variation correlated with geography was noted.

Habitat. Found only on the banks of rivers, most commonly on barren, silt-mixed sand.

Phylogenetic Relationships. Apparently the sister species of *B. balli* (Figs. 292, 293).

Bembidion argenteolum Ahrens

Bembidion Argenteolum Ahrens, 1812:23. TYPE material lost (see Lindroth, 1962:11). Type locality Halle, Germany.

Bembidium azureum Gebler, 1833:276.

Bembidium chalybaeum Sturm, 1843:36. *Nomen nudum.*

Bembicidium glabriusculum Motschulsky, 1845:272. Holotype male examined, in ZMUM, labelled: "Sitka [red label] / Bembidium glabriusculum Mihi, Sitka [handwritten on bordered paper] / [blank red rectangular label]." Type locality apparently Sitka, Alaska (presumably incorrect, as no other specimens of this species has been taken from the New World).

(*Bembidion argenteolum* v. *amethystinum* Meier, 1899:98. [Name unavailable as clearly intended to be infrasubspecific.])

Bembidion argenteolum var. *virens* Schilsky, 1908: 604 (not Gyllenhal, 1827:407). Types presumably in the Schilsky collection, Zool. Mus., Berlin (Horn and Kahle, 1937). Type locality Posen (=Poznan), Poland. (Original description gives no indication that author intended the name to be infrasubspecific, and thus the name is available [ICZN, Third edition, Article 45(g)].)

Derivation of Specific Epithet. From the Latin *argentum*, meaning silver, referring to the sparkling, metallic appearance of the elytral "silver spots."

Characteristics of Adult. (Figs. 7, 77, 88, 93, 97, 114, 131, 150, 167.)

Diagnostic combination. Large (SBL = 5.4–7.0 mm, generally over 5.8 mm); elytral mirrors on intervals 3 and 5, in some specimens on first five intervals, no distinct mirrors on intervals 6 or 7; pronotum lacking long basilateral carina, without midlateral seta; ventroapical setae of protarsomere 4 narrowly separated (Fig. 93); lateral projection on male protarsomere 3 lacking (Fig. 93).

Comparisons with related species. Adults are very similar to those of *B. alaskense* and *B. semenovi.* Larger than *B. alaskense*, shinier, silver spots not on intervals 2 or 4. Setae ed3 and ed5 located at anterior margin of silver spots; most specimens with at least one seta between elytral setae eo4 and eo5. Ventroapical setae of protarsomere 4 narrowly separated. Aedeagus of *B. argenteolum* generally larger, straighter, with a less evident ventrolateral bulge than *B. alaskense*. The only consistent difference noted was in the CSC flagellum: that of *B. argenteolum* has a narrower base and a less-sinuous dorsal margin. Duller than *B. semenovi,* with wider interval 3, and without lateral projection on male protarsomere 3.

Distinguished from the sympatric *B. velox* and *B. lapponicum* by the lack of midlateral pronotal setae, larger size, and (in some specimens) more distinct mirrors of elytral intervals 4 and 5.

This and the following two species form a taxonomically difficult complex of forms, which I call the *B. argenteolum*-subgroup. I follow Lindroth (1962, 1965) in treating it as three species (*B. argenteolum*, *B. alaskense*, and *B. semenovi*), although I am not entirely satisfied with this arrangement. *B. semenovi* is probably a distinct species, although it is possible that the holotype is simply an aberrant *B. argenteolum.* The distinctiveness of *B. alaskense* from *B. argenteolum* is more doubtful. While European *B. argenteolum* are quite different from Alaskan *B. alaskense*, the few specimens I have from the Lake Baikal region are somewhat intermediate (they are nearly the size of European *B. argenteolum*, but otherwise match Alaskan *B. alaskense*), suggesting that the distinct forms may simply be two extremes of one species. I discuss these specimens further under *B. alaskense.* However, the few specimens I have from the region between Lake Baikal and Alaska represent more typical *B. argenteolum*, indicating that the two forms are not simply ends of a cline. Because of this, and as the material before me from eastern Russia is rather meager, I will not synonymize the two names; more specimens from eastern Asia are needed to settle the problem.

Description. See Table 2 for character states. Additional traits follow. SBL = 5.4–7.0 mm. Mirrors with dark brass, coppery-red, aeneous, or green reflection; rest of dorsal surface dark bronze, purple, or blue; mirrors of many specimens contrasted in color with rest of dorsal surface. Appendages mostly infuscated, piceous, with ventral portion of antennomere 1, venter at base of antennomeres 2 through 4, and base of femora rufous. Pronotum with shiny disc. Elytra shinier than that of *B. alaskense*, about as shiny as pronotum. Pronotum convex, with rounded margins. Elytra convex, humeral margins longer and more angulate than in many *B. alaskense*, nearly extended to stria 5; striae slightly to moderately impressed; interval 3 distinctly wider than 2. Spermatheca varied; cornu more or less curved in most specimens (Fig. 167). No posterior lobe at base of spermathecal duct. Stylomeres long, as in Figure 150.

Characteristics of First Instar Larva.

Description. See Andersen (1966) for more details about all larval stages. He includes information about only a few of the first instar characters I have studied. Head pale, centrally darker. Judging from his figures 12–14, setae PR_{13}, ME_{15}, and TE_{11} are long, and PR_{10} is apparently present and long.

Specimens Examined. I have seen 126 adults from the following collections: BMNH, CAS, DRMa, HNHM, MCZ, UMHF, USNM, ZMLS.

Geographic Distribution. Isolated on Ireland; on the mainland from western France and northern Italy, to Scandinavia, and eastward to the Lena River and Ussuri River regions of Russia (Fig. 263; Netolitzky and Meyer, 1933). The type specimen of *B. glabriusculum* is labelled "Sitka," presumably referring to Sitka, Alaska; this is probably an error, as no *B. argenteolum* are known from North America.

Geographic Variation. None noted over Europe and western Siberia. The one female I have examined from far eastern Russia ("Ussuri," UMHF), is more deeply microsculptured than other specimens, but otherwise appears to be a normal *B. argenteolum*.

Habitat. On barren or nearly barren sand banks of rivers or lakes (Lindroth, 1945).

Phylogenetic Relationships. Most closely related to *B. alaskense* or *B. semenovi.*

Bembidion alaskense Lindroth

Bembidion alaskense Lindroth, 1962:9. HOLOTYPE male examined, in CAS, labelled: "Grants Cabin, Toms Lake, Alask. Pen., Alask. VII-8-1919 [handwritten] / Van Dyke Collection / Holotypus alaskense Lth. [red label, partly in Lindroth's handwriting]." Type locality Lake Brooks (=Toms Lake [Orth, 1967]), Alaska Peninsula, Alaska.

Bembidion colvillense Lindroth, 1965:126. HOLOTYPE male examined, in MCZ, labeled: "Umiat, Alaska Aug. 6, 1958 George E. Ball / MCZ Holotype 32753 [red label] / Holotypus colvillense Lindroth [red label, in Lindroth's handwriting]." Type locality Umiat, Alaska. **New synonymy.**

Notes About Synonymy. The type of *B. colvillense* Lindroth is more heavily microsculptured than most southern *B. alaskense*, with the mirror on interval 4 thereby fainter. While this mirror is fainter than those on intervals 3 and 5, it is still distinct, contrary to Lindroth's (1965) statement; the striae are also not particularly regular. In the *B. colvillense* holotype the unpigmented nature of the aedeagus makes interpretation of its structure difficult, but in visible aspects it appears identical to *B. alaskense*. A sample from the Killick River (AMor, UASM!), not far from the type locality of *B. colvillense*, contains specimens similar to the *B. colvillense* type, the *B. alaskense* type, and a range of intermediates. It thus seems clear that all specimens from the Colville and Killick rivers belong to *B. alaskense.*

Derivation of Specific Epithet. From "Alaska," state of capture of the type series.

Characteristics of Adult. (Figs. 1, 8, 47, 50, 92, 110, 115, 132, 146, 151, 168.)

Diagnostic combination. Small (SBL = 5.0–6.3 mm, Alaskan specimens 5.0–5.7

mm); elytral mirrors on intervals 3 and 5, in some specimens on intervals 3 through 5, no distinct mirrors on intervals 6 and 7; pronotum lacking long basilateral carina, without midlateral seta; ventroapical setae of protarsomere 4 widely separated (Fig. 92); lateral projection on male protarsomere 3 lacking.

Comparisons with related species. Belongs to the *B. argenteolum*-subgroup. Distinguished from *B. argenteolum* by smaller size, and generally darker appendages. Prothorax in most specimens with disc shiny, otherwise the microsculpture is stronger than most *B. argenteolum*, and thus the surface is duller. Silver spots in many *B. alaskense* specimens larger, extended onto intervals 2 and 4. Seta of silver spot located nearer center of spot. Interval 9 of elytra generally lacking setae between eo4 and eo5. Ventroapical setae of protarsomere 4 widely separated. See also the "Comparisons with related species" section under *B. argenteolum*.

From *B. lapponicum* and *B. carinula* distinct in lacking the midlateral pronotal seta, and in having more definite mirrors on interval 5 (and generally also 4).

Description. See Table 2 for character states. Additional traits follow. SBL = 5.0–6.3 mm. Darker than *B. argenteolum*. Dorsal surface dark copper, bronze, aeneous, or bluish, mirrors in many specimens slightly purplish or reddish. Appendages dark, piceous or black, except for the venter of the antennomere 1, the base of femora, and the pro- and mesotrochanters, which are rufous; tibiae slightly paler in a few specimens, as is the maxillary palpomere 2. Pronotum narrower than *B. argenteolum*, sides straighter, not as rounded. Humeral margin short to medium-long, extended to stria 5 or not, generally not as angulate as in *B. argenteolum;* striae slightly to moderately impressed, in many specimens disrupted (especially 3 and 4); interval 3 wide, in many specimens abruptly widened just around silver spots. Spermatheca (Fig. 168) as for *B. argenteolum*, cornu of varied shapes. Stylomeres as in Figure 151.

Characteristics of First Instar Larva. (Figs. 212, 227, 233, 236.)

Diagnostic combination. Head capsule wide, diffusely darker centrally, frontale without traces of spots (Fig. 212); parietal denticles large, thin (Figs. 227, 233); PR_{13}, ME_2, ME_{14}, TE_6, TE_{11} long; abdominal segment VIII with EP_1 less than one-half width of EP_2.

Comparisons with related species. Distinguished from the other species with centrally dark head capsules, *B. carinula*, by the large setae ME_2 and TE_6, and the smaller, more widely distributed parietal denticles of *B. alaskense*.

Description. See Table 2 for character states. Additional traits follow. LHw = 490–500 μm, LHl = 340–365 μm, LCl/LHl = 0.110–0.118. Three specimens measured. Frontale without denticulate microsculpture (or at most with a few denticles around sensillum FR_b). Parietale lacking microsculpture near coronal suture. Mandible with prominent denticles dorsally near MN_1. Head wide, LHw/LHl = 1.35–1.47 (n = 3).

Characteristics of Second Instar Larva.

Description. LHw = 700–750 μm (n = 2). Frontale with extra setae near FR_3, and lacking microsculpture posteriorly. Head and pronotum with accessory microsetae clearly over three times longer than wide. Microsculpture absent centrally on pronotum. Urogomphus with seven long setae.

Specimens Examined. I have seen 157 adults, 156 first instars, 23 second instars, and 27 third instars from the following collections: AMNH, AMor, BMNH, CAS, CNC, DRMa, HNHM, MCZ, OSUC, OSUO, UASM, USNM, ZIL, ZMLS.

Geographic Distribution. Known from Alaska, from the Alaska Peninsula in the south to the Brooks Range in the north (Fig. 264); also in the region of Lake Baikal (Fig. 263).

Geographic Variation. While there is much within-population variation in Alaska, southern specimens seem in general to be darker, shinier, and with shorter appendages than specimens from north of the Brooks Range. Genitalic variation appears uncorrelated with external variation or geography. Specimens from Lake Baikal are larger than Alaskan specimens (SBL = 5.4–6.3 mm, mean = 5.86 mm, S.D. = 0.31, n = 7 for Njurga Bay, Lake Baikal; SBL = 5.0–5.7 mm, mean = 5.33 mm, S.D. = 0.26, n = 10 for Lake Brooks, Alaska), but otherwise possess all of the distinguishing features of *B. alaskense:* widely separated ventroapical setae of protarsomere 4, sinuate flagella, etc.

Habitat. On the bank of Lake Brooks, Alaska, larvae and adults were abundant on a barren, dark, volcanic-sand beach. On the north slope of the Brooks Range in northern Alaska, specimens were found under flood debris on the barren sand-silt bank of the Killick River (A. V. Morgan, pers. comm.), and on the mostly barren sand-clay bank of the Colville River (Lindroth, 1962:126).

Phylogenetic Relationships. A member of the *B. argenteolum*-subgroup, but beyond that its relationships are unclear (Figs. 292, 293).

Bembidion semenovi Lindroth

Bembidion semenovi Lindroth, 1965:127. HOLOTYPE male examined, in ZIL, labeled: "[handwritten label in Cyrillic, mostly indecipherable to me, ends in '8.VIII.910 A. Jacobson'] / Bracteon sp.n.? [handwritten] / B (Chrysobracteon) ?semenovi sp.nov. [handwritten] Kryzhanovskij det./ Holotypus semenovi Lth. [red label, partly in Lindroth's handwriting]." Type locality (Lindroth, 1965:127): Black Irtysh R., near the mouth of the Kaldzhir R. (=Markakol' R.), approximately 140 km NNE Zaisan, Siberia.

Derivation of Specific Epithet. Patronym given to honor the coleopterist André Semenov-Tian-Shanskij.

Characteristics of Adult. (Figs. 9, 78.)

Diagnostic combination. Large (SBL = 6.1 mm), convex, shiny; interval 3 narrow, with small silver spots (Fig. 9); appendages pale rufous or rufotestaceous; pronotum without long basilateral carina, without midlateral seta; male protarsomere 3 with lateral projection (Fig. 78).

Comparisons with related species. Belongs to the *B. argenteolum*-subgroup. Difficult to distinguish from some specimens of *B. argenteolum*. Shinier, with narrower interval 3, and smaller silver spots. Appendages paler than *B. argenteolum*, with antennomere 1 entirely rufotestaceous. Protarsomere 3 of male with lateral projection (Fig. 78). Male genitalia of the holotype is identical in all studied aspects to that of *B. argenteolum* specimens. See also the "Comparisons with related species" section under *B. argenteolum*.

Description. See Table 2 for character states. Additional traits follow. SBL = 6.1 mm. Dorsal surface aeneous, mirrors with coppery tint. Appendages very pale, entirely rufotestaceous, although antennomeres 3 to 11 and tarsi slightly infuscated. Disc of pronotum slightly shinier than in *B. argenteolum*. Elytra very shiny; mirrors on intervals 2 to 5, none on 6 or 7; mirrors only slightly shinier than the background; silver spots inconspicuous. Pronotum shaped as in members of *B. argenteolum*, that is, convex with rounded sides. Elytra convex, humeral margins moderately long, almost extended to stria 5; striae straight, moderately impressed; interval 3 narrow.

Characteristics of First Instar Larva. Unknown.

Specimen Examined. Only the holotype seen (ZIL).

Geographic Distribution. Known only from the type locality (Fig. 263).

Habitat. Unknown.

Phylogenetic Relationships. Most closely related to *B. alaskense* and *B. argenteolum* (Figs. 292, 293).

Bembidion stenoderum Bates

Bembidium stenoderum, Bates 1873:300. TYPE, not examined, BMNH. Type locality Osaka, Japan.

Bembidion uenoshiba Jedlička, 1965a:94. HOLOTYPE female, examined, in National Museum of Czechoslovakia, Prague. Labelled: "UENOSHIBA nr OSAKA VII-12 1947 COLL. Yosio Yano [partly handwritten] / TYPUS [bordered, reddish-gray] / Mus. Nat. Prague 23945 Inv. [orange label] / uenoshiba sp. n. [handwritten] det Ing. Jedlička [upper surface of label pink] / Bembidion stenoderum Bates det DR Maddison 1986." Type locality Uenoshiba (part of Osaka), Japan. **New synonymy**.

Bembidion stenoderum mukdensis Kirschenhofer, 1984:59. HOLOTYPE male, not examined, in Kirschenhofer collection, Vienna. Type locality Shenyang (Mukden), China.

Derivation of Specific Epithet. From the Greek *stenos*, meaning narrow, referring to the narrow body of members of this species.

Characteristics of Adult. (Figs. 10, 116, 133, 152, 169.)

Diagnostic combination. Small and narrow, body fusiform (Fig. 10); surface shiny, with mirrors on intervals 3 through 5, and in most specimens with faint mirrors on intervals 6 and 7; ed3 and ed5 in large pit; prothorax sides little rounded, with wide base, and midlateral seta absent; humeral margin long, extended to stria 5; striae deeply engraved; generally with two setae in ed7 area. Aedeagus slender, with straight basal portion and ventrally bent apex (Fig. 116); sclerite complexes far removed from basal orifice; right lobe of CSC ridged; ostial microtrichial patch very small.

Comparisons with related species. The fusiform shape and other characters mentioned in the diagnosis are distinctive; specimens are not likely to be misidentified.

Description. See Table 2 for character states. Additional traits follow. SBL = 4.4–5.4 mm. Dorsal surface of body aeneous or bronze, mirrors purplish, silver spots bluish or aeneous. Appendages pale: most of antennomere 1 pale rufotestaceous, at least base of following three articles pale; legs infuscated at least at joints and on tarsi, slightly more generally infuscated in some examples. Sides of pronotum little sinuate, base wide (greatest width of prothorax at hind angles); basal tubercle relatively flat. Elytra tapered toward apex; humeral margins long, extended to inside stria 5; striae moderately to markedly impressed, more so than any other *Bracteon* (even stria 8 is more or less deepened throughout its length); stria 3 abruptly deeper around silver spots. Spermatheca varied, as in Figure 169; although cornu in some specimens shorter and straighter. Spermathecal duct without posterior lobe. Stylomeres as in Figure 152.

Characteristics of First Instar Larva. Unknown.

Specimens Examined. I have seen 44 adults from the following collections: BMNH, DRMa, HNHM, MCZ, UASM, USNM.

Geographic Distribution. Restricted to Japan and the neighboring mainland (Fig. 263).

Geographic Variation. None seen in the few specimens at hand from Japan. The only female I have seen from "China" (BMNH) is larger than average and quite dull. This form is considered a distinct subspecies (*B. s. mukdensis*) by Kirschenhofer (1984); I have not seen enough material to judge.

Habitat. Not known to me.

Phylogenetic Relationships. Unclear; may be related to *B. carinula* and relatives (Figs. 292, 293).

Bembidion carinula Chaudoir

Bembidium carinula Chaudoir, 1868:239. LECTOTYPE male designated by Lindroth 1963:237, in MNP, not examined. Type locality "*la Terre de Rupert*," Rupert's Land, former name for the entire drainage basin of Hudson's Bay, thus including most of northern Québec, Ontario, Manitoba, etc. (Lamb, 1971); not Rupert House, Québec, as stated by Lindroth (1963).

Bembidion tuberculatum Notman, 1929:157. HOLOTYPE female, examined by Lindroth (1962), in Staten Island Museum. Type locality Marquette, Michigan, U.S.A.

Derivation of Specific Epithet. From the Latin *carina*, meaning "keel" or "ridge," presumably referring to the prominent basilateral carina of pronota of adults.

Characteristics of Adult. (Figs. 12, 70, 117, 134, 145, 154, 170, 185, 187, 188.)

Diagnostic combination. Pronotum with long, distinct basilateral carina extended to base (Figs. 12, 70), as well as a midlateral setae; elytral mirrors present on interval 3, in some specimens on intervals 4 and 5, but not on intervals 6 through 8; aedeagus slender, with narrow basal orifice (Fig. 117).

Comparisons with related species. From the externally similar *B. lapponicum* and

B. velox, males can be best separated by characters of the aedeagus, and females by the elongate second stylomeres (longer than 400 μm in *B. carinula*, around 200 μm in *B. velox* and *B. lapponicum*). Aedeagus of *B. carinula* slenderer, with narrower basal orifice; right lobe of CSC unridged; ostial microtrichial patch smaller; with no dorsal field; dorsal plate with small sclerotized patch with dark, irregular borders; other *Bracteon* have dark dorsal plates (most notably *B. hesperium*), but in these the sclerotized region is more extensive. *B. carinula* members can be externally distinguished from *B. lapponicum* by the long basilateral pronotal carina, more convex pronota with more-rounded sides and less-divergent hind angles, and relatively narrower elytral interval 3. From *B. velox*, by the pronotal carina.

Some specimens of *B. carinula* have been confused with *B. balli*, especially old, worn, *B. carinula* in which the mirrors are invisible or unclear; the basilateral pronotal carina and genitalia are the best distinguishing features.

Description. See Table 2 for character states. Additional traits follow. SBL = 4.4–6.4 mm. Dorsal surface bronze, gray-bronze, coppery-red, dark bluish, or aeneous; mirrors in many specimens purplish or reddish; silver spots aeneous, blue, or bronze. Appendages in most specimens pale, with first four antennomeres rufotestaceous ventrally and basally, palpi partly pale, and legs rufotestaceous, femora and tibiae infuscated apically, tarsi dark. Other specimens, especially from Alberta and Saskatchewan, have the femur and tibia more extensively infuscated; in some only the bases of the femora are pale. In general, shinier than both *B. velox* and *B. lapponicum*. Pronotum frequently shinier than elytra. Mirrors on interval 5, when present, not more evident than on 4. Pronotum convex, sides sinuate, more definitely rounded than most specimens of *B. velox* or *B. lapponicum;* hind angle right or obtuse in many specimens. Humeral margins of elytra long, extended to stria 5 or nearly so; striae slightly to moderately impressed; interval 3 relatively narrow, not much wider than 2. Spermatheca as in Figure 170, with relatively short and straight cornu, and long, flat basal portion. Spermathecal duct with posterior lobe at base. Stylomeres as in Figure 154. Sternum X dark, asetose, clothed with small pegs (Fig. 185).

Characteristics of First Instar Larva. (Figs. 197, 198, 213, 228, 234, 243, 246, 250, 253, 256.)

Diagnostic combination. Head centrally darker, frontale without spots (Fig. 213); large, stout, closely set parietal egg bursters (Figs. 228, 234), PR_{13}, ME_{14}, and TE_{11} very short (Fig. 250); FR_1, FR_3, and segment VIII EP_1 as wide as nearby setae (Figs. 197).

Comparisons with related species. From the species with most similar larvae, *B. alaskense*, distinguished by the exceptionally large egg bursters and sensillar characters mentioned in the diagnosis.

Description. See Table 2 for character states. Additional traits follow. LHw = 450–460 μm, LHl = 340–360 μm, LCl/LHl = 0.094–0.104. Four specimens measured. Head pale with center diffusely darker, and with dark spot on center of frontale, or more generally pale brown. Frontale lacking pointed microsculpture (although two of the eight specimens studied had a few small denticles posteriorly). Mandibles lacking microsculpture (compare Fig. 198 with Figs. 199 and 239). Unlike most *Bracteon*, FR_5 is anterior to FR_4 in most specimens.

Characteristics of Second Instar Larva. (Fig. 260.)

Description. LHw = 630–665 μm (n = 2). Frontale with extra setae near FR_3, and lacking microsculpture posteriorly. Head and pronotum with accessory microsetae short, less than two times longer than wide. Microsculpture absent centrally on pronotum. Urogomphus with ten long setae (Fig. 260).

Specimens Examined. I have seen 2,248 adults, 57 first instars, and 4 second instars from the following collections: AMNH, AMor, BJCa, BMNH, CAS, CNC, CUIC, DHKa, DRMa, FMNH, GDND, HNHM, ICCM, JKLi, KUSM, MCZ, OSUO, ROM, SAEl, SMNH, UASM, UBC, UCB, UMHF, UMSP, UMMZ, USNM, ZIL.

Geographic Distribution. A common species, distributed from Newfoundland and New Jersey in the east, south to Kentucky, west to Iowa, British Columbia, and north to southeastern Yukon and western N. W. T. (Fig. 265). I have seen three specimens, probably mislabeled, with the following labels: "Or." (USNM), "Tex" (MCZ), and "ARIZONA Pena Blanca 20.VIII.1966" (AMNH). Lindroth's (1963: 237) record from Washington is based on a misidentified *B. lapponicum* (OSUO!).

Geographic Variation. Populations from west of Manitoba have a higher frequency of dark appendages; those from northern British Columbia and southern Yukon in general are more heavily microsculptured, with less regular basilateral carinae of pronota, and less convex pronota.

Habitat. This species often occurs on upper, dry sand banks of rivers and lakes. In Manitoba and eastward, it seems restricted to lake banks, but occurs frequently along large rivers in Saskatchewan and westward.

Phylogenetic Relationships. Apparently related to *B. lapponicum* and *B. velox;* possibly the sister group of *B. stenoderum* (Figs. 292, 293).

Bembidion velox (Linné)

Carabus velox Linné, 1761:222. TYPE material lost (see Lindroth, 1957a:335, 339). Type locality Fårö Island near Gotland, Sweden.

Elaphrus impressus Panzer, 1797, number 8. Location of type unknown. Type locality Germany.

Elaphrus striatus Paykull, 1798:175 (not Fabricius, 1792:179). Type presumably in Paykull collection, Naturhist. Riksmus., Stockholm (Horn and Kahle, 1937). Type locality Sweden.

Bembidium Güntheri Seidlitz, 1891:64. Location of TYPE unknown, according to Lindroth (1962:13). Type locality Petrosavodsk, Russia.

(*Bembidion velox* v. *semicyaneum* Meier, 1899:97. [Name unavailable as clearly intended to be infrasubspecific.])

(*Bembidium velox* L. ab. s. *bimaculatum* Uyttenboogaart, 1904:172 [not Kirby, 1837:52]. [Name unavailable as clearly intended to be infrasubspecific.])

(*Bembidium velox* ab. *nigrescens* Kuhnt, 1913:57. [Name unavailable as clearly intended to be infrasubspecific.])

(*Bembidion velox* ab. *moestum* Csiki, 1928:37; new name for *Bembidium velox* ab. *nigrescens* Kuhnt, 1913. [Name unavailable as clearly intended to be infrasubspecific.])

(*Bembidion velox* ab. *Evertsi* Csiki, 1928:37; new name for *Bembidium velox* ab. s. *bimaculatum* Uyttenboogaart, 1904. [Name unavailable as clearly infrasubspecific.])

Derivation of Specific Epithet. From the Latin *velox*, meaning "swift," referring no doubt to the rapid running of members of this typical *Bracteon* species, and the speed with which they take flight.

Characteristics of Adult. (Figs. 13, 118, 135, 155, 171.)

Diagnostic combination. Elytral interval 3 with distinct mirrors, in some specimens on 2 through 5 as well; pronotum without long basilateral carina; if basilateral carina present, then short, not extended to pronotal base, midlateral seta present. Aedeagus with right lobe of CSC ridged and far removed from basal orifice (Fig. 118); ostial microtrichial patch extended dorsally as a prominent dorsal field of long microtrichia; left-most central membranes with small, sparse, heavily sclerotized scales, sac thus with a peppered appearance; "pillow" with large scales lacking.

Comparisons with related species. The short basilateral carina of pronotum, isolated from the base, distinguishes adults of this species from those of *B. carinula.* As well, the elytra of *B. velox* are generally narrower and more nearly parallel-sided. Aedeagal characters of *B. velox,* as noted in the diagnoses, are also distinctive. Differences from *B. lapponicum* are given under that species.

Description. See Table 2 for character states. Additional traits follow. SBL = 4.6–6.0 mm. Dorsal surface dull bronze, coppery, aeneous, or bluish; mirrors coppery red or purplish, silver spots aeneous, bluish, or bronze. Appendages in most specimens pale; antennomere 1 entirely pale, or infuscated dorsally, antennomeres 2 through 4 pale basally; palpi dark apically, maxillary palpomere 2 pale; legs rufous, slightly infuscated at joints and on tarsi. Pronotum similar to that of *B. carinula*, with sides less rounded in most specimens. Humeral margin of elytra long, to interval 5 or beyond; striae slightly to moderately impressed; interval 3 relatively narrow. Spermatheca with short, apically hooked cornu, more tapered than in *B. lapponicum;* basal portion long, flat (Fig. 171). Spermathecal duct with no posterior lobe. Stylomeres as in Figure 155.

Characteristics of First Instar Larva. Unknown.

Specimens Examined. I have seen 195 adults from the following collections: AMNH, BMNH, CAS, CNC, HNHM, ICCM, MCZ, UMHF, USNM, ZMLS.

Geographic Distribution. In the Palearctic from western France to Scandinavia, north of the Alps, east to the Irtysh and Jenesei Rivers of Russia, and Shenyang, China (Netolitzky and Meyer, 1939; Lindroth, 1962; Fig. 266; Kirschenhofer, 1984).

Geographic Variation. None observed.

Habitat. On pure, completely barren sand (Lindroth, 1945). On larger lakes and river banks; also on banks of bodies of salt water (for example, the Baltic Sea [Lindroth, 1945]).

Phylogenetic Relationships. The inconclusive evidence available suggests a relationship with *B. carinula*, and possibly *B. stenoderum* (Figs. 292, 293).

Bembidion lapponicum Zetterstedt

Bembidium impressum Var. B. *lapponicum* Zetterstedt, 1828:6. LECTOTYPE male selected by Lindroth, 1963:239, in UML. Type locality Vittangi on Torne-älve, Sweden.

Bembidium latiusculum Motschulsky, 1845:272. TYPE material apparently lost, according to Lindroth (1962:13); Keleinikova (1976) does not include this name in her catalogue of the Motschulsky collection in Moscow. Type locality "en Dauria et au Kamtchatka," restricted to "'Dauria', that is Transbaicalia, Siberia" by Lindroth (1962:13).

Bembidium Jenisseense J. Sahlberg, 1880:14. LECTOTYPE female selected by Lindroth, 1963:239, in UMT. Type locality Imbatsk, Lower Jenissei, Russia.

Bembidium pugetanum Fall, 1916:13. HOLOTYPE male, examined, in MCZ. Labeled: "Seattle Wash O.B.J. [handwritten] / TYPE pugetanum / M.C.Z. Type 23865 [red label] / H. C. FALL COLLECTION." Type locality Seattle, Washington.

Derivation of Specific Epithet. From "Lapponia," or Lapland.

Characteristics of Adult. (Figs. 14, 44, 46, 51, 59, 61, 71, 119, 136, 156, 172.)

Diagnostic combination. Elytra with mirrors on interval 3, in most specimens with fainter mirrors on 2 through 5, rarely with very faint mirrors on 6 and 7; pronotum without long basilateral carina, with midlateral seta, and with hind angles prominent, flared outward (Fig. 14); aedeagus wide and short, with one prominent apical lobe (the "pillow") with large triangular scales (Fig. 119).

Comparisons with related species. Difficult to distinguish using external characters from *B. velox*, and to a lesser extent, *B. carinula*. The prothorax of *B. lapponicum* is flatter, with less rounded sides, and broader base with more protruded hind angles. Generally silver spots are wider and longer, with interval 3 wider as well. Legs are darker in most specimens. Aedeagus wider and much shorter than in *B. velox* and *B. carinula;* right lobe of CSC ridged as in *B. velox*, but the lobe is more basal, nearly touching the basal orifice; ostial microtrichial patch large, posteriorly with many comb-like scales extended upward as the dorsal field; central membranes not peppered, as scales are larger and less sclerotized; apically, the "pillow" is covered with large triangular scales; other *Bracteon* have similarly positioned lobes, but no other has such distinctive scales.

Description. See Table 2 for character states. Additional traits follow. SBL = 4.5–6.1 mm. Dorsal surface bronze, gray-bronze, bluish, or aeneous; mirrors purplish or coppery; silver spots aeneous, bluish, or bronze. Appendages dark, piceous, except for venter of antennomere 1, and femur at base, which are rufous or rufopiceous; some specimens have as well paler tibiae. Midlateral setae of pronotum present, rarely absent; only one specimen seen (from "Maalselven, Framnes," ZMLS!) without setae. Side margins of pronotum sinuate, little rounded, hind angles prominent, flared outward, acute in most specimens; basilateral carina thin, generally short, never extended to basal edge of pronotum. Humeral margin of elytra long, extended to inward of stria 5, longer than in *B. carinula;* striae slightly to moderately impressed; interval 3 wide, especially around silver spot. Spermatheca with long, distinctly curved cornu; basal portion long, flat (Fig. 172). Spermathecal duct with or without small posterior lobe. Stylomeres as in Figure 156.

Characteristics of First Instar Larva. (Figs. 206–209, 214, 229, 235.)

Diagnostic combination. Head capsule dark, without traces of spots on frontale (Fig. 214); prominent parietal denticles (Figs. 229, 235); setae ME_2 and TE_6 short, scale-like; seta ST_2 on segment IX present.

Comparisons with related species. From the similarly dark *B. balli* and *B. foveum*, distinguished by the shorter coronal suture and more prominent parietal denticles, as well as the short ME_2 and TE_6.

Description. LHw = 400–425 μm, LHl = 330–350 μm, LCl/LHl = 0.114–0.129. Three specimens measured. Head capsule dark, piceous, more or less uniform, or frontale darker centrally, paler laterally; parietale darker in front of PA_4 and PA_7.

Characteristics of Second Instar Larva. (Fig. 259.)

Description. LHw = 540 μm (n = 1). Frontale without extra setae near FR_3, and lacking microsculpture posteriorly. Head and pronotum with accessory microsetae short, less than two times longer than wide. Microsculpture absent centrally on pronotum. Urogomphus with nine long setae (Fig. 259).

Specimens Examined. I have seen 366 adults, 33 first instars, and 2 second instars from the following collections: AMNH, AMor, BMNH, CAS, CNC, DRMa, HNHM, ICCM, MCZ, OSUC, OSUO, UASM, UMHF, USNM, ZMLS.

Geographic Distribution. A widespread Holarctic species (Fig. 267; Lindroth, 1962), in the Old World from northernmost Scandinavia throughout much of Russia, south to Mongolian Peoples' Republic, east to Kamtchatka. In North America (Fig. 267b) common in the northwest, from Alaska east to the Anderson River; uncommon at scattered localities in the south from Washington, Oregon, Idaho, and Wyoming, east to central Saskatchewan.

Geographic Variation. Populations from the southern portion of the range in North America (central B. C., Alberta, and Saskatchewan southward) are more uniform than northern populations. Southern specimens are larger, with straighter, less-impressed striae, a generally smoother and shinier surface, with mirrors on intervals 2, 4, and 5 generally absent or very faint, and with a relatively narrow interval 3; some northern specimens are like this as well. The male genitalia appear identical to those of northern specimens. Unfortunately, the relative lack of collecting throughout much of the northern portions of British Columbia, Alberta, and Saskatchewan makes interpretation of this form difficult: it is unknown if the southern form is allopatric or sympatric with the northern form, or if a cline connects them. Further work may reveal the distinctiveness of the southern form, if so, it would take on the epithet "*pugetanum* Fall," most likely as a subspecies of *B. lapponicum*. The material I have at hand is too limited to identify clear patterns of variation in the Old World. Lindroth (1962) gives a brief discussion of Palearctic variation.

Habitat. Generally on barren sand banks of large rivers, less frequently around small rivers, and rarely around lakes (Lake Brooks, Alaska).

Phylogenetic Relationships. Perhaps part of a clade with *B. velox*, *B. stenoderum*, and *B. carinula* (Figs. 292, 293).

Bembidion punctatostriatum Say

Bembidium punctato-striatum Say, 1823b:83. NEOTYPE male designated by Lindroth and Freitag (1969:335), examined, in MCZ, labeled: "Rumney, N.H. V.51 Lindroth / Neotypus Bembidium punctatostriatum Say design Lth [red label, in Lindroth's handwriting] / Bembidion punctatostriatum Say det. Lindroth 68." Type locality Rumney, New Hampshire, designated by Lindroth, 1962:12.

Bembidium sigillare Say, 1834:437. TYPE material lost, see Lindroth and Freitag (1969:335). Type locality "Missouri" (probably present-day Nebraska, according to Lindroth, 1969:1113).

Bembidium stigmaticum Dejean, 1831:83. TYPE, examined by Lindroth (1962:12), in MNP. Type locality: "Amérique septentrionale."

Derivation of Specific Epithet. From the Latin *punctum*, meaning puncture, and *stria*, meaning furrow or line, referring to the punctate striae of this species.

Characteristics of Adult. (Figs. 11, 33, 34, 45, 48, 52, 60, 67, 72, 94, 120, 137, 153, 173.)

Diagnostic combination. Long and wide (Fig. 11); surface shiny, mirrors present on interval 3, but not on 6 and 7; mentum tooth parallel-sided, truncate, bulbous; prothorax with wide base and little-rounded sides (Fig. 11), with midlateral seta; humeral margin of elytra prominent, long, extended to stria 5 (Fig. 72); ostial patch of simple microtrichia large (Fig. 120).

Comparisons with related species. A distinctive species, not liable to be confused with other species. From the somewhat similar *B. lorquinii* distinguished externally by the wider body and presence of midlateral pronotal seta, and aedeagally by the usually unridged right CSC lobe and the prominent dorsal VSP ridge.

Description. See Table 2 for character states. Additional traits follow. SBL = 4.9–7.1 mm, rarely below 5.5 mm. Dorsal surface bronze or silver gray, mirrors coppery red or purplish, silver spots aeneous. Antennomere 1 ventrally pale; legs dark, piceous or black, with base of femora, pro- and mesotrochanters, as well as tibiae in most specimens, rufous or rufopiceous. Pronotum with slightly sinuate sides and wide base (about as wide as maximum width anterior to hind angles). Elytral humerus prominent, with long margin, extended to stria 5; striae shallow to moderately impressed. Spermatheca quite varied, in many specimens as in Figure 173; cornu curved or not, generally fairly long. Spermathecal duct with distinct bulb at base, but no posterior lobe. Stylomeres as in Figure 153.

Characteristics of First Instar Larva. (Figs. 194, 204, 215, 230, 237, 239, 241, 251, 254.)

Diagnostic combination. Head broad, pale, with 3-spotted frontale and 2-spotted parietale (Fig. 215); parietal denticles small; seta FR_3 thick but FR_1 thin; pronotum with extensive tubercles set in rows; basilateral corners of thoracic tergites with several extra small setae (setal groups gPR and gME, Figs. 237, 241), and posterolateral corner of abdomen with extra seta (TE_α, Fig. 251).

Comparisons with related species. The distinctly spotted head, microtuberculate pronotum, and setal groups gPR and gME combine to make *B. punctatostriatum* first instar larvae distinctive and unlikely to be misidentified.

Description. See Table 2 for character states. Additional traits follow. LHw = 440–505 μm, LHl = 370–390 μm, LCl/LHl = 0.128–0.130. Three to five specimens measured.

Characteristics of Second Instar Larva.

Description. LHw = 730 μm (n = 1). Frontale without extra setae near FR_3, and with microsculpture posteriorly. Head and pronotum with accessory microsetae less than two times longer than wide. Microsculpture present centrally on pronotum. Urogomphus with seven long setae.

Specimens Examined. I have seen 425 adults, 70 first instars, 1 second instar, and 1 third instar from the following collections: AMNH, BJCa, BMNH, CAS, CNC, CUIC, DHKa, DRMa, ICCM, JKLi, KUSM, MCZ, OSUC, OSUO, ROM, SMNH, UASM, UBC, UMMZ, USNM, ZIL.

Geographic Distribution. In the New World from New Brunswick and Maine south to Kentucky and Arkansas (Lindroth, 1962); in the west from Saskatchewan and Montana, to the Yukon, and Fort MacPherson, N. W. T.; apparently absent from the center of the continent (Fig. 268). I have seen three specimens labelled "TEX" (OSUC, USNM), and two labelled "Cal." (MCZ); both are doubtful records.

Geographic Variation. None noted.

Habitat. On the barren sand banks of large and small rivers, as well as lakes. Specimens frequent drier areas of the sand banks; on the North Saskatchewan River near Paynton, Saskatchewan, found at a considerable distance from the water.

Phylogenetic Relationships. B. punctatostriatum has proven to be the most difficult *Bracteon* to place phylogenetically. It shows characters linking it with the *B. argenteolum*-subgroup, *B. lapponicum,* and the *B. inaequale*-subgroup. It is more likely related to *B. lapponicum* and its relatives (Figs. 292, 293).

Bembidion hesperium Casey

Bembidium hesperum Fall, 1910:95 (not Crotch, 1867: 385). HOLOTYPE male, examined, in MCZ. Labeled: "Vanc. Id. 8/24/96 / hesperum TYPE [handwritten] / M.C.Z. Type 23862 [red label] / H.C. Fall Collection." Type locality Vancouver Island, British Columbia.

Bembidion hesperium Casey, 1918:9. New name for *B. hesperum* Fall.

Bembidion binarium Casey, 1918:9. LECTOTYPE male designated by Lindroth, 1975:115, in USNM. Type locality: California.

Derivation of Specific Epithet. From the Latin *hesperius,* meaning "western" or "of the evening." This lovely name might refer to either the place of residence of these animals, the western edge of North America, or to their dark tone.

Characteristics of Adult. (Figs. 15, 53, 64, 95, 121, 138, 157, 174.)

Diagnostic combination. Dark, shiny; mirrors thus somewhat obscured (Fig. 15), present on intervals 3 through 5; dorsal surface of elytra with sculpticells generally transverse (isodiametric only in deeply microsculptured females) (Fig. 64); pronotum with carina short or absent, lacking midlateral seta; stria 3 abruptly deeper around silver spots; basal portions of femora rufous; aedeagus with wide apex, right CSC lobe at most slightly ridged (Fig. 121).

Comparisons with related species. Adults of this species are the darkest *Bracteon,* and, along with *B. semenovi,* the shiniest. Most similar to *B. lorquinii,* with which it shares the lack of the midlateral seta of the pronotum. Besides luster, color, and genitalia, specimens can be distinguished by the more deeply engraved and punctate striae, smaller size, and proportionally wider body. Genitalic differences are described under *B. lorquinii* .

Description. See Table 2 for character states. Additional traits follow. SBL = 4.7–5.8 mm. Dorsal surface dark, with aeneous, bluish green, or bronze tint; mirrors coppery or purplish red; silver spots aeneous or bluish green. Appendages dark, for the most part piceous; antennomere 1 rufous ventrally; in most specimens basal portions of femora are rufous as well. Pronotum with sides slightly sinuate. Elytral humerus somewhat rounded, margin short, extended to stria 6 but not 5; striae slightly to moderately impressed; third deepened abruptly around silver spots. Spermatheca as in Figure 174; cornu fairly short, only slightly curved. Spermathecal duct without posterior lobe. Stylomeres as in Figure 157.

Characteristics of First Instar Larva.

Diagnostic combination. As for *B. lorquinii,* except that there is virtually no microsculpture near coronal suture. No other differences noted. LHw = 350–360 μm, LHl = 255–270 μm, LCl/LHl = 0.109–0.111. Two specimens measured. See Table 2 for full description.

Characteristics of Second Instar Larva.

Description. As for *B. lorquinii;* LHw = 540 μm (n = 2).

Specimens Examined. I have seen 417 adults, 52 first instars, 7 second instars, and 1 third instar from the following collections: AMNH, BJCa, BMNH, CAS, CNC, DHKa, DRMa, FMNH, GDND, HNHM, ICCM, MCZ, OSUO, UASM, UBC, USNM, ZIL.

Geographic Distribution. Restricted to the westernmost states, from around San Francisco, California, north to Washington, and in southernmost British Columbia (Fig. 269).

Geographic Variation. Specimens from the south (e.g., Klamath River, northern California, DRMa!) tend to be shinier, with more-transverse elytral sculpticells, and with flatter pronota with less rounded sides than specimens from the north (e.g., Nooksack River, northern Washington, DRMa!).

Habitat. Known only from the sandy banks of rivers; occasionally among vegetation.

Phylogenetic Relationships. A relatively basal member of the 2n = 20+XY clade; its sister group is not known (Figs. 292, 293).

Bembidion lorquinii Chaudoir

Bembidium lorquinii Chaudoir, 1868:239. LECTOTYPE male designated by Lindroth, 1963:235, in MNP. Type locality California.

B. lorquini auctorum.

Bembidion tacomae Casey, 1924:22. LECTOTYPE male designated by Lindroth, 1975:115, examined, in USNM. Labeled: "Wawawai Wn [handwritten] / CASEY bequest 1925 / TYPE USNM 36797 [red label] / tacomae Csy [handwritten] / LECTOTYPE tacomae Csy By C. H. Lindroth." Type locality Wawawai, Washington.

Notes About Synonymy. "*Bembidion lorquini*" is an incorrect subsequent spelling (ICZN, Third edition, Article 33[d]).

Derivation of Specific Epithet. Patronym honoring M. Lorquin, who sent the type series to M. H. Deyrolle, from whom Baron Chaudoir received them.

Characteristics of Adult. (Figs. 16, 122, 139, 158, 175.)

Diagnostic combination. Duller than *B. hesperium* (Fig. 16), with mirrors on intervals 3 through 5; elytral sculpticells isodiametric; pronotum with carina short or lacking, and without midlateral seta; stria 3 not as abruptly deepened around silver spots; femora black or piceous; aedeagus with ridged right CSC lobe, otherwise as in Figure 122.

Comparisons with related species. A large species, similar to *B. hesperium*. It is larger, more slender, and with a duller luster than specimens of that species. In addition, the striae of *B. lorquinii* are shallower, especially around the silver spots, and the punctures are smaller; ed3 and ed5 in smaller pit than in *B. hesperium;* apex of aedeagus narrower than in *B. hesperium;* right lobe elongate, consistently markedly ridged (at most only slightly so in *B. hesperium*); ostial microtrichial patch larger than in *B. hesperium,* with more extensive dorsal field; VSP with slightly more prominent, angulate dorsal ridge.

Description. See Table 2 for character states. Additional traits follow. SBL = 5.3–6.8 mm. Dorsal surface greenish-gray, gray-bronze, or bronze; mirrors purplish, coppery, or bronze; silver spots grayish, bronze, or aeneous. Appendages very dark, black or piceous, with only the pro- and mesotrochanters paler, rufopiceous. Pronotal side margins little sinuate; basilateral tubercle prominent. Humeral margins of elytra short, extended to stria 6 but not 5; striae slightly to moderately impressed, not abruptly deepened around silver spots. Spermatheca varied, in many specimens as in Figure 175. Spermathecal duct without posterior lobe. Stylomeres as in Figure 158.

Characteristics of First Instar Larva. (Fig. 216.)

I have not been able to distinguish larvae of *B. lorquinii* from most members of the *B. inaequale*-subgroup. The description below thus applies, with a few exceptions, to *B. lorquinii*, *B. zephyrum*, *B. levettei*, and *B. inaequale*.

Diagnostic combination. Head pale, with 3-spotted frontale, spots indistinct in some specimens (Fig. 216); parietale with small denticles, with denticulate microsculpture near coronal suture; pronotum lacking microsculpture; ME_2 and TE_6 large.

Comparisons with related species. *B. lorquinii* and *B. inaequale*-subgroup larvae are most similar to those of *B. balli* and *B. foveum*. However, the former have paler head capsules, with more prominently denticulate frontales, and lack lateral pronotal microtubercles.

Description. See Table 2 for character states. Additional traits follow. LHw = 380–390 μm, LHl = 295–300 μm, LCl/LHl = 0.119–0.133. Two specimens measured.

Characteristics of Second Instar Larva.

Description. LHw = 550 μm (n = 1). Frontale without extra setae near FR_3, and lacking microsculpture posteriorly. Head and pronotum with accessory microsetae clearly over three times longer than wide. Microsculpture absent centrally on pronotum. Urogomphus with seven long setae.

Specimens Examined. I have seen 389 adults, 16 first instars, and 2 second instars from the following collections: AMNH, BHar, BMNH, CAS, CNC, CUIC, DHKa, DRMa, FMNH, HNHM, ICCM, JKLi, MCZ, OSUO, UASM, UBC, UCB, UMMZ, USNM, ZIL.

Geographic Distribution. Similar to that of *B. hesperium*, but with an extension farther eastward. From near Los Angeles, California, east to western Nevada, north to Idaho and southwesternmost British Columbia (Fig. 270). I view the record from Colorado (Lindroth, 1963, USNM!) with suspicion.

Geographic Variation. None noted.

Habitat. Generally found on barren sandy banks of rivers. One population has been found near seepage on sandy Wreck Beach, on the Pacific Ocean banks of Vancouver, B. C. (BHar!). The water here is at least brackish, if not saline (B. Harrison, pers. comm.), making this population the only known *Bracteon*, other than *B. zephyrum* and *B. velox*, found next to salty water.

Phylogenetic Relationships. B. lorquinii belongs to the 2n = 20+XY clade, but its precise relationships with *B. hesperium* and the *B. inaequale*-subgroup are unresolved (Figs. 292, 293).

Bembidion zephyrum Fall

Bembidium zephyrum Fall, 1910:96. HOLOTYPE male, examined, in MCZ. Labeled: "Humboldt Co. CAL. / [male symbol] / zephyrum TYPE [handwritten] / M.C.Z. Type 23870 [red label] / H.C. Fall Collection / Bembidium zephyrum Fall." Type locality Humboldt County, California.

Bembidion zephyrum tristiculum Casey, 1924:22. LECTOTYPE male designated by Lindroth, 1975: 115, examined, in USNM. Labeled: "S. Oregon Kunf [spelling?] [handwritten] / CASEY bequest 1925 / TYPE USNM 36795 [red label] / tristiculum Csy [handwritten] / LECTOTYPE sbsp. tristiculum Csy By C. H. Lindroth." Type locality southern Oregon.

Bembidion marginosum Casey, 1924:23. LECTOTYPE male designated by Lindroth, 1975:115, examined, in USNM. Labeled: "Del Norte Co. CAL VI.2.10 / CASEY bequest 1925 / marginosum Csy [handwritten] / TYPE USNM 36793 [red label] / LECTOTYPE marginosum Csy By C. H. Lindroth." Type locality Del Norte County, California.

Derivation of Specific Epithet. From the Latin *zephyrus*, meaning "west wind." The beaches these beetles inhabit are swept over by winds blowing from the west across the Pacific Ocean.

Characteristics of Adult. (Figs. 19, 54, 79, 82, 84, 123, 140, 159, 176.)

Diagnostic combination. Wide, relatively flat; with prominent raised mirrors on intervals 2 through 7, in pattern of Figure 19; connection between anterior elytral mirrors and central mirrors absent or consisting of only a very thin mirror on interval 3; pronotum with carina small or absent, with wide lateral expansion and flared front angles; midlateral pronotal seta present; aedeagus with very broad ostial microtrichial patch; VSP with rounded, unscaled dorsal ridge (Fig. 123).

Comparisons with related species. Rather similar to *B. levettei*, with which it has been confused in the past. Specimens of *B. zephyrum* are generally brighter than those of *B. levettei*, with the copper or purple mirrors contrasted against the generally green or blue-green elytra. The mirror of the anterior portion of intervals 3 through 5 is connected to the more posterior mirrors only by a faint band on the interval 3 (Fig. 19); in related species (for example, *B. levettei*, Fig. 20) this band is a much more definite mirror. Mentum tooth not bulbous, against *B. levettei* and *B. inaequale;* incisions in mentum not as deep or outwardly directed as in *B. levettei* and *B. inaequale;* submentum with 4 setae, with medial setae absent, in contrast to 6 setae in *B. levettei*. The side margin of the pronotum is more explanate than in most specimens of related species; it flares out into a protruded front angle. Protarsomere 1 of males is noticeably wider and thicker than in *B. levettei* (compare Figs. 79 and 82 with 80 and 83), as are the associated adhesive setae (compare Fig. 84 with 85). Ostial microtrichial patch extensive, with apical comb-like scales, and a prominent dorsal field of microtrichia. VSP usually without the distinctly angulate and sclerotized dorsal ridge of *B. levettei* and other members of the group, dorsal ridge not angulate.

Description. See Table 2 for character states. Additional traits follow. SBL = 5.0–6.3 mm. Dorsal surface generally bluish green, although some specimens aeneous, with purplish, coppery red, or purplish black mirrors; this same contrast in color between shiny and dull areas of the elytra is also true of the pronotum. Appendages dark, piceous except for rufous pro- and mesotrochanters and base of femora. Pronotum with distinct shiny band on disc on each side close to midline; in some females outer mirrors rather faint, or, rarely, virtually absent (one female from Siltcoos Outlet, Oregon, OSUC!); interval 7 mirror connected to inner mirrors, although the connecting interval 6 mirror is occasionally faint or small. Pronotum wide, relatively flat, lateral margins expanded as protruded front angles. Elytral humerus somewhat rounded, short, not extended to stria 5; striae slightly to moderately impressed. Spermatheca as in Figure 176; cornu distinctly curved. Spermathecal duct without posterior lobe. Stylomeres as in Figure 159, of varied lengths (Fig. 3).

Characteristics of First Instar Larva. (Fig. 217.)

Diagnostic combination. As for *B. lorquinii*, except color paler, flavous; head generally, but not always, with distinct spotted pattern. LHw = 380–410 μm, LHl = 315–320 μm, LCl/LHl = 0.117–0.119. Two specimens measured. See Table 2 for full description.

Characteristics of Second Instar Larva.

Description. As for *B. lorquinii*.

Specimens Examined. I have seen 1,162 adults, 22 first instars, and 1 second instar from the following collections: AMNH, BJCa, BMNH, CAS, CNC, CUIC, DHKa, DRMa, FMNH, HNHM, MCZ, OSUO, UASM, UBC, UCB, UMSP, UMMZ, USNM, ZIL.

Geographic Distribution. Found mainly on the Pacific coast of North America, from San Francisco to the Queen Charlotte Islands (Fig. 271); only a few specimens have been found at inland localities. Inland specimens from Creston, B. C., reported by Lindroth (1962, 1963) as *B. zephyrum*, are actually members of *B. levettei levettei* (CNC, UBC!).

Geographic Variation. None noted in external features. However, the length of S2 in females varies considerably (from 190 μm to 325 μm); this variation is correlated with geography (Fig. 3), but apparently not with body size (although careful measurements to support this claim are lacking). Except for the only two known *B. zephyrum* females from central California (San Francisco) (CAS!), Californian specimens have shorter S2s than do specimens from Bandon, Oregon, and northward; southernmost Oregon is a zone of intermediates.

Habitat. For the most part restricted to sandy beaches of the Pacific Ocean, where it is sometimes abundant under driftwood.

Phylogenetic Relationships. A relatively basal member of the extensively mirrored *Bracteon* (Figs. 292, 293).

Bembidion levettei Casey

Bembidion levettei Casey, 1918:9. LECTOTYPE male designated by Lindroth, 1975:114, examined, in USNM. Labeled: "Col / CASEY bequest 1925 / TYPE USNM 36793 [red label] / levettei Csy [handwritten] / LECTOTYPE levettei Csy By C. H. Lindroth." Type locality Colorado.

Bembidion carrianum Casey, 1924:23. LECTOTYPE female designated by Lindroth, 1975:115, examined, in USNM. Labeled: "Edmonton Alta 1.VII.1920 F.S. Carr / CASEY bequest 1925 / carrianum Csy [handwritten] / TYPE USNM 36800 [red label] / LECTOTYPE carrianum Csy By C. H. Lindroth." Type locality Edmonton, Alberta.

Derivation of Specific Epithet. Patronym honoring G. M. Levette, a physician and amateur entomologist who collected the type specimen (Ewan, 1950). *Bembidion carrianum* Casey, treated here as a subspecies of *B. levettei*, is a patronym honoring the amateur coleopterist F. S. Carr.

Characteristics of Adult. (Figs. 20, 21, 55, 80, 83, 85, 103–106, 111, 124, 125, 141, 160, 161, 177, 180–182.)

Diagnostic combination. Mirrors on intervals 2 through 7, in pattern of Figures 20, 21; anterior elytral mirrors generally connected to middle mirrors by a broad mirror on interval 3; mirrors on intervals 6 and 7 located nearer anterior silver spot, broadly connected to inner mirrors; pronotum with carina short or absent, front angle not flared outward, midlateral seta present; VSP with both basins and dorsal ridge scaled (a few specimens lack or have only very small scales) (Figs. 124, 125).

Comparisons with related species. This and the following three species form the *B. inaequale*-subgroup. They share extensive elytral mirrors, straight CSC flagella, 10 pairs of autosomal chromosomes, and similar larvae.

Many specimens confused with the other two North American species with mirrors on elytral intervals 6 and 7, *B. zephyrum* and *B. inaequale*. Distinguished from *B. zephyrum* by characters mentioned under that species's account. As well, leftmost central membranes of internal sac with large, heavily sclerotized scales, unlike those found in *B. zephyrum*. From *B. inaequale* distinct in having the outer mirrors near the anterior silver spot; these outer mirrors are generally connected to the inner mirrors in *B. levettei*.

Description. See Table 2 for character states. Additional traits follow. SBL = 4.8–6.1 mm. Dorsal surface greenish-gray, aeneous, or bronze; mirrors purplish, reddish, or coppery; silver spots greenish-gray, aeneous, or bronze. Appendages dark, piceous except extreme base of legs and (in a few specimens only) venter of antennomere 1 rufous. Pronotum with distinctly contrasted shiny discal band near midline present or faint; with a small "silver spot" near the lateral edge of this band. Sides of pronotum moderately sinuate. Humeral margins of elytra short, not extended to stria 5; striae slightly to moderately impressed. Spermatheca varied; with very long cornu, slightly to distinctly curved, basal portion short (Fig. 177). Spermathecal duct without posterior lobe. Stylomeres as in Figures 160, 161; no consistent differences observed between the subspecies.

Characteristics of First Instar Larva. (Fig. 231.)

Diagnostic combination. As for *B. lorquinii*. LHw = 380–420 μm, LHl = 315–355 μm, LCl/LHl = 0.137–0.155. Six specimens measured. See Table 2 for complete description.

Characteristics of Second Instar Larva. (Fig. 218.)

Description. As for *B. lorquinii*. LHw = 580–625 μm (n = 2).

Specimens Examined. I have seen 1,606 adults, 36 first instars, 9 second instars, and 1 third instar from the following collections: AMNH, AMor, BJCa, BMNH, CAS, CNC, CUIC, DHKa, DRMa, FMNH, GDND, HNHM, ICCM, ISAs, JKLi, KUSM, MCZ, OSUO, ROM, SMNH, UASM, UBC, UMSP, UMMZ, USNM, ZIL.

Geographic Distribution. B. levettei levettei is found in the western mountains, from southern British Columbia and southwestern Alberta to Idaho, Wyoming, Colorado, and northernmost New Mexico (Fig. 272). I have seen as well one specimen from Washington, and another labelled "Cal." (MCZ!). *B. levettei carrianum* is transamerican, from Newfoundland and Labrador west through Minnesota to central Alberta, British Columbia, and north into Alaska and N. W. T. (Fig. 272).

Geographic Variation. This variable species consists of two distinct forms, which I treat as subspecies, *B. levettei levettei* and *B. levettei carrianum*. The two forms are, as far as known, allopatric, with no signs of intergradation (although intermediate localities have not been well collected). One form is strictly southern and montane, and the other almost exclusively more northern or lowland (Fig. 272). The only exceptions I have seen are three specimens from Fort Collins, Colorado (CAS!). Two of these males have genitalia of the *B. levettei carrianum* form, and yet they are within the known range of *B. levettei levettei*, far from the range of *B. levettei carrianum*. The third male is genitally intermediate between the two subspecies. The significance of these three specimens is uncertain; more material is needed from northern Colorado.

Bembidion levettei levettei specimens are distinguished from *B. levettei carrianum* primarily by male genitalia: members of *B. levettei levettei* lack the basodorsal lobe of the internal sac possessed by members of *B. levettei carrianum* (compare Fig. 125 with 124) (46 specimens of *B. levettei levettei* examined, 66 of *B. levettei carrianum*). In inverted internal sacs, this lobe of *B. levettei carrianum* is manifest as a characteristic bulge of the anterior edge of the ostial cavity (Fig. 103, arrow). *B. levettei levettei* aedeagi are generally larger, more curved ventrally, with a wider apex, but there are exceptions to these characters. However, there are a few somewhat consistent differences in external characters. Members of *B. levettei levettei* tend to be larger and shinier than *B. levettei carrianum*, with the mirrors more contrasted in luster and color to the surrounding surface. This includes not only the mirrors of the elytra, but also the shiny areas of the pronotum, which are generally a shiny purplish contrasted against the dull grayish green of the rest of the pronotum. Mirrors on elytral intervals 5 through 7 tend to be a bit more extensive, and are positioned slightly more posteriad (compare Fig. 20 with 21). The striae of *B. levettei levettei* are a bit deeper (at least in northern populations). The elytra are slightly more parallel-sided, and relatively larger than the pronotum; the sides of the pronotum are less rounded (Fig. 20). Stria 4 is more frequently straight in *B. levettei levettei*. Most of these external characters are rather vague, and none consistently distinguish the two subspecies.

Habitat. B. levettei members are found most commonly on barren sand or sand-silt banks of rivers; also on creek and lake banks.

Phylogenetic Relationships. The relationships within the *B. inaequale*-subgroup are unclear (Figs. 292, 293); indeed, I am not certain that the two subspecies of *B. levettei* are themselves sister taxa.

Bembidion inaequale Say

Bembidium inaequalis Say, 1823a:151. NEOTYPE male designated by Lindroth and Freitag (1969: 335), examined, in MCZ, labeled: "Mt Pleasant Ia Apr 28 1934 Knutson / inaequale det. Darlington / Neotypus Bembidium inaequale Say design Lth [red label, in Lindroth's handwriting] / Bembidion inaequale Say s.str.det. Lindroth 68." Type locality Mount Pleasant, Iowa.

Bembidium arenarium Dejean, 1831:80. TYPE, examined by Lindroth (1962:7), in MNP. Type locality: "Amérique septentrionale".

Bembidium lacustre LeConte, 1848:451. HOLOTYPE female, examined, in MCZ. Labeled: "[grayish-green circle] / 428 / Type 5491 [red label] / *var.* lacustre Lec. [handwritten] / Bembidion inaequale Say Det Lindroth 1951." Type locality Lake Superior, according to Lindroth (1962:7).

Bembidion opaciceps Casey, 1918:8. LECTOTYPE female designated by Lindroth, 1975:115, examined, in USNM. Labeled: "Cal. / CASEY bequest 1925 / TYPE USNM 36794 [red label] / opaciceps Csy [handwritten] / LECTOTYPE opaciceps Csy By C. H. Lindroth." Type locality California.

Derivation of Specific Epithet. From the Latin *inaequalis*, referring to the unequal surface of the elytra.

Characteristics of Adult. (Figs. 22, 23, 73, 74, 126, 142, 162, 178.)

Diagnostic combination. Mirrors present on intervals 2 through 7; outer mirrors on intervals 6 and 7 near posterior silver spots, frequently isolated from inner mirrors (Figs. 22, 23); pronotum with carina short or absent, midlateral seta present or absent; aedeagus with prominent ventral bulge and hooked apex (Fig. 126); extensive dorsal field of comb-like scales; VSP scaly, as in *B. levettei.*

Comparisons with related species. Belongs to the *B. inaequale*-subgroup. Adults are generally smaller than those of *B. levettei*, from which they differ externally by small silver spots, and the mirror on elytral intervals 6 and 7 being positioned near the posterior silver spot. Generally the outer mirror is a small spot, isolated from the inner mirrors, but in many specimens it is broadly connected to inner mirrors. Eastern members of *B. inaequale* are more readily distinguished from *B. levettei* specimens by the narrow forebody with deeply punctured striae, and pale tibia.

Description. See Table 2 for character states. Additional traits follow. SBL = 4.3–5.9 mm. Dorsal surface ranging from dark bronze or dark aeneous to gray green, aeneous, or bluish green; mirrors dark purplish black, dark bronze, or coppery, or reddish. Antenna with first four antennomeres pale, at least basally, or more generally infuscated; tibia centrally pale, rufous or rufotestaceous with slight metallic tint; femora basally pale; western specimens with more generally infuscated legs. Faint discal shiny patch flanked by dull patches on pronotum. Pronotum varied, from convex and narrow to flat and wide. Transverse basal impression of elytra not as pronounced as in *B. levettei*, in many specimens absent; humeral margin short to medium in length, not extended to stria 5; striae slightly to markedly punctate; 5 and 6 in many specimens interrupted at outer mirror; 4 in many specimens interrupted. Spermatheca quite varied; cornu slightly curved, length varied, as short as in Figure 179 or nearly as long as in *B. levettei* (Fig. 177). Spermathecal duct without posterior lobe. Stylomeres as in Figure 162.

Characteristics of First Instar Larva. (Fig. 193.)

Diagnostic combination. As for *B. lorquinii.* LHw = 330–400 μm, LHl = 260–340 μm, LCl/LHl = 0.111–0.161. Four specimens measured. See Table 2 for complete description.

Characteristics of Second Instar Larva.

Description. As for *B. lorquinii.*

Specimens Examined. I have seen 1,802 adults, 62 first instars, 4 second instars, and 2 third instars from the following collections: AMNH, AMor, BJCa, BMNH, CAS, CNC, CUIC, DEUN, DHKa, DRMa, FMNH, GDND, HNHM, ICCM, ISAs, JHAc, JKLi, KUSM, MCZ, OSUO, ROM, SMNH, UASM, UBC, UCB, UMSP, UMMZ, USNM, UWLW, ZIL.

Geographic Distribution. In North America from Nova Scotia, south to Georgia and Alabama, west to Kansas, Colorado, and California, north to Alaska (Fig. 273).

Geographic Variation. This species shows considerable geographic variation. Lindroth (1963) divided *B. inaequale* into two subspecies, but I do not consider them discrete enough to be recognized. Adults from east of the Great Plains ("*B. inaequale inaequale*," Fig. 22) are generally more somber in color, have paler legs, shinier luster, narrower body (especially the forebody), and deeper elytral punctures; they lack the midlateral pronotal seta. Specimens from the western mountains ("*B. inaequale opaciceps*," Fig. 23) are wider and more robust; the microsculpture is deeper, with surface therefore duller; pronotum wider with less sinuate sides and broader base; midlateral setae present in most specimens; striae much shallower, with less impressed punctures; shoulder margin a bit longer. The two forms are quite different. However, there is a broad zone of intermediates, from Alberta and Manitoba south to Colorado, Wyoming, and Nebraska. Within this intergradation zone there is also notable variation, with Alberta and Saskatchewan specimens being: larger, more reddish, with smaller silver spots, restricted to interval 3; with mirrors more extensive, outer mirrors frequently not isolated. Making the picture more complex are five specimens from Nampa, Idaho (ICCM!), which appear quite like intergrade specimens from western Nebraska, even though they are from well within the range of the western form. I feel that a detailed morphometric study of the patterns of geographic variation in this species is necessary before any clear division into subspecies is undertaken.

Habitat. Found on river, creek, and lake banks. Generally among sparse vegetation on a silt-sand substrate.

Phylogenetic Relationships. *B. inaequale* is either the sister species of *B. levettei levettei*, *B. levettei carrianum*, the *B. litorale*-*B. conicolle* line, or a combination thereof (Figs. 292, 293).

Bembidion litorale (Olivier)

Elaphrus litoralis Olivier, 1790:6. Location of type unknown, according to Lindroth (1962:6). Type locality Paris, France.

Elaphrus paludosus Panzer, 1794, number 4. Location of type unknown. Type locality Nürnberg, Germany.

Bembidium elegans Germar, 1824:27. Location of type unkown. Type area Transsylvania.

Bembidium var. *caeruleum* Krynicki, 1832:85 (not Serville, 1826:76). Type presumably in Krynicki collection, University of Charkow (Horn and Kahle, 1937). Type locality undesignated. (Name available as original description does not give clear indication that the name is intended to be infrasubspecific.)

(*Bembicidium palmosum* var. *evanescens* Dalla Torre, 1877:53 [not Wollaston, 1877:18]. Presumably "*palmosum* Pnz" is an emendation of "*paludosum* Panzer." [Name unavailable as intended as infrasubspecific.])

(*Bembidium littorale* v. *nigrans* Barthe, 1912:234. [Name unavailable as infrasubspecific, as indicated by "Ça et là avec le type." (Barthe, 1912:234).])

(*Bembidium litorale* ab. *melanoticum* Wagner, 1915: 307. [Name unavailable as intended as infrasubspecific.])

(*Bembidion litorale* ab. *krynickii* Csiki, 1928:35; new name for *Bembidium* var. *coeruleum* Krynicki, 1832. [Name not available, as Csiki considered it of infrasubspecific rank.])

B. littorale auctorum.

Derivation of Specific Epithet. From the Latin *litoralis*, meaning "of the shore," referring to the beachside habitat of these beetles.

Characteristics of Adult. (Figs. 17, 56, 81, 127, 143, 163, 179.)

Diagnostic combination. Mirrors on intervals 2 through 7, outer mirrors broadly connected or isolated from inner mirrors; pronotum basally constricted (Fig. 17), somewhat convex, lacking carina, midlateral setae present or absent; male protarsomere adhesive setae narrow (as in Fig. 86); aedeagus stout (Fig. 127), with dorsally bent ventral margin of the ostial cavity; VSP large, with unscaled (but occasionally striated) dorsal ridge; ostial microtrichial patch narrow, dense.

Comparisons with related species. Belongs to the *B. inaequale*-subgroup. Males of this species have exceptionally thin basal protarsomeres, with small adhesive setae, traits they share with members of the closely related *B. conicolle*. *B. litorale* has a more convex prothorax with more rounded sides (that is, much more basally constricted) than does *B. conicolle*. Other differences from *B. conicolle* are described under that species.

Both Netolitzky (1940, 1942) and Lindroth (1962) considered the eastern populations of *B. litorale*-like *Bracteon* to belong to a separate species, *B. conicolle*. O. L. Kryzhanovskij (pers. comm., 1983) suggests that *B. conicolle* and *B. litorale* belong to the same polytypic species. I have decided to treat the forms as distinct species, in good part because the limited material before me prevents a definitive conclusion (and thus I would prefer to err on the side of conservancy), but also because of the nature of the geographic variation. The few (11) specimens I have from a zone of sympatry, the Lena River, belong to two forms. Two females (Ust Kut, UMHF!) with convex, rounded prothorax, possessing midlateral setae, ed3 and ed5 in center of silver spots, and outer mirrors isolated, are typical *B. litorale* members. Nine specimens (Ust Aldan, Aldan, Ust Kut, Ust Vilui, UMHF!) are more similar to typical *B. conicolle*, having flatter, less rounded prothoraces, lacking midlateral setae, having ed3 and ed5 at or near the anterior edge of silver spots, and having outer mirrors broadly connected to inner mirrors or partly isolated. However, most of the characters Lindroth (1962) uses to separate the species are inconstant (especially the isolation of the outer mirrors), and the differences between the forms are rather slight. Kryzhanovskij's suggestion of synonymy of the two names thus deserves greater attention than I have been able to give it; an examination of geographic variation of *B. litorale*-like *Bracteon* based on more extensive material is warranted.

Description. See Table 2 for character states. Additional traits follow. SBL = 5.2–5.9 mm. Dorsal surface bronze gray, bronze, or greenish gray; mirrors dark bronze gray, or purplish. Appendages dark, with venter of antennomere 1, base of legs, and venter of tibiae paler (rufous or rufopiceous). Deeply microsculptured, and therefore quite dull. Shinier specimens show a slight silver spot on the prothorax. Convex pronotum, sides distinctly rounded, greatest width well before middle; base narrow. Humeral margins of elytra short, not extended to stria 5; striae slightly to moderately impressed. Spermatheca as in Figure 179; cornu straight, basal bulb small. Spermathecal duct without posterior lobe. Stylomeres as in Figure 163.

Characteristics of First Instar Larva. Unknown.

Characteristics of Second and Third Instar Larvae.

Diagnostic combination. Described by Andersen (1966); he does not provide information on the characters I studied.

Specimens Examined. I have seen 241 adults from the following collections: AMNH, BMNH, CAS, HNHM, ICCM, MCZ, UMHF, USNM, ZMLS.

Geographic Distribution. A Palearctic species, found from the British Isles and Spain, to Greece, north to Finland, and east across Asia to the Lena River (Lindroth, 1962; Fig. 274).

Geographic Variation. None noted.

Habitat. On banks of rivers and small lakes, on fine sand often mixed with silt; bank often sparsely vegetated (Lindroth, 1945). The habitat is thus similar to that of *B. inaequale*.

Phylogenetic Relationships. B. litorale is the sister species of *B. conicolle*, or of *B. levettei* + *B. inaequale* (Figs. 292, 293).

Bembidion conicolle Motschulsky

Bembidium conicolle Motschulsky, 1845:273. LECTOTYPE female designated by Lafer (1975), examined, in ZMUM, labeled: "Mt. Hamar-Dab [red label] / Bembidium conicicolle mihi, Mt. Ham. Dab [handwritten on bordered paper] / Lectotypus Bembidion conicolle Motsch. Lafer det. [red label]." Type locality Hamar Daban Mountains, near Lake Baikal, Russia

Bembicidium conicicolle Motschulsky, 1850:16; unjustified emendation of *Bembidium conicolle* Motschulsky, 1845.

Bembidion baikalo-ussuricum Netolitzky, 1940:163. HOLOTYPE male, examined by Lindroth (1962: 7), in Naturh. Mus. Vienna. Type locality Nikolsk-Ussurisk, north of Vladivostok, Russia. For notes on synonymy, see Lafer (1975).

Bembidion baicaloussuricum auctorum.

Derivation of Specific Epithet. Presumably referring to the trapezoidal pronotum of members of this species.

Characteristics of Adult. (Figs. 18, 86, 128, 144, 164.)

Diagnostic combination. Mirrors on intervals 2 through 7, outer mirrors broadly connected or isolated from inner mirrors; pronotum only slightly basally constricted (Fig. 18), relatively flat, generally with small carina, midlateral setae present or absent; male protarsomere adhesive setae narrow; aedeagus narrower than in *B. litorale*, with less curved ostial sclerotized strip (Fig. 128); VSP large, with unscaled (but occasionally striated) dorsal ridge; ostial microtrichial patch narrow, thick.

Comparisons with related species. Belongs to the *B. inaequale*-subgroup. Very similar to specimens of *B. litorale*. The prothorax of *B. conicolle* is flatter, with straighter sides and a wider base than that of *B. litorale;* the midlateral seta is constantly absent in *B. conicolle*, only inconstantly so in *B. litorale.* A minute laterobasal carina is present in most *B. conicolle*, but in no *B. litorale.* The outer mirrors are broadly connected to the inner elytral mirrors in most, but not all, specimens. Stria 4 is generally straighter (although in some specimens it is abruptly sinuate); ed3 and ed5 are at the anterior margin of the silver spot in most specimens. Aedeagus very similar to that of *B. litorale* (compare Figs. 127 and 128); slenderer, VSP usually thinner, with anterior basin shallower, ventral margin thus appearing straighter in side view; ostial cavity without markedly bent ventral margin.

Distinguished from the North American *B. levettei* by the lack of the prothoracic seta and the narrow protarsomere of the male.

Description. See Table 2 for character states. Additional traits follow. SBL = 5.3–5.7 mm. Stylomeres as in *B. litorale;* see Figure 164.

Characteristics of First Instar Larva. Unknown.

Specimens Examined. I have seen 21 adults from the following collections: HNHM, UMHF, ZMLS.

Geographic Distribution. From the Lena River, Lake Baikal, and Mongolian Peoples' Republic, east to the Ussur region and Japan (Fig. 274; Lindroth, 1962).

Geographic Variation. None noted.

Habitat. Not known to me.

Phylogenetic Relationships. This species is probably most closely related to *B. litorale* or to *B. levettei* + *B. inaequale* (Figs. 292, 293).

PHYLOGENY OF *BRACTEON*

Introduction

Of primary importance in deciphering the course of biotic history is the discovery of the pattern of splitting of lineages, and of the manner in which traits have been transmitted along lineages. But breeding ties of past organisms cannot be observed directly, and so some secondary indicators of genealogical relationship must be sought. The only evidence we have for a group such as *Bracteon* is that provided by the characteristics of living species; the few *Bracteon* fossils offer little information.

The hypotheses of phylogenetic branching pattern and character state evolution to be chosen for a group such as *Bracteon* are those that best explain the diversity in extant organisms. It is important that we strive to make our hypotheses of character evolution and phylogeny to be the "best explanatory hypotheses" not just in isolation but also within a broader framework. We have to consider them in the context of hypotheses about related groups and of established notions about genetics, development, evolutionary ecology, etc. For example, we must make sure that we choose hypotheses for our study group ("ingroup") that allow for "acceptable" hypotheses of related group ("outgroup") evolution; we do this by using some form of outgroup analysis. We must also make certain our hypotheses are consistent with our background assumptions about evolutionary rates, developmental constraints, etc. This striving for compatibility of our hypotheses with the rest of biological knowledge is important whatever our phylogeny reconstruction methods might be. But which background assumptions are justifiable?

Two divergent opinions form the focus of one of the most crucial controversies in systematics today: Felsenstein (1982, 1983, 1988) recommends that we choose the phylogeny that confers on the data the greatest likelihood of observation under a particular model of evolution; Farris (1983) believes we should choose the phylogeny that allows us to most simply account for the observed distribution of character states, without relying on stochastic evolutionary models. We could choose the most-parsimonious hypothesis (*sensu* Farris) either for purely aesthetic reasons (because parsimonious hypotheses are pleasing), or as they might be viewed, through their simplicity and presumed greater testability, as appropiate Popperian devices to stimulate future research, or because some stochastic model of evolution judges parsimony to be a good estimator of phylogeny (see Sober, 1988). A number of different stochastic models might so judge parsimony, but these have only been partially explored (Felsenstein, 1988), and all of the models examined to date are to greater or lesser extent biologically unrealistic. The same can be said of any particular maximum likelihood method. We are therefore left in the uncomfortable position of using a method which could be justified if the characters studied evolve according to some realistic, but unknown, model.

For morphological data such as that available for *Bracteon*, I have no clearly defensible stochastic models of character evolution that would allow us to build statistical estimation methods. My algorithmic analysis will therefore be based on parsimony methods.

Before delving into the phylogeny of *Bracteon* and its near relatives, I will discuss briefly its more distant relatives.

The Phylogenetic Context of *Bracteon*

Suprageneric Relationships within the Supertribe Trechitae. While relationships of major lineages of Trechitae are not crucial for my study of *Bracteon*, they provide a useful context within which to consider the evolution of *Bracteon* and its near relatives. Below I review a few aspects of trechites, concentrating on the tribe Bembidiini.

Four tribes are included within the supertribe: Trechini, Zolini, Pogonini, and Bembidiini (Kryzhanovskij, 1976; Erwin, 1985). Virtually no cladistic studies on the higher-level relationships of the members of these tribes have been published. Erwin's (1972, 1982) papers are the only available works, and these only deal with a very few aspects of bembidiine phylogeny. Other studies include Jeannel (1941), Barr (1971), Schuler (1971), and Perrault (1981), but the character analysis in these is somewhat vague or not explicit. A complete analysis of major evolutionary patterns within trechites is far beyond the scope of the present work.

Figure 275 presents some names of major groups of trechites, and hypotheses of some possible aspects of their phylogeny; it is based mainly on the previously cited works. The meager cladistic structure illustrated in the figure is in doubt: the monophyly of the groups shown, and their relationships, have not been adequately demonstrated.

Monophyly of Bembidiini. The tribe Bembidiini includes thousands of species of carabids with small or minute adults, which occur throughout the world. The only known derived character linking members of the Bembidiini are the subconical, narrow, and short apical palpomeres (Erwin, 1982). However, some trechines (for example, *Oxytrechus* Jeannel and *Perileptus* Schaum) also have relatively small terminal palpomeres. A bembidiine-like palpus occurs as well in the aberrant genus *Gehringia* Darlington, a genus with doubtful affinities to bembidiines (D. Maddison, 1985a). There is some uncertainty about the nature of palpomere evolution, and thus about bembidiine monophyly; the character needs to be studied in more detail.

Generic Relationships within Bembidiini. Members of the tribe containing *Bembidion* are organized by some workers into the three subtribes Anillina, Tachyina, and Bembidiina. All are worldwide groups, with the small tachyines being predominantly tropical, the larger bembidiines mainly temperate, and the minute, soil-dwelling anillines occurring in unglaciated regions.

Erwin (1982) proposes that Anillina is a polyphyletic grade derived from the tachyine *Paratachys* Casey and its allies. *Limnastis* Motschulsky and relatives, plus *Horologion* Valentine are also presumably derived from this same group (Barr, 1971; Erwin, 1982).

Among Bembidiina, Erwin (1972) considers *Asaphidion* and *Bembidion* to be sister groups, indicated by common possession of the (presumably derived) brush on male internal sacs. This character state is not found in other Bembidiina, but it is found as well in the tachyine *Xystosomus* Schaum (Erwin, 1973). Another genus of doubtful affinities is the Australian *Tasmanitachoides* Erwin, now placed in the Tachyina (Erwin, 1972). *Phrypeus* is considered by Erwin (1972) to be the sister group of *Asaphidion* + *Bembidion*, with *Bembidarenas* being the sister group of that whole assemblage. Erwin does not treat *Zecillenus*, but in this scheme it would presumably fall outside of the *Asaphidion* + *Bembidion* group because of its supposedly primitive lack of a brush sclerite. Perrault (1981), in contrast, considers the lack of a brush sclerite in *Bembidarenas* and *Phrypeus* (and presumably *Zecillenus*) to be derived, and would include these within *Bembidion* (sens. lat.). A more certain sorting of these genera awaits extensive character analysis, including study of promising characters such as male protarsal vestiture, testicular structure, etc.

Monophyly of Bembidion. The only character typically cited (Erwin, 1972; Lindroth, 1980) linking *Bembidion* members is the brush sclerite of the male internal sac (Figs. 99–102, 107). However, *Asaphidion* and *Xystosomus* also possess such a brush, and thus it cannot be considered an autapomorphy of *Bembidion* as the genus now stands. I know of no other possible synapomorphy of members of the genus, and *Bembidion* may be paraphyletic or polyphyletic, with one or more of the less-inclusive genera of Bembidiina derived from within it.

Cladistic Structure of *Bracteon* and Related *Bembidion*

No cladistic analysis of relationships of subgenera of *Bembidion* has been published. Erwin and Kavanaugh (1981) present the only available cladistic analysis of members of the genus, but they deal with relationships within two species groups only, distantly related to *Bracteon*.

The main attempt at tracing lineages within the genus was made by Jeannel (1941), with modifications of his scheme proposed by Perrault (1981, 1982). These works, however, did not include a cladistic character analysis. Jeannel (1941) lists seven phylogenetic series within the French bembidiine fauna: *Ocys*, *Cillenus*, *Notaphus*, *Bembidion*, *Peryphus*, *Odontium*, and *Asaphidion*. Based on the South American fauna, Jeannel (1962) later removed *Plataphus* from the *Peryphus* series. He does not discuss the interrelationships of these eight series.

Netolitzky (1942), in contrast, distinguished two major phyletic series in his studies of *Bembidion*, the *Notaphus* series (with "free" ed3 and ed5), and the *Peryphus* series (with ed3 and ed5 attached to stria). He presents a number of other series of evolving lines (based on changes in form of mentum tooth, humeral margin, etc.) interwoven with these two series, but the discussion is lacking clear hypotheses of relationships of taxa.

Perrault (1982) also views *Bembidion* as comprising two major lineages, but of different compositions than Netolitzky's. According to Perrault, *Bembidion* originated in the tropics, with an ancient separation of two stocks leading to the eastern Southern Hemisphere forms on one hand, and to the speciose Northern Hemisphere and South American taxa on the other.

In my opinion, none of these views have been corroborated, and at present must be considered very tentative working hypotheses.

I herein present a first attempt at a cladistic analysis of *Bembidion*, including 52 taxa from a number of subgenera, with hopes that this initial contribution will serve as a starting point for future phylogenetic studies in the genus. Because my main interest is with *Bracteon*, most of my effort is placed there.

Methods

I have examined 85 traits in the 18 taxa of *Bracteon*, 38 other *Bembidion*, as well as *Asaphidion alaskanum* (Tables 2, 4, and 5). I thus have 18 taxa in my study group (ingroup), and 39 outgroup taxa. Some of the characters (for example, 10, 26, 28, and

32) have been used in the past to group *Bembidion* into subgenera or species-groups; others vary only within the outgroups, and are constant within *Bracteon*. These are included primarily for the evidence they might offer regarding outgroup relationships. Table 3 presents the number of specimens examined for each entry in Table 2; sample sizes for Tables 4 and 5 are contained therein.

I have conducted an analysis using traditional Hennigian argumentation, not employing a computer (which I will call the "traditional analysis"), as well as a computer-aided, fully algorithmic parsimony analysis of these data (which I will call the "algorithmic analysis"). Before going into details about each analysis, I describe the gathering and weighing of evidence.

Choice of characters

In choosing evidence for my cladistic analysis, I have discarded about 50 characters after preliminary investigation. Characters eliminated were those that proved: (1) to be too difficult to interpret states of a given specimen without resorting to expensive SEM or other excessively time-consuming work; (2) to have too much variation within species, requiring much more time to document accurately than was available. I also avoided characters that required extensive measurements. While some of the characters used are inherently quantitative (such as length of some larval setae), the organisms exhibit discrete conditions that could readily be distinguished by eye. After this pruning, 85 characters remained.

Hypothesizing transformation networks

For each character, all changes between states were equally weighted, with one major exception. All multistate characters whose traits were considered as ordered in a transformation series were treated as linearly ordered, reversible characters. Thus, a character ordered into a 0↔1↔2 transformation series implies that a 0↔2 change is of greater weight than a 0↔1 change. The only multistate characters not fitting into this category were characters 34 and 64, which were treated as unordered characters.

Character weighting

Initial analyses were conducted with equal weighting of characters. I should note that this equality of inter-character weighting is somewhat artificial, as some of the characters are weighted more than others simply by the way I coded the characters. I divided some characters into two states (say 0 and 1), others into three (say A, B, and C); the characters with more states are naturally weighted more highly than the ones with less, but this does not necessarily reflect greater genetic diversity requiring higher weights. Without knowing considerably more about *Bembidion*, it is not possible to determine whether the genetic distance between 0 and 1 is any more or less than that between A and B or A and C. However, in the face of ignorance, I think that this (somewhat questionable) equality of weights is the best that can be done.

Two additional weighting schemes were explored. In the first, I weighted against all characters that were subject to observational error, that is, I doubted I could distinguish character states consistently, or I felt the sample sizes were too small. In this weighting scheme, error-prone characters were given a weight of 1, other characters a weight of 2. The characters I judged to be error-prone are: 8, 11, 15, 16, 27, 28, 32, 35–38, 40, 45, 46, 51, 60, 64, 70, 73, 82, 83. In the second, I weighted against error-prone characters, as well as those that were polymorphic in at least two species. The relative decrease in weight is based on the assumption that polymorphisms which are maintained are less reliable phylogenetic indicators (see Kluge and Farris, 1969; Hecht and Edwards, 1976). In addition, the numerical algorithms used for dealing with polymorphic data are biologically unrealistic (they do not allow for ancestral polymorphisms), thus leaving the treatment of such characters questionable. By this weighting scheme, characters that were both error-prone and overly polymorphic were given a weight of 1, those that suffered from only one problem a weight of 2, and all other characters a weight of 3. The characters which show polymorphism in two or more species are: 3–11, 21, 25 27–29, 35, 40, 45–46, 51, 57, 60, 75, and 82.

Traditional analysis

Many of the non-numerical approaches used by systematists are essentially less-rigorous versions of maximum likelihood estimation, or a parsimony approach, or an amalgam of the two. The rigorous portions of these mental techniques are by necessity shorter and less complex than those used in computers, and, as expected, they are therefore less powerful. The non-rigorous portions make up for some of this lack of depth by allowing inclusion of more information in the analysis. However, these non-rigorous, more intuitive portions of the method lack openness to critical examination. (The hypotheses they produce are open to critical examination, as are all hypotheses, but the methods are not.)

Of the non-numerical methods currently used for inferring the phylogeny of a group of organisms, almost all involve an initial assessment as to which states of a character were present in an ancestor of the ingroup. Methods proposed for inferring which states are ancestral (or which derived) are numerous, and have been reviewed by Crisci and Stuessy (1980), de Jong (1980), Stevens (1980), Arnold (1981), and others. The three methods most widely discussed today are outgroup analysis, the ontogenetic method, and the paleontologic method. The debate in the literature on the relative merits of these techniques, carried on by Nelson (1978), Patterson (1982), Voorzanger and van der Steen (1982), and W. Maddison *et al.* (1984), among many others, is unfortunately nearly irrelevant for ground beetle systematics: the ontogeny and fossil record of carabids, including *Bracteon*, are so poorly known that these methods are for the most part inapplicable; only outgroup analysis is available.

A number of outgroup analysis procedures have been proposed (see Watrous and Wheeler, 1981; W. Maddison *et al.*, 1984). When outgroups are adequately resolved cladistically, the character states of the most recent common ancestor of the ingroup plus its sister group are estimated via an outgroup algorithm (W. Maddison *et al.*, 1984), and then a second step of resolving the ingroup assuming those ancestral states is taken.

These hypotheses of ancestral state can then be used to corroborate the monophyly of subgroups that possess derived states (Hennig, 1966). Two steps are thus involved: initial hypothesizing of ancestral states, and resolution of the ingroup. Rigorous techniques of argument for this second step are more or less undeveloped, although Watrous and Wheeler's (1981) functional outgroup/functional ingroup routine (equivalent to Kavanaugh's [1978] "character correlation" method and Clark's [1978] "ingroup analysis") is a useful, albeit imperfect, method of searching for most-parsimonious trees (see W. Maddison *et al.*, 1984 for a discussion of some of its problems).

However, when outgroups are imprecisely resolved, the outgroups and ingroups must be resolved simultaneously to guarantee the globally most-parsimonious ingroup cladogram. One could imagine doing this mentally, by a reciprocal illumination technique that would entail resolution of part of the ingroup, then part of the outgroup, then a portion of the ingroup, and so on, until all the data provided by the characters were used. Such a technique has not been rigorously developed, and even if it were, it would probably suffer from some of the same problems as the functional outgroup/functional ingroup approach. Nonetheless, it may be the best we could do without lengthy calculations best done by a computer. Further discussion of the relationship between techniques of argument and the globally most-parsimonious cladogram is given by W. Maddison *et al.* (1984).

The use of the outgroup analysis procedure of W. Maddison *et al.* (1984) followed by a traditional, non-numerical ingroup resolution procedure could encompass a search for the most-parsimonious tree. It might thus seem to be simply a non-numerical version of computerized parsimony analysis, with less hope of successfully finding the most-parsimonious tree. However, it does have the advantage over available most-parsimonious-tree searching programs in that the systematist is likely to subconsciously include in the analysis data not incorporated in an algorithmic analysis, data acquired over years of examining the organisms.

I will briefly outline my traditional analysis; a more complete, step-by-step description of the analysis can be found in D. Maddison (1985c). To begin the traditional analysis, I first used some of the characters listed in Tables 2, 4, and 5 to infer a few aspects of the cladistic structure of *Bembidion* (Fig. 276).

I then chose, as ancestral to *Bracteon*, a state that allows for a simple hypothesis of outgroup evolution, using the outgroup algorithm of W. Maddison *et al.* (1984). This procedure was complicated by the fact that the relationships were uncertain for *Bracteon* outgroups (Fig. 276), and so the algorithm could not be applied directly. This uncertainty in outgroup structure reflects the large number of possible resolutions of relationships. For this study the number of possible full resolutions of near-outgroup (*Pseudoperyphus* + *Odontium* subgeneric-group) structure shown in Figure 276 is 1.9 trillion (see Felsenstein, 1978). The outgroup algorithm could be applied to each possible resolution, and for each a set of possible ancestral state assessments could be obtained; but this would be dreadfully time-consuming. Fortunately, for some characters the outgroup uncertainties are irrelevant for the outgroup analysis, and an unequivocal ancestral state assessment is produced; this occurs when all possible resolutions yield the same most-parsimonious hypothesis of ancestral state (for example, if the character is invariant among the outgroups). But for most characters, different outgroup resolutions will yield different assessments of ancestral state. For these characters, I determined as many distinct assignments of ancestral states as possible, by inspection of the tree and distribution of states. Consider, for example, character 2. If *B. americanum* is the sister group of *B. bifossulatum*, and *Ochthedromus* the sister group of *Bracteon*, with (*B. chloropus* + *B. fusiforme*) + *B. aeneipes* the next-most distant sister group, then the ancestral state assessment for *Bracteon* is state 2 (slight mirrors present). If, however, *B. durangoense* is the sister group of *Bracteon*, with *B. robusticolle* next down the line, then state 0 is the assessment. Another arrangement of outgroups would yield state 1; no arrangements would yield state 3. Thus the set of possible ancestral state assessments is {0, 1, 2}. Other characters were treated similarly. For each, I condensed outgroup information, recording the range of preferred ancestral states. Taking these into account will at least partly allow for simple hypotheses of outgroup evolution. It is not an ideal technique, as character interactions are not taken into account (W. Maddison *et al.*, 1984).

The next step in the analysis is the deciphering of lineages within *Bracteon*. Not all 85 characters are useful for this. Fifteen of the characters are invariant within *Bracteon;* these include some of the characters that were used to infer outgroup relationships shown in Figure 276. As well, outgroup analysis indicated that in over 20 of the 70 remaining characters, the outgroup information at hand provided no initial clue as to ancestral states of *Bracteon*. The assessments of ancestral states for the remaining characters lead to hypotheses of derived states within *Bracteon* plus its stem group. Seventeen of these characters showed only states autapomorphic for single species, and thus they provide no evidence for joining species together. The remaining 30 or so characters form the basis for the next step of the analysis. To infer clades within *Bracteon*, I attempted to find a phylogeny that would be as consistent as possible with a monophyletic origin of each set of species sharing derived characters; that is, I tried to propose as few origins of derived states as possible. I further refined the phylogeny by then incorporating information from all of the other characters. A multistep procedure was used, with cladistic structure slowly being built up, this cladistic structure then allowing me to begin to understand evolution in the initially uninterpretable characters. The procedure used was thus similar to Watrous and Wheeler's (1981) functional outgroup/functional ingroup method. I cannot describe it more explicitly, as it was not done rigorously.

I then reexamined this initial cladogram and tried to improve it by mentally rearranging some of the branches. The resulting phylogeny is presented in Figure 277. Because of conflicting evidence, I was most uncertain about the placement of *B. punctatostriatum*, and, to a lesser extent, *B. stenoderum* and *B. carinula*.

Algorithmic analysis

After the traditional analysis was completed, most-parsimonious trees were searched for by the computer program PAUP versions 3.0q and 3.0s (Swofford, 1991). A few searches were also made by Hennig86 version 1.5 (Farris, 1988). In the PAUP analyses several terminal taxa were coded as polymorphic, and steps within polymorphic terminal taxa are added to the treelength. As Hennig86 cannot accept polymorphic terminal taxa, all polymorphic terminal taxa were recoded for ordered characters using additive binary recoding. This has the effect of treating the multistate taxa as having uncertain state, rather than polymorphisms, but this does not affect relative treelengths, and thus does not affect judging the parsimony of a tree.

The trees discovered were analyzed using MacClade version 3.0 (Maddison and Maddison, 1992). MacClade's Compare Two Tree Files facility was used to determine those characters that consistently supported one set of trees over another set of trees. MacClade was also used to determine branch lengths and examine character evolution. The data matrix is included on computer disk with version 3.0 of MacClade, or it can be requested from the author.

Four searches were conducted on a restricted set of taxa (only the 18 *Bracteon* taxa, or *Bracteon* plus *B. striatum*). The characters were either equally weighted or error-prone characters were weighted against (see "Character Weighting," above). PAUP's branch and bound searching was used to guarantee discovery of the shortest trees. Strict consensus trees of the trees resulting from these 4 searches are shown in Figures 278–281.

The remaining searches were conducted on the full set of taxa from Tables 2, 4, and 5, excluding *B. scopulinum*, *B. obscurellum*, *B. petrosum*, and *B. "kuprianovi-#1."* These four outgroup species were removed because preliminary searches with PAUP indicated that slight rearrangements among them were vastly inflating the number of equally parsimonious trees, thus significantly impairing the searches for short trees. This probably would not have much impact on inferred *Bracteon* phylogeny, as in this preliminary search these taxa were well removed from *Bracteon*, and were clustered down near the base of *Bembidion*. All PAUP searches on the set of 53 taxa were conducted using tree-bisection-reconnection (TBR) branch rearranging, with MAXTREES set to 1,000, STEEPEST DESCENT turned off, and zero-length branches collapsed. For some runs, the CHUCK option was used with CHUCKLEN set to 1 greater than the length of the shortest trees and NCHUCK set to 40. For each set of character weights, multiple searches were conducted, each beginning with a tree built by a random addition sequence. Five Hennig86 searches were conducted, beginning with the different starting points provided by mhennig, mhennig*, hennig, hennig*, and tread (the latter providing a bush). Each of these were given to the branch rearranger, bb*.

Characters 5, 6, 11, 45, 46, and 48 in the data matrix are inapplicable for some taxa. For example, those taxa without an ostial sclerotized strip (character 47), cannot be said to have a beaded or unbeaded strip (character 48). This is indicated by a "—" in the entries for those taxa in Tables 2, 4, and 5. In the algorithmic analysis, these entries were treated as missing data. Since the analyses were completed in 1989, the dangers of treating inapplicable entries as missing data have come to light (Platnick *et al.*, 1991; Nixon and Davis, 1991; W. Maddison, in press). A preliminary reanalysis was done to study the effect of treating inapplicable entries as missing data, and is described below, under "Recoded data matrix, equal weights." All other analyses examined the unrecoded matrix.

I will first describe the results of three analyses with the unrecoded matrix. These analyses differ in the relative weights applied to characters. After a description of the analysis on the recoded matrix, I present a summary of all numerical analyses. For the trees found, the treelength, consistency index, and retention index (Archie, 1989; Farris, 1989) are given.

Full Data Matrix, Equal Weights. In total, 545 equally parsimonious trees were found by PAUP in 1,167 searches, including 224 trees that were also found by Hennig86. All were of length 653, with a consistency index of 0.490, and a retention index of 0.643.

There was variation among the different PAUP searches in the collection of most-parsimonious trees discovered. For example, one search produced a collection of 84 trees, all of which were rather similar one to another, but which differed from the collections of trees found by some other searches. The collection of trees resulting from a single search is one "island" of trees (D. Maddison, 1991). In total this data matrix yields 12 islands of most-parsimonious trees, with 1, 8, 12, 12, 32, 36, 40, 44, 48, 68, 84, and 160 trees respectively, for a total of 545 trees. In the 1,167 searches conducted, each island was found more than once, with the island of 32 trees encountered most rarely (in 10 searches) and the island of 84 trees encountered most frequently (in 192 searches).

The strict consensus tree of the 545 trees, shown in Figure 282, is relatively unresolved. However, this does not mean that the 545 trees are all very different from one another, as there are only 5 distinct sorts of trees. One hundred and forty of the trees, comprising all of 3 islands and parts of 3 others, have *Bracteon* as a clade (Fig. 283). Eighty-eight of the trees in 3 islands have *B. balli* and *B. foveum* excluded from *Bracteon*, with *B. striatum* the sister group of the rest of *Bracteon* (Fig. 284). Two hundred and sixty-eight trees in 4 islands have the clade containing *B. argenteolum*, *B. alaskense*, and *B. semenovi* far removed from the rest of *Bracteon*, and placed within the complex of North American and East Asian *Odontium* related to *B. aenulum* and *B. fusiforme* (Fig. 285). Forty-eight trees in one island have a similar arrangement, but with *B. stenoderum* also included with the *B. argenteolum* clade (Fig. 286). A single tree (Fig. 287), the only member of an island, itself isolated in an island of 82 trees of length 654, has *Bracteon* shattered into 3 clades, with 7 species including *B. argenteolum* and *B. velox* contained within the *B. aenulum–B. fusiforme* clade, *B. punctatostriatum* the sister of *Ochthedromus*, and the rest of *Bracteon* the sister of *B. persimile* + *B. foraminosum*.

Ideally, trees close to the most parsimonious should also be examined. For this data set, there are many thousands of trees of length 654. Most of these result from slight rearrangements on the structure of outgroups; these slight rearrangements do not yield significantly longer trees because of the relatively small number of characters included in the analysis that provide evidence about outgroup structure. A tree of length 654 is of interest if some characters prefer it over trees of length 653, but a tree of length 654 that only differs from a 653 tree in that it violates the evidence provided by one character is of lesser interest. Many of the trees of length 654 fall into the latter category. The vast numbers of trees in the latter category make it impractical to examine all trees of length 654. I have therefore confined my analysis to most-parsimonious trees.

While many trees just slightly longer than 653 steps exist for this data set, the vast majority of trees are much longer. I used PAUP to count the length of a random sample of 1,000,000 trees (each tree equiprobable) (Fig. 288). The shortest tree sampled was of length 980, the longest 1,178; the mean treelength is 1,107. As the longest conceivable tree for this data set is less than or equal to 1237 (the length of a bush of a "hard polytomy" [W. Maddison, 1989]), and the shortest known tree 653, the vast majority of possible trees are in a narrow range near the top of the scale, far above the observed shortest tree. This is also indicated by the value of the g_1 statistic, which, at −0.36, indicates a treelength distribution significantly more skewed than one would expect if the data contained no phylogenetic structure (Hillis and Huelsenbeck, 1992).

If the PAUP search is constrained to conform to the basic structure inferred by my traditional analysis, the shortest trees it could find in 171 searches was 657, 4 steps longer than the shortest trees. Two hundred and seventy-three such trees were found, in 4 islands.

Error-prone Characters Relatively Devalued. Five hundred PAUP searches yielded two islands (one found 33 times, the other found 49 times), totalling 120 trees of length 1,086, consistency index of 0.513, and retention index of 0.651 (Fig. 289); these trees place the 3 species around *B. argenteolum* outside of *Bracteon*, and are very similar to one of the classes of trees found in the equal weighting analysis. Sixty-eight searches by PAUP, enforcing the constraint that *Bracteon* is monophyletic, yielded 4 trees of length 1,088 (in one island that was found 10 times); thus, the shortest tree maintaining *Bracteon* as a clade is 2 steps longer than the shortest known tree. Under equal weighting, these 4 trees are among the most-parsimonious trees; they are part of the island of 44 trees of length 653. A portion of one of these four trees is presented in Figures 294–296. No Hennig86 search was conducted.

Error-prone and Polymorphic Characters Relatively Devalued. Nine hundred and sixty-three searches in PAUP yielded two islands (one found 18 times, one found 64 times), totalling 21 trees of length 1,406, consistency index of 0.484, and retention index of 0.647 (Fig. 290). These trees are very similar to those inferred under the previous weighting scheme; in fact, there are 9 trees in common. Two hundred searches by PAUP, enforcing the constraint that *Bracteon* is monophyletic, yielded 50 trees of length 1,407, in two islands (each found 10 times); thus, the shortest tree maintaining *Bracteon* as a clade is one step longer than the shortest known tree (4 of these trees are the same trees found with only error-prone characters devalued). Five Hennig86 searches, using the same options as those used for the equal weighting analysis, yielded in total 33 trees of length 1,407, with 24 of those showing *Bracteon* monophyletic.

Recoded Data Matrix, Equal Weights. To study possible problems in these analyses caused by treating inapplicable characters as missing data, an analysis was conducted on a recoded data matrix.

In recoding the matrix, each set of dependent characters was combined into one character. For example, character 48, having a beaded or unbeaded ostial sclerotized strip, is not applicable to beetles without an ostial sclerotized strip (character 47). In combining these two characters into one, larger, multistate character whose states are the absence of a strip, the presence of an unbeaded strip, or the presence of a beaded strip, the problems caused by the dependencies between the separate characters can be avoided.

For this matrix, the sets of dependent characters were combined as follows. Characters 1, 6, and 11 were fused into a character with five states: 0 = silver spots absent; 1 = silver spots present, restricted to third interval, contained setae near anterior end; 2 = silver spots present, restricted to third interval, contained seta centrally located; 3 = silver spots present, extended into fourth interval, contained setae near anterior end; 4 = silver spots present, extended into fourth interval, contained setae centrally located. A step matrix (Maddison and Maddison, 1992) was built and applied to this combined character in the analysis. It was presumed that it was one step to gain or loose a restricted silver spot, one step to extend the silver spot onto the fourth interval, and one step to change the position of the setae. Characters 4 and 5 were fused into an ordered character with five states: 0 = mirrors on intervals 6 or 7 absent; 1 = intervals 6 or 7 slightly shinier; 2 = intervals 6 or 7 with slight mirrors; 3 = interval 7 with distinct, isolated mirror; 4 = interval 7 with distinct mirror continuous with inner mirrors. Characters 44, 45, and 46 were combined into a character with 11 states: 0 = ostial microtrichial patch absent; 1 = patch small, without scales; 2 = patch medium, without scales; 3 = patch medium, with few comb-like scales; 4 = patch medium, with extensive scales; 5 = patch medium-large, without scales; 6 = patch medium-large, with few comb-like scales; 7 = patch large, without scales; 8 = patch large, with few comb-like scales; 9 = patch large, with extensive scales; 10 = patch large, with extensive scales that are sparse and small. The step matrix applied to this character presumes that it is one step to gain a small ostial microtrichial patch with no scales, one step with each increase in size of the patch or increase in the extent of scales, and one step between states 9 and 10. Characters 47 and 48 were combined into a three-state unordered character: 0 = ostial sclerotized strip absent; 1 = ostial sclerotized strip present, without beaded texture; 2 = ostial sclerotized strip present, with beaded texture.

For this recoded matrix, the length of the 545 trees found in the initial algorithmic analysis varied from 650 to 652. These treelengths are as calculated by PAUP, which does not include the steps within two polymorphic taxa (*B. inaequale* and *B. litorale*) for the character formed by the merger of characters 1, 6 and 11. MacClade includes some of these steps, and reports treelengths of 652 to 654. Treelengths will be reported using PAUP's calculations.

Most-parsimonious trees for this recoded matrix were searched in two ways. First, 100 searches were conducted with starting trees produced using random addition sequences, and subsequent TBR branch rearrangements, with NCHUCK set to 25, and CHUCKLEN set to 651. These searches yielded two islands of trees of length 650. The first island contained 44 trees, and was found five times; the second island contained 5,482 trees, and was found six times. Second, 12 searches were conducted, using as starting trees each of the 12 islands of trees found in the algorithmic analysis of the unrecoded matrix, again using TBR branch rearrangements. Three of these searches produced the same island of 44 trees of length 650, with the remaining searches finding various islands of trees of length 651.

The trees found in this preliminary analysis of the recoded matrix do not dramatically alter the conclusions drawn from the previous analyses. The island of 44 trees contained the same trees as island-44 in the unrecoded data matrix, including the tree partially shown in Figures 294–296.

These trees are included within the trees whose consensus is depicted in Figure 283, and show a monophyletic *Bracteon*. Thus, both unweighted analyses suggest the possibility of a monophyletic *Bracteon*. Trees in the island of 5,482 trees showed a novel pattern: *Ochthedromus* is split in two, with the two *B. bifossulatum* subspecies moving within *Bracteon* (Fig. 291). The diversity present among the 5,482 trees is mostly within the outgroups, as there are only 48 distinct relationships among *Bracteon* plus *B. bifossulatum* exhibited among these trees. This results in the relatively well-resolved ingroup relationships shown in Figure 291. For the unrecoded matrix, these trees are one step longer than the most parsimonious. Thus, among most-parsimonious trees without a monophyletic *Bracteon*, recoding the matrix tipped the balance slightly to favor trees with *B. bifossulatum* contained within *Bracteon*, in contrast to the trees for the unrecoded matrix, which show pieces of *Bracteon* scattered among *Odontium* and *Ochthedromus*. It should be noted, however, that this analysis does not include one of the characters that supports the monophyly of *Ochthedromus*, that is, the presence of about 10 long setae on the submentum of *Ochthedromus* adults. If this character were included, then the 5,482 trees would not be among the most parsimonious.

Discussion

Traditional versus Algorithmic Analyses. Two taxa judged to be of uncertain relationships in the traditional analysis, *B. stenoderum* and *B. punctatostriatum*, were placed in different places in the two studies. In the traditional analysis, *B. stenoderum* was placed in the *B. argenteolum* group; in the algorithmic analysis, it was placed within the *B. carinula-B. velox-B. lapponicum* clade, except for the one island in the unweighted analysis which placed *B. stenoderum* with the *B. argenteolum* group, but outside of *Bracteon* proper. *B. punctatostriatum* was placed, in all shortest trees, with weighted and unweighted characters, as sister to the *B. carinula-B. velox-B. lapponicum* clade, except for one single tree (Fig. 287) which places it as the sister to *Ochthedromus*.

Using MacClade's Compare Two Tree Files chart, I compared all 545 most-parsimonious trees, with the 273 trees of length 657 that preserves the structure inferred from the traditional analysis. All traditional analysis trees differ from all most-parsimonious trees in requiring at least one extra step in larval characters 73 (ME_2 length) and 75 (TE_6 length). Examination of the tracings of evolution of these two characters provided by MacClade indicates that the placement in Figure 277 of *B. punctatostriatum* outside of the *B. carinula-B. velox-B. lapponicum* clade, with which it shares shorter ME_2 and TE_6 setae, is the reason for this difference. Of course, these two characters only account for 2 of the 4 steps by which the traditional analysis trees differ from the most-parsimonious trees. Other combinations of characters must account for the other 2 steps.

However, allowing *B. punctatostriatum* to join the *B. carinula-B. velox-B. lapponicum* clade, but maintaining the rest of the structure in Figure 277, does not help. The shortest trees found under this constraint were again of length 657. The only character in which these trees are consistently longer than the most parsimonious is character 25 (pronotal carina shape and size). While placing *B. punctatostriatum* with *B. carinula* and relatives is supported by characters 73 and 75, the decrease in number of steps of these two characters is evidently balanced by an increase in number of steps of other characters.

The extra length present in these trees consistent with the traditional analysis is a result of the differing placement of *B. punctatostriatum*, *B. stenoderum* and relatives, not in the outgroup structure. That the outgroup structure presumed in the traditional analysis is not the constraint causing less-than-most-parsimonious trees can be seen by PAUP searches in which the outgroup structure was constrained as in Figure 277, but the ingroup was not constrained. Such searches yielded 4 trees of length 653, indicating that the problem was not solely in the outgroup structure.

Other than these relative minor differences between placement of *B. punctatostriatum*, *B. stenoderum* and relatives, the traditional and algorithmic analyses inferred the same basic structure of *Bracteon*, except for one profound difference: the shattering of *Bracteon* into 2 or 3 clades in some of the equal weighted trees, and all of the most-parsimonious trees under unequal weighting.

Is Bracteon *Monophyletic?* Two characters suggest that *Bracteon* is monophyletic. One derived state possibly linking *Bracteon* is the presence of elytral silver spots around ed3 and ed5. Some near-outgroup species also have the elytral surface around ed3 and ed5 modified, but in different ways from *Bracteon*. For example, *Ochthedromus* and *B. (Odontium) foraminosum* specimens have the region around ed3 and ed5 foveolate. In *B. foraminosum* the microsculpture is distinctly modified around the setae, with the sculpticells stretched. However, no distinct, granulate silver spots are present in either group. Another trait, perhaps associated with the development of the silver spots, is the movement of elytral setae ed3 and ed5 into the middle of interval in *Bracteon*, not attached to the stria. In all trees found in which *Bracteon* was not monophyletic, these two characters (numbers 1 and 10) exhibit more evolutionary steps than in the trees found in which *Bracteon* is monophyletic; these are the only characters that exhibit this pattern.

Several characters, however, speak against the monophyly of *Bracteon*. Using MacClade's Compare Two Tree Files chart, I have analyzed the characters that support shattering of *Bracteon* into two or more clades, by comparing those trees that maintain the subgenus as monophyletic with others that don't. There are three kinds of trees with shattered *Bracteon* that need to be examined.

Trees with *B. balli* and *B. foveum* separate from the rest of *Bracteon* are not consistently better for any particular character than are the trees with *Bracteon* intact. Presumably a combination of characters that favor the trees with *B. balli* and *B. foveum* removed from *Bracteon* compensate for the increased length in characters 1 and 10.

Trees with the *B. argenteolum-alaskense-semenovi* clade (with or without *B. stenoderum*) removed from *Bracteon* were among the most-parsimonious trees found under equal weighting, and formed the entire collection of most-parsimonious trees under the other two weighting schemes investigated. In all cases, these trees were favored over trees with *Bracteon* intact by characters 9 (midlateral pronotal seta), 27 (elytral basal impression), 60 (Y chromosome size), and 63 (frontale microsculpture behind FR_3). In the trees found when error-prone characters were devalued, two or more other larval characters also supported the shattered *Bracteon*, including character 65 and character 61 or 64. By placing the *B. argenteolum-alaskense-semenovi* clade within the *B. aenulum-B. fusiforme* complex, all of which lack a midlateral pronotal seta, the explanation of evolution of this trait becomes simpler. The *B. argenteolum-alaskense-semenovi* clade lacks the basal impression on the elytra characteristic of most *Bracteon*. The small Y-chromosomes of *B. alaskense* are shared among *Bracteon* only with *B. carinula;* removal of *B. alaskense* and related species from *Bracteon* is thus suggested by this trait. Finally, in characters 63 and 65, the lack of microsculpture at the back of the frontale in first instar larvae, as well as the large eggbursters, both suggest relationship to *B. aenulum*.

The odd tree of Figure 287 was supported over those of Figure 283 primarily on the basis of a large number of larval characters (61–63, 65, 66, 70).

Are these characters that speak against a monophyletic *Bracteon* good evidence of relationship? The lability of larval characters is not well known in carabids. However, it is clear that midlateral pronotal setae are quite labile, being lost frequently in carabids (note that three of the *Bembidion* species examined are polymorphic for this trait; see also Darlington, 1971b). If this untrustworthy character were omitted from the analysis, the balance would be tipped in favor of *Bracteon* monophyly. This, plus the fact that the silver spots exhibited by all *Bracteon* are unique within carabids, leads me to (tentatively) prefer the hypothesis that *Bracteon* is monophyletic.

Bold and Cautious Hypotheses. I choose to present both bold and cautious hypotheses of *Bracteon* phylogeny, in order to dispel acceptance of a single hypothesis. Weakly supported hypotheses, presented in the name of Popperian science as hypotheses to test, can be carelessly transformed through the literature into confidently accepted notions.

A relatively bold hypothesis of *Bracteon* relationships is shown in Figure 292. This figure summarizes the common elements in those trees among the most-parsimonious trees (with equal weighting) that show *Bracteon* monophyletic, as well as the most-parsimonious trees (under the two other weighting schemes, and under equal weighting of the recoded matrix) with the constraint that *Bracteon* is monophyletic. Note that it is also consistent with those trees inferred with one or no outgroups considered (Figs. 278–281). This indicates that, except for the shattering of *Bracteon* in some parsimonious trees, the addition of outgroups did not alter the inferred structure of *Bracteon* itself (except, of course, to indicate its root).

As a complement to the relatively bold hypothesis presented in Figure 292, a more cautious view is illustrated in Figure 293. The latter is a summary of all of the trees summarized in Figure 292, plus all of the rest of the most-parsimonious trees inferred under all three weighting schemes, as well as the trees found from the recoded matrix. Note that some structure is present in the conservative tree of Figure 293 outside of *Bracteon*. *B. interventor* is the sister group of the rest of the examined *Bembidion;* the subgenera *Hirmoplataphus* (*B. concolor* and *B. salebratum*) and *Pseudoperyphus* are suggested to be monophyletic. Some aspects of the structure of *Pseudoperyphus* also are constant across trees. The *Odontium* subgeneric group is monophyletic in almost all of the trees. There is one exception. Forty of the trees, among the most parsimonious if error-prone and polymorphic characters are devalued, and if *Bracteon* is forced to be monophyletic, show *Pseudoperyphus* interposed between a clade containing *B.* sp. nr. *aenulum*, *B. chloropus*, *B. fusiforme*, and *B. aeneipes* and the rest of the *Odontium* subgeneric group. *Odontium* is not monophyletic in the most-parsimonious trees. However, the shortest trees in which *Odontium* is a clade are only two steps longer than the most parsimonious (length = 655, based on 115 searches by PAUP), and thus the evidence against the monophyly of *Odontium* is not strong.

Summary. Four major hypotheses should be considered plausible, and examined more in future studies: that *Bracteon* is monophyletic, with relationships as shown in Figure 292, or that *B. balli* and *B. foveum* are outside of the rest of *Bracteon* (Fig. 284), or that *B. argenteolum*, *B. alaskense,* and *B. semenovi* are actually more closely related to the *B. aenulum*-*B. fusiforme* complex (Figs. 285, 286, 289, 290), or that *B. bifossulatum* belongs within *Bracteon* (Fig. 291). These hypotheses are most-parsimonious, or nearly so, for all weighting schemes used, and for the unrecoded and recoded matrices. All four hypotheses should be considered if one uses the phylogenetic conclusions presented here as the foundation for some ecological, behavioral, or physiological studies. However, if one wants a bolder phylogenetic hypothesis to test, I recommend that of Figure 292.

Fossil Material

The oldest *Bracteon* fossils are fragments from the Beaufort Formation of Banks and Meighen islands. They are apparently Middle to Late Miocene, approximately 7–13 million years before the present (Matthews, 1976, 1977, 1979). I have examined 12 of these fragments, as well as 2 Early Holocene/Late Pleistocene fragments from Vermont (all JVMa!), identifiable with some certainty as *Bracteon*. Character states of these pieces are shown in Table 6.

Unfortunately, exact placement of any of these specimens on an inferred phylogeny is impossible, due to the lack of visible character states. Nonetheless, some assignments can be made.

For example, specimen B7 from Banks Island (JVM 3-73) is clearly a fragment of a *Bracteon* elytron (as a silver spot is present), but third interval elytral mirrors are lacking. The specimen thus belongs to the *B. balli*-*B. foveum* line, the stem-group of the rest of *Bracteon* (from a lineage predating the evolution of mirrors), or from the stem-group of *Bracteon*.

Some of the other elytral fragments possess mirrors, and thus belong to the "mirrored clade" of *Bracteon*. Placement beyond this is difficult, and of questionable validity. The specimens are phenetically most similar in visible features to *B. levettei*, but many of these similarities are symplesiomorphies. Cladistically they could fall nearly anywhere within the mirrored *Bracteon*.

The most notable features of the three pronota are the lack of a long basilateral carina and the presence of midlateral setae. There are a number of *Bracteon* lineages to which they might belong. As with the elytral fragments, the known pronota unfortunately contribute scant information about *Bracteon* evolution.

A few Pleistocene fragments have also been discovered. The only specimen from North America with which I am familiar is an elytron, probably of *B. levettei*, from southern Ontario; this specimen is from well within the range of present-day *B. levettei*. Coope (1969, 1979b) reports *B. velox* from Late Würm Glacial (Zone I) and Early Windermere Interstadial (13,200–12,000 years b. p.) deposits in Britain. This species is not extant in Britain, although it occurs across the English Channel in France (Fig. 266). From Glacial sediments just predating the Windermere Interstadial of the Isle of Man (about 19,000 years b. p.), fragments of *B. lapponicum* have been discovered (Coope, 1977, 1979a). *B. lapponicum* is now absent from the British Isles, occurring in northern Scandinavia (Fig. 267); its presence 19,000 years ago in Britain reflects the cooler climate at the time (Coope, 1977, 1979a). *B. litorale* is known from Early Windermere Interstadial (13,200–12,000 years b. p.) deposits in the British Isles (Coope, 1979b); this is within the modern geographic distribution of the species. The Pleistocene material, therefore, contains possibly Recent species in not-unexpected localities.

GENERAL PATTERNS OF EVOLUTION IN *BRACTEON*

A few general patterns in the data are worthy of note and discussion. The patterns pose more questions than they answer, and are noted here more for incentive they may provide for future research, than for the conclusions they yield.

Evolution of Mirrors

A most noticeable feature of many adult *Bracteon* is the presence of elytral mirrors. Why mirrors evolved is a puzzle. The mosaic pattern created by the mirrors is similar to that produced by pigment in other *Bembidion* (for example, many members of *Notaphus*). Microsculpturally mosaic elytra have evolved independently a number of times in caraboids (a few examples are *Systolosoma*, *Elaphrus*, *Opisthius*, *Scopodes*, *Tillius*, and *Asaphidion*). Perhaps the mosaic pattern confuses potential predators; at least in humans, "these patches tend to catch the eye of the observer and to draw his attention away from the shape which bears them" (Cott, 1940:48). Or perhaps mirrors are for thermoregulatory purposes; or perhaps there is some other function (see Lindroth, 1974b); or perhaps there is no function at all.

In his study of *Elaphrus*, Goulet (1983) notes a striking correlation between overall shininess of the beetles and substrate moisture, with shinier beetles occurring on wetter soils; as well, more extensively mirrored *Elaphrus* tend to occur on wetter substrates. Within *Bracteon*, the limited knowledge I have of habitats reveals no correlation between microsculpture and substrate. For example, unmirrored, dull beetles such as *B. foveum* and *B. balli* coexist in the same microhabitat with extensively mirrored, relatively shiny species such as *B. levettei*. Goulet (1983) explains the patterns he notes as resulting from evolutionary development of crypsis in response to predation; clearly, no such explanation is readily available for *Bracteon*. I cannot think of adaptive reasons for the divergence of microsculpture.

Evolution of Larvae

The *Bracteon* larvae with the most primitive features are found in the clade with 20 autosomes (*B. hesperium* + *B. lorquinii* + *B. inaequale*-subgroup). Almost all of the evolution of larvae detected within *Bracteon* has taken place within the less-mirrored members of the mirrored clade (Fig. 295). Genitalic characters show changes in similar parts of the tree as do adult external characters (compare Fig. 296 with 294), with the exception of *B. punctatostriatum*, which shows many derived features of adult structure, but may have no derived features detected in genitalia. Again, it is difficult to select any specific hypothesis explaining these patterns without more basic data about the natural history of *Bracteon* species.

One notable correlate is the presence in *B. carinula* of both the longest second stylomeres (Fig. 154) and the largest egg bursters (Figs. 228 and 234) of any *Odontium* subgeneric group members. Perhaps the long S2s are suited for laying eggs in an unusual microhabitat, a place that requires tougher chorion, which in turn requires larger egg bursters. A comparative study of the habits of *B. carinula* and related species, as well as discovery of larvae of the long-stylomered *B. robusticolle*, could provide rewarding tests of this hypothesis.

HISTORICAL MOVEMENTS OF *BRACTEON* LINEAGES

As with phylogeny reconstruction, historical biogeography can be approached from either a statistical or parsimony perspective. One could produce maximum likelihood estimates of the biogeographic history of a group, if one built a general model of the biogeographic behavior of lineages of the animals, and used it with presumed phylogenetic and geologic history. This would involve background assumptions about the dispersal abilities, natural history, etc., of the organisms. Such an analysis could be conducted with or without the aid of a computer. To my knowledge, statistical biogeographic methods for single clades (as opposed to whole biotas [Rosen, 1978, Simberloff, *et al.*, 1981]) remain wholly undeveloped. The reasons for this probably include the mathematical difficulties involved, as well as the lack of sufficient knowledge about most groups necessary to apply such techniques. Such methods would undoubtedly be opposed by cladists seeking to produce patterns using a minimum of process hypotheses; they would instead use cladistic biogeographic techniques. These techniques choose hypotheses that invoke vicariance as much as possible, and dispersal as little as possible, in explaining geographic distributions. This is advocated by its practictioners as a parsimony method, because the number of hypothesized dispersal events is minimized. The explanations I present for geographic distributions of *Bracteon* species invoke a mixture of vicariance and dispersal, and were arrived at with traditional (non-numerical) methods.

Dispersal has undoubtedly played a prominent role in the history of *Bracteon*, and has resulted in the sympatry (Table 1) and the wide ranges of most of the taxa. As can be seen from the distribution maps (Figs. 261–274), many *Bracteon* are widespread with coincident ranges. For example, within the Nearctic region, *B. carinula*, *B. punctatostriatum*, *B. levettei*, and *B. inaequale* are all transamerican, occurring from the Yukon Territory south into the contiguous United States. This overlap of species ranges has led to a clouding of vicariant patterns. One should thus expect only a few fragments of the geographic history of these widespread, lowland forms to be detectable. If one takes a cautious approach, and uses the phylogeny of Figure 293 as a foundation for biogeographic studies (Fig. 297), the lack of resolution in that phylogeny will lead to uncertainties in the inferences made. Ecological requirements of *Bracteon* lineages, when more thoroughly known, might provide additional clues.

Eight of the 18 taxa have restricted distributions (*B. balli*, *B. semenovi*, *B. stenoderum*, *B. hesperium*, *B. lorquinii*, *B. zephyrum*, *B. levettei levettei*, and *B. conicolle*). Three of these, *B. balli*, *B. semenovi*, and *B. conicolle*, are all near the edge of the range of what may be their widespread sister-groups.

B. balli occupies a small area in Alberta and Saskatchewan (Fig. 261), just within the southernmost limit of the range of *B. foveum* (Fig. 262). A relatively recent vicariance event may have split the common ancestor of these two species, with subsequent dispersal of one or both forms until *B. foveum* attained sympatry with *B. balli*. *B. foveum* populations presumably spent Quaternary glaciations in Nearctic Beringia or in the Palearctic, although they may have been south of the ice sheets in North America. However, it does seem most reasonable that *B. balli* occurred south of the ice sheets, with invasion northward upon glacial retreat. Indeed, the ice sheets may have been the barrier that allowed differentiation of the ancestral *B. foveum*-*B. balli* stock into the two extant species.

B. semenovi is only known from the holotype, found in a region which has been scantily collected (Fig. 263). The full range of the species is unknown, and thus biogeographic hypotheses about the species must be considered tentative. Nonetheless, it does seem reasonable to presume an isolation of a southern portion of the proto-*B. argenteolum*-*B. semenovi* stock resulting in divergence and separation of *B. argenteolum* and *B. semenovi*. An east-west vicariance probably resulted in the production of the *B. alaskense* lineage. The lack of cladistic resolution of the *B. argenteolum*-subgroup may be indicative of an actual trichotomy, that is, a near-simultaneous formation of the *B. semenovi* and *B. alaskense* lineages.

The 2n = 20+XY clade originated in the Nearctic, with most of its history in that region. Only relatively recently has one of its stocks (*B. litorale*-*B. conicolle*) invaded the Old World, with subsequent differentiation of eastern *B. conicolle* from western *B. litorale* (Fig. 274).

The three primitive species of the 2n = 20+XY clade (*B. hesperium*, *B. lorquinii*, and *B. zephyrum*) are isolated in western North America from British Columbia south to California (Figs. 269–271), whereas the derived members of the *B. inaequale*-subgroup are more widespread in the eastern and northern Nearctic, and in the Palearctic (Fig. 297). The Pacific coastal forms may have arisen as buddings from a more widespread Nearctic stock, with one of the buddings (that leading to *B. zephyrum*) invading the seashore. However, a full explanation of this pattern awaits a resolution of their relationships.

The relatives of *Bracteon*, *Odontium* and *Ochthedromus*, are predominantly southern groups. Within both the New and Old World, species of the latter two groups increase in numbers southward, at the expense of *Bracteon* diversity. *Bracteon* are thus more cool-adapted than their relatives, and probably have been throughout their history; whether the entire *Odontium* subgeneric group assemblage originated as cool or warm adapted animals, is not known.

Exactly when the ancestor of *Bracteon* arose is a mystery. It clearly was before the Late Miocene; in fact, the mirrored clade was already in existence by then. I hesitate to speculate age of origin, because of the lack of an adequate fossil record, and the lack of well-supported, detailed biogeographic hypotheses.

CONCLUSIONS

Darlington (1971a), in his review of the history of *Bembidion* systematics, notes the shift in emphasis from the time of Casey to that of Lindroth. From a view of systematics as a sorting of dead specimens, to Lindroth's studies of populations of living, evolving creatures, the change has encompassed an increasing knowledge of the organisms and their histories. Erwin and Kavanaugh's (1981, in prep.) studies have continued the progress, adding female genitalic characters to our data base, as well as introducing cladistic techniques. I have incorporated more adult structural characters, as well as larval and chromosomal features, along with modified cladistic techniques.

But, as always, much remains to be done; a few avenues of research that appear to me to be potentially valuable are worthy of note. I have only skimmed the surface of geographic variability of *Bracteon* species. *B. inaequale, B. lapponicum*, the *B. argenteolum*-subgroup, and *B. litorale-B. conicolle* all require further analysis. A study of external structural variation is warranted, as is that of any other character that might help sort out patterns of gene flow. Numerous morphological characters await study, including the microsculpture of the internal sac of male genitalia, as well as molecular data. A great aid to further phylogenetic analysis of *Bracteon* would be a more thorough study of interrelationships of outgroups. Examination of adults and larvae of *B. aenulum* and its East Asian relatives is crucial to the resolution of the issue of *Bracteon* monophyly. Some of the pathways of *Bracteon* evolution may then become clearer.

ACKNOWLEDGMENTS

Most of this work was done during my tenure as a Master's student with George E. Ball. With his wealth of understanding of living creatures, and his care for his work and his people, he has served as an inspiration and an invaluable source of advice.

R. C. Fox and my brother, Wayne P. Maddison, have been similarly significant sources of enthusiasm, encouragement, and wisdom, for which I am very grateful. Wayne's help in obtaining copies of literature should not go unmentioned. R. H. Gooding graciously acted as my supervisor during G. E. Ball's administrative leave, as well as fulfilling, along with R. C. Fox and G. E. Ball, the duties of being a member of my supervisory committee. The three members of my committee also thoroughly and competently reviewed an earlier version of the manuscript.

I heartily thank Diane Hollingdale, Kerry P. Irons, and, most especially, Helen M. Amerongen for all the help they provided. Helen's aid during the last stages of the study was vital for the maintenance of progress and my sanity; she also helped tremendously with photography.

Many people aided me in various technical endeavours. W. P. Maddison, G. E. Ball, N. E. Stork, F. A. H. Sperling, J. E. O'Hara, K. C. Jope of the United States National Park Service, J. H. Acorn, and K. P. Fennie helped in collecting specimens. D. J. Larson and J. Andersen provided advice for raising larvae. H. Goulet obtained larvae of eastern *B. inaequale* and a few other eastern *Bembidion* for me. T. Nakane sent some valuable specimens of *Bracteon* and related groups from Japan. T. L. Erwin and H. Goulet suggested important techniques for studying male genitalia. D. A. Craig helped me with matters microscopic and photomicroscopic. G. Braybrook patiently taught me how to use the SEM, and provided other necessary services. F. A. H. Sperling translated some essential papers from German to English; K. P. Fennie provided a translation of Keleinokova (1976). R. E. Roughley borrowed the type and only known specimen of *B. semenovi*, and hand-carried it from Leningrad so that I might study it. A. Sen and B. K. Mitchell aided my study of sensilla by providing advice and bibliographic help. F. Martin Brown informed me of the identity of the man after whom *B. levettei* was named. Florence Boisse-Kilgo's thorough editorial efforts improved many details in the text. I sincerely thank all of these people.

Yves Bousquet brought to my attention several important papers and a specimen I would have otherwise missed. I am especially thankful for his discovery that the correct name of these beetles is *Bracteon*!

For his making pre-release copies of PAUP available, and for his patience, I am very grateful to David L. Swofford. Edward O. Wilson graciously allowed me to conduct my many PAUP analyses on his computer. I am also grateful to James M. Carpenter, for performing the Hennig86 analyses.

To all of the curators of collections listed in "Specimens Examined," I express my gratitude for their help in obtaining much of the material on which this study is based.

Comments on the manuscript by J. K. Liebherr and an anonymous reviewer were especially helpful.

This work was funded primarily by NSERC Grant A-1399 to G. E. Ball, and in part by a grant from the Alfred P. Sloan Foundation. Publication was supported in part by funds from E. O. Wilson.

LITERATURE CITED

AHRENS, A. 1812. Beiträge zur Kenntniss deutscher Käfer. Neueste Schriften der Naturforschenden Gesellschaft zu Halle, **2:** 1–40.

ALI, H. A. 1967. The higher classification of the Carabidae and the significance of internal chacracters [*sic*] (*Coleoptera*). Bulletin de la Société Entomologique d'Egypte, **51:** 211–231.

ANDERSEN, J. 1966. The larval stages of the genus *Bembidion* Latr. (Col. Carabidae) I. The larvae of the subgenus *Chrysobracteon* Net. and *B. dentellum* ThunB. Norsk Entomologisk Tidsskrift, **13:** 440–453.

———. 1970. Habitat choice and life history of Bembidiini (Col., Carabidae) on river banks in central and northern Norway. Norsk Entomologisk Tidsskrift, **17:** 17–65.

———. 1978. The influence of the substratum on the habitat selection of Bembidiini (Col., Carabidae). Norwegian Journal of Entomology, **25:** 119–138.

ANDREWES, H. E. 1921. Notes on Oriental Carabidae-II. Some new species of *Bembidium* from Java and Indo-China. The Entomologist's Monthly Magazine, **7**(third series): 248–252.

———. 1935. The fauna of British India, including Ceylon and Burma. Coleoptera. Carabidae Vol. II. Harpalinae I. London: Taylor and Francis Publishers. 323 pp.

ANTOINE, M. 1955. Coléoptères carabiques du Maroc (Première partie). Mémoires de la Société des Sciences Naturelles et Physiques du Maroc. Nouvelle Série. Zoologie, **1:** 1–177.

ARCHIE, J. W. 1989. Homoplasy excess ratios: New indices for measuring levels of homoplasy in phylogenetic systematics and a critique of the consistency index. Systematic Zoology, **38:** 253–269.

ARNOLD, E. N. 1981. Estimating phylogenies at low taxonomic levels. Zeitschrift für zoologische Systematik und Evolutionsforschung, **19**: 1–35.

BAEHR, M. 1979. Vergleichende Untersuchungen am Skelett und an der Coxalmuskulatur des Prothorax de Coleoptera. Ein Beitrag zur Klärung der phylogenetischen Beziehungen der Adephaga (Coleoptera, Insecta). Zoologica. Originalabhandlungen aus dem Besamtgebiet der Zoologie, **44:** 1–76.

BALL, G. E. 1972. Classification of the species of the *Harpalus* subgenus *Glanodes* Casey (Carabidae: Coleoptera). The Coleopterists Bulletin, **26:** 179–204.

BALL, G. E., AND D. SHPELEY. 1983. The species of eucheiloid Pericalina: Classification and evolutionary considerations (Coleoptera: Carabidae: Lebiini). The Canadian Entomologist, **115:** 743–806.

BARR, T. C., JR. 1971. *Micratopus* Casey in the United States (Coleoptera: Carabidae: Bembidiinae). Psyche, **78:** 32–37.

BARTHE, E. 1912. Tableaux analytiques pour la détermination des Carabidae de la région francorhénane, comprenant toutes les espèces, variétés, races et aberrations. Miscellanea Entomologica. Revue Entomologique Internationale, **20:** 225–240.

BASILEWSKY, P. 1968. Contributions à l'étude des coléoptères carabiques de la région Malgache. V. Les Bembidiinae de Madagascar et des îles voisines. Annales de la Société Entomologique de France N.S., **4:** 515–548.

———. 1972. La faune terrestre de l'Ile Sainte-

Hélène. II.-Insectes. 9. Coleoptera. 1. Fam. Carabidae. Annales du Musée Royal de l'Afrique Centrale, **192:** 11–84.

Bates, H. W. 1873. On the geodephagous Coleoptera of Japan. The Transactions of the Entomological Society of London, **1873:** 219–322.

———. 1883. Supplement to the geodephagous Coleoptera of Japan, chiefly from the collection of Mr. George Lewis, made during his second visit, from February 1880, to September, 1881. The Transactions of the Entomological Society of London, **1883:** 205–290.

———. 1891. Additions to the carabideous fauna of Mexico, with remarks on some of the species previously recorded. The Transactions of the Entomological Society of London, **1891:** 223–278.

Bauer, T. 1971. Zur Biologie von *Asaphidion flavipes* L. (Col., Carabidae). Entomologische Zeitschrift, **81:** 154–164.

———. 1975. Zur Biologie und Autökologie von *Notiophilus biguttatus* F. und *Bembidion foraminosum* Strm. (Coleopt., Carabidae) als Bewohner ökologisch extremer Standorte. Zum Lebensformtyp des visuell jagenden Räbers unter den Laufkäfern (II). Zoologischer Anzeiger, **194:** 305–318.

Bedel, L. 1879. Faune des coléoptères du bassin de la Seine. Annales de la Société Entomologique de France, série 5, **9:** 1–128. [Not seen.]

———. 1881. Faune des Coléoptères du bassin de la Seine. Première partie. Annales de la Société Entomologique de France [volume hors série], **1:** xxiv + 359.

Bils, W. 1976. Das Abdomende weiblicher, terrestisch lebender Adephaga und seine Bedeutung für die Phylogenie. Zoomorphologie, **84:** 113–193.

Boldori, L. 1939. Larve di *Asaphidion* (Coleopt. Carab.). Bollettino della Societa Entomologica Italiana, **71:** 98–105.

Bousquet, Y., and H. Goulet. 1984. Notation of primary setae and pores on larvae of Carabidae (Coleoptera: Adephaga). Canadian Journal of Zoology, **62:** 573–588.

Bousquet, Y., and A. Larochelle. In press. Catalogue of the Geadephaga (Coleoptera: Trachypachidae, Rhysodidae, Carabidae including Cicindelini) of America north of Mexico. Memoirs of the Entomological Society of Canada.

Bøving, A. 1911. Nye bidrag til Carabernes Udviklingshistorie. II. Larver af slaegterne *Tachypus*, *Cillenus*, *Trechus*, *Clivina*, *Zabrus*, *Anisodactylus*. Entomologiske Meddelelser, **4:** 129–180.

Carr, F. S. 1932. New arctic Coleoptera. The Canadian Entomologist, **64:** 191–192.

Casey, T. L. 1918. A review of the North American Bembidiinae. Memoirs on the Coleoptera, **8:** 1–223.

———. 1924. Additions to the known Coleoptera of North America. Memoirs on the Coleoptera, **11:** 1–347.

Cerruti, M. 1939. Larva del *Tachys parvulus* Dej. (Coleop. Carab.). Memorie della Societa Entomologica Italiana, **17:** 121–124. [Not seen.]

Chaudoir, M. de. 1868. Observations synonymiques sur les *Carabiques* de l'Amérique septentrionale et descriptions d'espèces nouvelles de ce pays. Revue et Magazine de Zoologie, **20**(second series): 239–245.

Clark, W. E. 1978. The weevil genus *Sibinia* Germar: Natural history, taxonomy, phylogeny, and zoogeography, with revision of the New World species (Coleoptera: Curculionidae). Quaestiones Entomologicae, **14:** 91–387.

Coope, G. R. 1969. The contribution that the Coleoptera of Glacial Britain could have made to the subsequent colonisation of Scandinavia. Opuscula Entomologica, **34:** 95–108.

———. 1977. Fossil coleopteran assemblages as sensitive indicators of climatic changes during the Devensian (Last) cold stage. Philosophical Transactions of the Royal Society of London, Series B, **280:** 313–340.

———. 1979a. Late Cenozoic fossil Coleoptera: evolution, biogeography, and ecology. Annual Review of Ecology and Systematics, **10:** 247–267.

———. 1979b The Carabidae of the glacial refuge in the British Isles and their contribution to the post glacial colonization of Scandinavia and the North Atlantic islands, pp. 407–424. *In* T. L. Erwin, G. E. Ball, D. R. Whitehead, and A. L. Halpern (eds.), Carabid Beetles: Their Evolution, Natural History, and Classification. The Hague: Dr. W. Junk Publishers. 635 pp.

Cott, H. B. 1940. Adaptive Coloration in Animals. London: Metheun. xxxii + 508 pp.

Cooper, K. W. 1990. Linear, longitudinal markings on the outer elytral surface of beetles: interneurs or striae? Quaestiones Entomologicae, **26:** 695–699.

Coyne, J. A., H. A. Orr, and D. J. Futuyma. 1988. Do we need a new species concept? Systematic Zoology, **37:** 190–200.

Crisci, J. V., and T. F. Stuessy. 1980. Determining primitive character states for phylogenetic reconstruction. Systematic Botany, **5:** 112–135.

Crotch, G. R. 1867. On the Coleoptera of the Azores. Proceedings of the Scientific Meetings of the Zoological Society of London, **1867:** 359–391.

Csiki, E. 1928. Carabidae: Mormolycinae, Harpalinae I, pp. 1–226. *In* W. Junk and S. Schenkling (eds.), Coleopterorum Catalogus. Berlin: W. Junk. Vol. 2, part 97.

Dalla Torre, C. W. von. 1877. Synopsis der Insecten Oberösterreichs. Verein für Naturkunde in österreich ob der Enns, Linz, Jahresbericht, **8:** 15–74.

Daley, P. F., and M. F. Ryan. 1979. Ultrastructure of antennal sensilla of *Nebria brevicollis* (Fab.)

(Coleoptera: Carabidae). International Journal of Insect Morphology and Embryology, **8:** 169–181.

Darlington, P. J., Jr. 1959. The *Bembidion* and *Trechus* (Col.: Carabidae) of the Malay Archipeligo. Pacific Insects, **1:** 331–345.

———. 1962. Australian carabid beetles X. *Bembidion*. Breviora, **162:** 1–12.

———. 1971a. Modern taxonomy, reality, and usefulness. Systematic Zoology, **20:** 341–365.

———. 1971b. The carabid beetles of New Guinea. Part IV. General considerations, analysis and history of fauna; taxonomic supplement. Bulletin of the Museum of Comparative Zoology, **142:** 129–337.

Dejean, P. F. M. A. 1831. Spécies général des Coléoptères de la collection de M. le Comte Dejean. Vol. 5, pp. I–VIII, 1–384. Paris.

Dobzhansky, T. 1937. Genetics and the origin of species. First edition. New York: Columbia University Press. xvi + 364 pp.

Elias, S. A. 1984. Coleoptera from two subarctic localities in Canada with ecological notes and six new distribution records. The Coleopterists Bulletin, **38:** 142–144.

Emden, F. I. van. 1942. A key to the genera of larval Carabidae (Col.). Transactions of the Royal Entomological Society of London, **92:** 1–99.

Erwin, T. L. 1972. Two new genera of bembidiine carabid beetles from Australia and South America with notes on their phylogenetic and zoogeographic significance (Coleoptera). Breviora, **383:** 1–19.

———. 1973. Studies of the subtribe Tachyina (Coleoptera: Carabidae: Bembidiini), Part I: A revision of the Neotropical genus *Xystosomus* Schaum. Smithsonian Contributions to Zoology, **140:** 1–39.

———. 1974. Studies of the subtribe Tachyina (Coleoptera: Carabidae: Bembidiini) Supplement A: lectotype designations for New World species, two new genera, and notes on generic concepts. Proceedings of the Entomological Society of Washington, **76:** 123–155.

———. 1975. Studies of the subtribe Tachyina (Coleoptera: Carabidae: Bembidiini), Part III: Systematics, Phylogeny, and Zoogeography of the genus *Tachyta* Kirby. Smithsonian Contributions to Zoology, **208:** i–68.

———. 1982. Small terrestrial ground-beetles of Central America (Carabidae: Bembidiina and Anillina). Proceedings of the California Academy of Sciences, **42:** 455–496.

———. 1984. Studies of the Tribe Bembidiini (Coleoptera: Carabidae): Lectotype designations and species group assignments for *Bembidion* species described by Thomas L. Casey and others. Pan-Pacific Entomologist, **60:** 165–187.

———. 1985. The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles, pp. 437–472. *In* G. E. Ball (ed.), Taxonomy, Phylogeny and Zoogeography of Beetles and Ants: A Volume Dedicated to the Memory of Philip Jackson Darlington, Jr. (1904–1983). The Hague: Dr. W. Junk Publishers. xiii + 514 pp.

Erwin, T. L., and D. H. Kavanaugh. 1981. Systematics and zoogeography of *Bembidion* Latreille: I. The *carlhi* and *erasum* groups of western North America (Coleoptera: Carabidae, Bembidiini). Entomologica Scandinavica Supplement, **15:** 33–72.

Erwin, T. L., and L. L. Sims. 1984. Carabid beetles of the West Indies (Insecta: Coleoptera): A synopsis of the genera and checklists of tribes of Caraboidea, and of the West Indian species. Quaestiones Entomologicae, **20:** 351–466.

Ewan, J. 1950. Rocky Mountain Naturalists. University of Denver Press. xiv + 358 pp.

Fabricius, J. C. 1775. Systema Entomologiae. Lipsiae, 832 pp.

———. 1792. Entomologia Systematica. Emendata et aucta. Secundum classes, ordines, genera, species. Adjectis synonimis, locis, observationibus, descriptionibus. I: i–xx, 1–330 + 538 pp. Hafniae.

Fall, H. C. 1910. Miscellaneous notes and descriptions of North American Coleoptera. Transactions of the American Entomological Society, **36:** 89–197.

———. 1916. Three new Coleoptera from Washington state. Bulletin of the Brooklyn Entomological Society, **11:** 13–14.

Farris, J. S. 1983. The logical bases of phylogenetic analysis, pp. 7–36. *In* N. Platnick and V. Funk (eds.), Advances in Cladistics. Volume 2. Proceedings of the Second Meeting of the Willi Hennig Society. New York: Columbia University Press. x + 218 pp.

———. 1988. Hennig86, version 1.5. Computer program distributed by the author, 41 Admiral Street, Port Jefferson Station, NY 11776, U.S.A.

———. 1989. The retention index, and the rescaled consistency index. Cladistics, **5:** 417–419.

Felsenstein, J. 1978. The number of evolutionary trees. Systematic Zoology, **27:** 27–33.

———. 1982. Numerical methods for inferring evolutionary trees. The Quarterly Review of Biology, **57:** 379–404.

———. 1983. Parsimony in systematics: biological and statistical issues. Annual Review of Ecology and Systematics, **14:** 313–333.

———. 1988. Phylogenies from molecular sequences: inference and reliability. Annual Review of Genetics, **22:** 521–565.

Gardner, J. C. M. 1938. Immature Stages of Indian Coleoptera (23), Carabidae. Indian Forest Records, **3:** 149–157.

Gebler, F. A. 1833. Notae et addidamenta ad catalogum coleopterorum Sibiriae Occidentalis et confinis tatariae operis C. F. von Ledebours. Reise in das Altaigebirge und die soongarische Kirgisensteppe. Bulletin de la Société Impériale des Naturalistes de Moscou, **6:** 262–309.

Germar, E. F. 1824. Coleopterorum species novae aut minus cognitae, descriptionibus illustratae.

Halle: J. C. Hendel and sons. I, pp. I–XXIV, 1–624.

GERSDORF, E. 1937. Okologische-faunistische Untersuchungen über die Carabiden der mecklenburgischen Landschaft. Zoologische Jahrbücher, Abteilung für Systematik, ökologie, und Geographier der Tiere, **70:** 17–86.

GORDON, R. D. 1985. The Coccinellidae (Coleoptera) of America North of Mexico. Journal of the New York Entomological Society, **93:** 1–912.

GOULET, H. 1977. Technique for the study of immature Coleoptera in glycerine. The Coleopterists Bulletin, **31:** 381–382.

———. 1983. The genera of Holarctic Elaphrini and species of *Elaphrus* Fabricius (Coleoptera: Carabidae): classification, phylogeny, and zoogeography. Quaestiones Entomologicae, **19:** 219–482.

GUSE, G.-W., AND K. HONOMICHL. 1980. Die digitiform Sensillen auf dem Maxillarpalpus von Coleoptera. II. Feinstruktur bei *Agabus bipustulatus* (L.) und *Hydrobius fuscipes* (L.). Protoplasma, **103:** 55–68.

GYLLENHAL, L. 1827. Insecta Svecica. Classis I. Coleoptera sive Eleuterata. I(IV). Apud Friedericum Fleischer, Lipsiae.

HATCH, M. H. 1950. Studies on the Coleoptera of the Pacific Northwest. II. Carabidae: Bembidiini. The Pan-Pacific Entomologist, **26:** 97–106.

———. 1951. Studies on the Coleoptera of the Pacific Northwest. IV. Carabidae, Dytiscidae, Gyrinidae. Bulletin of the Brooklyn Entomological Society, **46:** 113–122.

HAYWARD, R. 1897. On the species of *Bembidium* of America North of Mexico. Transactions of the American Entomological Society, **24:** 32–143.

———. 1901. Synonymical notes on *Bembidium* and descriptions of new species. Transactions of the American Entomological Society, **27:** 156–158.

HECHT, M. K., AND J. L. EDWARDS. 1976. The methodology of phylogenetic inference above the species level, pp. 3–51. *In* M. K. Hecht, P. C. Goody, and B. M. Hecht (eds.), Major Patterns in Vertebrate Evolution. NATO Advanced Study Institutes Series. New York: Plenum Press. ix + 908 pp.

HENNIG, W. 1966. Phylogenetic Systematics. Urbana: University of Illinois Press. xiii + 263 pp.

HILLIS, D. M., AND J. P. HUELSENBECK. 1992. Signal, noise, and reliability in molecular phylogenetic analyses. Journal of Heredity, **83:** 189–195.

HLAVAC, T. F. 1971. Differentiation of the carabid antennal cleaner. Psyche, **78:** 51–66.

HONOMICHL, K. 1980. Die digitiform Sensillen auf dem Maxillarpalpus von Coleoptera. I. Vergleichend-topographische Untersuchung des kutikulären Apparates. Zoologischer Anzeiger, **204:** 1–12.

HONOMICHL, K., AND G.-W. GUSE. 1981. Digitiform sensilla on the maxillar palp of Coleoptera. III. Fine structure in *Tenebrio molitor* L. and *Dermestes maculatus* De Geer). Acta Zoologica, **62:** 17–25.

HORN, W., AND I. KAHLE. 1937. Uber entomologische Sammlungen Entomologen und Entomo-Museologie. Entomologische Beihefte, 2–5: vi + 536 pp.

HOWDEN, A. T. 1976. *Pandeleteius* of Venezuela and Colombia (Curculionidae: Brachyderinae: Tanymecini). Memoirs of the American Entomological Institute, **24:** 1–310.

HŮRKA, K. 1978. Bestimmunstabellen für die Gattungen ausgewählter Käferfamilien 5.2. Carabidae, pp. 51–69. *In* B. Klausnitzer (ed.), Ordnung Coleoptera (Larven). The Hague: Dr. W. Junk. vi + 378 pp.

JEANNE, C. 1971. Carabiques de la Péninsule Ibérique (12^e note). Bulletin de la Société Linnéenne de Bordeaux, **1:** 203–220.

JEANNEL, R. 1941. Coléoptères Carabiques, Première Partie. Faune de France, 39. Paris: Lechevalier. 571 pp.

———. 1962. Les Trechides de la Paléantarctide occidentale. Biologie de l'Amérique Australe, étude de la Faune du Sol, **1:** 527–655.

JEDLIČKA, A. 1961. Drei neue *Bembidion*-Arten aus Japan (Coleoptera, Carabidae). Annales Historico-Naturales Musei Nationalis Hungarici (Pars Zoologica), **53:** 311–312.

———. 1965a. Monographie des Tribus Bembidiini aus Ostasien (Coleoptera, Carabidae). Entomologische Abhandlungen, **32:** 79–199.

———. 1965b. Neue Carabiden aus den Samml. des Riksmuseum in Stockholm. Entomologisk Tidskrift, **86:** 202–208.

JONG, R. DE. 1980. Some tools for evolutionary and phylogenetic studies. Zeitschrift für zoologische Systematik und Evolutionsforschung, **18:** 1–23.

JUBERTHIE, C., AND Z. MASSOUD. 1977. L'équipement sensoriel de l'antenne d'un coléoptère troglobie, *Aphaenops cryticola* Linder (Coleoptera: Trechinae). International Journal of Insect Morphology and Embryology, **6:** 147–160.

KAVANAUGH, D. H. 1978. The Nearctic species of *Nebria* Latreille (Coleoptera: Carabidae: Nebriini): classification, phylogeny, zoogeography, and natural history. Unpublished PhD thesis. University of Alberta, Edmonton.

———. 1979. Studies of the Nebriini (Coleoptera: Carabidae), III. New Nearctic *Nebria* species and subspecies, nomenclatural notes, and lectotype designations. Proceedings of the California Academy of Sciences, **42:** 87–133.

KELEINIKOVA, S. I. 1976. Motschulsky's types of Coleoptera in the collection of the Zoological Museum MGU. I. Carabidae. [In Russian.] Sbornik Trudov Gosudarstvennogo Zoologicheskogo Museya, **15:** 183–224.

KIRBY, W. 1837. Insects. *In* J. Richardson (ed.), Fauna Boreali-Americana; or the Zoology of the Northern Parts of British America. 4: 1–325.

KIRK, V. M. 1972. Identification of ground beetle larvae found in cropland in South Dakota. Annals of the Entomological Society of America, **65:** 1349–1356.

KIRSCHENHOFER, E. 1984. Neue paläarktische Bembidiinae unter besonderer Berücksichtigung der von Eigin Suenson in Ostasien durchgeführten Aufsammlungen (Col. Carabidae) 1. Teil, *Bembidion* Latreille.

KLUGE, A. G., AND J. S. FARRIS. 1969. Quantitative phyletics and the evolution of anurans. Systematic Zoology, **18:** 1–32.

KRYNICKI, J. 1832. Enumeratio coleopterorum rossiae meridionalis et praecipue in Universitatis Caesareae Charkoviensis circulo obvenientium, quae annorum 1827–1831 spatio observavit. Bulletin de la Société Impériale des Naturalistes de Moscou, **5:** 65–179.

KRYZHANOVSKIJ, O. L. 1976. An attempt at a revised classification of the family Carabidae (Coleoptera). Entomological Review, **55:** 56–64.

———. 1983. Coleoptera. Vol I, no. 2. Adephaga (Part 1). Fauna of the U.S.S.R., new series no. 128. Leningrad. 341 pp.

KUHNT, P. 1913. Illustrierte bestimmungs-tabellen der Käfer Deutschlands. Ein Handbuch zum genauen und leichten Bestimmen aller in Deutschland vorkommenden Käfer. Stuttgart: E. Schweizerbart'sche verlagsbuchhandlung, Nägele and Dr. Sproesser. 1138 pp.

LAFER, G. S. 1975. On the ground beetle species of *Chrysobracteon* Net. and *Bracteon* Bed. subgenera, genus *Bembidion* Latr. (Coleoptera, Carabidae) from Primorye, U.S.S.R., pp. 58–61. *In* Entomophagi Sovetskogo Dal-nego Vostoka, Trudy biologo-pochvennogo Instituta, Novaia Seria, volume 27.

LAMB, W. K. 1971. Canada's Five Centuries. From Discovery to Present Day. Toronto: McGraw-Hill. 327 pp.

LANDRY, J.-F., AND Y. BOUSQUET. 1984. The genus *Omophron* Latreille (Coleoptera: Carabidae): redescription of the larval stage and phylogenetic considerations. The Canadian Entomologist, **116:** 1557–1569.

LAROCHELLE, A. 1975. Notes sur l'activité diurne de quelques Carabidae du Québec. Annales de la Société Entomologique du Québec, **20:** 3–6.

———. 1977. *Bembidion* du Québec: groupe *inaequale*. Fabreries, **3:** 38–40.

LARSSON, S. G. 1939. Entwicklungstypen und Entwicklungszeiten der dänischen Carabiden. Entomologiske Meddelelser, **20:** 277–560.

———. 1941. Larver. *In* V. Hansen (ed.), Biller XI. Sandspringere og løbebiller. Danmarks Fauna, **47:** 243–380. [Not seen.]

———. 1968. Larverne. *In* V. Hansen (ed.), Biller XXIV. Sandspringere og løbebiller (Cicindelidae og Carabidae). Danmarks Fauna, **76:** 282–433.

LATREILLE, P. A. 1802. Histoire naturelle, générale et particulière des crustacés et des insectes. Familles naturelles des genres, vol. 3. Paris. 467 pp.

LECONTE, J. L. 1848. A descriptive catalogue of the geodephagous Coleoptera inhabiting the United States east of the Rocky Mountains. Annals of the Lyceum of Natural History of New York, **4:** 173–233, 334–474.

———. 1851. Descriptions of new species of Coleoptera, from California. Annals of the Lyceum of Natural History of New York, **5:** 125–216.

———. 1878. The Coleoptera of the alpine regions of the Rocky Mountains. Bulletin of the United States Geological and Geographical Survey of the Territories, **4:** 447–480.

LINDROTH, C. H. 1940. Zur Systematik fennoskandischer Carabiden. 4–12. *Bembidion*-Studien. Notulae Entomologicae, **19:** 63–99.

———. 1945, 1949. Die fennoskandischen Carabidae. I. Göteborgs Kungliga Vetenskap och Vitterhets-Samhälles Handlingar Ser. B4. I: 709 pp., II: 277 pp., III: 911 pp.

———. 1954. Random notes on North American Carabidae (Coleopt.). Bulletin of the Museum of Comparative Zoology, **111:** 117–161.

———. 1955. The carabid beetles of Newfoundland, including the French islands St. Pierre and Miquelon. Opuscula Entomologica, Supplementum XII, 168 pp.

———. 1957a. The Linnean species of carabid beetles. Journal of the Linnean Society-Zoology, **43:** 325–341.

———. 1957b. The principal terms used for male and female genitalia in Coleoptera. Opuscula Entomologica, **22:** 241–256.

———. 1962. Revision of the subgenus *Chrysobracteon* Net., genus *Bembidion* Latr. (Col. Carabidae). Opuscula Entomologica, **27:** 1–18.

———. 1963. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Part 3. Opuscula Entomologica, Supplementum XXIV, pp. 201–408.

———. 1965. Two new species of subg. *Chrysobracteon* (genus *Bembidion*), from Alaska and Siberia (Col. Carabidae). Opuscula Entomologica, **30:** 125–128.

———. 1969. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Part 6. Opuscula Entomologica, Supplementum XXXIV, pp. 945–1192.

———. 1974a. Coleoptera, Carabidae. Handbook for the Identification of British Insects, **4:** 1–148.

———. 1974b. On the elytral microsculpture of carabid beetles (Col. Carabidae). Entomologica Scandinavica, **5:** 251–264.

———. 1975. Designation of holotypes and lectotypes among ground beetles (Coleoptera, Carabidae) described by Thomas L. Casey. The Coleopterists Bulletin, **29:** 109–147.

———. 1976. Genus *Bembidion* Latreille (Coleoptera: Carabidae) in New Zealand: a revision. New Zealand Journal of Zoology, **3:** 161–198.

———. 1980. A revisionary study of the taxon *Cil-*

lenus Samouelle, 1819 and related forms (Coeloptera [*sic*]: Carabidae, Bembidiini). Entomologica Scandinavica, **11:** 179–205.

Lindroth, C. H., and R. Freitag. 1969. North American ground-beetles (Coleoptera, Carabidae, excluding Cicindelinae) described by Thomas Say: designation of lectotypes and neotypes. Psyche, **76:** 326–361.

Linné, C. von. 1761. Fauna Suecica. Sistens Animalia Sueciae Regni: Mammalia, Aves, Amphibia, Pisces, Insecta, Vermes. Distributa per classes & ordines, genera & species, cum differentiis specierum, synonymis auctorum, nominibus incolarum, locis natalium, descriptionibus insectorum. Second edition. Stockholm: Laurent Salv. 578 pp.

Maddison, D. R. 1985a. The discovery of *Gehringia olympica* Darlington (Coleoptera: Carabidae), pp. 35–37. *In* G.E. Ball (ed.), Taxonomy, Phylogeny and Zoogeography of Beetles and Ants: A Volume Dedicated to the Memory of Philip Jackson Darlington, Jr. (1904–1983). The Hague: Dr. W. Junk Publishers. xiii + 514 pp.

———. 1985b. Chromosomal diversity and evolution in the ground beetle genus *Bembidion* and related taxa (Coleoptera: Carabidae: Trechitae). Genetica, **66:** 93–114.

———. 1985c. Systematics of the Holarctic ground-beetle subgenus *Chrysobracteon* Netolitzky and related *Bembidion* Latreille (Coleoptera: Carabidae). Master's thesis, Department of Entomology, University of Alberta, Edmonton.

———. 1991. The discovery and importance of multiple islands of most-parsimonious trees. Systematic Zoology, **40:** 315–328.

Maddison, W. P. 1989. Reconstructing character evolution on polytomous cladograms. Cladistics, **5:** 365–377.

———. In press. Missing data versus missing characters in phylogenetic analysis. Systematic Biology.

Maddison, W. P., M. J. Donoghue, and D. R. Maddison. 1984. Outgroup analysis and parsimony. Systematic Zoology, **33:** 83–103.

Maddison, W. P., and D. R. Maddison. 1992. MacClade: Analysis of phylogeny and character evolution. Version 3.0. Sunderland, Massachusetts: Sinauer Associates. xi + 398 pp.

Matthews, J. V., Jr. 1976. Insect fossils from the Beaufort Formation: geological and biological significance. Geological Survey of Canada Paper, 76–1B: 217–227.

———. 1977. Tertiary Coleoptera fossils from the North American arctic. The Coleopterists Bulletin, **31:** 297–308.

———. 1979. Late Tertiary carabid fossils from Alaska and the Canadian Archipelago, pp. 425–445. *In* T. L. Erwin, G. E. Ball, D. R. Whitehead, and A. L. Halpern (eds.), Carabid Beetles: Their Evolution, Natural History, and Classification. The Hague: Dr. W. Junk Publishers. 635 pp.

Mayr, E. 1940. Speciation phenomena in birds. American Naturalist, **74:** 249–278.

Meier, W. 1899. Über Abänderungen einiger Coleopteren-Arten, welche bei Hamburg gefunden wurden. Entomologische Nachrichten, **25:** 97–102.

Moore, B. P. 1979. Chemical defense in carabids and its bearing on phylogeny, pp. 193–203. *In* T. L. Erwin, G. E. Ball, D. R. Whitehead, and A. L. Halpern (eds.), Carabid Beetles: Their Evolution, Natural History, and Classification. The Hague: Dr. W. Junk Publishers. 635 pp.

Morawitz, A. 1862. Vorläufige Diagnosen neuer Coleopteren aus Südost-Sibirien. Bulletin de l'Académie Impériale des Sciences, Leningrad, **5:** 231–265. [Not seen.]

Mörch, O. A. L. 1853. Catalogus Conchyliorum quae reliquit d. Alphonso d'Aquirra and Gadea Comes de Yoldi. **2:** 18.

Morita, S. 1987. Notes on the Bembidiinae (Carabidae) of Japan. I. *Bembidion kaszabi* Jedlička. Entomological Review of Japan, **42:** 109–110.

Motschulsky, V. von. 1845. Insectes de la Sibérie rapportés d'un voyage fait en 1839 et 1840. Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg, **13:** 1–274.

———. 1850. Die Kaefer Russlands. I. Insecta Carabica. Moscow: Gautier. vii + 91 pp. + 9 tables.

———. 1859. Coléoptères nouveaux de la Californie. Bulletin de la Société Impériale des Naturalistes de Moscou, **32:** 122–185.

Müller, J. 1918. Bestimmungstabelle der *Bembidion*-Arten Europas und des Mittelmeergebietes. Koleopterologische Rundschau, **7:** 26–117.

———. 1926–1927. Tableaux de détermination des coléoptères d'Europe. Heft LXXXIX (89). Carabidae. Genre *Bembidium* Latr. d'Europe et de la région méditerranéenne. Miscellanea Entomologica, **29–30:** 1–100. [French translation of Müller (1918).]

Nelson, G. 1978. Ontogeny, phylogeny, paleontology, and the Biogenetic Law. Systematic Zoology, **27:** 324–345.

———. 1983. Reticulation in cladograms, pp. 105–111. *In* N. Platnick and V. Funk (eds.), Advances in Cladistics. Volume 2. Proceedings of the Second Meeting of the Willi Hennig Society. New York: Columbia University Press. x + 218 pp.

Netolitzky, F. 1910. Bemerkungen zur Systematik in der Gattung *Bembidion* Latr. Wiener Entomologische Zeitung, **29:** 209–228.

———. 1914a. Die Bembidiini in Winklers Catalogus. I–II. Entomologische Blätter, **10:** 50–55, 164–176.

———. 1914b. *Bembidion (Bracteon) fusiforme* nov. spec. (Col.). Entomologische Mitteilungen, **3:** 168–169.

———. 1921. Catalogus systematicus specierum palaearcticarum generis *Bembidion* Latr. (Carabidae). Archiv für Naturgeschichte, Series A, **87:** 185–229.

———. 1926. Bemerkungen über *Bembidion*-Larven. Entomologische Blätter, **22:** 117–119.

———. 1927. Gedanken über die Urform und das natürlische System der Bembidiini und der mit ihnen nächstverwandten Carabidengruppen. Koleopterologische Rundschau, **13:** 100–112.

———. 1928. *Bembidion Gebieni* n. sp. aus China. Koleopterologische Rundschau, **14:** 168.

———. 1931. Kritisches zum Katalog der Harpalinae von Csiki, etc. Deutsche entomologische Zeitschrift, 153–167.

———. 1940. Bestimmungstabellen der *Bembidion*-Arten Europas, Asiens und Afrikas. Buletinul Facultăţii de Ştiinţe din Cernăuţi, **13**(1939): 144–179.

———. 1942, 1943. Bestimmungstabelle der *Bembidion*-Arten des paläarktischen Gebietes. Koleopterologische Rundschau, **28:** 29–124, **29:** 1–70.

NETOLITZKY, F., AND P. MEYER. 1933. Die Verbreitung des *Bembidion argenteolum* Ahr. Entomologische Blätter, 29(4): 2 unnumbered pages and 1 map.

———. 1939. Die Verbreitung des *Bembidion velox* L. (Besonders dem Norden und Osten eigen). Entomologische Blätter, 35(4): 4 unnumbered pages and 1 map.

NETTMAN, H.-K. 1986. Carabid systematics and chromosome numbers, pp. 235–254. *In* P. J. den Boer, M. L. Luff, D. Mossakowski, and F. Weber (eds.), Carabid Beetles. Their Adaptations and Dynamics. Stuttgart: Gustav Fischer. 551 pp.

NIXON, K. C., AND J. I. DAVIS. 1991. Polymorphic taxa, missing values and cladistic analysis. Cladistics, **7:** 233–241.

NOTMAN, H. 1929. A new species of *Bembidion* from Lake Superior (Coleoptera, Carabidae). Journal of the New York Entomological Society, **37:** 157–158.

OLIVIER, A. G. 1790. Entomologie, ou histoire naturelle des insectes, avec leurs caractères génériques et spécifiques, leur description, leur synonymie et leur figure eluminée. Coléoptères. Vol. 2. Paris. 485 pp.

ORTH, D. J. 1967. Dictionary of Alaska Place Names. Geological Survey Professional Paper 567. Washington: U. S. Government Printing Office. 1084 pp + 12 maps.

PANZER, G. W. F. 1794. Faunae Insectorum Germanicae, initia. Deutschlands Insecten. Vol. 20: 4. Nürnberg, Felsecker.

———. 1797. Faunae Insectorum Germanicae, initia. Deutschlands Insecten. Vol. 40: 8. Nürnberg, Felsecker.

PATTERSON, C. 1982. Morphological characters and homology, pp. 21–74. *In* K. A. Joysey and A. E. Friday (eds.), Problems of phylogenetic reconstruction. Systematics Association Special Volume 21. London: Academic Press. x + 442 pp.

PAWLOWSKI, J. 1974. Biegaczowate—Carabidae podrodziny Bembidiinae, Trechinae. Klucze do oznaczania owadów Polski, No. 82, **19**(3b): 1–94. [Not seen.]

PAYKULL, G. 1798. Fauna Suecica. Insecta. I. Joh. F. Edman, Uppsala. 358 pp.

PERRAULT, G. G. 1981. Etudes sur la tribu des Bembidiini (Coleoptera, Carabidae) I. Notes sur la classification supraspécifique. Nouvelle Revue d'Entomologie, **11:** 237–250.

———. 1982. Etudes sur la tribu des Bembidiini s. str. (Coleoptera, Carabidae). II. Révision du sous-genre *Cyclolopha* (Casey). Entomologica Basiliensia, **7:** 89–126.

PERRIS, E. 1862. Histoire des insectes du pin maritime. Supplément aux coléoptères et rectifications. Annales de la Société Entomologique de France, Sér. 4, **2:** 173–243, pl. 5–6.

PLATNICK, N. I., C. E. GRISWOLD, AND J. A. CODDINGTON. 1991. On missing entries in cladistic analysis. Cladistics, **7:** 337–343.

RAYNAUD, P. 1976a. Description de deux larves de Coléoptères Carabiques. Entomops, **38:** 195–198.

———. 1976b. Description de cinq larves de Coléoptères Carabiques. Entomops, **40:** 275–284.

———. 1977. Description de deux larves de Coléoptères Carabiques. Entomops, **41:** 8–12.

REED, E. C. 1874. On the Coleoptera Geodephaga of Chile. Proceedings of the Zoological Society (London), **1874:** 48–70, plate XIII.

REICHARDT, H. 1977. A synopsis of the genera of neotropical Carabidae (Insecta: Coleoptera). Quaestiones Entomologicae, **13:** 346–493.

REY, C. 1887. Essai d'études sur certaines larves de coléoptères et description de quelques espèces inédites ou peu connues. Beaune, 1887. 126 pp., 2 pl. [Not seen.]

ROBERTSON, J. G. 1961. Ovariole numbers in Coleoptera. Canadian Journal of Zoology, **39:** 245–263.

ROSEN, D. E. 1978. Vicariant patterns and historical explanation in biogeography. Systematic Zoology, **27:** 159–188.

ROŻEK, M. 1981. Karyological studies of Bembidiinae (Coleoptera, Carabidae). I. Chromosome number and sex-determining system in six species of the genus *Bembidion* Latr. Folia Biologica (Kraków), **29:** 119–122.

RYE, B. G. 1908. Biller. I. Løbebiller. Danmarks Fauna. 178 pp.

SAHLBERG, J. 1880. Bidrag till Nordvestra Sibiriens Insektfauna. Coleoptera. Insamlade under expeditionerna till Obi och Jenessej 1876 och 1877. I. Cicindelidae, Carabidae, Dytiscidae, Hydrophilidae, Gyrinidae, Dryopidae, Georyssidae, Limnichidae, Heteroceridae, Staphilinidae, och Micropeplidae. Kongilga Svenska Vetenskapsakademiens Handlingar, **17:** 1–115 + 1 plate.

SAY, T. 1823a. Descriptions of coleopterous insects collected in the late expedition to the Rocky Mountains, performed by order of Mr. Calhoun, Secretary of War, under the command of Major

Long. Journal of the Academy of Natural Sciences (Philadelphia), **3:** 139–216.

———. 1823b. Descriptions of insects of the families of Carabici and Hydrocanthari of Latreille, inhabiting North America. Transactions of the American Philosophical Society, **2:** 1–109.

———. 1834. Descriptions of new North American insects and observations on some already described. Transactions of the American Philosophical Society, new series, **4:** 409–470.

Schaum, H. R. 1859. Drei neue Carabicinen-Larven. Berliner entomologische Zeitschrift, **3:** 35–41.

Schildknecht, H., U. Maschwitz, and H. Winkler. 1968. Zur Evolution der Carabiden-Wehrdrüsensekrete. Uber Arthropoden-Abwehrstoffe XXXII. Die Naturwissenschaften, **55:** 112–117.

Schilsky, J. 1908. XII. Beitrag zur deutschen Käferfauna. Deutsche Entomologische Zeitschrift, pp. 604–608.

Schiødte, J. C. 1867. De Metamorphosi Eleutheratorum Observationes. Bidrag til Insekterns Udviklingshistorie. Naturhistorisk Tiddsskrift, **3:** 415–552.

Schuler, L. 1959. Le genre *Microserrulula* Netolitzky (Bembidiini Jeannel, Col. Trechidae). Les formes multispires. Revue française d'Entomologie, **26:** 96–105.

———. 1960. Les spermathèques dans la tribu des Bembidiini Jeannel (Col. Trechidae). Revue française d'Entomologie, **27:** 24–48.

———. 1971. Les Trechinae de France. L'inversion de la valeur systématique des organes génitaux males et femelles. Nouvelle Revue d'Entomologie, **1:** 265–274.

Seidlitz, G. 1891. Die Kaefer (Coleoptera) der deutschen ostseeprovinzen Russlands. Fauna Baltica, second edition. lvi + 192 + 819 pp. Königsberg.

Serrano, J. 1981a. Chromosome numbers and karyotypic evolution of Caraboidea. Genetica, **55:** 51–60.

Serrano, J. 1981b. A chromosome study of Spanish Bembidiidae and other Caraboidea (Coleoptera, Adephaga). Genetica, **57:** 119–129.

Serrano, J. 1981c. Male achiasmatic meiosis in Caraboidea. Genetica, **57:** 131–137.

Serrano, J. 1984. New chromosome numbers of Spanish Caraboidea (Coleoptera, Adephaga). Genética Ibérica, **34**(1982): 63–82.

Serville, J. G. A. 1826. Faune Française, Insectes. Coléoptères. 240 pp. [Not seen.]

Silvey, J. K. G. 1935. An investigation of the burrowing inner-beach insects of some fresh-water lakes. Papers from the Michigan Academy of Arts, Science and Letters, **21:** 655–697.

Simberloff, D., K. L. Heck, E. D. McCoy, and E. F. Connor. 1981. There have been no statistical tests of cladistic biogeographic hypotheses, pp. 40–63. *In* G. Nelson and D. E. Rosen (eds.), Vicariance Biogeography: a Critique. New York: Columbia University Press. xvi + 593 pp.

Simpson, G. G. 1961. Principles of Animal Taxonomy. New York: Columbia University Press. xii + 247 pp.

Smith, S. G. 1960. Chromosome numbers of Coleoptera. II. Canadian Journal of Genetics and Cytology, **2:** 66–88.

Smrz, J. 1979. über die Larven der *Bembidion* (*Peryphus*)-Arten (Coleoptera, Carabidae, Bembidiinae). Acta entomologica bohemoslovaca, **76:** 244–254.

Sober, E. 1988. Reconstructing the Past. Parsimony, Evolution, and Inference. Cambridge: MIT press. xiii + 265 pp.

Spence, J. R., and J. F. Sutcliffe. 1982. Structure and function of feeding in larvae of *Nebria* (Coleoptera: Carabidae). Canadian Journal of Zoology, **60:** 2382–2394.

Stebbing, E. P. 1914. Indian Forest Insects of Economic Importance. Coleoptera. London: Eyre & Spottiswoode, Ltd. xvi + 648 pp.

Stevens, P. F. 1980. Evolutionary polarity of character states. Annual Review of Ecology and Systematics, **11:** 333–358.

Stork, N. E. 1980. A scanning electron microscope study of tarsal adhesive setae in the Coleoptera. Zoological Journal of the Linnean Society, **68:** 173–306.

Sturm, J. 1825. Deutschlands Fauna in Abbildungen nach der Natur mit Beschreibungen. V. Abtheilungen Die Insecten. Vol. 6, 188 pp.

———. 1843. Catalog der Kaefer-Sammlung. Nürenberg: J. Sturm. 386 pp.

Swofford, D. L. 1991. PAUP (Phylogenetic Analysis Using Parsimony), version 3.0q. Illinois Natural History Survey, 607 E. Peabody Drive, Champaign, IL 61820 U.S.A.

Thompson, R. G. 1979. Larvae of North American Carabidae with a key to the tribes, pp. 209–291. *In* T. L. Erwin, G. E. Ball, D. R. Whitehead, and A. L. Halpern (eds.), Carabid Beetles: Their Evolution, Natural History, and Classification. The Hague: Dr. W. Junk Publishers. 635 pp.

Turin, H., J. Haeck, and R. Hengeveld. 1977. Atlas of the carabid beetles of The Netherlands. Amsterdam: North-Holland Publishing Company. 228 pp.

Uéno, S.-I. 1955. Marine insects of the Tokara Islands. VII. New species and new subspecies of the subfamily Trechinae (Coleoptera, Harpalidae). Publications of the Seto Marine Biological Laboratory, **4:** 403–413.

Uyttenboogaart, D.L. 1904. *In* Everts, Tweede Lijst van soorten en varieteiten nieuw voor de Nederlandsche fauna, sedert de uitgave der "Coleoptera Neerlandica" bekend geworden. Tijdschrift voor Entomologie, **47:** 172–176.

Voorzanger, B., and W. J. van der Steen. 1982. New perspectives on the Biogenetic Law? Systematic Zoology, **31:** 202–205.

Wagner, H. 1915. Beiträge zur Coleopterenfauna der Mark Brandenburg II. Entomologische Mitteilungen, **4:** 300–309.

Wanntorp, H.-E. 1983. Reticulated cladograms and the identification of hybrid taxa, pp. 81–88. *In* N. Platnick and V. Funk (eds.), Advances in Cladistics. Volume 2. Proceedings of the Second Meeting of the Willi Hennig Society. New York: Columbia University Press. x + 218 pp.

Watrous, L. E., and Q. D. Wheeler. 1981. The out-group comparison method of character analysis. Systematic Zoology, **30:** 1–11.

Whitehead, D. R. 1972. Classification, phylogeny, and zoogeography of *Schizogenius* Putzeys (Coleoptera: Carabidae: Scaritini). Quaestiones entomologicae, **8:** 131–348.

Wiley, E. O. 1978. The evolutionary species concept reconsidered. Systematic Zoology, **27:** 17–26.

———. 1981. Phylogenetics. The Theory and Practice of Phylogenetic Systematics. New York: John Wiley and Sons. xv + 439 pp.

Wollaston, T. V. 1877. Coleoptera Sanctae-Helenae. London: John Van Voorst. xv + 256 pp.

Xambeau, V. 1894. Mœurs et métamorphoses d'insectes. 5ᵉ mémoire. Annales de la Société Linnéenne de Lyon, **41:** 107–156.

Zacharuk, R. Y., P. J. Albert, and F. W. Bellamy. 1977. Ultrastructure and function of digitiform sensilla on the labial palp of a larval elaterid (Coleoptera). Canadian Journal of Zoology, **55:** 569–578.

Zetterstedt, J. W. 1828. Fauna Insectorum Lapponica, Part I. Hammone: Librariea Schulziana, xx + 563 pp.

Table 1. Sympatry in *Bracteon*. Species abbreviations: bl = *B. balli*, fo = *B. foveum*, ar = *B. argenteolum*, al = *B. alaskense*, sm = *B. semenovi*, st = *B. stenoderum*, ca = *B. carinula*, vx = *B. velox*, lp = *B. lapponicum*, pn = *B. punctatostriatum*, hs = *B. hesperium*, lq = *B. lorquinii*, ze = *B. zephyrum*, lvl = *B. levettei levettei*, lvc = *B. levettei carrianum*, in = *B. inaequale*, lt = *B. litorale*, co = *B. conicolle*. Other abbreviations: S = species found sympatrically but not known to occur at exact same locality, M = species found microsympatrically, together on the same beach, · = specimens not known to occur sympatrically.

Species	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
B. balli	—																	
B. foveum	M	—																
B. argenteolum	·	S	—															
B. alaskense	·	S	·	—														
B. semenovi	·	·	·	·	—													
B. stenoderum	·	·	·	·	·	—												
B. carinula	M	M	·	·	·	·	—											
B. velox	·	M	M	·	·	·	·	—										
B. lapponicum	M	M	M	M	·	·	M	·	—									
B. punctatostriatum	M	M	·	·	·	·	M	·	M	—								
B. hesperium	·	·	·	·	·	·	·	·	S	S	—							
B. lorquinii	·	·	·	·	·	·	·	·	S	S	M	—						
B. zephyrum	·	·	·	·	·	·	·	·	S	S	S	S	—					
B. levettei levettei	·	·	·	·	·	·	·	·	S	M	S	S	·	—				
B. levettei carrianum	M	M	·	M	·	·	M	·	M	M	·	·	·	·	—			
B. inaequale	M	M	·	S	·	·	M	·	M	M	M	M	S	M	M	—		
B. litorale	·	M	M	·	·	·	·	M	M	·	·	·	·	·	·	·	—	
B. conicolle	·	M	S	S	·	S	·	·	S	·	·	·	·	·	·	·	M	—

Table 2. Character states in *Bracteon*. Species abbreviations: bl = *B. balli*, fo = *B. foveum*, ar = *B. argenteolum*, al = *B. alaskense*, sm = *B. semenovi*, st = *B. stenoderum*, ca = *B. carinula*, vx = *B. velox*, lp = *B. lapponicum*, pn = *B. punctatostriatum*, hs = *B. hesperium*, lq = *B. lorquinii*, ze = *B. zephyrum*, lvl = *B. levettei levettei*, lvc = *B. levettei carrianum*, in = *B. inaequale*, lt = *B. litorale*, co = *B. conicolle*. Other symbols: "0, 1" = taxon dimorphic, with both states 0 and 1; "0–2" = taxon polymorphic, with states 0 through 2; "?" = character state unknown; "—" = character state not applicable. Number of specimens examined for each entry listed in Table 3.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
Adult external characters																		
1. Silver spots 0 = absent; 1 = present	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2. Mirrors on interval 3 0 = absent; 1 = very slightly shinier; 2 = slight mirrors; 3 = distinct mirrors	1	1	3	3	2	3	3	3	3	3	2, 3	3	3	3	3	3	3	3
3. Mirrors on intervals 4 or 5 0 = absent; 1 = very slightly shinier; 2 = slight mirrors; 3 = distinct mirrors	1	1	2, 3	2, 3	2	3	0–2	0–2	0–3	0–2	3	3	3	3	3	3	3	3
4. Mirrors on intervals 6 or 7 0 = absent; 1 = very slightly shinier; 2 = slight mirrors; 3 = distinct mirrors	0	0	0, 1	0	0	0, 2	0	1	0, 2	1	0, 2	1	2, 3	3	3	3	3	3
5. Interval 7 mirror isolated? 0 = no; 1 = yes	—	—	—	—	—	0	—	—	0	—	0	—	0	0	0	0, 1	0, 1	0, 1
6. Silver spot on interval 4? 0 = no, restricted to 3rd; 1 = yes	0	0	0	0, 1	0	0	0	0	0	0	0, 1	0, 1	0, 1	1	1	0, 1	0, 1	0, 1
7. Elytral sculpticell shape 0 = isodiametric; 1 = slightly transverse; 2 = transverse	0	0	0	0	0	0	0	0	0	0	0–2	0	0	0	0	0	0	0
8. Suborbital setae 0 = absent, Fig. 60; 1 = short and sparse; 2 = denser, Fig. 59	1, 2	1, 2	2	2	2	1, 2	2	2	2	0	1	0, 1	2	2	2	0–2	2	2
9. Midlateral pronotal setae 0 = absent; 1 = present	1	1	0	0	0	0	1	1	1	1	0	0	1	1	1	0, 1	0, 1	0
10. ed3 and ed5: position relative to 3rd stria 0 = "free," in interval; 1 = attached to stria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE 2. CONTINUED.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
11. ed3 and ed5: position relative to silver spot 0 = anterior end of spot; 1 = center of spot	0	0, 1	0	1	0	0	0, 1	0	0, 1	0	0	0	1	0, 1	0, 1	0, 1	0, 1	0
12. Setae between eo4 and eo5 (average number) (discrete coding for numerical analysis: 0 = <0.40; 1 = 0.40–0.80; 2 = 1.8–2.1; 3 = >3.0)	0.05	0.80	1.8	0.10	4	0	0.40	0	0.09	2.1	0	0.07	0	0	0	0.04	0	0.14
13. Number setae ed7 area (average number) (discrete coding for numerical analysis: 1 = 0.90–1.1; 2 = 1.9–2.1)	1	1.1	0.92	1	1	1.9	1	1	1.1	1	1	1	1	1	1	1	1	1
14. Male adhesive setae 0 = narrow, Fig. 86; 1 = wide, Figs. 84, 85	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
15. Protarsomere 4 ventroapical setae 0 = less flattened, more circular, Fig. 94; 1 = apically flattened, wide, Fig. 96	1	1	0	0	0	1	1	1	1	0	1	1	1	1	1	1	1	?
16. Protarsomere 4 setal separation 0 = narrow, Figs. 93–96; 1 = wide, Fig. 92	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17. Mandible shape 0 = curved, Fig. 25; 1 = straight, narrow, Fig. 28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18. Lacinia shape 0 = curved, Figs. 44–48; 1 = straight, narrow, Fig. 42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19. Lacinia width 0 = narrow, Figs. 46, 47; 1 = wide, Fig. 48	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0

TABLE 2. CONTINUED.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
20. Mentum tooth shape 0 = triangular, trapezoid; 1 = subrectangular; 2 = rectangular, with deep lateral incisions	0	0	0	0	0	0	0	0	0	2	0	0	2	2	2	2	0	2
21. Mentum tooth emarginate? 0 = no; 1 = yes	0	0	0, 1	0, 1	1	0	0	0	0	0	0, 1	1	0, 1	0	0	0	1	0, 1
22. Mentum tooth bulbous? 0 = flat; 1 = slightly bulbous; 2 = distinctly bulbous	0	0	0	0	0	0	0	0	0	2	0	0	0	2	2	2	0	1
23. Mentum epilobes 0 = absent, Figs. 52, 55; 1 = indistinct; 2 = distinct, Figs. 49–51	2	2	2	2	2	2	2	2	2	0	2	2	2	0	0	0	2	2
24. Pronotal shape 0 = rounded sides; 1 = trapezoid, prominent anterior corners	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25. Pronotal carina 0 = absent; 1 = short, separated from base, Fig. 71; 2 = long, separated from base; 3 = long, attached to base, Fig. 70	0, 1	0, 1	0, 1	0	0	1	3	0, 1	1	0, 1	0, 1	0, 1	0, 1	0, 1	0, 1	0, 1	0	0, 1
26. Metasternum 0 = unbordered; 1 = bordered	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27. Elytral basal impression 0 = absent; 1 = slight; 2 = definite	2	2	0	0	0	0	1, 2	0, 1	1	0, 1	1, 2	2	2	2	2	0–2	1, 2	1, 2
28. Angulate humeral margin 0 = absent; 1 = short, Figs. 69, 73; 2 = moderate, Figs. 68, 70; 3 = long, Figs. 71, 72	1, 2	1	2	1	2	3	2	3	3	3	1	1	1	1	1	1	1	1
29. Stria 4 shape 0 = straight; 1 = slightly sinuate; 2 = distinctly sinuate	0	0	0	0	0	0	0	0	0	0	0	0	0–2	0–2	2	2	1, 2	0, 1

TABLE 2. CONTINUED.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
30. Elytra around ed3 and ed5 0 = not foveolate; 1 = slightly foveolate; 2 = foveolate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31. Elytral punctures 0 = circular; 1 = slightly transverse; 2 = transversely stretched	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0, 1	0	0
32. Stria 8 depth 0 = as shallow as 7th anteriorly; 1 = slightly deeper than 7th anteriorly; 2 = distinctly deeper than 7th anteriorly	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0, 1	0	0
33. Interval 5 posteriorly 0 = flat; 1 = ridged	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34. Subapieal elytral plica 0 = absent; 1 = internal only, not connected to epipleuron; 2 = connected to epipleuron	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
35. Male protarsomere 3 shape 0 = no lateral projection, Figs. 75–77; 1 = slight projection; 2 = prominent projection, Fig. 78	0	0	0	0, 1	2	0	0	0	0, 1	0	0	0	0	0	0	0	0	0
36. Protarsomere 4 projection 0 = absent, minute, Figs. 90–94; 1 = very short; 2 = short, Fig. 95; 3 = long, Fig. 96	3	3	0	0	1	3	3	3	2	0	2	2	2	2	2	2	2	2
Male genitalia																		
37. Flagellar sheath 0 = as Figs. 112, 113, 117–128; 1 = dark and hooked, Figs. 114–116	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
38. Flagellar sheath sculpture 0 = without long, thin scales; 1 = with long, thin scales	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE 2. CONTINUED.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
39. CSC right lobe 0 = absent; 1 = present, ventral margin narrow; 2 = present, ventral margin moderate; 3 = present, ventral margin wide	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
40. CSC right lobe ridge 0 = no ridge; 1 = slightly; 2 = distinctly	0	0	0	0	0	2	0	2	2	0, 1	0, 1	2	0	0	0	0	0	0
41. VSP dorsal ridge 0 = not angled, Figs. 112–120; 1 = very slightly; 2 = slightly; 3 = sharply angled, Figs. 124–128	0	0	0	0	0	0	0	0	0	0	1	2	1	3	3	3	3	3
42. VSP dorsal ridge sculpture 0 = unscaled; 1 = slightly scaled; 2 = distinctly scaled	2	2	2	2	2	0	0	0	0	0	0	0	0	2	2	2	0	0
43. Dark spot on flagellar sheath 0 = absent; 1 = present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
44. Ostial microtrichial patch size 0 = absent; 1 = small, Fig. 116; 2 = medium (not dorsal), Figs. 114, 115; 3 = large; 4 = very large, dense, dorsal, Figs. 112, 113	4	4	2	2	2	1	2	4	4	4	4	4	4	4	4	4	4	4
45. Ostial scales 0 = comb-like scales larger; 1 = combs sparse, small	0	0	—	—	—	—	—	—	0	—	0	—	0	—	—	—	—	—
46. Ostial microtrichial patch 0 = comb-like scales absent; 1 = combs few; 2 = combs extensive; 3 = combs extensive, sparse, small	2	2	0	0	0	0	0	0	1	0	0, 1	0	2	0	0	0	0	0
47. Ostial sclerotized strip 0 = absent, Figs. 123, 124; 1 = present, Figs. 126–128	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1

TABLE 2. CONTINUED.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
48. Ostial strip sculpture 0 = not beaded; 1 = beaded	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0	0
49. Pillow with scales 0 = absent; 1 = present, Fig. 119	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
50. Internal sac, leftmost central membrane 0 = small scales; 1 = large scales, Fig. 108	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51. Ventral bulge 0 = absent; 1 = slight; 2 = distinct, Fig. 126	0	0	0, 1	1	0	0	0	0	0	0	0, 1	0, 1	0, 1	0	0	2	0	0
52. Aedeagal apex 0 = straighter; 1 = abruptly ventrally bent	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Female genitalia																		
53. Vaginal sclerotized plate 0 = absent; 1 = present	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
54. Spermatheca apically indented? 0 = no; 1 = yes	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0
55. Stylomere 1 setal length 0 = absent; 1 = short, Fig. 154; 2 = medium; 3 = long, Fig. 152	2	2	2	2	?	3	1	2	2	2	2	2	2	2	2	2	2	2
56. Stylomere 2 length (μm, average) **B. zephyrum* varies from 190 to 325 micrometers (discrete coding for numerical analysis: 0 = <210; 1 = 210–300; 2 = 300–400; 3 = >400)	168	171	361	310	?	154	410	194	188	198	219	174	*	186	169	158	190	167
57. Number dorsolateral sensilla	2	2	2–4	3, 4	?	2	4–6	1, 2	1, 2	2, 3	0	1, 2	1–3	2, 3	2, 3	1, 2	2	2
58. Sternum X setae 0 = very short, nubbin-like; 1 = longer	1	1	1	1	?	1	0	1	1	1	1	1	1	1	1	1	1	1

TABLE 2. CONTINUED.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
Chromosomes																		
59. Pairs of autosomes, count for *B. litorale* from Nettman (1986) (Discrete coding for numerical analysis: 0 = 10; 1 = 11; 2 = 12; 6 = 16; 7 = 17)	11	11	?	11	?	?	11	?	11	11	10	10	10	10	10	10	17	?
60. Y chromosome size 0 = absent; 1 = small, <⅔ autosome size; 2 = medium, ⅔–1 autosome size; 3 = large, about autosome size	3	3	?	1	?	?	1	?	3	3	2	2	3	?	2, 3	2	?	?
First instar larva																		
61. Frontale with three spots 0 = not distinctly; 1 = slightly; 2 = distinctly	2	2	0	0	?	?	0	?	0	2	2	2	0–2	2	2	2	?	?
62. Head (other than spots) 0 = light; 1 = centrally dark; 2 = dark	2	2	1	1	?	?	1	?	2	0	0	0	0	0	0	0	?	?
63. Frontale behind FR_3 0 = microsculpture absent, Figs. 227, 228; 1 = laterally only, microsculpture slight; 2 = laterally only, Figs. 229, 231; 3 = centrally, Fig. 230	2	2	?	0	?	?	0	?	2	3	2	2	2	2	2	2	?	?
64. Frontale: anteriorly behind FR_3 0 = microsculpture absent; 1 = single-toothed denticles; 2 = rare multitoothed combs; 3 = some multitoothed combs	2	3	?	0	?	?	0	?	1	1	1	1	1	1	1	1	?	?
65. Parietal eggbursters 0 = small denticles, Figs. 226, 230, 231; 1 = small teeth, Figs. 227, 229; 2 = large teeth, spaced; 3 = large teeth, clustered, Fig. 228	0	0	?	1	?	?	3	?	1	0	0	0	0	0	0	0	?	?

TABLE 2. CONTINUED.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
66. Pronotal microtubercles 0 = absent; 1 = present only laterally; 2 = laterally, faint centrally; 3 = absent between PR_{14}; 4 = absent only before PR_{14}; 5 = prominent throughout	1	1	?	0	?	?	0	?	2	4	0	0	0	0	0	0	?	?
67. FR_1 width 0 = <½ FR_2 width; 1 = >½ FR_2 width	0	0	?	0	?	?	1	?	1	0	0	0	0	0	0	0	?	?
68. FR_3 width 0 = <½ FR_2 width; 1 = >½ FR_2 width	0	0	?	0	?	?	1	?	1	1	0	0	0	0	0	0	?	?
69. PR_4 length 0 = very short; 1 = short, Fig. 241; 2 = long, Fig. 240	2	2	?	2	?	?	2	?	2	1	2	2	2	2	2	2	?	?
70. PR_{10} length 0 = absent; 1 = short, Fig. 243; 2 = medium, Fig. 244; 3 = long, Fig. 242	3	3	?	3	?	?	1	?	3	0	3	3	3	3	3	3	?	?
71. gPR and gME lateral setae 0 = absent; 1 = present, Figs. 237, 241	0	0	?	0	?	?	0	?	0	1	0	0	0	0	0	0	?	?
72. PR_{13} length 0 = short; 1 = long	1	1	1	1	?	?	0	?	1	1	1	1	1	1	1	1	?	?
73. ME_2 length VS = very short, Fig. 246; S = short; M = medium, Fig. 247; L = long, Fig. 248	3	3	?	3	?	?	0	?	0	1	3	3	3	3	3	3	?	?
74. ME_{14} length 0 = very short; 1 = short; 2 = medium; 3 = long	3	3	3	3	?	?	0	?	3	3	3	3	3	3	3	3	?	?
75. TE_6 length 0 = very short, Fig. 253; 1 = short, Fig. 254; 2 = long, Fig. 252	2	2	?	2	?	?	0	?	0	1	2	2	2	2	2	2	?	?

TABLE 2. CONTINUED.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
76. TE_{11} length 0 = very short, Fig. 250; 1 = short; 2 = long, Fig. 248	2	2	2	2	?	?	0	?	2	2	2	2	2	2	2	2	?	?
77. TE_{11} shape 0 = narrow, parallel-sided, Fig. 249; 1 = basally wide, tapered, Fig. 248	1	0	?	1	?	?	?	?	1	1	1	1	1	1	1	1	?	?
78. TE_{α} 0 = absent; 1 = present, Fig. 251	0	0	?	0	?	?	0	?	0	1	0	0	0	0	0	0	?	?
79. EP_1 length 0 = short, Fig. 251; 1 = long, Fig. 248	1	1	?	1	?	?	1	?	1	0	1	1	1	1	1	1	?	?
80. Segment VIII EP_1 width 0 = <⅓ EP_2 width; 1 = >½ EP_2 width	0	0	?	0	?	?	1	?	1	?	0	0	0	0	0	0	?	?
81. Seta ST_2 on segment IX 0 = absent; 1 = present, Fig. 256	0	0, 1	?	0	?	?	1	?	1	0	0	0	0	0	0	0	?	?
82. Mandible mesal margin 0 = shelf absent, Fig. 200; 1 = minute shelf; 2 = narrow shelf, Fig. 199; 3 = wide shelf, Fig. 198	2	2	?	0	?	?	3	?	3	1	0	0	0	0	0	0	?	?
Second instar larva																		
83. Extra setae near FR_3 0 = absent; 1 = present	0	?	?	1	?	?	1	?	0	0	0	0	0	0	0	0	?	?
84. L2 stipites 0 = 3 outer setae; 1 = 4 outer setae	0	?	?	0	?	?	0	?	0	0	0	0	0	0	0	0	?	?
85. Long urogomphus setae, see Figs. 258–260 0 = 7 = setae; 2 = 9 setae; 3 = 10 setae	0	?	?	0	?	?	3	?	2	0	0	0	0	0	0	0	?	?

TABLE 3. NUMBERS OF SPECIMENS OF *BRACTEON* STUDIED. LARGER NUMBERS (E.G., "100") APPROXIMATE. DOTS ("·") INDICATE NO SPECIMENS EXAMINED FOR THIS CHARACTER. SPECIES ABBREVIATIONS: BL = *B. BALLI*, FO = *B. FOVEUM*, AR = *B. ARGENTEOLUM*, AL = *B. ALASKENSE*, SM = *B. SEMENOVI*, ST = *B. STENODERUM*, CA = *B. CARINULA*, VX = *B. VELOX*, LP = *B. LAPPONICUM*, PN = *B. PUNCTATOSTRIATUM*, HS = *B. HESPERIUM*, LQ = *B. LORQUINII*, ZE = *B. ZEPHYRUM*, LVL = *B. LEVETTEI LEVETTEI*, LVC = *B. LEVETTEI CARRIANUM*, IN = *B. INAEQUALE*, LT = *B. LITORALE*, CO = *B. CONICOLLE*.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
1. Silver spots	150	300	100	100	1	20	500	50	200	200	100	100	500	100	500	700	100	20
2. Mirrors on interval 3	150	300	100	100	1	20	500	50	200	200	100	100	500	100	500	700	100	20
3. Mirrors on intervals 4 or 5	150	300	100	100	1	20	500	50	200	200	100	100	500	100	500	700	100	20
4. Mirrors on intervals 6 or 7	20	20	20	20	1	20	50	20	20	20	20	20	100	50	100	100	50	20
5. Interval 7 mirror isolated?	·	·	·	·	1	20	·	·	20	·	20	·	100	50	100	100	50	20
6. Silver spot on interval 4?	10	10	10	10	1	10	10	10	10	10	10	10	10	10	10	10	10	10
7. Elytral sculpticell shape	6	6	6	6	1	15	6	6	6	6	6	6	6	6	6	6	6	6
8. Suborbital setae	6	7	7	7	1	7	7	7	7	7	7	7	7	7	7	7	7	7
9. Midlateral pronotal setae	150	300	100	100	1	20	500	50	200	200	100	100	500	100	500	700	100	20
10. ed3 and ed5: position relative to 3rd stria	10	10	10	10	1	10	10	10	10	10	10	10	10	10	10	10	10	10
11. ed3 and ed5: position relative to silver spot	20	10	20	10	1	10	10	10	10	15	10	10	10	10	10	10	10	10
12. Setae between eo4 and eo5	20	20	20	20	1	12	20	11	11	14	10	14	15	15	15	30	13	7
13. Number setae ed7 area	12	12	12	12	1	12	12	12	12	12	12	12	12	12	12	20	12	12
14. Male adhesive setae	5	5	2	2	1	2	2	2	2	2	2	2	2	2	2	4	2	2
15. Protarsomere 4 ventroapical setae	5	5	5	7	1	6	6	4	5	5	5	6	4	3	2	2	3	2
16. Protarsomere 4 setal separation	6	6	10	7	1	6	6	4	7	8	7	6	6	7	7	11	7	2
17. Mandible shape	6	6	6	6	1	6	6	6	6	6	6	6	6	6	6	12	6	6
18. Lacinia shape	6	6	6	6	1	6	6	6	6	6	6	6	6	6	6	12	6	6
19. Lacinia width	6	6	6	6	1	6	6	6	6	6	6	6	6	6	6	12	6	6
20. Mentum tooth shape	6	9	6	8	1	7	8	10	10	12	8	8	8	8	10	20	7	3
21. Mentum tooth emarginate?	6	9	6	8	1	7	8	10	10	12	8	8	8	8	10	20	7	3
22. Mentum tooth bulbous?	6	9	6	8	1	7	8	10	10	12	8	8	8	8	10	20	7	3
23. Mentum epilobes	6	9	6	8	1	7	8	10	10	12	8	8	8	8	10	20	7	3
24. Pronotal shape	150	300	100	100	1	20	500	50	200	200	100	100	500	100	500	700	100	20
25. Pronotal carina	16	20	20	20	1	20	70	30	40	20	20	20	20	20	20	20	20	20
26. Metasternum	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2	4	2	2
27. Elytral basal impression	12	20	12	12	1	12	25	12	12	12	12	12	12	12	12	12	12	12
28. Angulate humeral margin	20	20	8	8	1	8	8	8	8	8	8	8	8	8	8	8	8	8
29. Stria 4 shape	150	300	100	100	1	20	500	50	200	200	100	100	500	100	500	700	100	20
30. Elytra around ed3 and ed5	150	300	100	100	1	20	500	50	200	200	100	100	500	100	500	700	100	20
31. Elytral punctures	6	6	6	6	1	6	6	6	6	6	6	6	6	6	6	6	6	6

TABLE 3. CONTINUED.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
32. Stria 8 depth	6	6	6	6	1	6	6	6	6	6	6	6	6	6	6	6	6	6
33. Interval 5 posteriorly	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2	4	2	2
34. Subapical elytral plica	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2	4	2	2
35. Male protarsomere 3 shape	5	4	10	7	1	5	4	5	7	5	6	5	6	3	3	6	4	3
36. Protarsomere 4 projection	7	7	6	4	1	7	5	4	6	6	6	6	5	6	8	11	6	4
37. Flagellar sheath	3	3	3	3	1	3	3	3	3	3	3	3	3	3	3	3	3	3
38. Flagellar sheath sculpture	3	3	3	3	1	3	3	3	3	3	3	3	3	3	3	3	3	3
39. CSC right lobe	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
40. CSC right lobe ridge	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
41. VSP dorsal ridge	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
42. VSP dorsal ridge sculpture	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
43. Dark spot on flagellar sheath	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
44. Ostial microtrichial patch size	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
45. Ostial scales	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
46. Ostial microtrichial patch	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
47. Ostial sclerotized strip	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
48. Ostial strip sculpture	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
49. Pillow with scales	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
50. Internal sac leftmost central membrane	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
51. Ventral bulge	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
52. Aedeagal apex	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
53. Vaginal sclerotized plate	5	6	7	5	·	3	5	5	5	5	5	5	5	5	5	9	3	2
54. Spermatheca apically indented?	3	3	3	3	·	3	3	3	3	3	3	3	3	3	3	3	3	3
55. Stylomere 1 setal length	5	6	7	5	·	3	5	5	5	5	5	5	5	5	5	9	3	2
56. Stylomere 2 length	3	3	4	4	·	3	3	3	3	3	3	3	43	3	5	6	3	2
57. Number dorsolateral sensilla	5	6	7	5	·	3	5	5	5	5	5	5	5	5	5	9	3	2
58. Sternum X setae	5	6	7	5	·	3	5	5	5	5	5	5	5	5	5	9	3	2
59. Pairs of autosomes	10	29	·	11	·	·	17	·	30	10	9	7	10	5	38	24	?	·
60. Y chromosome size	4	8	·	5	·	·	7	·	9	4	3	2	3	2	11	8	·	·
61. Frontale with three spots	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
62. Head (other than spots)	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
63. Frontale behind FR_3	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
64. Frontale: anteriorly behind FR_3	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
65. Parietal eggbursters	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·

TABLE 3. CONTINUED.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	co
66. Pronotal microtubercles	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
67. FR_1 width	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
68. FR_3 width	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
69. PR_4 length	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
70. PR_{10} length	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
71. gPR and gME lateral setae	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
72. PR_{13} length	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
73. ME_2 length	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
74. ME_{14} length	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
75. TE_6 length	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
76. TE_{11} length	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
77. TE_{11} shape	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
78. TE_α	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
79. EP_1 length	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
80. Segment VIII EP_1 width	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
81. Seta ST_2 on segment IX	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
82. Mandible mesal margin	4	4	·	6	·	·	6	·	5	8	8	7	5	4	7	9	·	·
83. Extra setae near FR_3	2	·	·	3	·	·	2	·	1	1	2	1	1	1	2	2	·	·
84. L2 stipites	2	·	·	3	·	·	2	·	1	1	2	1	1	1	2	2	·	·
85. Long urogomphus setae	2	·	·	3	·	·	2	·	1	1	2	1	1	1	2	2	·	·

TABLE 4. CHARACTER STATES IN *ASAPHIDION ALASKANUM*, *BEMBIDION* DISTANTLY RELATED TO *BRACTEON*, AND *PSEUDOPERYPHUS*. SPECIES ABBREVIATIONS: ASA = *ASAPHIDION ALASKANUM* WICKHAM, QUA = *B. QUADRIMACULATUM* (LINNÉ) (FROM ALBERTA), TIM = *B. TIMIDUM* LECONTE, GRA = *B. GRAPHICUM* CASEY, UMB = *B. UMBRATUM* LECONTE, SCO = *B. SCOPULINUM* KIRBY, OBS = *B. OBSCURELLUM* MOTSCHULSKY, PET = *B. PETROSUM* GEBLER, CNC = *B. CONCOLOR* KIRBY, SAL = *B. SALEBRATUM* LECONTE, PLN = *B. PLANATUM* LECONTE, KUP = *B. "KUPRIANOVI-#1"* (THIS IS THE LARGER AND DARKER OF THE TWO SPECIES PRESENTLY INCLUDED WITHIN *B. KUPRIANOVI*), OBT = *B. OBTUSUM* SERVILLE, INV = *B. INTERVENTOR* LINDROTH, RUF = *B. RUFOTINCTUM* HAYWARD, INT = *B. INTEGRUM* CASEY, HON = *B. HONESTUM* SAY, ANT = *B. ANTIQUUM* DEJEAN, S17 = *B.* "SP. 17", CHA = *B. CHALCEUM* DEJEAN. OTHER SYMBOLS, INCLUDING THOSE FOR CHARACTER STATES, AS IN TABLE 2.

Character	Asa	qua	tim	gra	umb	sco	obs	pet	cnc	sal	pln	kup	obt	inv	ruf	int	hon	ant	s17	cha
Adult external characters																				
Number of specimens	6	6	6	6	6	6	6	6	6	6	6	5	6	6	6	6	6	6	6	6
1. Silver spots	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2. Mirrors on interval 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3. Mirrors on intervals 4 or 5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4. Mirrors on intervals 6 or 7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5. Interval 7 mirror isolated?	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6. Silver spot on interval 4?	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7. Elytral sculpticell shape	2	—	0	2	0	2	0–2	2	2	2	0	2	2	2	0	2	0	0–2	2	2
8. Suborbital setae	2	1	0, 1	0, 1	0	0	0	0	1	0	1, 2	2	0	0, 1	1	0	2	2	1	1, 2
9. Midlateral pronotal setae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
10. ed3 and ed5: position relative to 3rd stria	—	0, 1	0	0	0	1	1	1	1	1	1	1	1	0, 1	1	1	1	1	1	1
11. ed3 and ed5: position relative to silver spot	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12. Setae between eo4 and eo5	0	0	0	0	0	0	0	0	0.13	0	0.25	0	0	0.14	0.14	0.14	0	0.15	0.17	0.08
13. Number setae ed7 area	1.1	1	1	1	1	1	1	1.1	1	1	1	1	1	1	1	1	1	1	1	1
14. Male adhesive setae	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?
15. Protarsomere 4 ventroapical setae	0	0	0	1	?	1	?	1	1	?	1	1	?	0	1	1	1	1	1	1
16. Protarsomere 4 setal separation	1	1	0	0	0	0	0	0	0	0	0	0	?	1	0	0	0	0	0	0
17. Mandible shape	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18. Lacinia shape	0	?	?	0	?	?	?	0	?	?	0	0	?	0	0	0	0	0	0	0
19. Lacinia width	0	?	?	?	?	?	0	0	?	?	0	0	0	1	0	0	0	0	0	0
20. Mentum tooth shape	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21. Mentum tooth emarginate?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
22. Mentum tooth bulbous?	0	0	0	0	2	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
23. Mentum epilobes	2	2	2	2	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2

TABLE 4. CONTINUED.

Character	Asa	qua	tim	gra	umb	sco	obs	pet	cnc	sal	pln	kup	obt	inv	ruf	int	hon	ant	s17	cha
24. Pronotal shape	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25. Pronotal carina	0	3	3	2	2	0, 1	2	2	2	0, 1	2	2	1, 2	1, 2	0	0	0	0	0	0
26. Metasternum	0	1	1	1	1	1	1	1	1	1	1	1	?	0	0	0	0	0	0	0
27. Elytral basal impression	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28. Angulate humeral margin	0	0	0	0	0	0	0	0	0	1	0	1	2, 3	3	0	0	0	0	0	0
29. Stria 4 shape	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30. Elytra around ed3 and ed5	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
31. Elytral punctures	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32. Stria 8 depth	?	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
33. Interval 5 posteriorly	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0
34. Subapical elytral plica	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
35. Male protarsomere 3 shape	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36. Protarsomere 4 projection	0	0	2	2	2	?	?	3	?	?	2	?	?	0	?	2	2	2	?	2
Male genitalia																				
Number of specimens	2	2	2	1	1	2	2	1	2	2	2	2	2	1	3	2	3	4	4	4
37. Flagellar sheath	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0
38. Flagellar sheath sculpture	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	1	1	1
39. CSC right lobe	?	1	1	0	0	1	1	1	1	1	1	0	1	0	3	3	3	3	3	3
40. CSC right lobe ridge	?	0	0	?	?	0	0	0	0	0	0	?	0	?	0	0	0	0	0	0
41. VSP dorsal ridge	?	?	?	?	?	?	0	0	0	0	0	0	0	?	0	0	0	0	0	0
42. VSP dorsal ridge sculpture	?	?	?	?	?	?	0	?	2	2	2	2	?	?	0	0	0	0	1	0
43. Dark spot on flagellar sheath	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
44. Ostial microtrichial patch size	0	0	0	0	0	4	3	2	2	3	4	4	1	2	3	4	4	4	3	4
45. Ostial scales	—	—	—	—	—	0	—	0	—	—	—	0	—	0	0	0	0	0	—	—
46. Ostial microtrichial patch	—	—	—	—	—	2	0	2	0	0	0	2	0	2	1	2	2	1, 2	0	0
47. Ostial sclerotized strip	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
48. Ostial strip sculpture	—	—	—	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	—
49. Pillow with scales	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE 4. CONTINUED.

Character	Asa	qua	tim	gra	umb	sco	obs	pet	cnc	sal	pln	kup	obt	inv	ruf	int	hon	ant	s17	cha
50. Internal sac leftmost central membrane	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
51. Ventral bulge	0	0	0	0	0	0	0	0	0	0	0	0	0, 1	1	0	0	2	1	1	1
52. Aedeagal apex	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Female genitalia																				
Number of specimens	2	2	2	1	2	2	1	3	2	2	2	2	1	2	1	2	1	2	1	3
53. Vaginal sclerotized plate	1	1	0	1	1	0	0	0, 1	1	1	1	1	1	1	0	0	0	0	0	0
54. Spermatheca apically indented?	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0
55. Stylomere 1 setal length	0	2	0	2	2	2	2	0, 2	3	2	0	2	0	0	3	3	3	3	3	3
56. Stylomere 2 length	170	130	95	140	125	125	160	150	140	125	250	170	110	165	170	190	170	220	190	160
57. Number dorsolateral sensilla	2, 3	2, 3	2	2	2	1–3	1, 2	1, 2	2, 3	2	0	2, 3	2	2	2, 3	2, 3	1, 2	2, 3	3, 4	2
58. Sternum X setae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Chromosomes																				
Number of specimens	10	4	3	5	4	3	2	7	2	2	7	2	4	7	8	4	3	12	8	11
59. Pairs of autosomes	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	16	12
60. Y chromosome size	1	?	?	1	1	?	?	0	2, 3	2, 3	1	1	1	?	?	2	2	2	1	2
First instar larva																				
Number of specimens	1	2	1	3	2	1	1	3	3	5	1	1	2	5		1		1		4
61. Frontale with three spots	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	?	0	?	0
62. Head (other than spots)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	?	0	?	0
63. Frontale behind FR_3	2	1	2	2	2	1	0	1	2	2	1	1	1	2	?	2	?	0	?	2
64. Frontale: anteriorly behind FR_3	1	?	3	3	3	1	?	1	1	2	1	1	1	1	?	3	?	0	?	3
65. Parietal eggbursters	1	0	0	0	0	0	0	0	0	0	1	0	0	1	?	0	?	0	?	0
66. Pronotal microtubercles	5	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	?	0	?	0
67. FR_1 width	1	0	0	0	0	0	0	0	0	0	1	0	0	0	?	0	?	0	?	0
68. FR_3 width	1	0	0	0	0	0	0	0	0	0	1	0	0	0	?	0	?	0	?	0
69. PR_4 length	0	2	2	2	2	2	2	2	2	2	2	2	2	2	?	2	?	2	?	2
70. PR_{10} length	0	3	3	3	3	3	3	3	3	3	3	3	3	3	?	2	?	2	?	3
71. gPR and gME lateral setae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	?	0	?	0

TABLE 4. CONTINUED.

Character	Asa	qua	tim	gra	umb	sco	obs	pet	cnc	sal	pln	kup	obt	inv	ruf	int	hon	ant	s17	cha
72. PR_{13} length	?	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	?	1	?	1
73. ME_2 length	3	3	3	3	3	3	3	3	3	3	3	3	3	3	?	3	?	2	?	3
74. ME_{14} length	?	3	3	3	3	3	3	3	3	3	3	3	3	3	?	3	?	3	?	3
75. TE_6 length	1	2	2	2	2	2	2	2	2	2	2	2	2	2	?	2	?	2	?	2
76. TE_{11} length	?	2	2	2	2	2	2	2	2	2	2	2	2	2	?	2	?	2	?	2
77. TE_{11} shape	?	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	?	1	?	1
78. TE_a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	?	0	?	0
79. EP_1 length	0	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	?	1	?	1
80. Segment VIII EP_1 width	?	1	1	0	0	1	1	1	1	1	1	1	1	0	?	0	?	?	?	1
81. Seta ST_2 on segment IX	0	0	0	0	0	0	0	0	1	1	0	0	0	0	?	0	?	?	?	0
82. Mandible mesal margin	0	1	1	2	2	3	2	0, 2	2	0, 2	2	3	2	0	?	2	?	3	?	3
Second instar larva																				
Number of specimens				1	1		1	1	1	1				1				1		
83. Extra setae near FR_3	?	?	?	0	0	?	0	0	0	0	?	?	?	0	?	?	?	0	?	?
84. L2 stipites	?	?	?	1	1	?	0	0	0	0	?	?	?	0	?	?	?	0	?	?
85. Long urogomphus setae	?	?	?	0	0	?	0	0	0	0	?	?	?	0	?	?	?	0	?	?

TABLE 5. CHARACTER STATES IN *OCHTHEDROMUS* AND *ODONTIUM*. SPECIES ABBREVIATIONS: AME: *B. AMERICANUM* DEJEAN, BIF: *B. BIFOSSULATUM BIFOSSULATUM* LECONTE, CHE: *B. BIFOSSULATUM CHEYENNENSE* CASEY, CHP: *B. CHLOROPUS* BATES, FUS: *B. FUSIFORME* NETOLITZKY, AEP: *B. AENEIPES* BATES, NRA: *B.* SP. NR. *AENULUM*, AEN: *B. AENULUM* HAYWARD, DUR: *B. DURANGOENSE* BATES, ARZ: *B. ARIZONAE* LINDROTH, CNF: *B. CONFUSUM* HAYWARD, SCU: *B. SCULPTURATUM* (MOTSCHULSKY), CRT: *B. CARINATUM* (LECONTE), COX: *B. COXENDIX* SAY, ROB: *B. ROBUSTICOLLE* HAYWARD, PRS: *B. PERSIMILE* MORAWITZ, STR: *B. STRIATUM* (FABRICIUS), FOR: *B. FORAMINOSUM* STURM, BOW: *B. BOWDITCHII* LECONTE. OTHER SYMBOLS, INCLUDING THOSE FOR CHARACTER STATES, AS IN TABLE 2.

Character	ame	bif	che	chp	fus	aep	nra	aen	dur	arz	cnf	scu	crt	cox	rob	prs	str	for	bow
Adult external characters																			
Number of specimens	4	6	6	3	3	6	2	6	4	6	6	5	2	6	4	6	6	6	6
1. Silver spots	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2. Mirrors on interval 3	0	2	2	1	2	2	0	0	0	0	0	0	0	1	0	1	1	1	1
3. Mirrors on intervals 4 or 5	0	2	2	1	2	2	0	0	0	0	0	0	0	1	0	1	1	1	1
4. Mirrors on intervals 6 or 7	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
5. Interval 7 mirror isolated?	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6. Silver spot on interval 4?	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7. Elytral sculpticell shape	0	1	1	0	0	0	2	0	0	2	2	1	1	0	0–2	0	0	0	0
8. Suborbital setae	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0, 1	0, 1	2	1	0
9. Midlateral pronotal setae	1	1	1	0	0	0	0	0	0	0	1	1	1	0, 1	1	1	1	1	1
10. ed3 and ed5: position relative to 3rd stria	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0, 1	1
11. ed3 and ed5: position relative to silver spot	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12. Setae between eo4 and eo5	0	0	0.14	0	0	0.10	0	0	0	0	0.08	0	0.33	0.08	0	0.10	0.08	0.08	0.29
13. Number setae ed7 area	1	1	1	1	1	1.1	1	1	1	1	1	1	1	0.94	1	1	1	1	1.1
14. Male adhesive setae	?	1	1	1	1	1	1	1	1	1	1	?	1	1	1	?	1	?	1
15. Protarsomere 4 ventroapical setae	?	1	1	?	?	?	1	1	?	1	1	1	1	1	?	1	1	?	1
16. Protarsomere 4 setal separation	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17. Mandible shape	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
18. Lacinia shape	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
19. Lacinia width	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20. Mentum tooth shape	1	0	2	0	0	0	0	0	0	1	2	2	0	0	0	0	0	0	0
21. Mentum tooth emarginate?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22. Mentum tooth bulbous?	0	0	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
23. Mentum epilobes	2	2	2	2	2	2	2	2	2	2	0	2	2	1	2	2	2	2	2
24. Pronotal shape	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
25. Pronotal carina	0	0	0	0	0	0	0	0	1	1	1	2	1	1	3	1	0, 1	0	0, 1
26. Metasternum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27. Elytral basal impression	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0, 1	0, 1	0, 1
28. Angulate humeral margin	2	1, 2	1, 2	3	3	3	3	3	3	3	3	3	3	3	3	3	2	1, 2	2
29. Stria 4 shape	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE 5. CONTINUED.

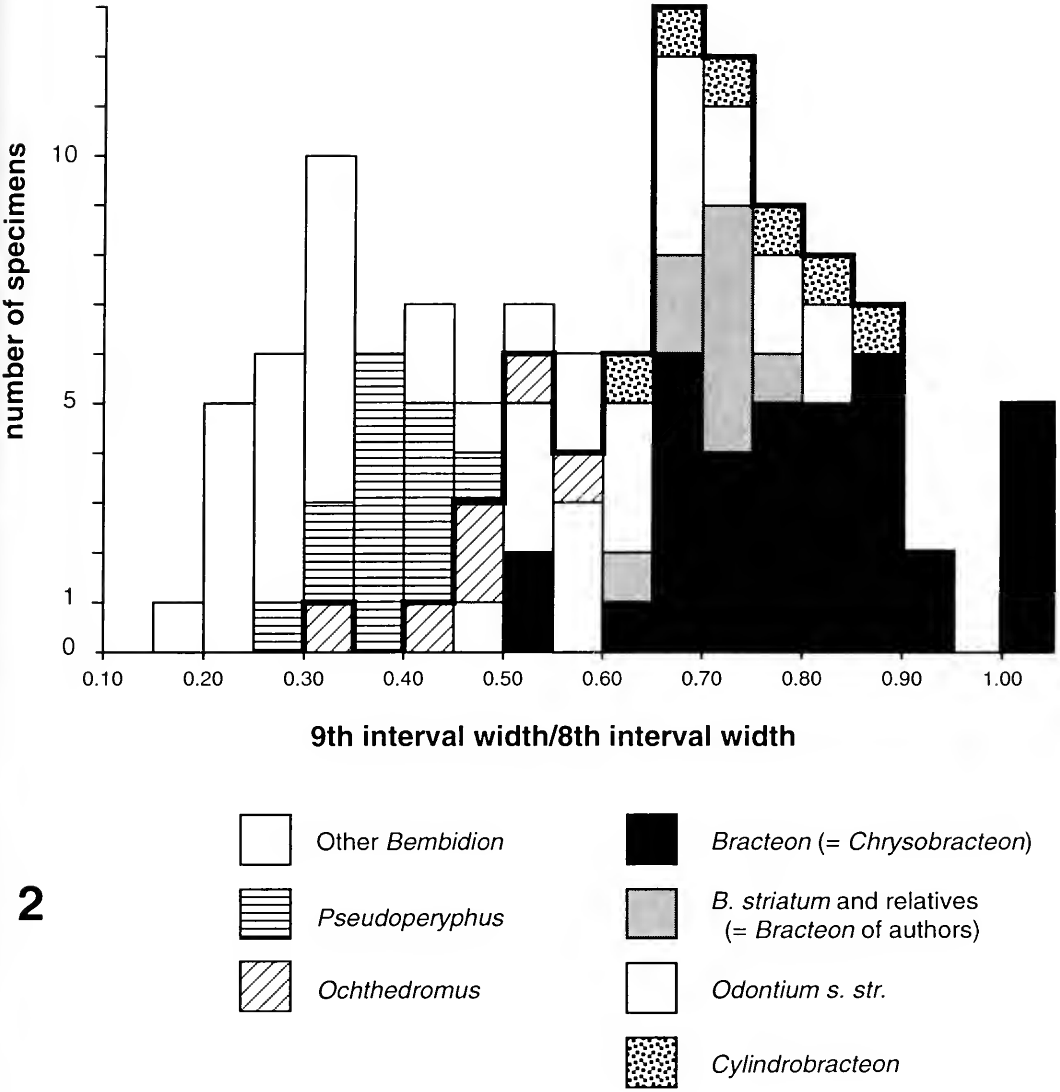
Character	ame	bif	che	chp	fus	aep	nra	aen	dur	arz	cnf	scu	crt	cox	rob	prs	str	for	bow
30. Elytra around ed3 and ed5	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
31. Elytral punctures	0	0	0	0	0	0	0	0	0	2	1	2	2	1	0	0	0	0	0
32. Stria 8 depth	1	1	1	2	2	2	2	1	0	1	1	1	1	1	1	0	0	0	0
33. Interval 5 posteriorly	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34. Subapical elytral plica	2	2	2	2	2	2	0	0	2	1	1	2	2	2	2	2	2	2	2
35. Male protarsomere 3 shape	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36. Protarsomere 4 projection	?	3	?	?	?	2	3	3	2	3	3	3	2	2	?	2	2	3	3
Male genitalia																			
Number of specimens	1	3	3	1	1	2	1	2	1	4	4	1	1	3	1	2	2	2	4
37. Flagellar sheath	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
38. Flagellar sheath sculpture	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39. CSC right lobe	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1
40. CSC right lobe ridge	0	0	0	0	0	0	0	0	2	0	0	0	0	0, 2	0	1, 2	?	1	0
41. VSP dorsal ridge	0	0	0	0	0	0	0	0	3	0	0	0	2	2	0	0	0	0	0
42. VSP dorsal ridge sculpture	2	2	2	2	1	0	0	1	2	0	0	?	0	1	0	2	2	2	0
43. Dark spot on flagellar sheath	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	?	0	0	0
44. Ostial microtrichial patch size	4	4	4	2	1	0	2	4	4	4	4	4	4	4	4	4	4	4	4
45. Ostial scales	—	—	—	0	—	—	—	0	0	1	1	1	—	—	0	0	—	0	—
46. Ostial microtrichial patch	0	0	0	1	0	—	0	1	1	1	1	1	0	0	2	1	0	1	0
47. Ostial sclerotized strip	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	?	0	1
48. Ostial strip sculpture	1	1	1	—	—	0	—	—	—	—	—	—	—	—	—	—	?	—	0
49. Pillow with scales	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50. Internal sac leftmost central membrane	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
51. Ventral bulge	0, 1	2	1, 2	0	0	0	0	0	0	0, 1	0	0	0	0	0	1	0	0, 1	0
52. Aedeagal apex	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Female genitalia																			
Number of specimens	1	1	1			1		3	1	1	3			3	1	1	2	1	3
53. Vaginal sclerotized plate	0	0	0	?	?	0	?	0	0	0	0	?	?	0	0	0	0	0	0
54. Spermatheca apically indented?	0	0	0	?	?	0	?	0	0	0	0	?	?	0	0	0	0	0	0
55. Stylomere 1 setal length	2	2	2	?	?	1	?	3	2	3	3	?	?	2	1	2	2	2	2
56. Stylomere 2 length	130	200	180	?	?	180	?	110	160	170	190	?	?	195	360	190	190	180	180
57. Number dorsolateral sensilla	2	2	2, 3	?	?	2	?	4, 5	2, 3	3	2, 3	?	?	1–3	3	2	2–4	2, 3	1, 2
58. Sternum X setae	1	1	1	?	?	1	?	1	1	1	1	?	?	1	1	1	1	1	1

TABLE 5. CONTINUED.

Character	ame	bif	che	chp	fus	aep	nra	aen	dur	arz	cnf	scu	crt	cox	rob	prs	str	for	bow
Chromosomes																			
Number of specimens	2	5	1					4		4	7			23			2		7
59. Pairs of autosomes	11	11	11	?	?	?	?	11	?	11	11	?	?	11	?	?	11	?	11
60. Y chromosome size	?	?	?	?	?	?	?	1	?	1	1	?	?	1	?	?	1	?	1
First instar larva																			
Number of specimens			3					1			1			3				2	7
61. Frontale with three spots	?	?	2	?	?	?	?	1	?	?	2	?	?	2	?	?	?	2	2
62. Head (other than spots)	?	?	0	?	?	?	?	0	?	?	0	?	?	0	?	?	?	0	0
63. Frontale behind FR_3	?	?	2	?	?	?	?	0	?	?	2	?	?	2	?	?	?	2	2
64. Frontale: anteriorly behind FR_3	?	?	3	?	?	?	?	0	?	?	3	?	?	3	?	?	?	3	3
65. Parietal eggbursters	?	?	0	?	?	?	?	2	?	?	0	?	?	0	?	?	?	0	0
66. Pronotal microtubercles	?	?	3	?	?	?	?	0	?	?	1	?	?	1	?	?	?	0	0
67. FR_1 width	?	?	0	?	?	?	?	0	?	?	0	?	?	0	?	?	?	0	0
68. FR_3 width	?	?	0	?	?	?	?	0	?	?	0	?	?	0	?	?	?	0	0
69. PR_4 length	?	?	2	?	?	?	?	2	?	?	2	?	?	2	?	?	?	2	2
70. PR_{10} length	?	?	1	?	?	?	?	3	?	?	3	?	?	3	?	?	?	3	3
71. gPR and gME lateral setae	?	?	0	?	?	?	?	0	?	?	0	?	?	0	?	?	?	0	0
72. PR_{13} length	?	?	1	?	?	?	?	1	?	?	1	?	?	1	?	?	?	1	1
73. ME_2 length	?	?	2	?	?	?	?	3	?	?	3	?	?	3	?	?	?	3	3
74. ME_{14} length	?	?	3	?	?	?	?	3	?	?	3	?	?	3	?	?	?	3	3
75. TE_6 length	?	?	1	?	?	?	?	2	?	?	2	?	?	2	?	?	?	2	2
76. TE_{11} length	?	?	2	?	?	?	?	2	?	?	2	?	?	2	?	?	?	2	2
77. TE_{11} shape	?	?	1	?	?	?	?	1	?	?	1	?	?	1	?	?	?	1	1
78. TE_a	?	?	0	?	?	?	?	0	?	?	0	?	?	0	?	?	?	0	0
79. EP_1 length	?	?	1	?	?	?	?	1	?	?	1	?	?	1	?	?	?	1	1
80. Segment VIII EP_1 width	?	?	0	?	?	?	?	0	?	?	0	?	?	0	?	?	?	0	0
81. Seta ST_2 on segment IX	?	?	0	?	?	?	?	0	?	?	0	?	?	0	?	?	?	0	0
82. Mandible mesal margin	?	?	0	?	?	?	?	1	?	?	1	?	?	0	?	?	?	0	0
Second instar larva																			
Number of specimens								1			1			1				1	
83. Extra setae near FR_3	?	?	?	?	?	?	?	0	?	?	0	?	?	0	?	?	?	0	?
84. L2 stipites	?	?	?	?	?	?	?	0	?	?	0	?	?	0	?	?	?	0	?
85. Long urogomphus setae	?	?	?	?	?	?	?	0	?	?	0	?	?	0	?	?	?	0	?

Table 6. Character states of *Bracteon* fossils. The two Columbia Bridge specimens are from an early Holocene, late Pleistocene locality from Vermont. The other specimens are from the Miocene Beaufort Formation. Lot number JVM 3-73 is from Banks Island; all the rest are from Meighen Island. Numbers in front of characters are those from Table 2. For numbered characters, state code matches those in Table 2; for others, code as follows: **body part**: E = elytron, P = pronotum; **3rd interval width**: W = distinctly wider than 2nd, N = as wide as second; **ed5 pit shape**: C = circular. "?" symbolizes missing data.

	Lot number and *Specimen number*													
	Columbia Bridge		**JVM 3-73**						**JVM 5-73**		**MRA 8-3-75-1**	**MRA 8-1-75-4**		
Character	*A1*	*A2*	*B2*	*B3*	*B4*	*B5*	*B6*	*B7*	*B3*	*B5*	*B4*	*A4*	*A5*	*B5*
Body part	E	E	E	E	E	E	E	E	E	P	E	P	P	E
1. Silver spots	1	?	1	1	1	1	1	1	1	?	1	?	?	1
2. Mirrors on 3rd?	3	?	3	3	3	?	?	0	3	?	3	?	?	3
3. Mirrors on 4th and 5th?	?	?	3	3	3	?	?	0	3	?	?	?	?	3
7. Sculpticell shape	0	?	0	0	0	0	0	0	0	?	0	?	?	0
9. Midlateral setae	?	?	?	?	?	?	?	?	?	1	?	1	1	?
10. ed3/5 and stria	0	0	0	0	0	0	0	0	0	?	0	?	?	?
11. ed3/5 and silver spot	1	?	0	0	0	0	0	?	0	?	0	?	?	0
25. Pronotal carina	?	?	?	?	?	?	?	?	?	1	?	0	1	?
28. Humeral margin	2	1	?	1	2	?	1	?	?	?	2	?	?	?
29. Stria 4 straight?	0	0	0	0	0	0	0	?	?	?	0	?	?	?
Interval 3 width	W	?	W	W	W	W	W	W	W	?	W	?	?	W
ed5 pit shape	?	?	?	?	?	?	?	C	?	?	?	?	?	?



2

Figure 2. Histogram of ratio (interval 9 width)/(interval 8 width) of studied *Bembidion* species. Two or three specimens measured of most species. Included are all *Bembidion* species of Tables 2, 4, and 5. Results for *Odontium* subgeneric group members are enclosed by a thick black line. The divisions between *Odontium*, *Cylindrobracteon*, and the *B. striatum* group are those recognized by Netolitzky (1942) and Lindroth (1962); note that I include all three within subgenus *Odontium* (see discussion in text).

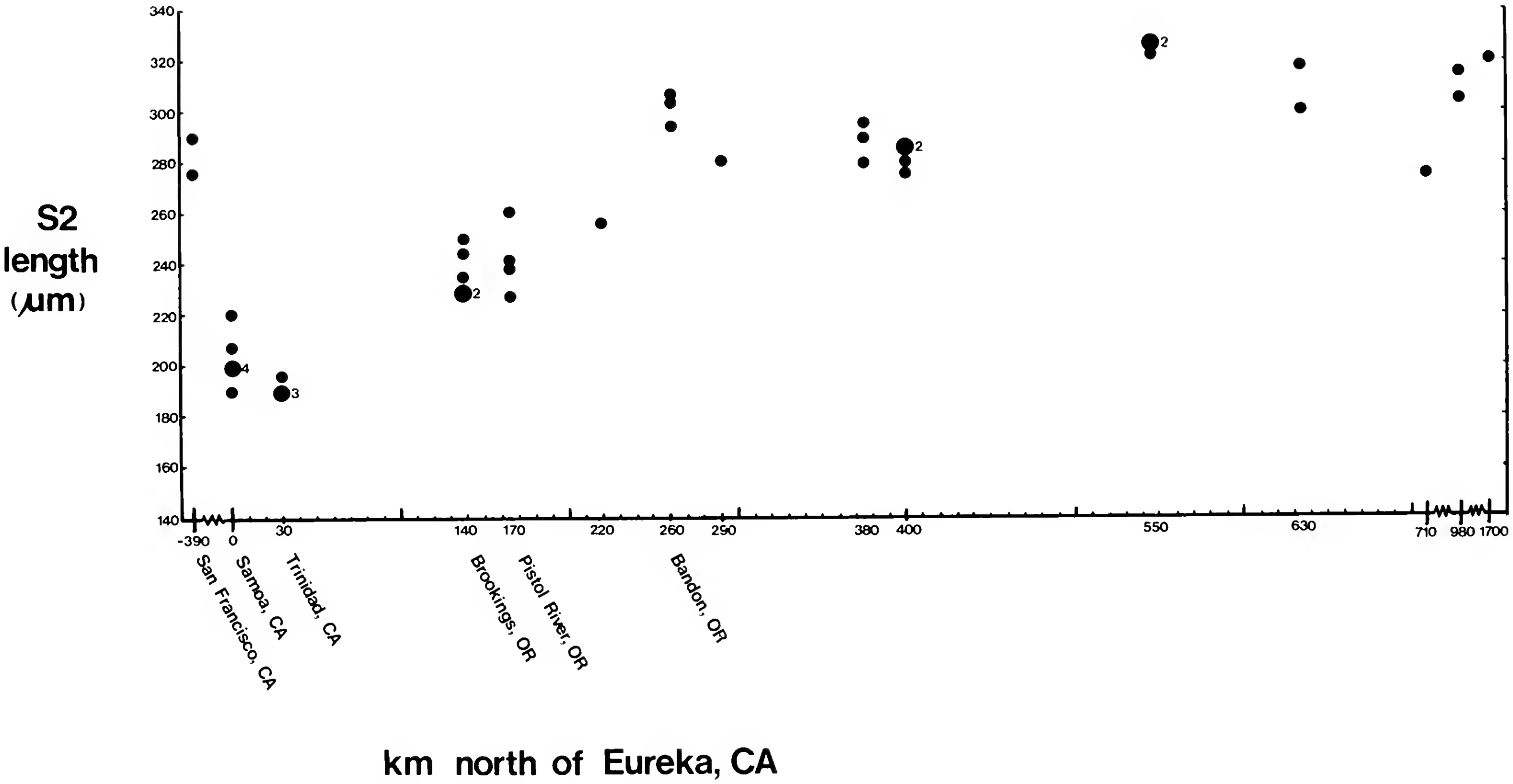


Figure 3. Geographic variation of *B. zephyrum* female second stylomere length.

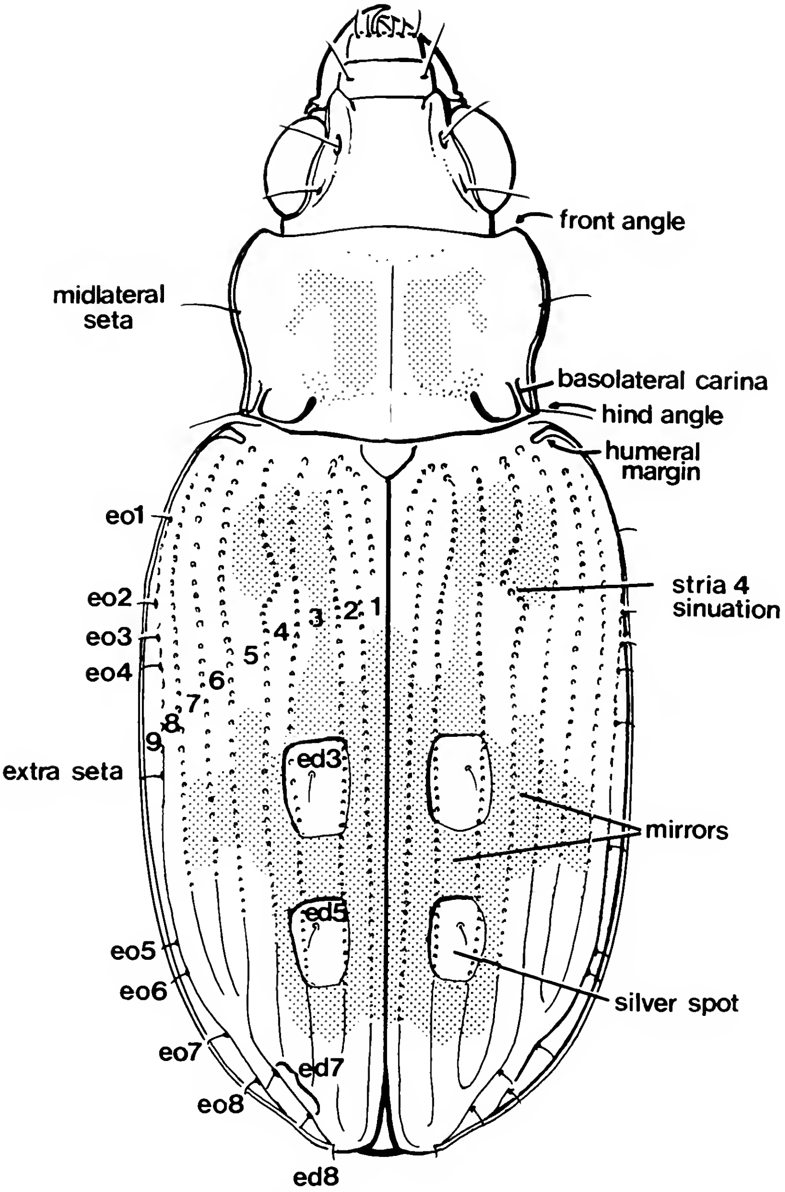
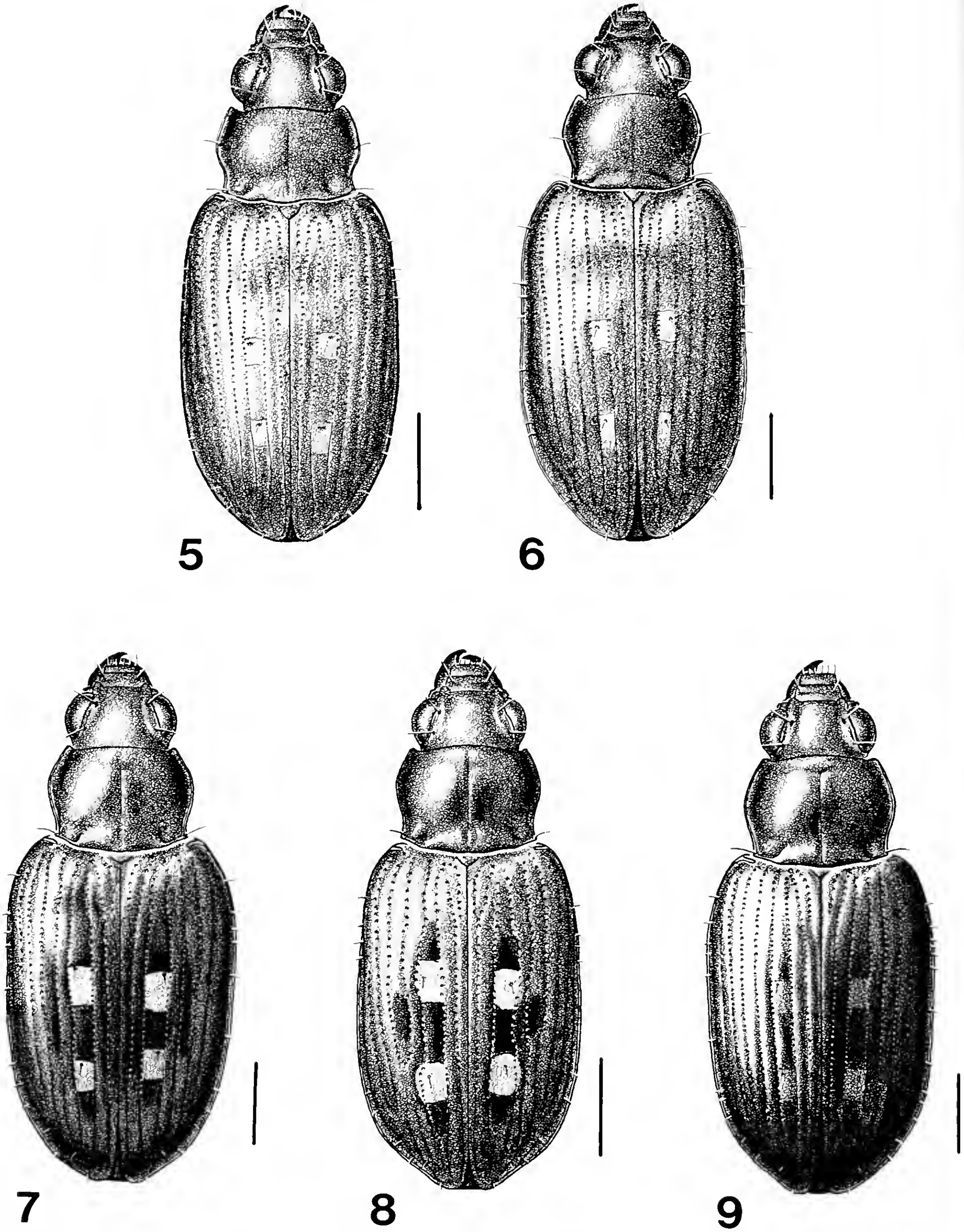
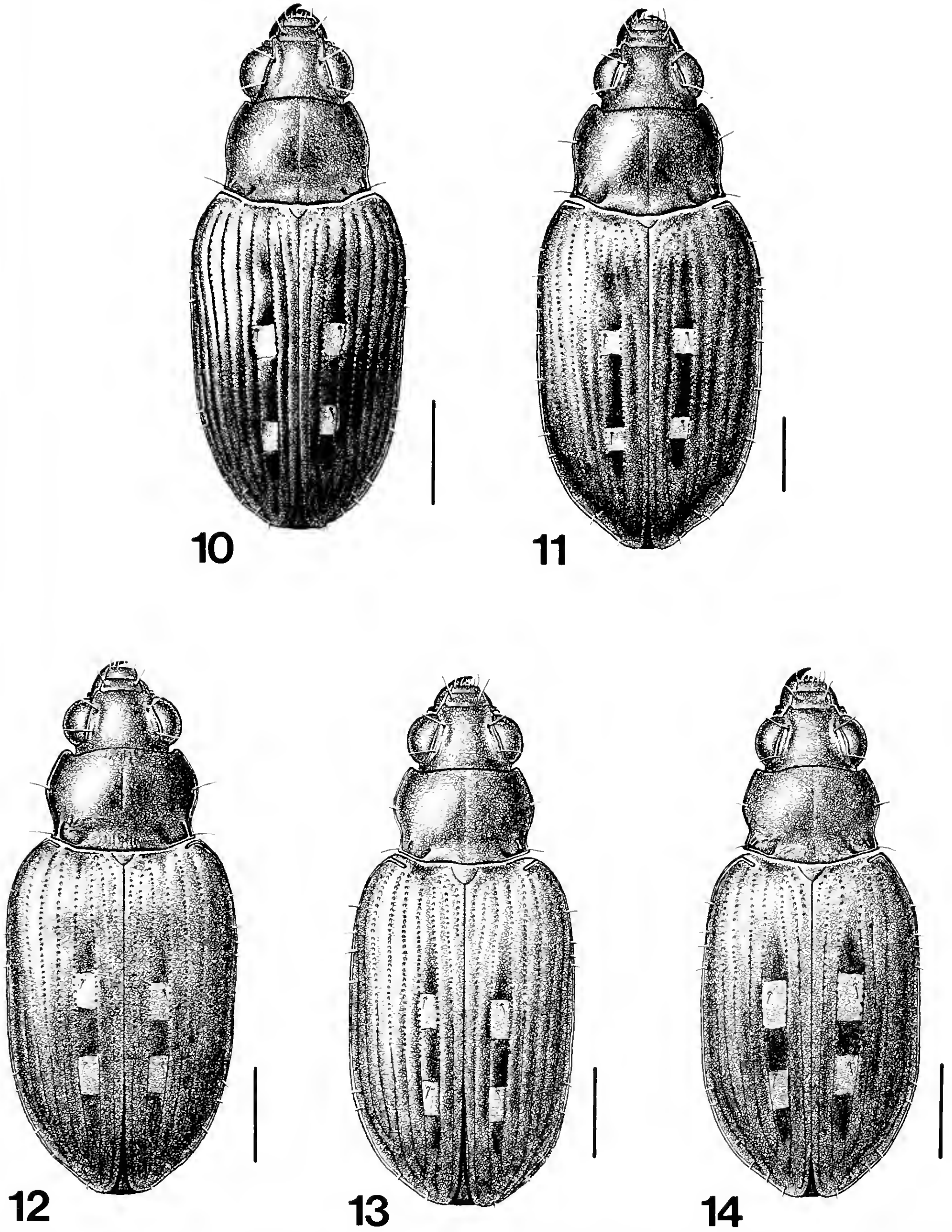


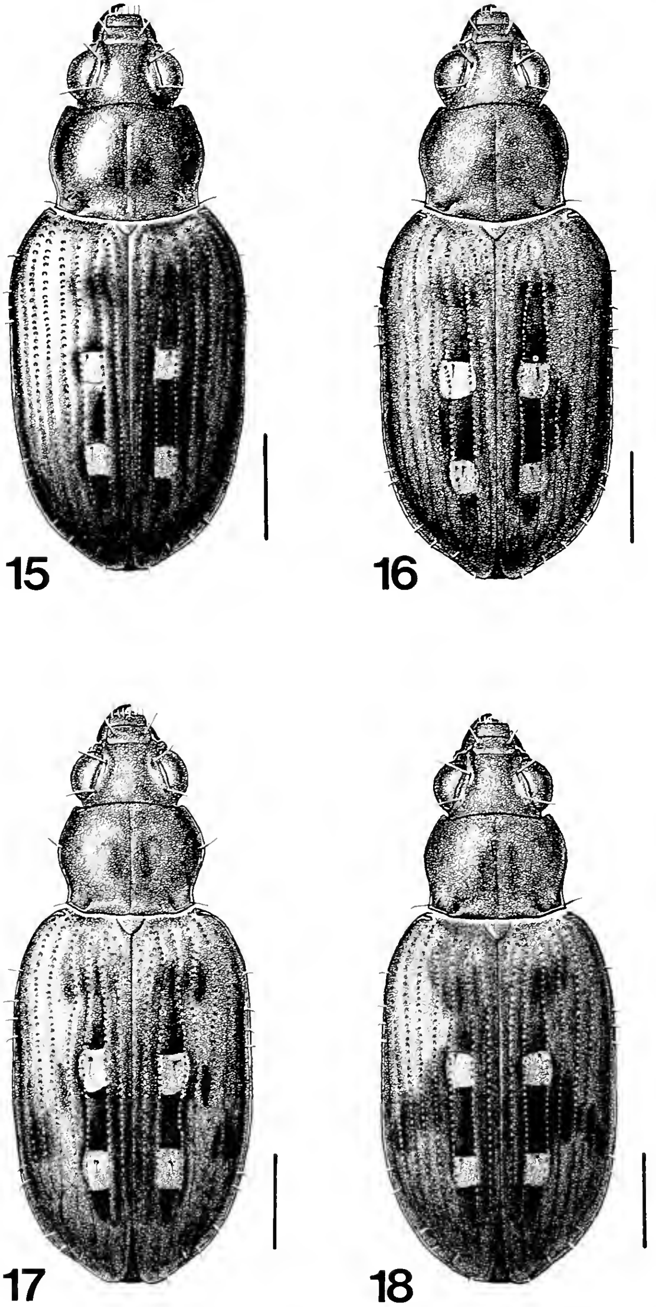
Figure 4. Diagrammatic dorsal view of imaginary *Bracteon* adult illustrating structures and terms. Elytral setal codes (eo1, ed3, and so on) follow nomenclature of Erwin and Kavanaugh (1981). Note that in *Bracteon*, there is either one or (as shown) two setae in the ed7 area. Transverse basal impression of elytron is located at stria 4 sinuation. Elytral intervals are numbered.



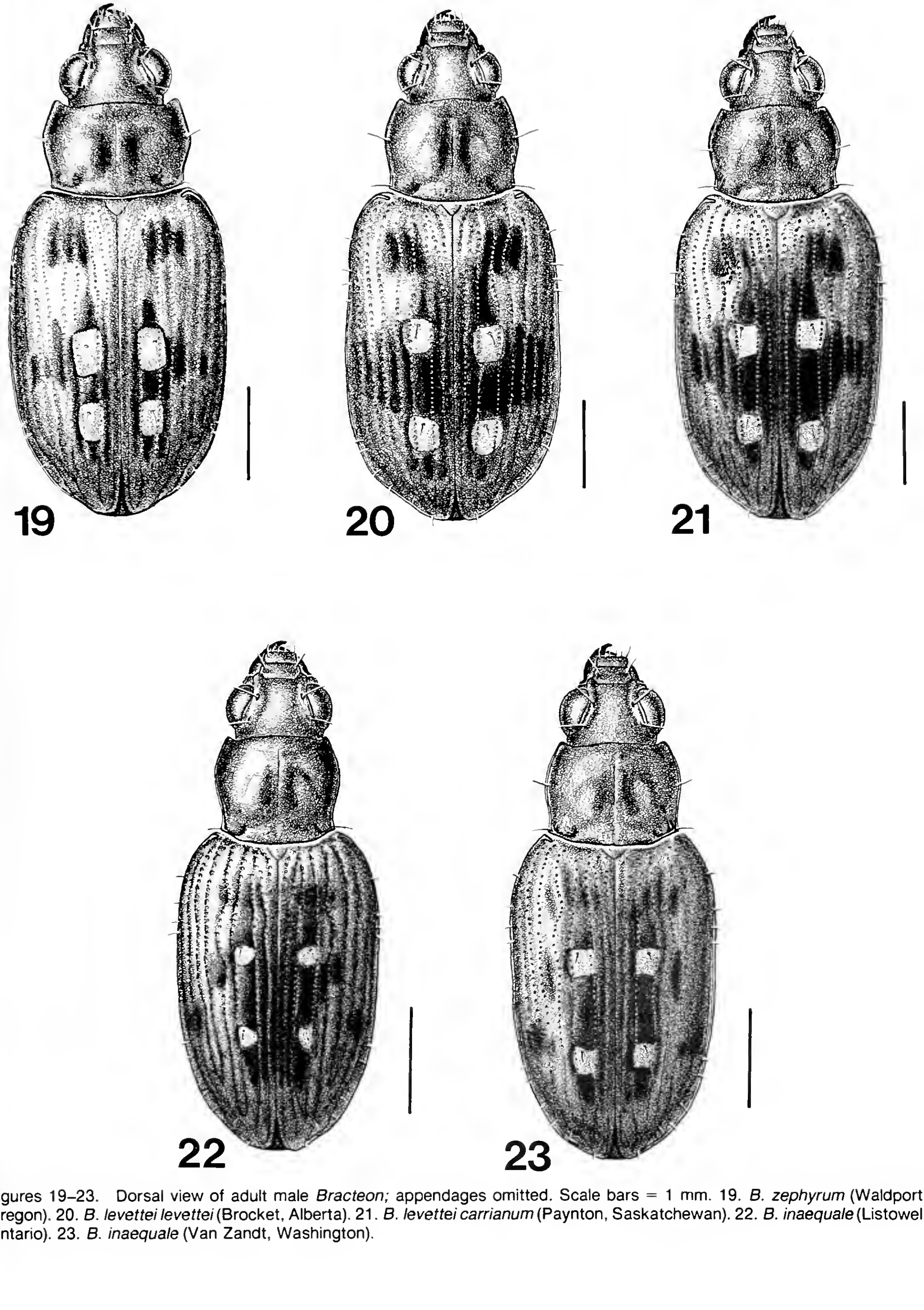
Figures 5–9. Dorsal view of adult male *Bracteon;* appendages omitted. Scale bars = 1 mm. 5. *B. balli* (Maymont, Saskatchewan). 6. *B. foveum* (Frenchman Butte, Saskatchewan). 7. *B. argenteolum* (Mora, Sweden). 8. *B. alaskense* (Lake Brooks, Alaska). 9. *B. semenovi* (Black Irtysh R., Russia)



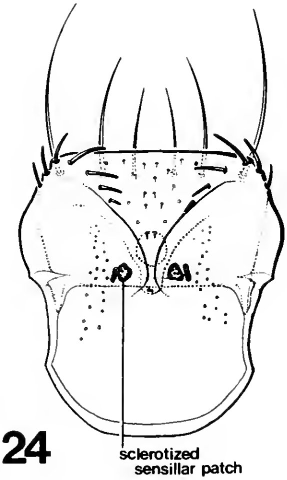
Figures 10–14. Dorsal view of adult male *Bracteon;* appendages omitted. Scale bars = 1 mm. 10. *B. stenoderum* (Kyoto, Japan). 11. *B. punctatostriatum* (Spring Creek Basin, Alberta). 12. *B. carinula* (North Saskatchewan River north of Lloydminster, Saskatchewan). 13. *B. velox* (Irtysh R., Russia). 14. *B. lapponicum* (Old Crow, Yukon).

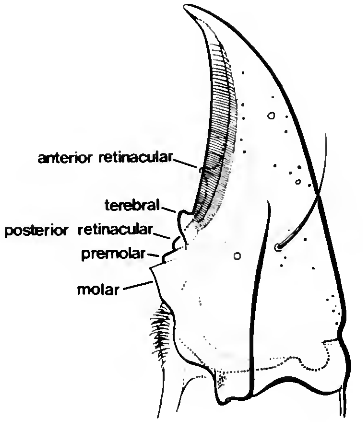


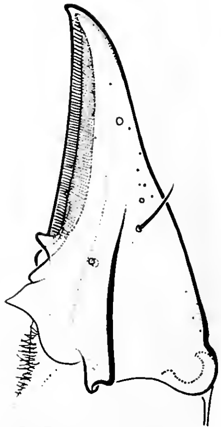
Figures 15–18. Dorsal view of adult male *Bracteon;* appendages omitted. Scale bars = 1 mm. 15. *B. hesperium* (Van Zandt, Washington). 16. *B. lorquinii* (Lockwood, Nevada). 17. *B. litorale* (Emsdetten, Germany). 18. *B. conicolle* (Ulan-Baator, Mongolian Peoples' Republic).

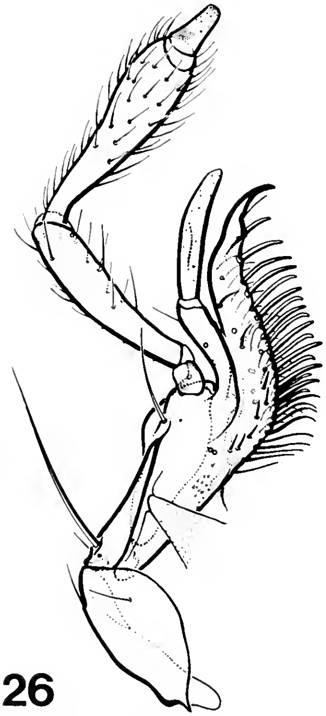


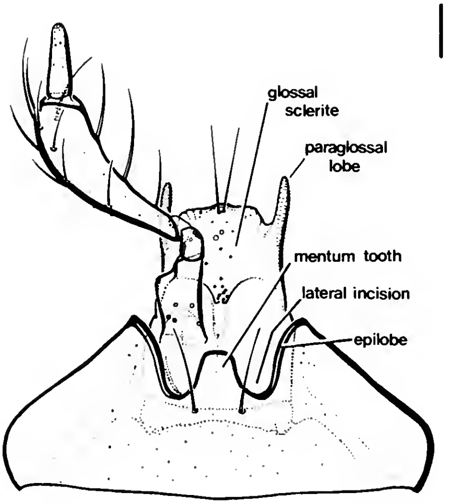
Figures 19–23. Dorsal view of adult male *Bracteon;* appendages omitted. Scale bars = 1 mm. 19. *B. zephyrum* (Waldport, Oregon). 20. *B. levettei levettei* (Brocket, Alberta). 21. *B. levettei carrianum* (Paynton, Saskatchewan). 22. *B. inaequale* (Listowel, Ontario). 23. *B. inaequale* (Van Zandt, Washington).


24


25

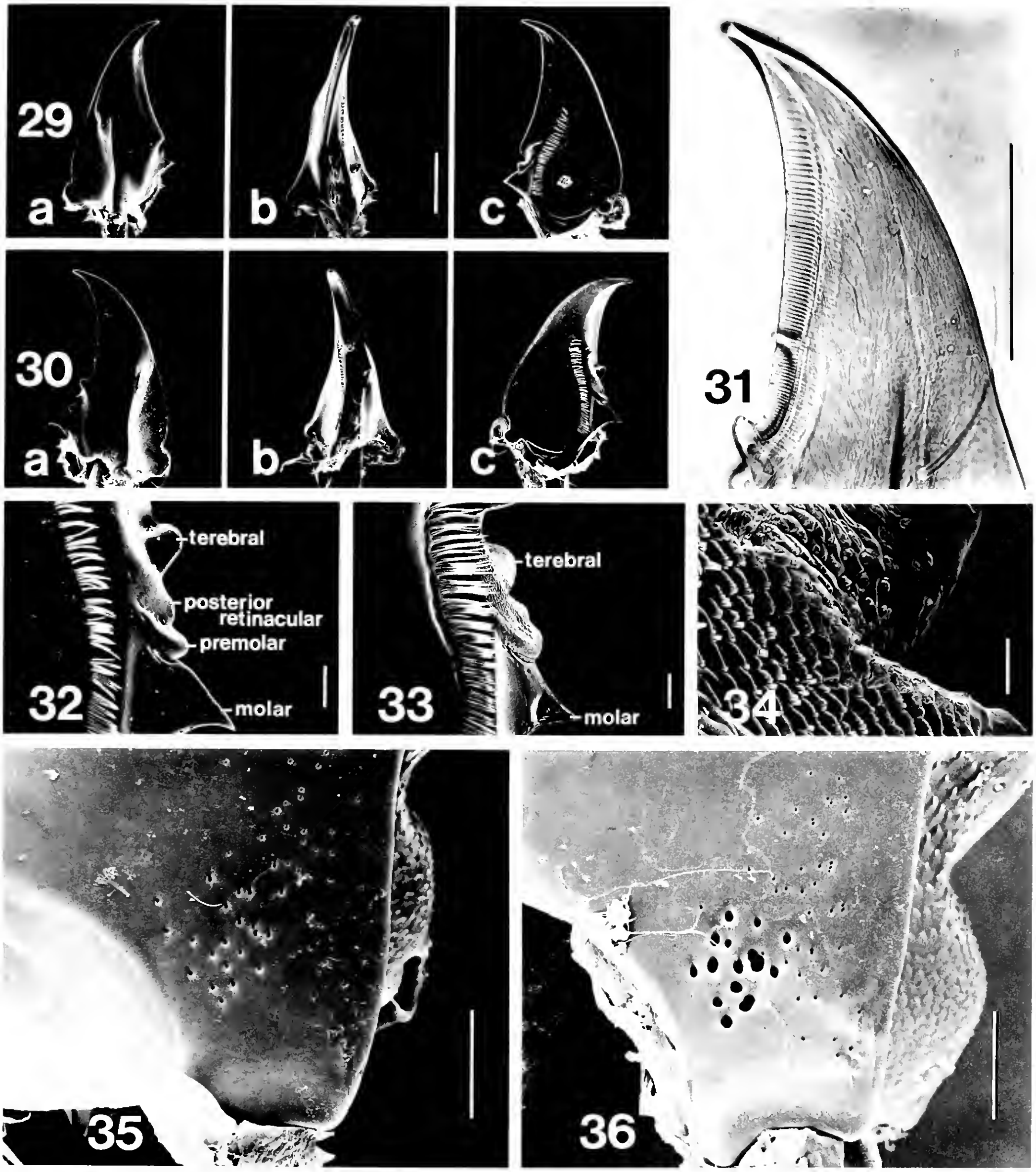

28


26

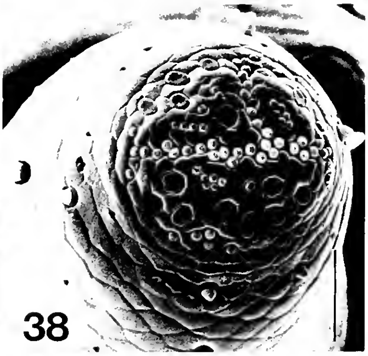

27

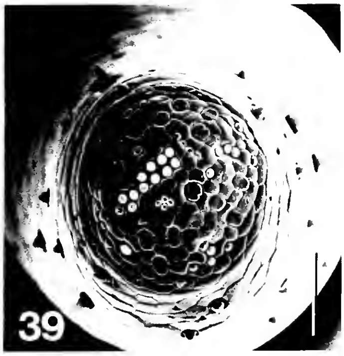
Figures 24–27. Cleared mouthpart structures of adult *B. foveum*. All figures at same scale; scale bar = 100 μm. 24. Ventral view of labrum. 25. Dorsal view of right mandible. 26. Ventral view of right maxilla. 27. Ventral view of mentum, ligula, and right labial palpus.

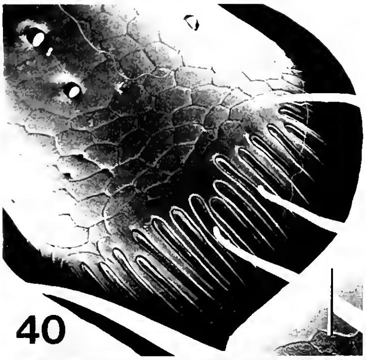
Figure 28. Dorsal view of cleared right mandible of *B. confusum*. Same scale as Figures 24–27.

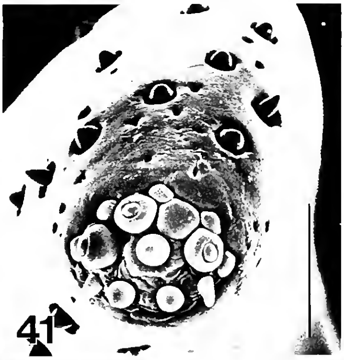


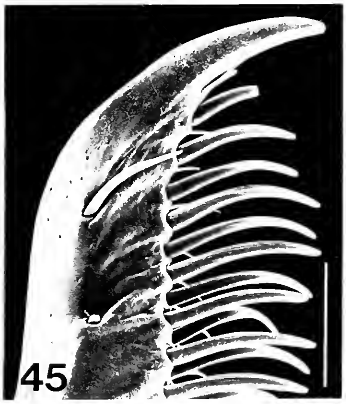
Figures 29–36. Mandibles of *Bracteon*. 29. Left mandible of *B. foveum*. Scale bar = 200 μm. (**a.** Dorsal view. **b.** Mesal view. **c.** Ventral view.) 30. Right mandible of *B. foveum*. Scale bar = 200 μm. (**a.** Dorsal view. **b.** Mesal view. **c.** Ventral view.) 31. Cleared right mandible of *B. foveum*, showing mesal pore canals. Scale bar = 200 μm. 32. Basal mesal edge of right mandible of *B. foveum*, ventral view. Scale bar = 40 μm. 33. Basal mesal edge of right mandible of *B. punctatostriatum*, ventral view. Scale bar = 40 μm. 34. Microsculpture around terebral tooth of right mandible of *B. punctatostriatum*. Scale bar = 10 μm. 35. Dorsal surface of right mandible of *B. balli*, near dorsal condyle. Scale bar = 40 μm. 36. Dorsal surface of right mandible of *B. foveum*, near dorsal condyle. Scale bar = 40 μm.



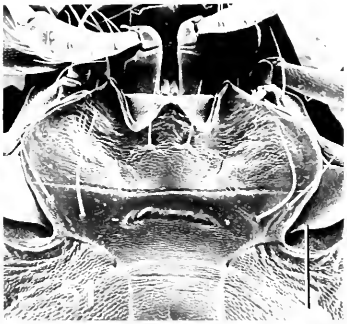


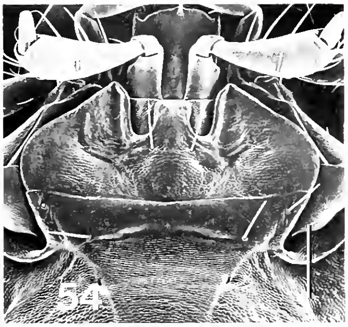


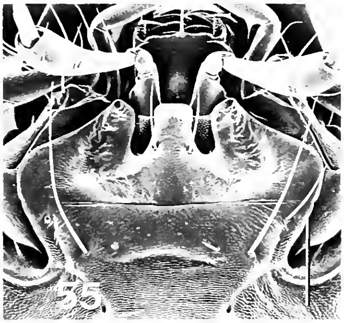


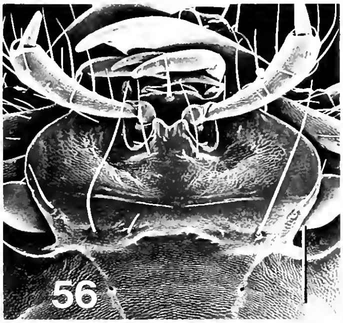


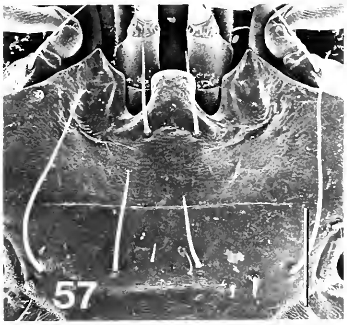
Figures 37–41. Mouthpart sensilla of adult *Bracteon*. Scale bars = 10 μm. 37. Epipharynx of *B. foveum*, right side near epipharyngeal hump, ventral view. 38. Apex of maxillary palp of *B. foveum*. 39. Apex of labial palp of *B. foveum*. 40. Digitiform sensilla at base of maxillary palp of *B. balli*. 41. Apex of galea of *B. foveum*.

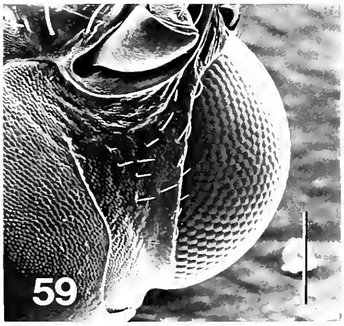


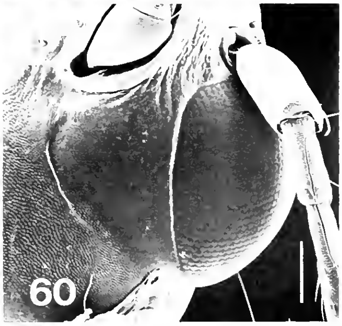


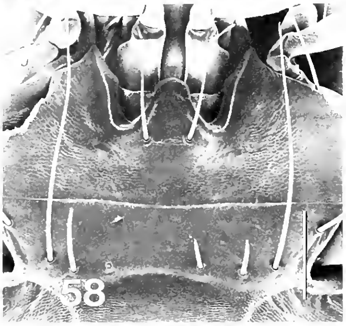










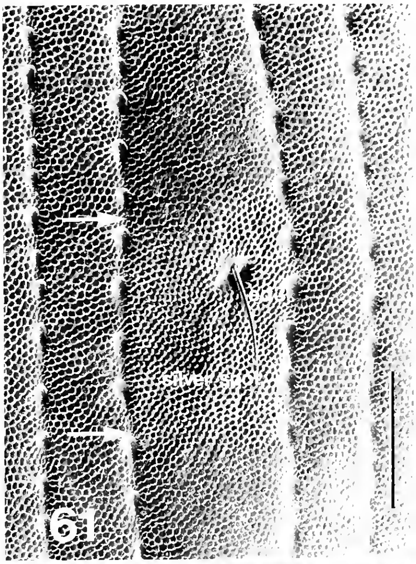


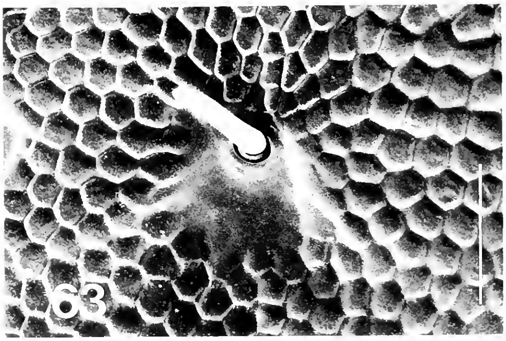
Figures 49–58. Menta of *Bembidion* adults, ventral view. Scale bars = 200 μm. 49. *B. balli*. 50. *B. alaskense*. 51. *B. lapponicum*. 52. *B. punctatostriatum*. 53. *B. hesperium*. 54. *B. zephyrum*. 55. *B. levettei carrianum*. 56. *B. litorale*. 57. *B. bifossulatum cheyennense*. 58. *B. bifossulatum bifossulatum*.

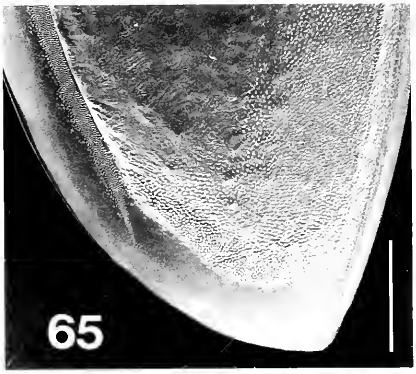
Figures 59–60. Lateroventral views of *Bracteon* heads. Scale bars = 200 μm. 59. *B. lapponicum*. 60. *B. punctatostriatum*.

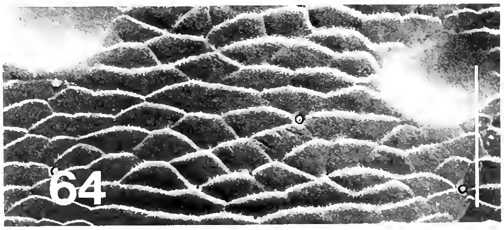
⟵

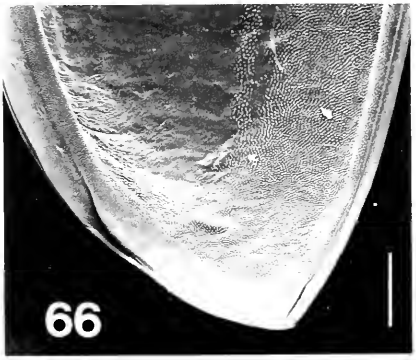
Figures 42–48. Right laciniae of *Bembidion*. Scale bars = 100 μm. 42. *B. confusum*, dorsal view. 43. *B. bowditchii*, dorsal view. 44. *B. lapponicum*, ventral view. Note subapical ridge (arrow). 45. *B. punctatostriatum*, ventral view. 46. *B. lapponicum*, dorsal view. 47. *B. alaskense*, dorsal view. 48. *B. punctatostriatum*, dorsal view.

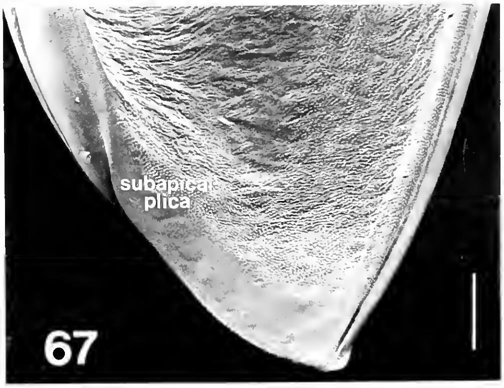






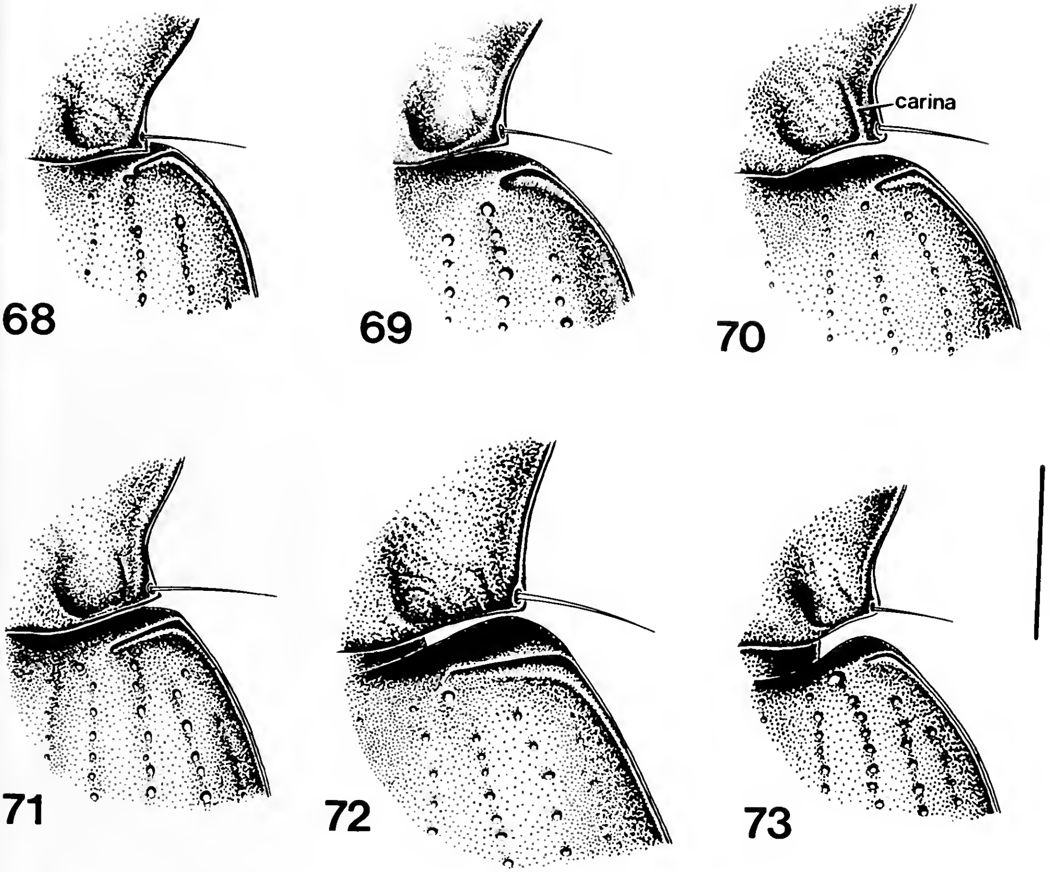


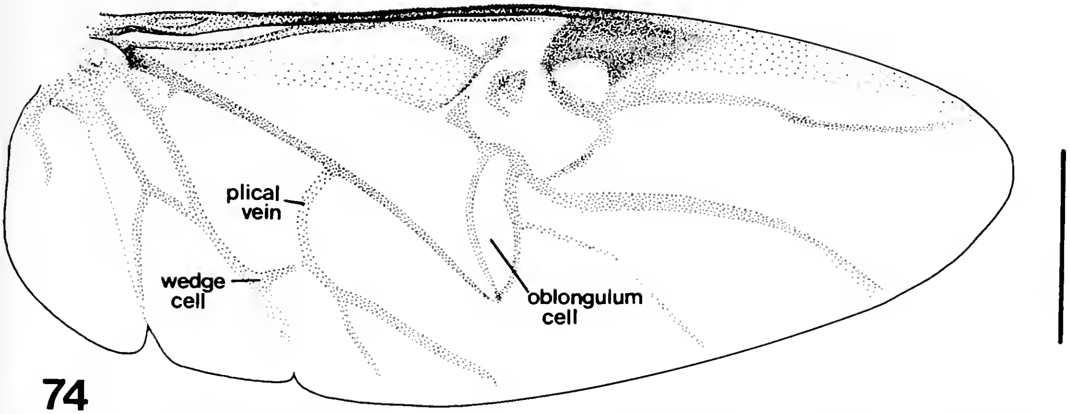




Figures 61–64. Elytral structure, dorsal surface. 61. Right elytron, *B. lapponicum*, around seta ed3. Arrows indicate anterior and posterior limits of silver spot. Scale bar = 200 μm. 62. *B. balli*, microsculpture around seta ed3 in silver spot of elytron. Scale bar = 40 μm. 63. *B. foveum*, microsculpture around seta ed3 in silver spot of elytron. Scale bar = 40 μm. 64. *B. hesperium* male, microsculpture of elytron in interval 6. Scale bar = 40 μm.

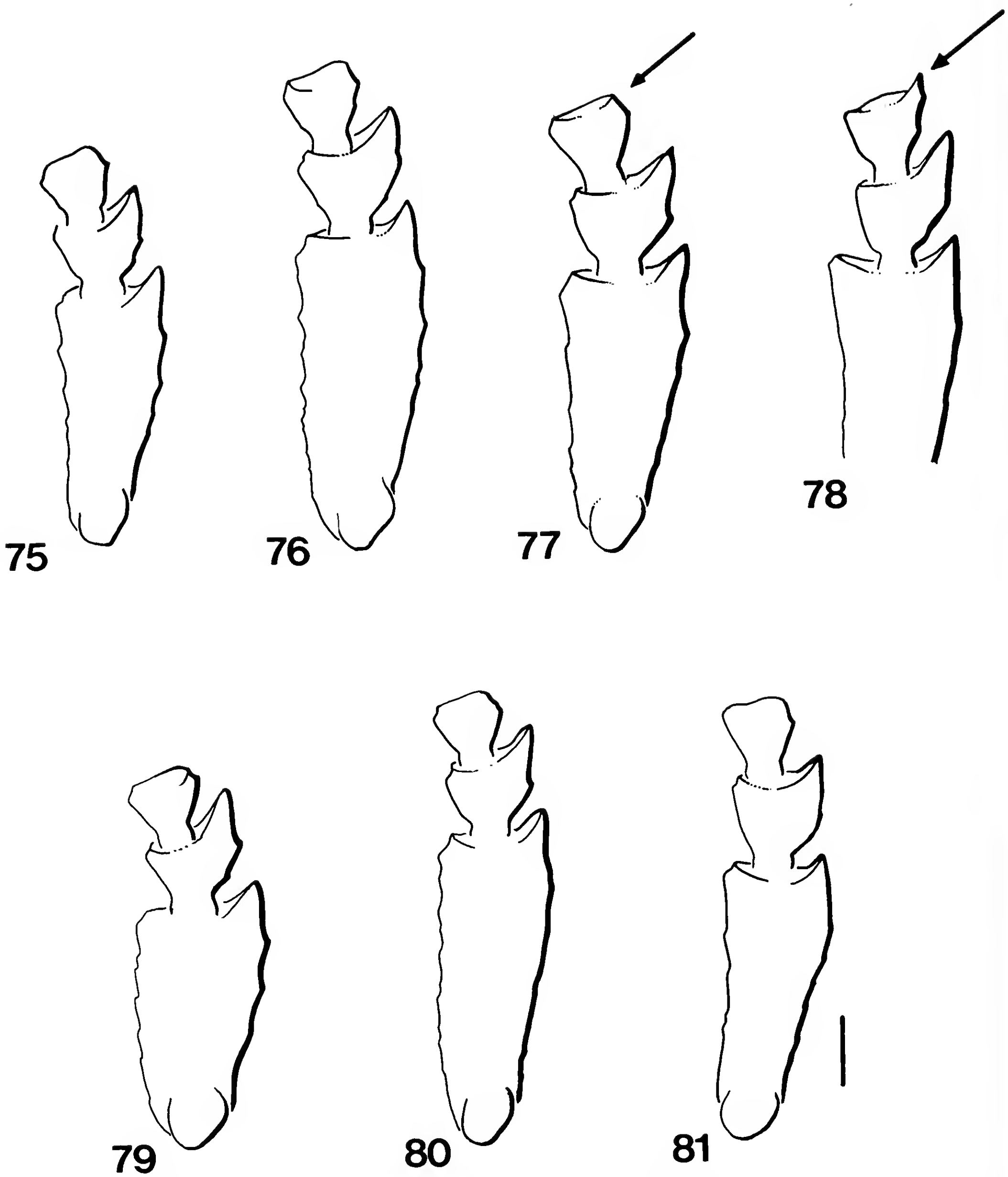
Figures 65–67. Ventral surface of elytral apex, showing subapical plica. Scale bars = 200 μm. 65. *B. aenulum*. 66. *B. confusum*. 67. *B. punctatostriatum*.



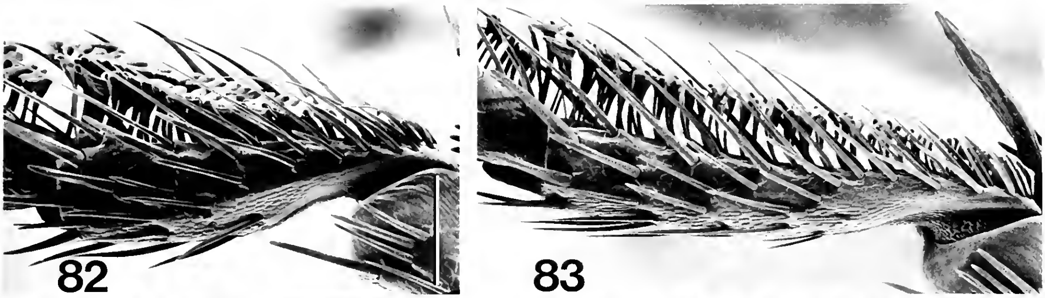


Figures 68–73. Shoulder region of *Bracteon*. Scale bar = 0.5 mm. 68. *B. balli*. 69. *B. foveum*. 70. *B. carinula*. 71. *B. lapponicum*. 72. *B. punctatostriatum*. 73. *B. inaequale*.

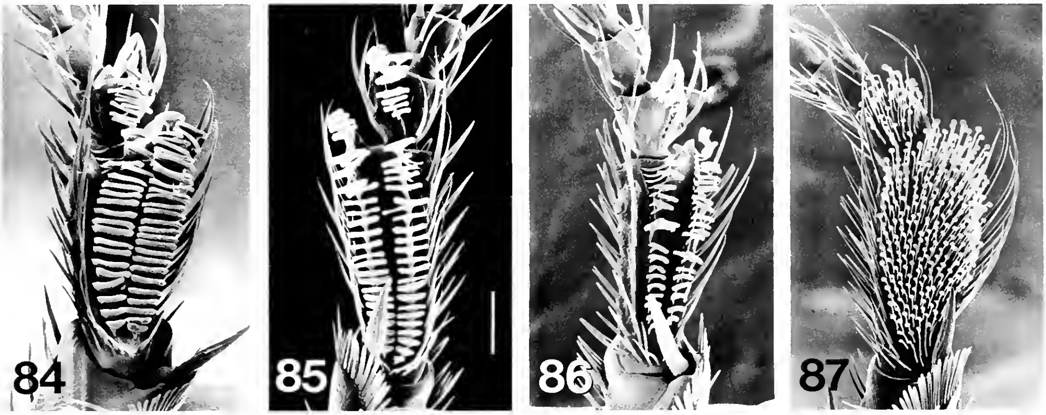
Figure 74. Right metathoracic wing of *B. inaequale*. Scale bar = 1 mm.



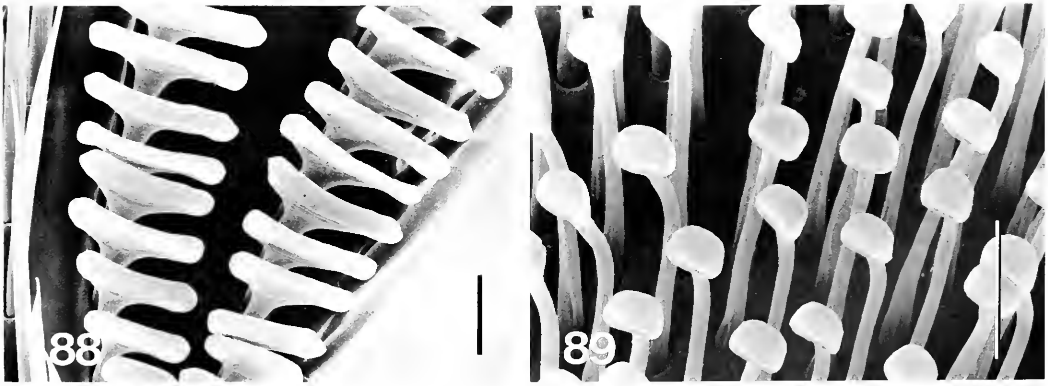
Figures 75–81. First three male left protarsomeres of *Bracteon*, dorsal view. Scale bar = 100 μm. 75. *B. balli.* 76. *B. foveum.* 77. *B. argenteolum.* Note lack of lateroapical projection on protarsomere 3. 78. *B. semenovi.* Note lateroapical projection on protarsomere 3. 79. *B. zephyrum.* 80. *B. levettei levettei.* 81. *B. litorale.*



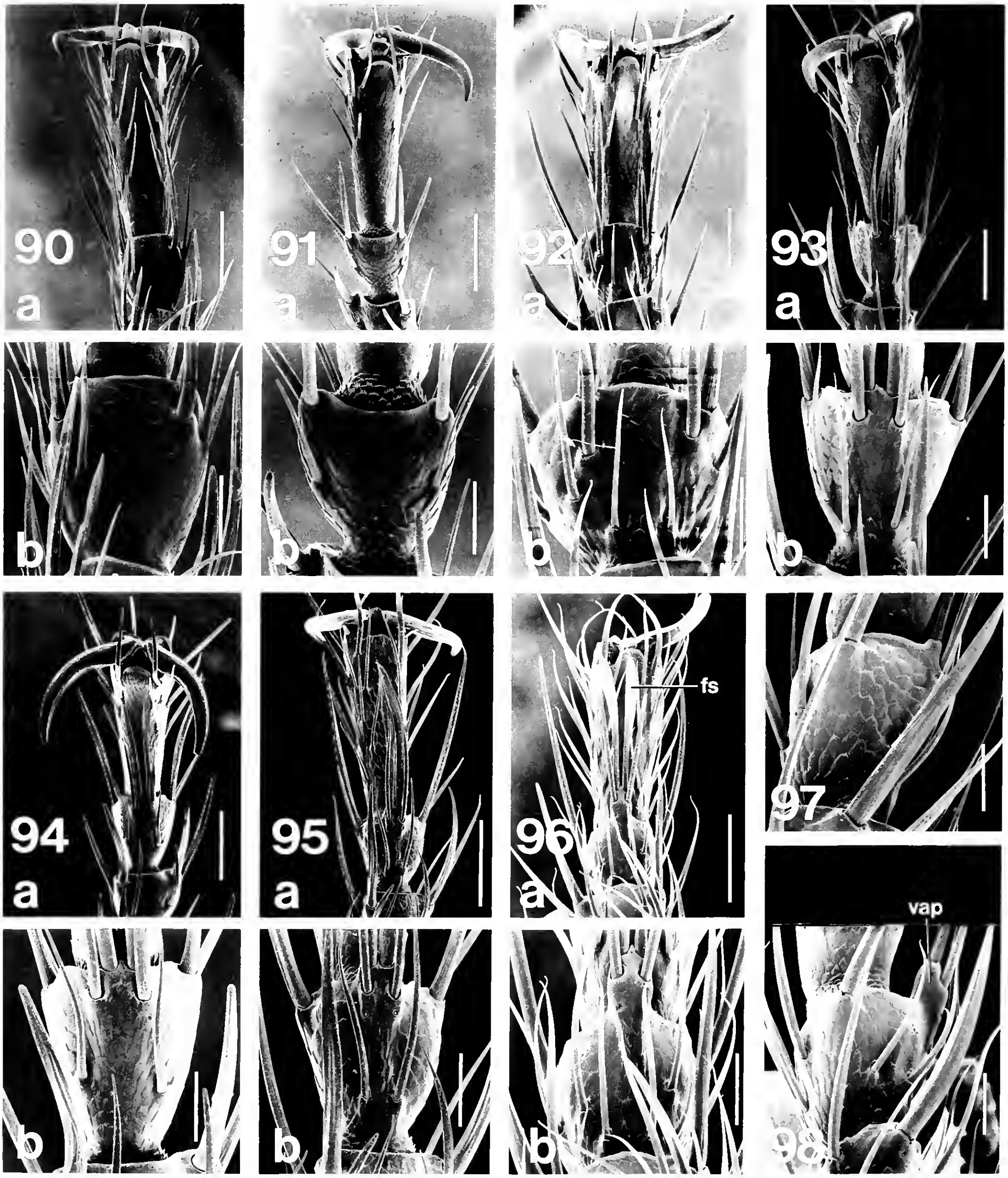
Figures 82, 83. Lateral view of male protarsomere 1. Scale bar = 100 μm; 82. *B. zephyrum*. 83. *B. levettei levettei*.



Figures 84–87. Ventral view of male protarsus. Scale bar = 100 μm. 84. *B. zephyrum*. 85. *B. levettei carrianum*. 86. *B. conicolle*. 87. *Asaphidion alaskanum*.

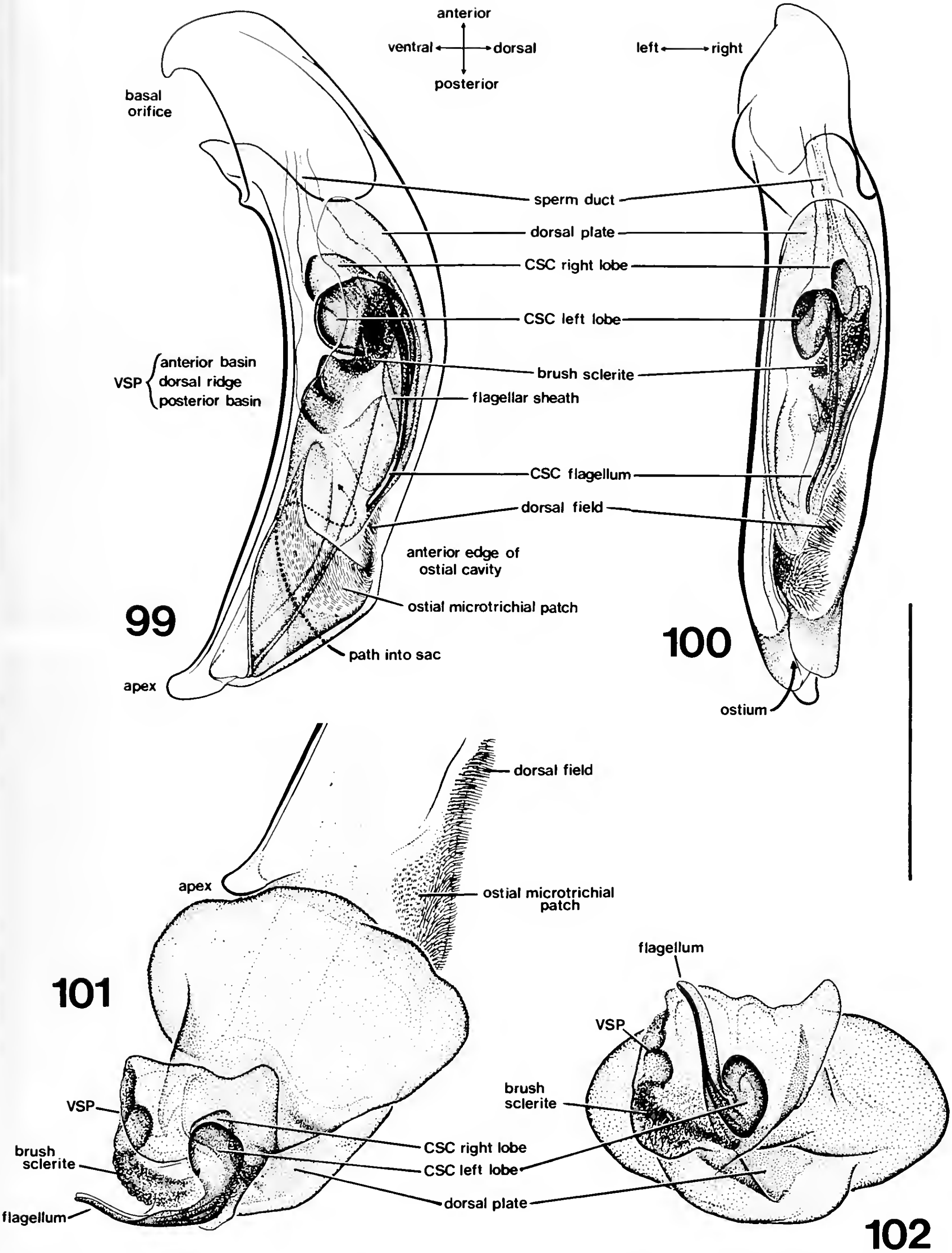


Figures 88, 89. Ventral view of male protarsomere 1, showing adhesive setae. Scale bars = 20 μm. 88. *B. argenteolum*. 89. *Asaphidion alaskanum*.

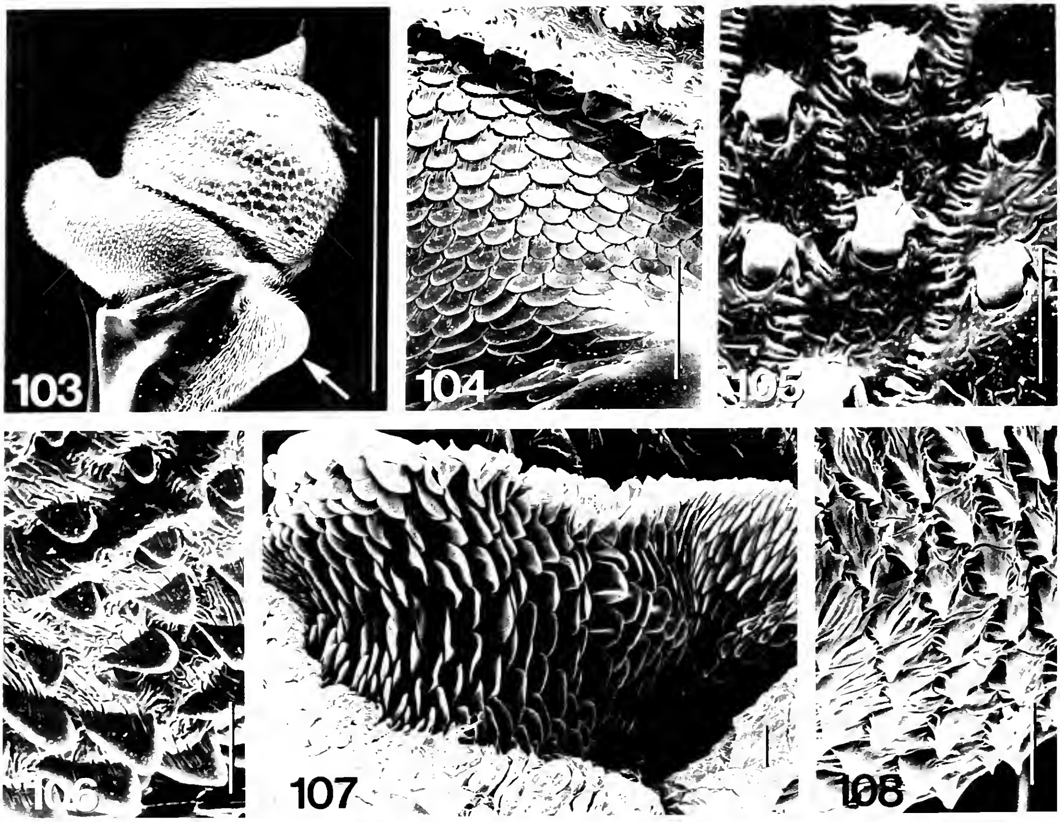


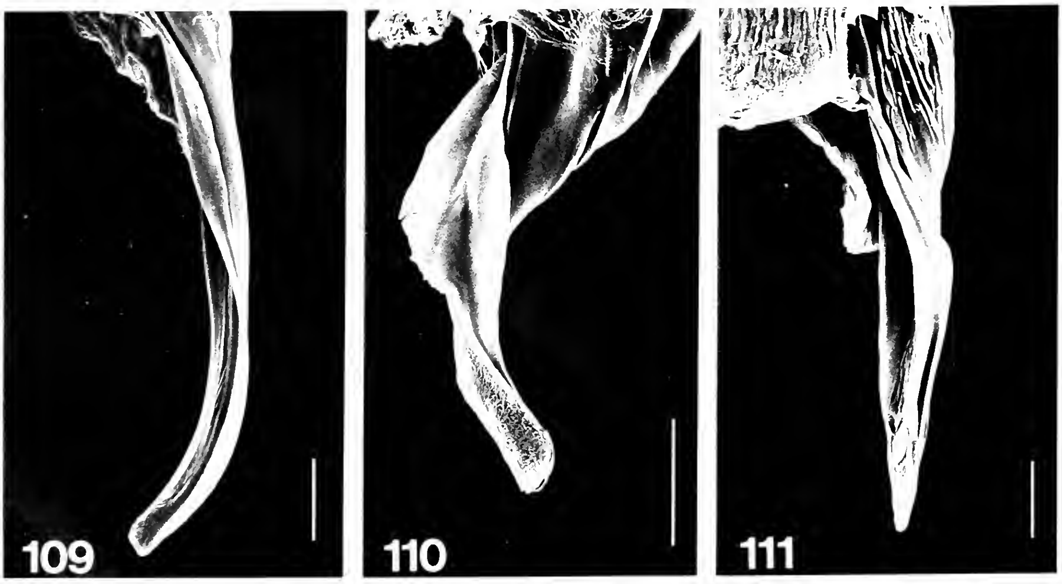
Figures 90–96. Ventral view of male protarsomeres. **a**: protarsomeres 4 and 5; scale bars = 100 μm. **b**: protarsomere 4; scale bars = 40 μm. 90. *Asaphidion alaskanum.* 91. *Bembidion interventor.* 92. *B. alaskense.* 93. *B. argenteolum.* 94. *B. punctatostriatum.* 95. *B. hesperium.* 96. *B. balli.* fs: flattened ventroapical setae of protarsomere 4.

Figures 97, 98. Lateral view of male protarsomere 4. Scale bars = 40 μm. 97. *B. argenteolum.* 98. *B. balli.* vap: ventroapical projection.



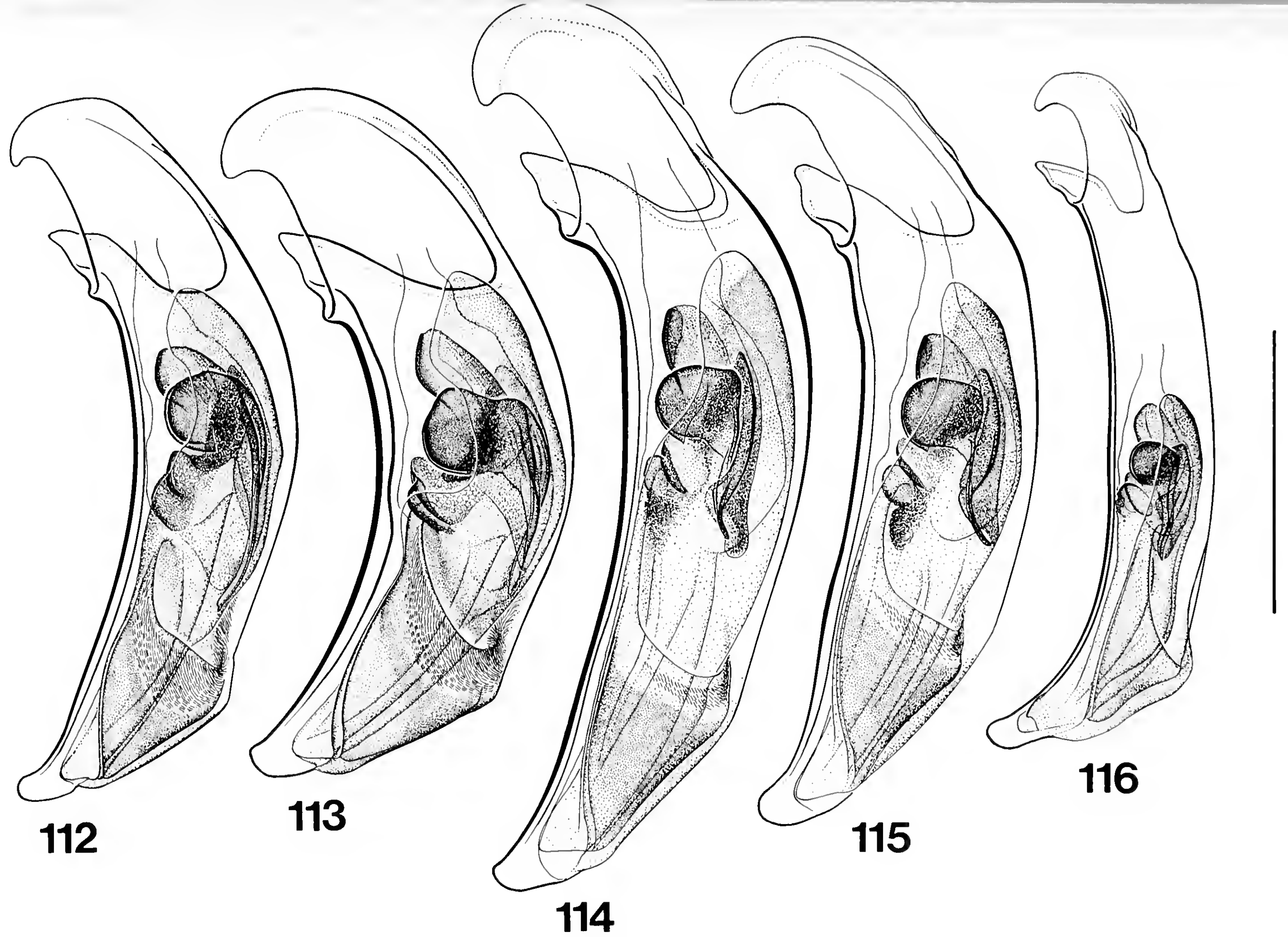
Figures 99–102. Median lobe of male aedeagus of *B. balli;* most membrane microsculpture omitted. Scale bar = 0.5 mm. 99. Left lateral view of median lobe, internal sac inverted. 100. Dorsal view of median lobe, internal sac inverted. 101. Left lateral view of everted internal sac. 102. Apex of everted internal sac.



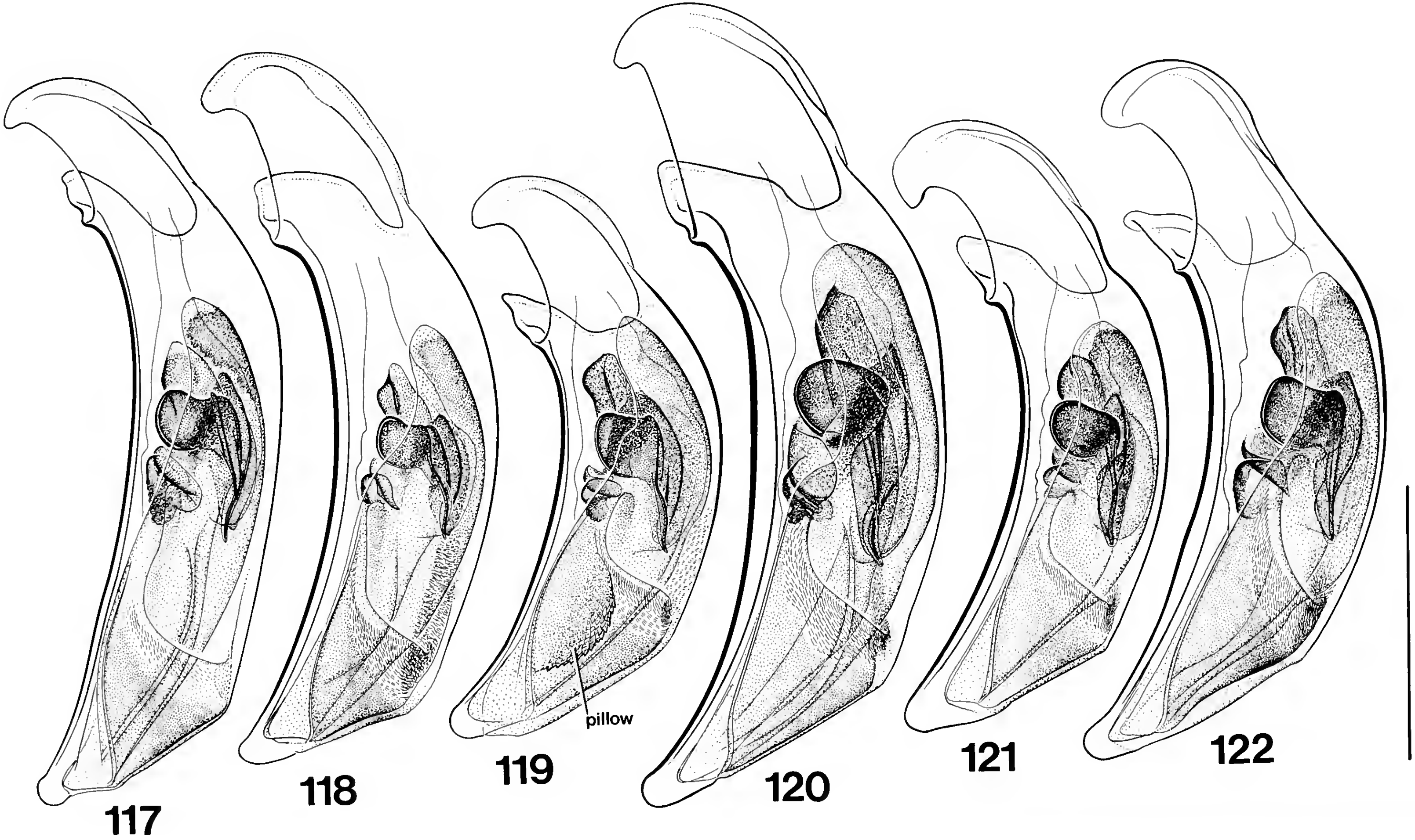


Figures 103–108. Internal sac microsculpture. 103. Everted internal sac of *B. levettei carrianum*, left lateral view. Arrow indicates basodorsal lobe. Scale bar = 500 μm. 104. Everted internal sac of *B. levettei carrianum*, microsculpture on left lateral face near ostial flag. Scale bar = 50 μm. 105. Everted internal sac of *B. levettei carrianum*, microsculpture on left lateral face. Scale bar = 20 μm. 106. Everted internal sac of *B. levettei carrianum*, microsculpture on right lateral face. Scale bar = 20 μm. 107. Everted internal sac of *B. bifossulatum cheyennense*, showing brush sclerite. Scale bar = 20 μm. 108. Everted internal sac of *B. chalceum*, showing large scales. Scale bar = 20 μm.

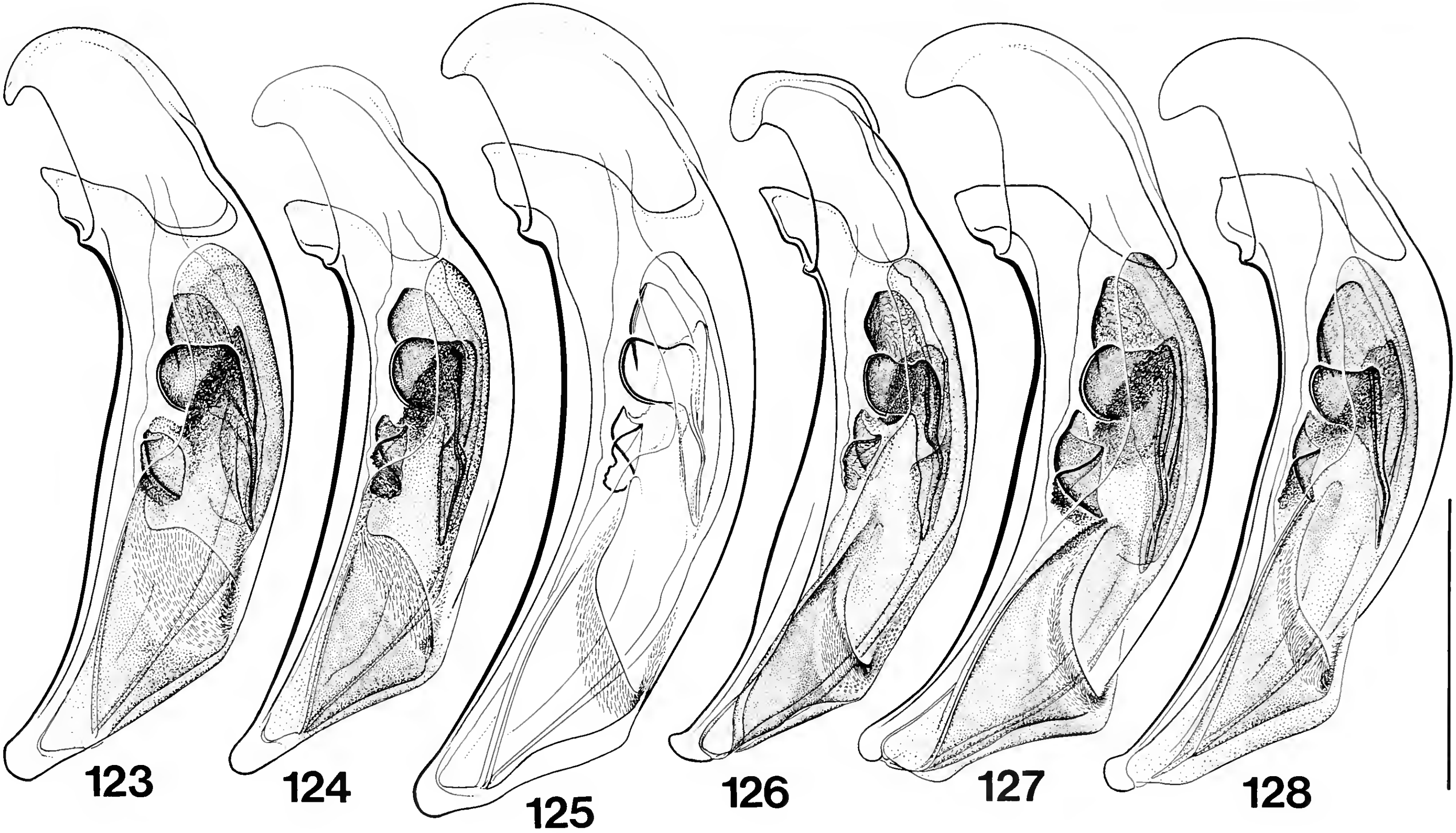
Figures 109–111. Left lateral view of flagella of *Bracteon*. View slightly more ventral than in Figures 129–144. Scale bars = 40 μm. 109. *B. balli*. 110. *B. alaskense*. 111. *B. levettei carrianum*.



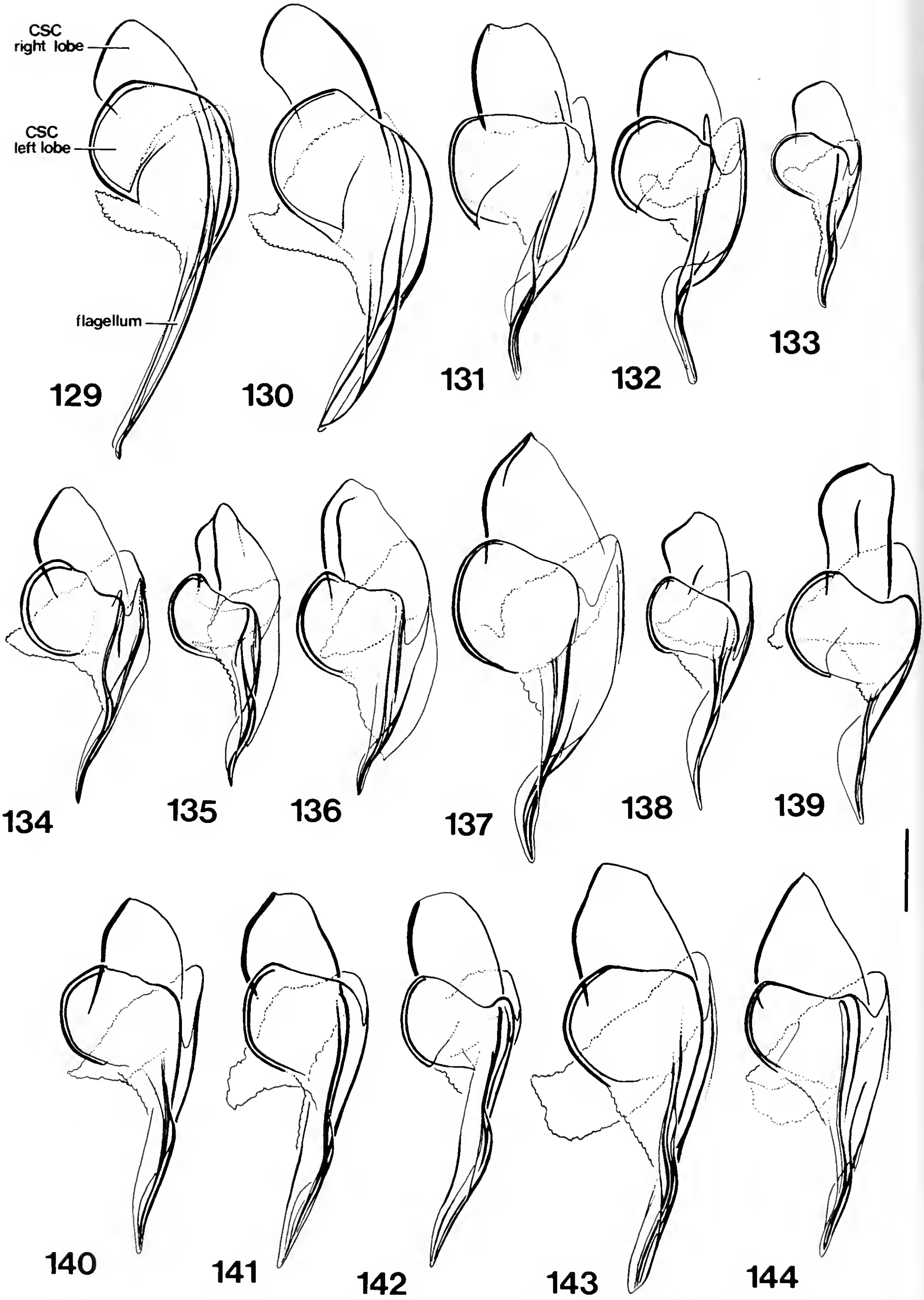
Figures 112–116. Median lobe of aedeagus, left lateral view. Scale bar = 0.5 mm. 112. *B. balli*. 113. *B. foveum*. 114. *B. argenteolum*. 115. *B. alaskense*. 116. *B. stenoderum*.



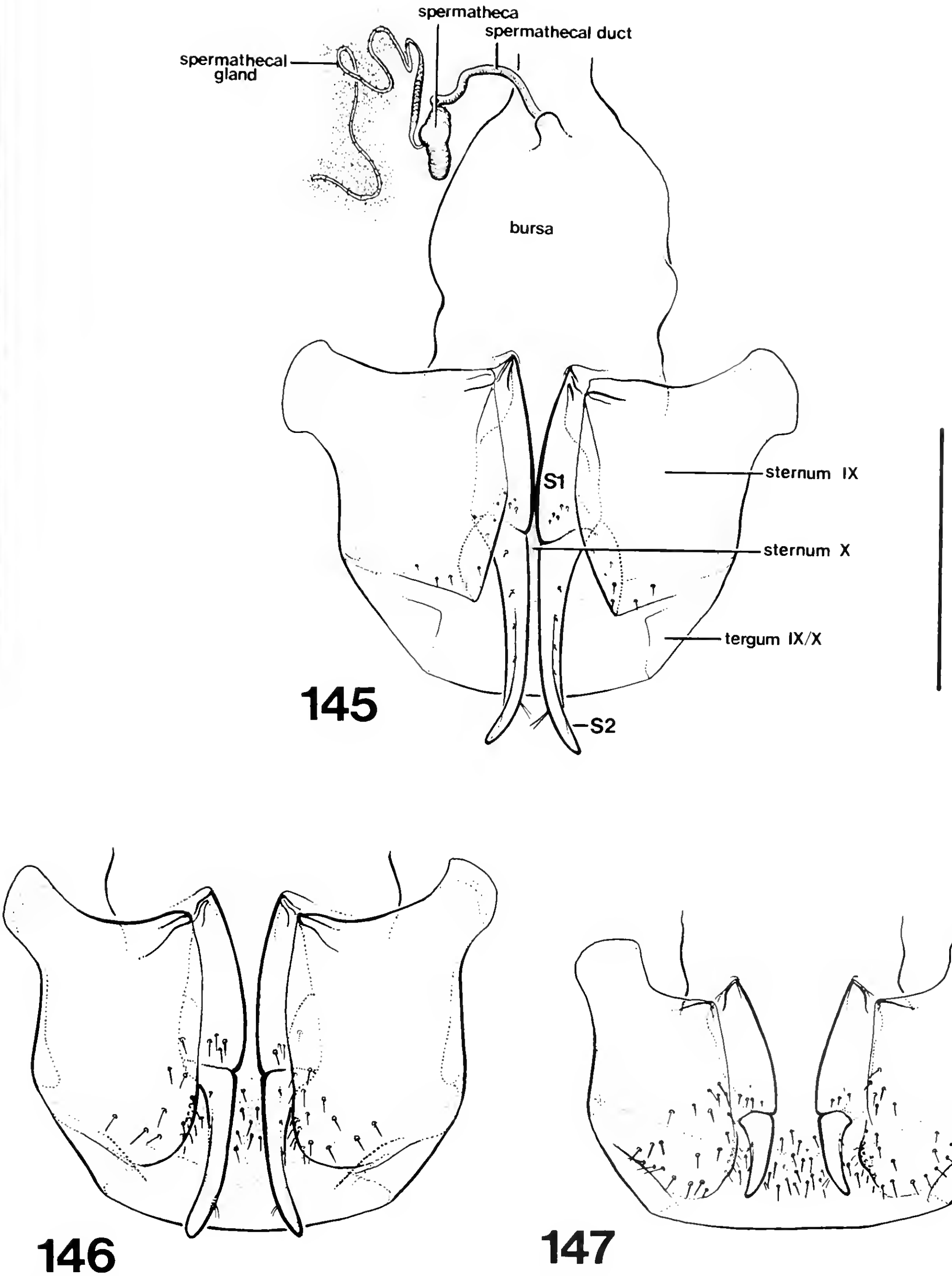
Figures 117–122. Median lobe of aedeagus, left lateral view. Scale bar = 0.5 mm. 117. *B. carinula*. 118. *B. velox*. 119. *B. lapponicum*. 120. *B. punctatostriatum*. 121. *B. hesperium*. 122. *B. lorquinii*.



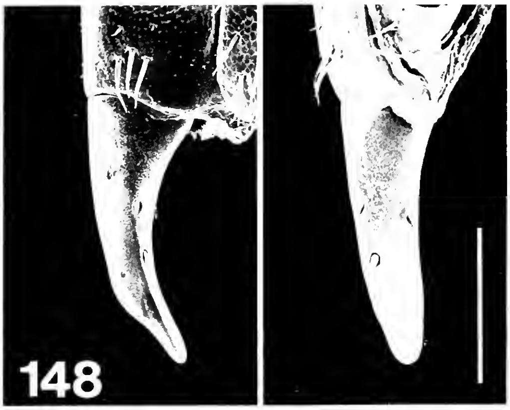
Figures 123–128. Median lobe of aedeagus, left lateral view. Scale bar = 0.5 mm. 123. *B. zephyrum*. 124. *B. levettei carrianum*. 125. *B. levettei levettei*. 126. *B. inaequale*. 127. *B. litorale*. 128. *B. conicolle*.

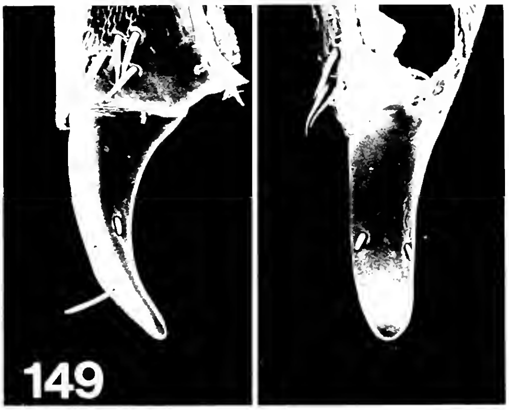


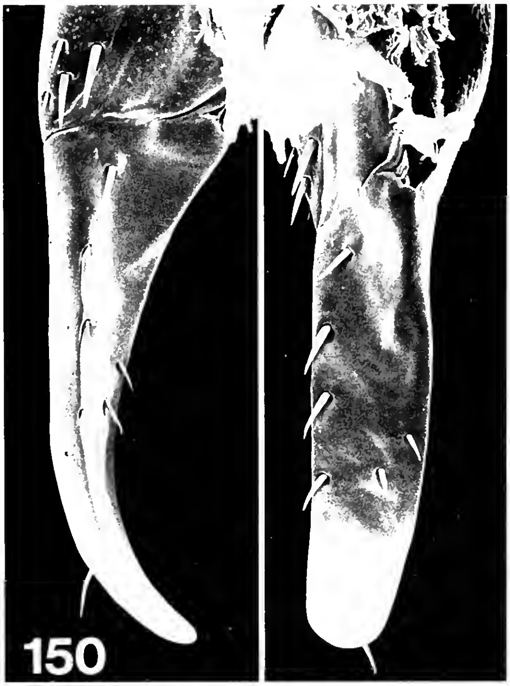
Figures 129–144. Central sclerite complex of male internal sac, with outline of brush sclerite, left lateral view. Scale bar = 100 μm. 129. *B. balli*. 130. *B. foveum*. 131. *B. argenteolum*. 132. *B. alaskense*. 133. *B. stenoderum*. 134. *B. carinula*. 135. *B. velox*. 136. *B. lapponicum*. 137. *B. punctatostriatum*. 138. *B. hesperium*. 139. *B. lorquinii*. 140. *B. zephyrum*. 141. *B. levettei carrianum*. 142. *B. inaequale*. 143. *B. litorale*. 144. *B. conicolle*.



Figures 145–147. Ventral view of cleared, inverted female genitalia. Scale bar = 0.5 mm. 145. *B. carinula.* 146. *B. alaskense.* 147. *B. balli.*

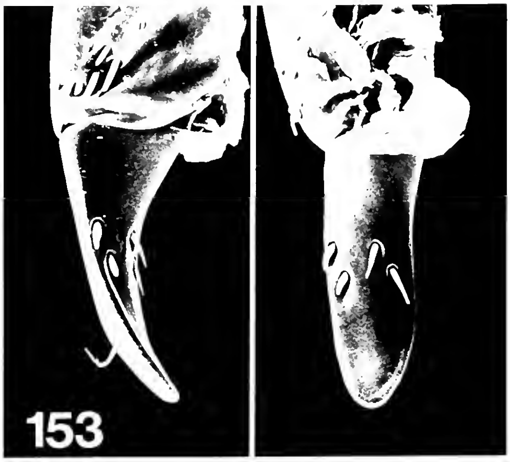

148


149

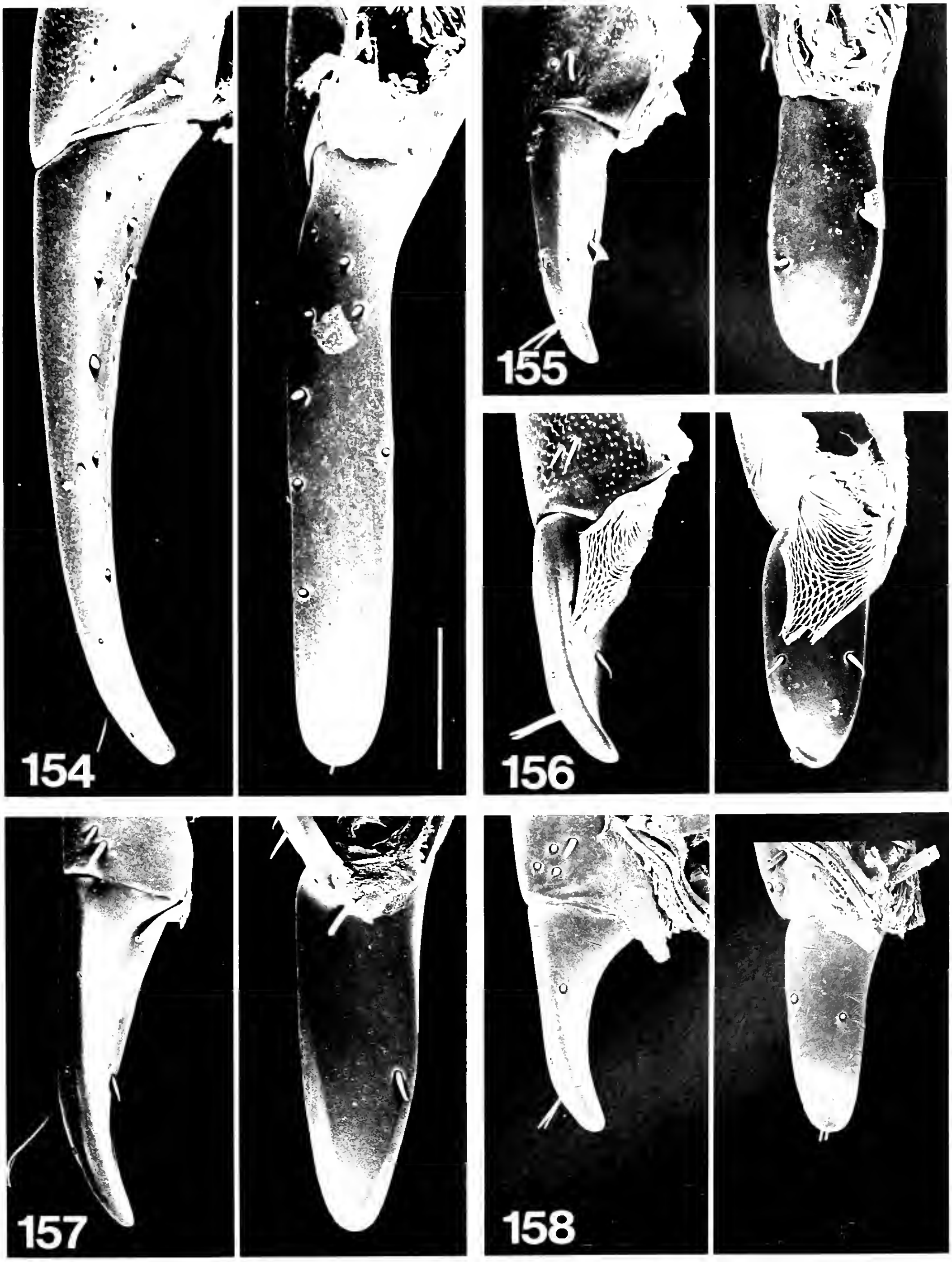

150


151


152

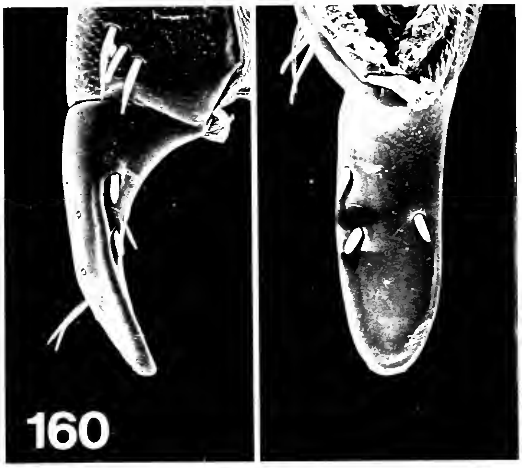

153

Figures 148–153. First and second left stylomeres of female genitalia. Scale bar = 100 μm; all figures at same scale. **Left-hand picture**: dorsal view. **Right-hand picture**: left lateral view. 148. *B. balli*. 149. *B. foveum*. 150. *B. argenteolum*. 151. *B. alaskense*. 152. *B. stenoderum*. 153. *B. punctatostriatum*.

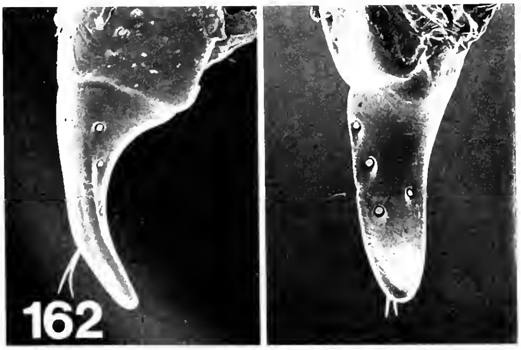


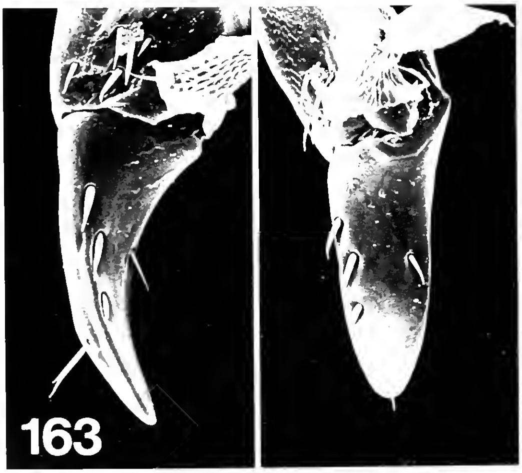
Figures 154–158. First and second left stylomeres of female genitalia. Scale bar = 100 μm; all figures at same scale. **Left-hand picture**: dorsal view. **Right-hand picture**: left lateral view. 154. *B. carinula*. 155. *B. velox*. 156. *B. lapponicum*. 157. *B. hesperium*. 158. *B. lorquinii*.

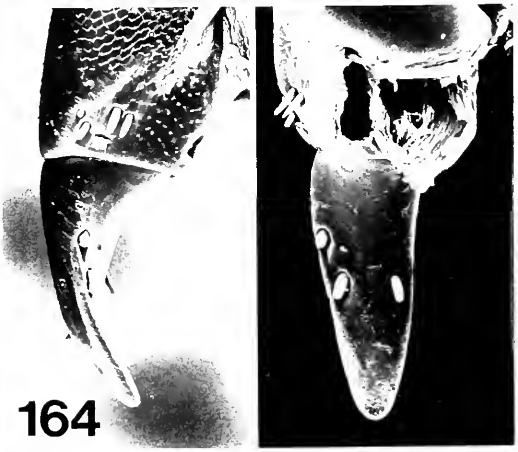

159


160

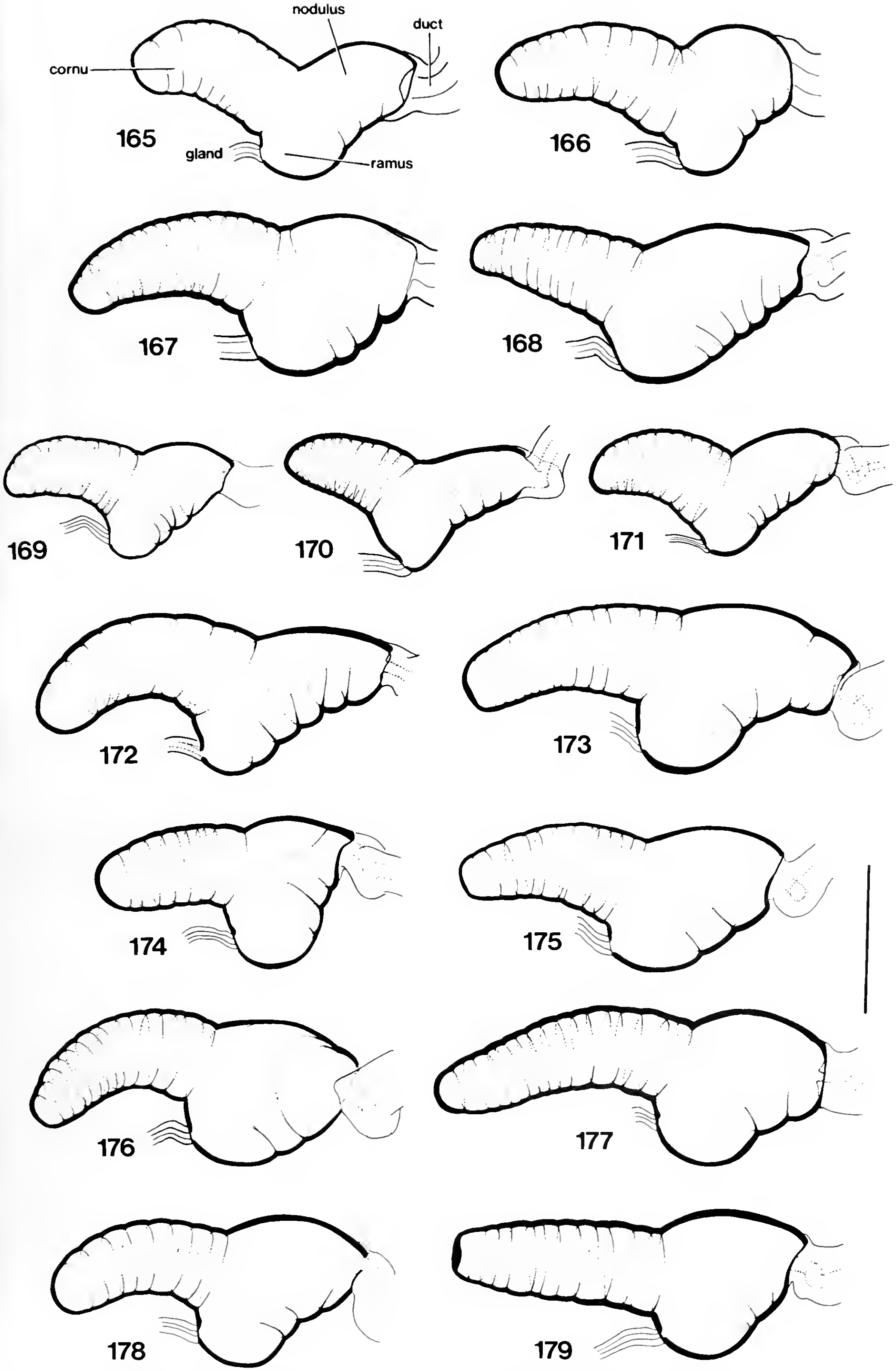

161


162

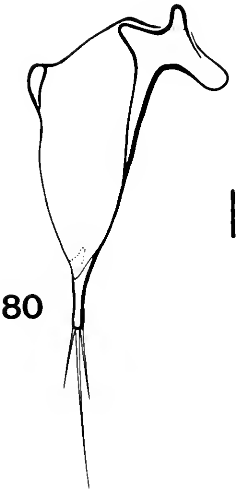

163


164

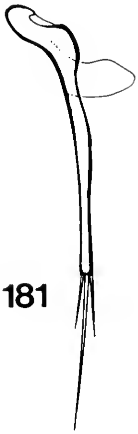
Figures 159–164. First and second left stylomeres of female genitalia. Scale bar 100 μm; all figures at same scale. **Left-hand picture**: dorsal view. **Right-hand picture**: left lateral view. 159. *B. zephyrum*; specimen from northern Oregon. 160. *B. levettei levettei*. 161. *B. levettei carrianum*. 162. *B. inaequale*. 163. *B. litorale*. 164. *B. conicolle*.



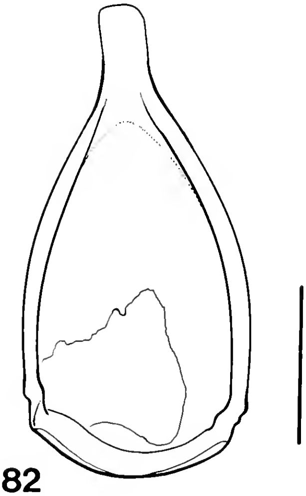
Figures 165–179. Spermathecae of *Bracteon*. Scale bar = 100 μm; all figures at same scale. 165. *B. balli*. 166. *B. foveum*. 167. *B. argenteolum*. 168. *B. alaskense*. 169. *B. stenoderum*. 170. *B. carinula*. 171. *B. velox*. 172. *B. lapponicum*. 173. *B. punctatostriatum*. 174. *B. hesperium*. 175. *B. lorquinii*. 176. *B. zephyrum*. 177. *B. levettei carrianum*. 178. *B. inaequale*. 179. *B. litorale*.



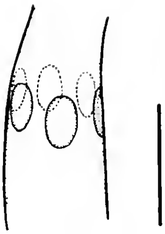
180



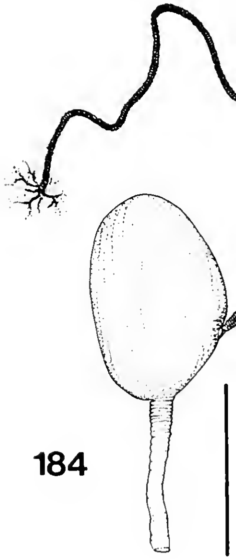
181



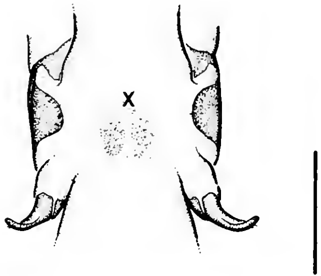
182



183

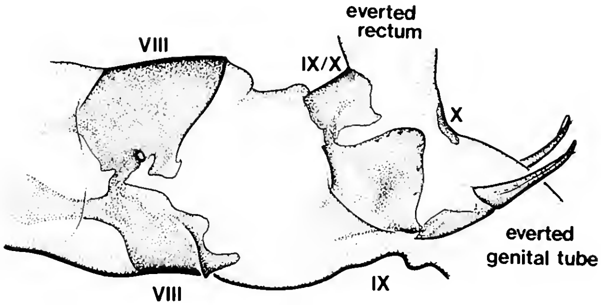


184



185

186



187

Figure 180. Left paramere of *B. levettei carrianum*. Right lateral view. Scale bar = 100 μm.

Figure 181. Right paramere of *B. levettei carrianum*. Left lateral view. Scale as previous figure.

Figure 182. Ring sclerite of *B. levettei carrianum*. Scale bar = 0.5 mm.

Figure 183. Rectal pads of *B. foveum*. Scale bar = 0.5 mm.

Figure 184. Cleared pygidial defense structures of *B. balli*. Left dorsal view. Scale bar = 0.5 mm.

Figures 185–187. Everted female genitalia. Scale bar = 0.5 mm. 185. Dorso-apical view of everted female genitalia of *B. carinula*. 186. Dorso-apical view of everted female genitalia of *B. balli*. 187. Left lateral view of everted female genitalia of *B. carinula*.

188

189

Figures 188, 189. Proventriculi of *Bembidion*. Scale bars = 100 μm. 188. *B. carinula*. 189. *B. (Ocys) harpaloides*. Only one of four lobes shown.

Figure 190. North Saskatchewan River bank at Paynton Ferry, Saskatchewan. Habitat of *B. balli*, *B. foveum*, *B. carinula*, *B. lapponicum*, *B. punctatostriatum*, and *B. levettei carrianum*, as well as the related *B. coxendix* and *B. bifossulatum cheyennense*.

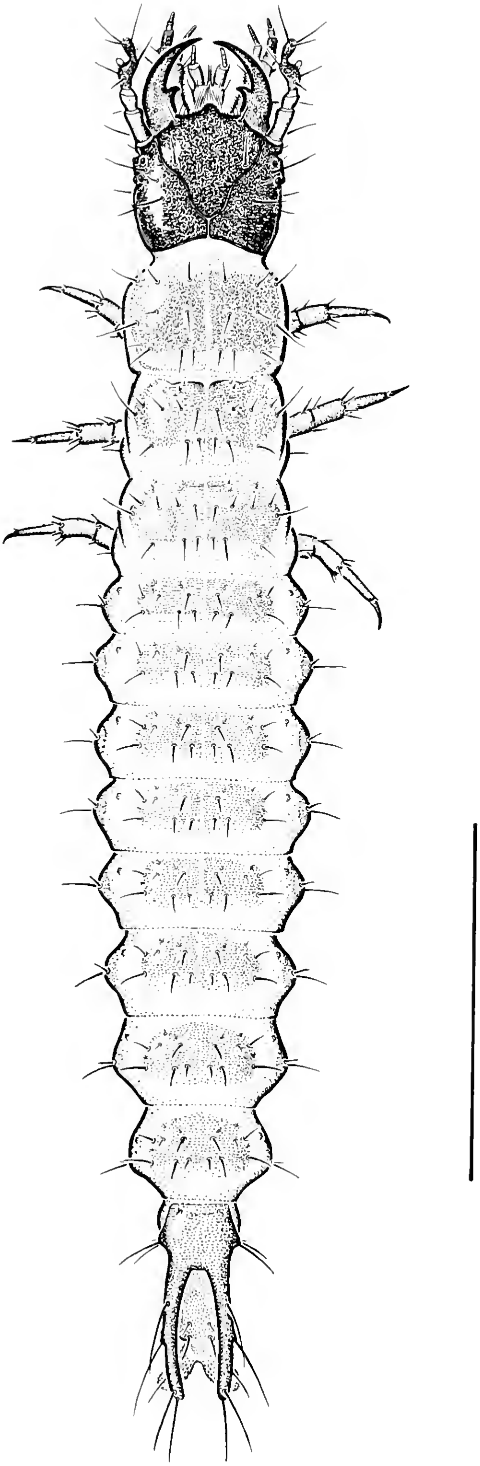
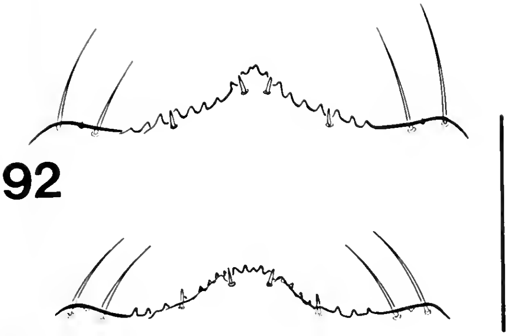
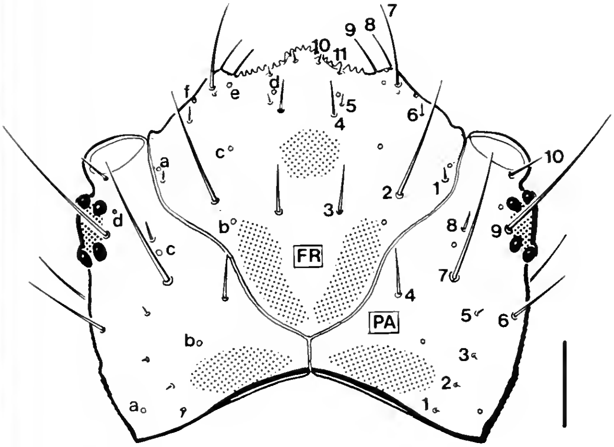


Figure 191. Dorsal view of first instar *B. balli* larva. Scale bar = 1 mm.

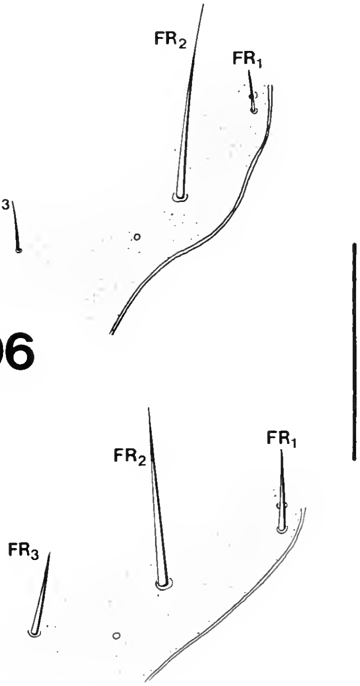

192

193


195



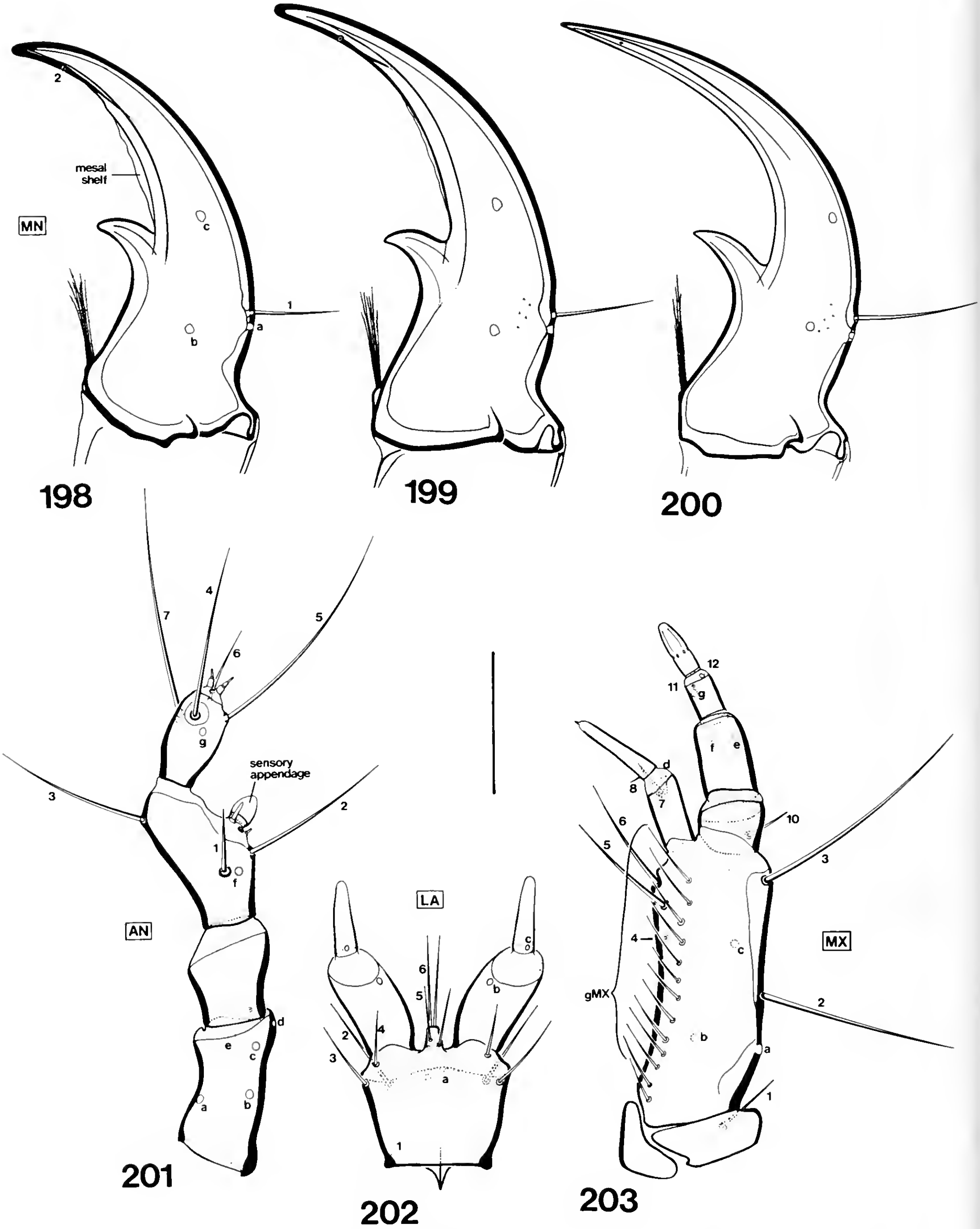
194



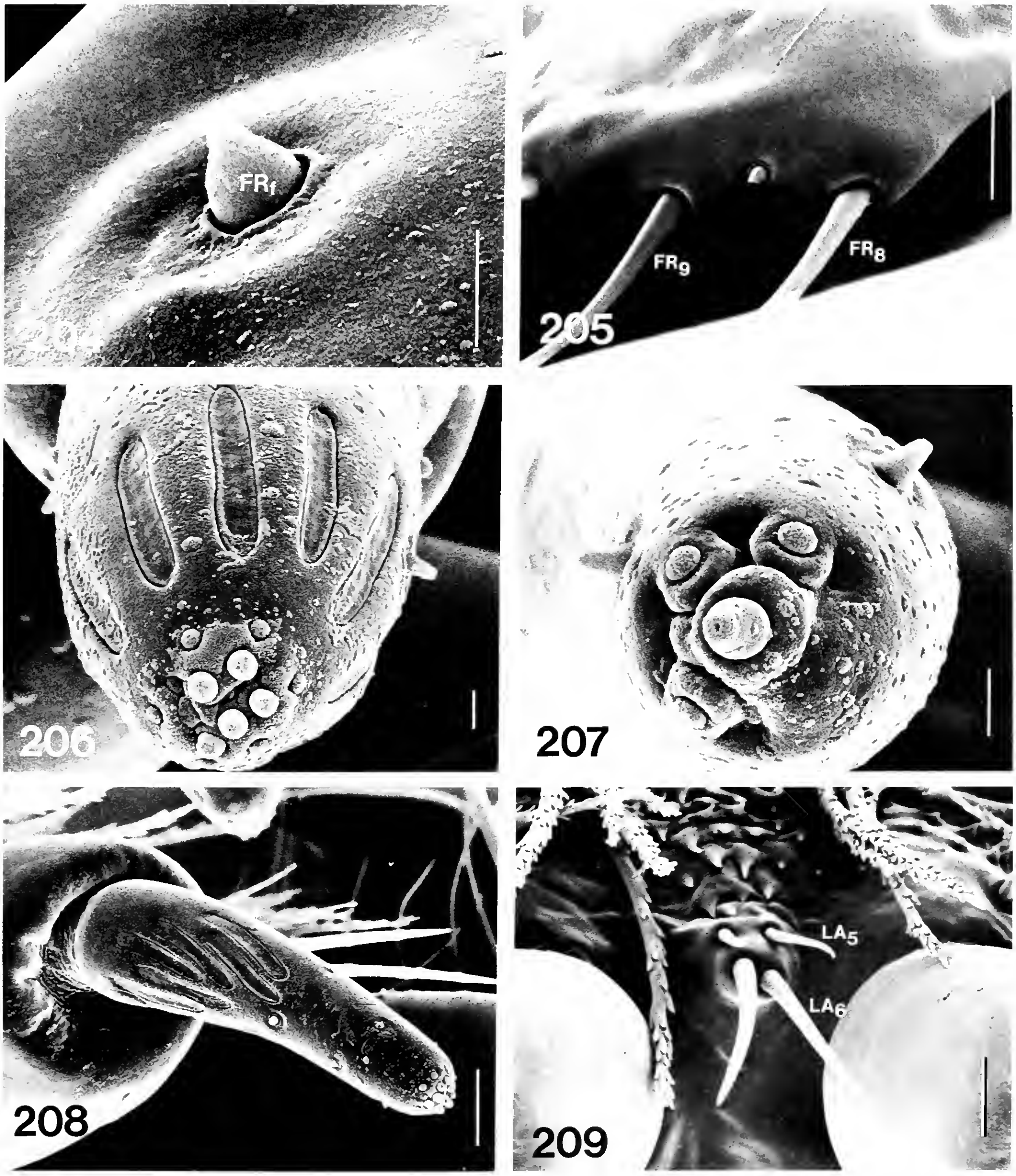
196

197

Figures 192–197. Bembidiine larvae. Boxed letters represent the two-letter sclerite or organ code used for sensillar nomenclature (Bousquet and Goulet, 1984). Scale bars all 100 μm, except for Figure 195, for which scale bar = 10 μm. Figure 192 at same scale as Figure 193. Figure 196 at same scale as Figure 197. 192. Nasale of first instar *B. coxendix*. 193. Nasale of first instar *B. inaequale*. 194. Head of first instar *B. punctatostriatum*, dorsal view. 195. Apex of seta FR_2 of first instar *Asaphidion alaskanum*. 196. Right central portion of frontale of first instar *B. balli*. 197. Right central portion of frontale of first instar *B. carinula*.



Figures 198–203. Cleared head structures of larval *Bembidion*. Scale bar = 100 μm. Boxed letters represent the two-letter sclerite or organ code used for sensillar nomenclature. 198. Right mandible of first instar *B. carinula*, dorsal view. Note wide mesal shelf. 199. Right mandible of first instar *B. foveum*, dorsal view. Note narrow mesal shelf. 200. Right mandible of first instar *B.* (*Odontium*) *coxendix*, dorsal view. 201. Right antenna of first instar *B. foveum*, dorsal view. 202. Labium of first instar *B. foveum*, dorsal view. 203. Right maxilla of first instar *B. foveum*, dorsal view.

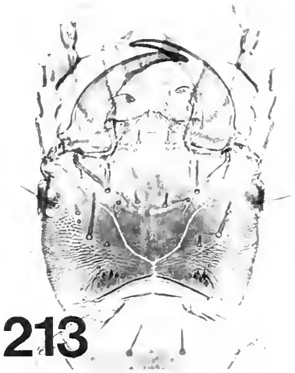


Figures 204–209. Structures of larval *Bracteon*. 204. Sensillum FR_f in first instar *B. punctatostriatum*. Scale bar = 2 μm. 205. Small sensillum between FR_8 and FR_9 in first instar *B. foveum*. Scale bar = 10 μm. 206. Apex of maxillary palpus of first instar *B. lapponicum*. Scale bar = 2 μm. 207. Apex of galea of first instar *B. lapponicum*. Scale bar = 2 μm. 208. Apical article of labial palpus of first instar *B. lapponicum*. Scale bar = 10 μm. 209. Anterior view of ligular region of *B. lapponicum*. Note quadrisetose ligula and multiply branched setae. Scale bar = 20 μm.


210


211


212

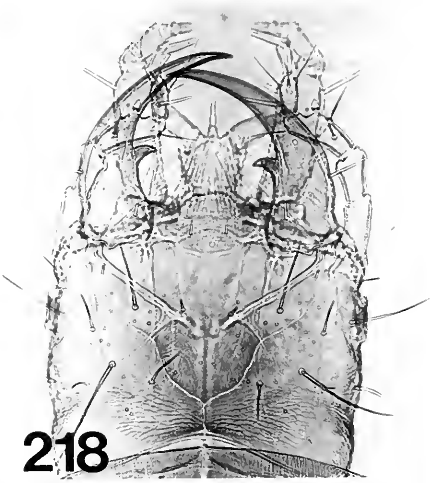

213


214

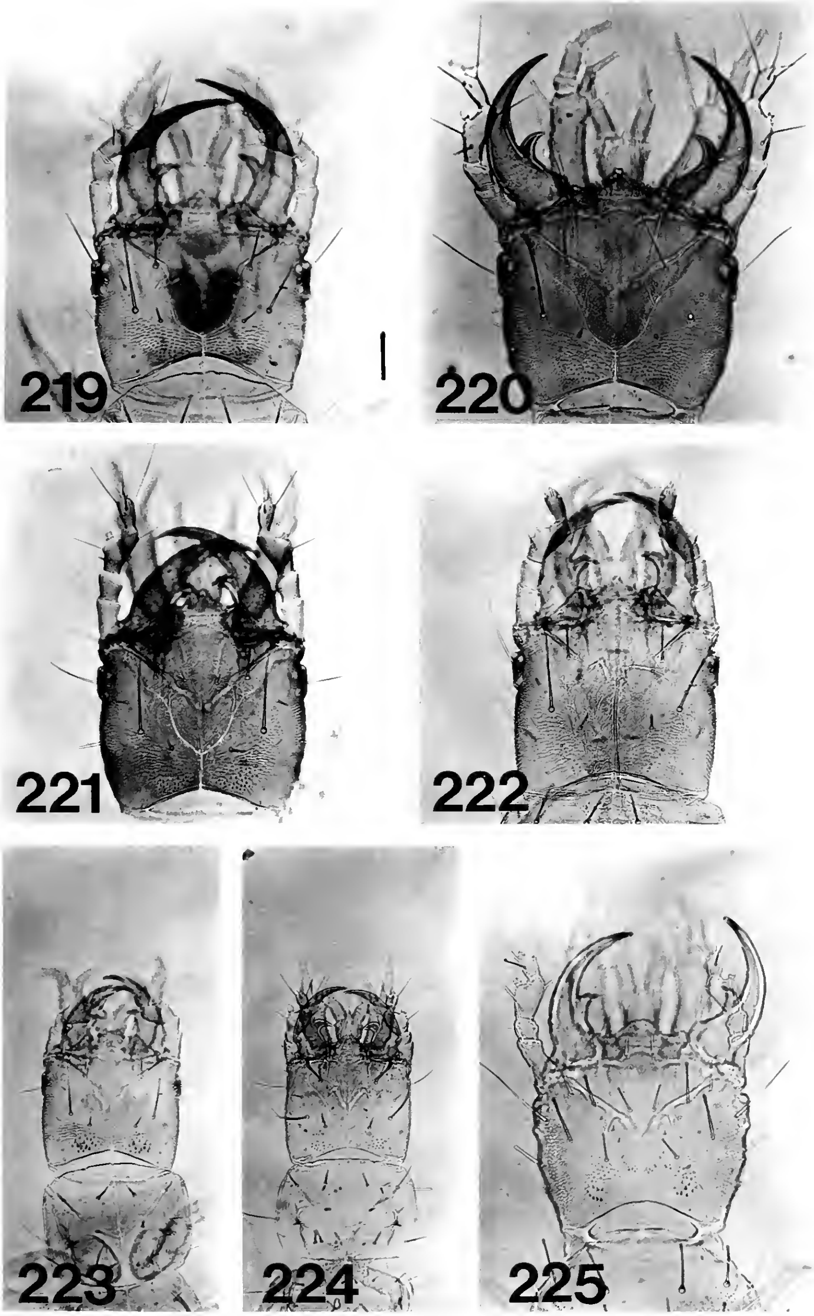

215


216

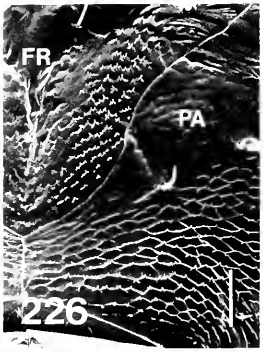

217

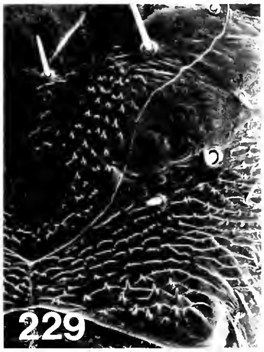

218

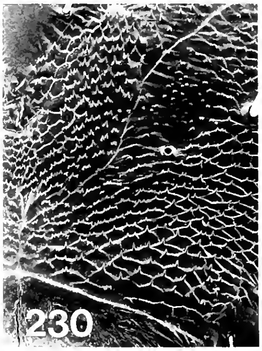
Figures 210–217. Cleared heads of first instar larvae. Scale bar = 100 μm; all figures at same scale. 210. *B. balli*. 211. *B. foveum*. 212. *B. alaskense*. 213. *B. carinula*. 214. *B. lapponicum*. 215. *B. punctatostriatum*. 216. *B. lorquinii*. 217. *B. zephyrum*. Figure 218. Cleared head of second instar *B. levettei levettei* larva. Same scale as Figures 210–217.

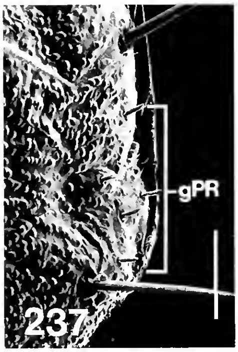


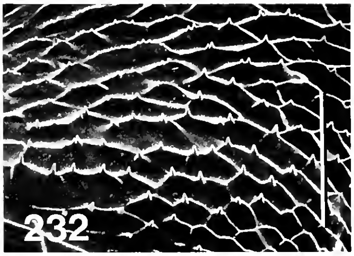
Figures 219–225. Cleared heads of first instar larvae. Scale bar = 100 μm; all figures at same scale. 219. *B. coxendix.* 220. *B. bifossulatum cheyennense.* 221. *B. chalceum.* 222. *B. antiquum.* 223. *B. aenulum.* 224. *B. obtusum.* 225. *Asaphidion alaskanum.*

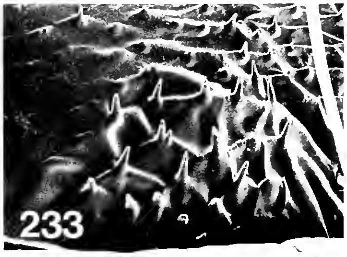


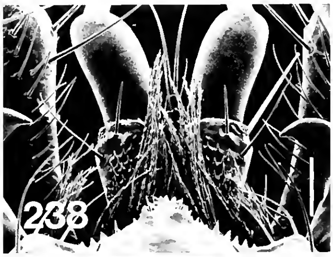


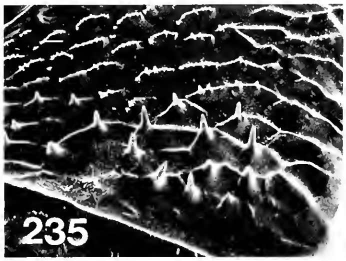








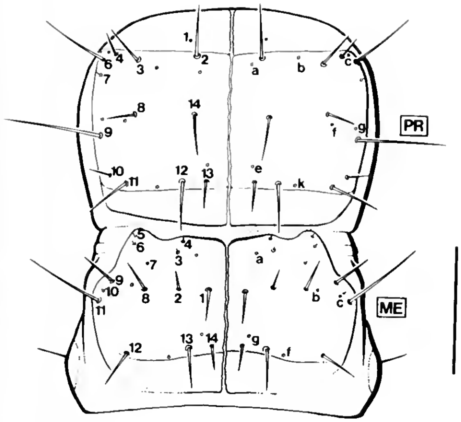




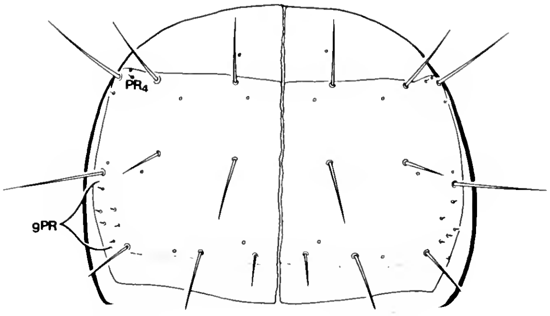
Figures 226–231. First instar *Bracteon*, central and right portions of posterior part of head. Scale bar = 40 μm. 226. *B. foveum*. 227. *B. alaskense*. 228. *B. carinula*. 229. *B. lapponicum*. 230. *B. punctatostriatum*. 231. *B. levettei levettei*.

Figures 232–235. Parietal egg bursters. Scale bar = 40 μm. 232. *B. foveum*. 233. *B. alaskense*. 234. *B. carinula*. 235. *B. lapponicum*.

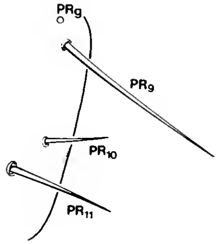
Figures 236–239. First instar *Bracteon*. Scale bars = 40 μm. 236. Right basal corner of pronotum of *B. alaskense*. 237. Right basal corner of pronotum of *B. punctatostriatum*. 238. Dorsal view of nasale and mouth cavity of *B. foveum*. 239. Dorsal view of right mandible of *B. punctatostriatum* near seta MN_1.



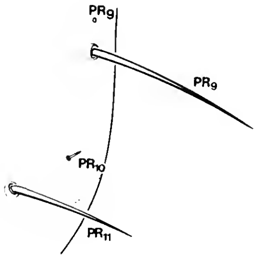
240



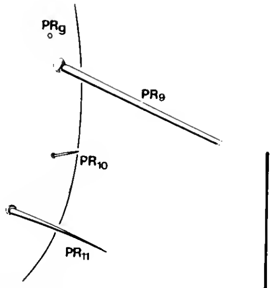
241



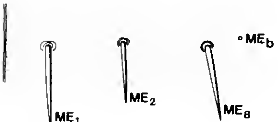
242



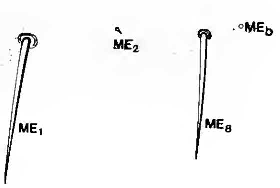
243



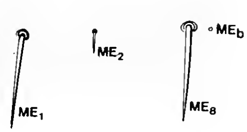
244



245

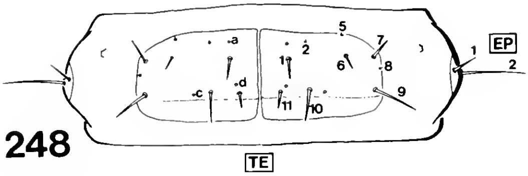


246

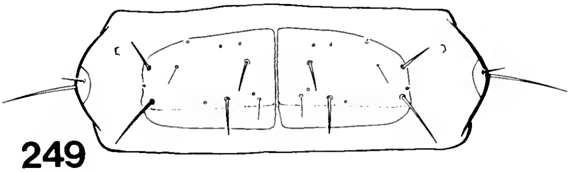


247

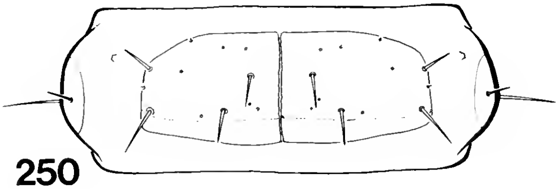
Figures 240–247. Thoraces of larval *Bembidion.* Boxed letters represent the two-letter sclerite or organ code used for sensillar nomenclature. Figure 240 at same scale as Figure 241; scale bar = 200 μm. Figures 242–247 at same scale; scale bar = 100 μm. 240. Pronotum and mesonotum of first instar *B. balli.* 241. Pronotum of first instar *B. punctatostriatum.* 242. Right basilateral corner of pronotum of first instar *B. balli.* 243. Right basilateral corner of pronotum of first instar *B. carinula.* 244. Right basilateral corner of pronotum of first instar *B. integrum.* 245. Right-central portion of mesonotum of first instar *B. balli.* 246. Right-central portion of mesonotum of first instar *B. carinula.* 247. Right-central portion of mesonotum of first instar *B. antiquum.*



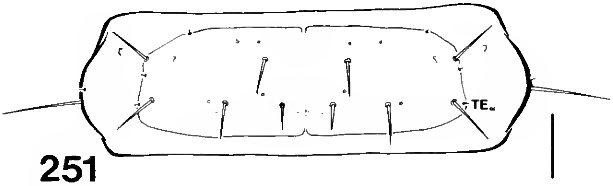
248



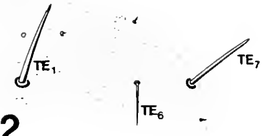
249



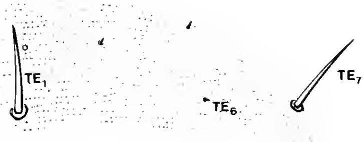
250



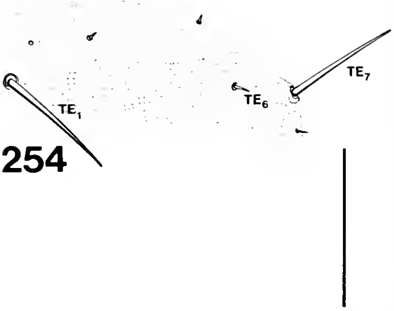
251



252



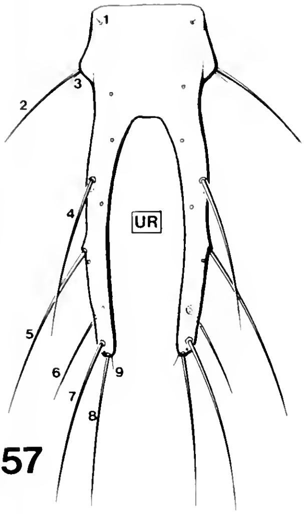
253



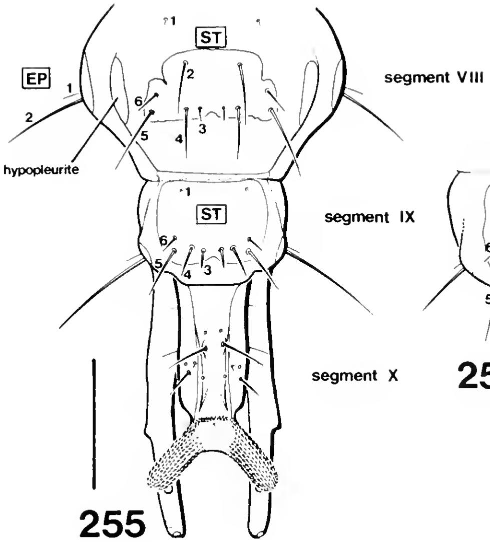
254

Figures 248–251. Second abdominal terga of first instar *Bracteon.* Boxed letters represent the two-letter sclerite or organ code used for sensillar nomenclature. All at same scale; scale bar = 100 μm. 248. *B. balli.* 249. *B. foveum.* 250. *B. carinula.* 251. *B. punctatostriatum.*

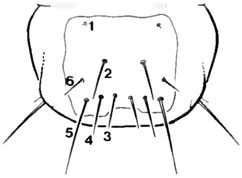
Figures 252–254. Right anterior portion of second abdominal terga of first instar *Bracteon,* showing variation in sizes of seta TE_6. All at same scale; scale bar = 100 μm. 252. *B. balli.* 253. *B. carinula.* 254. *B. punctatostriatum.*



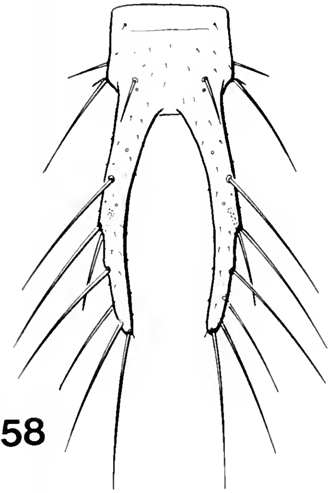
257



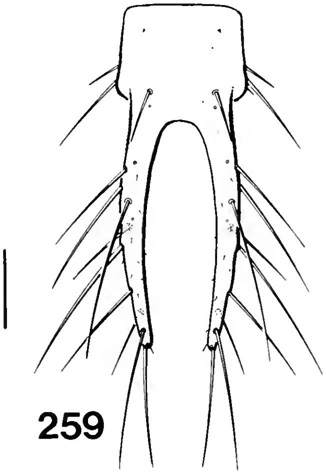
255



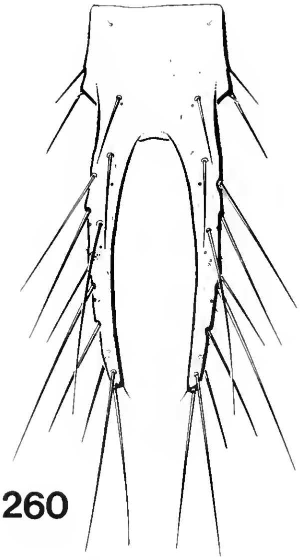
256



258



259



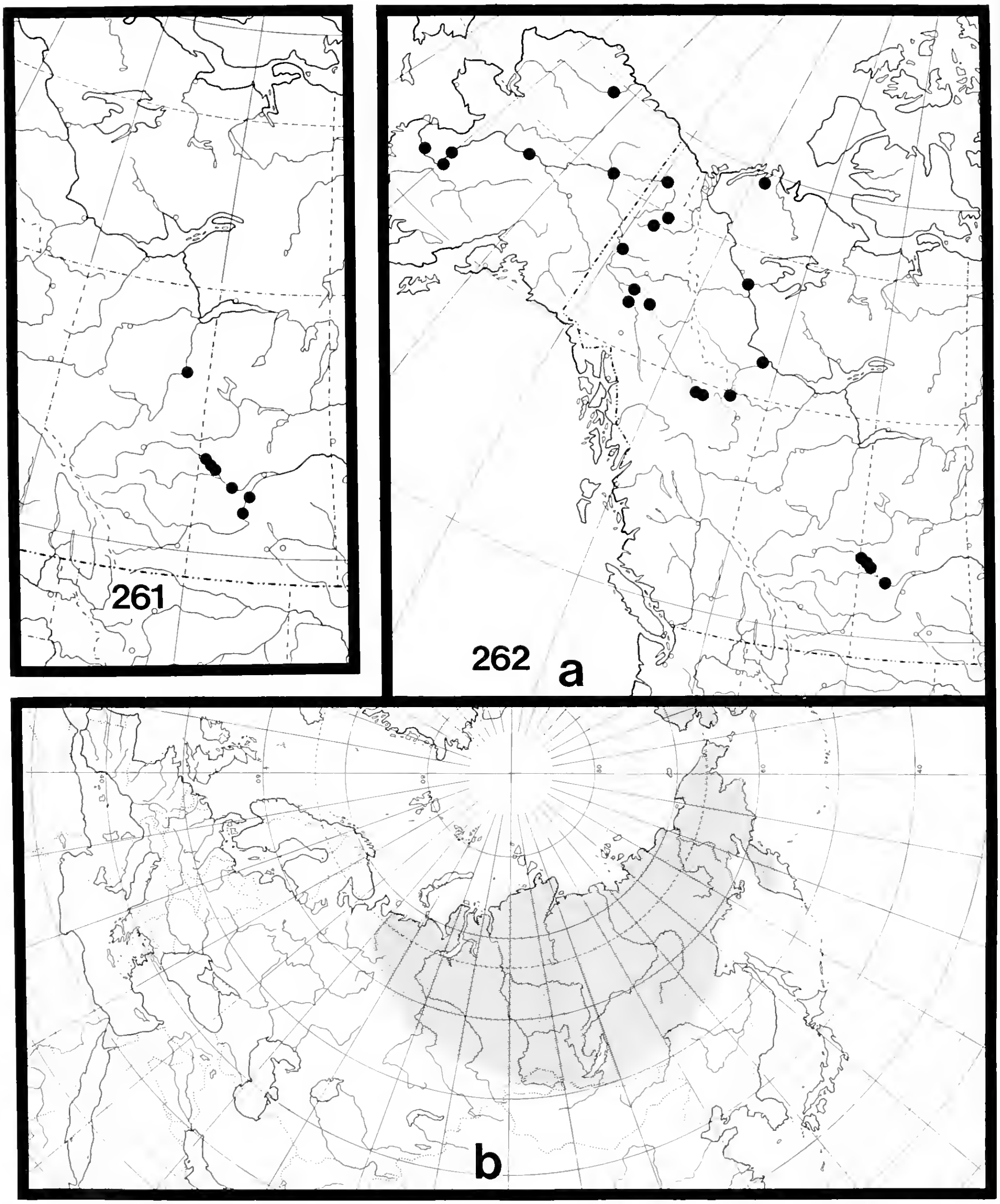
260

Figure 255. Ventral view of abdominal segments VIII through X of first instar *B. balli*. Scale bar = 200 μm.

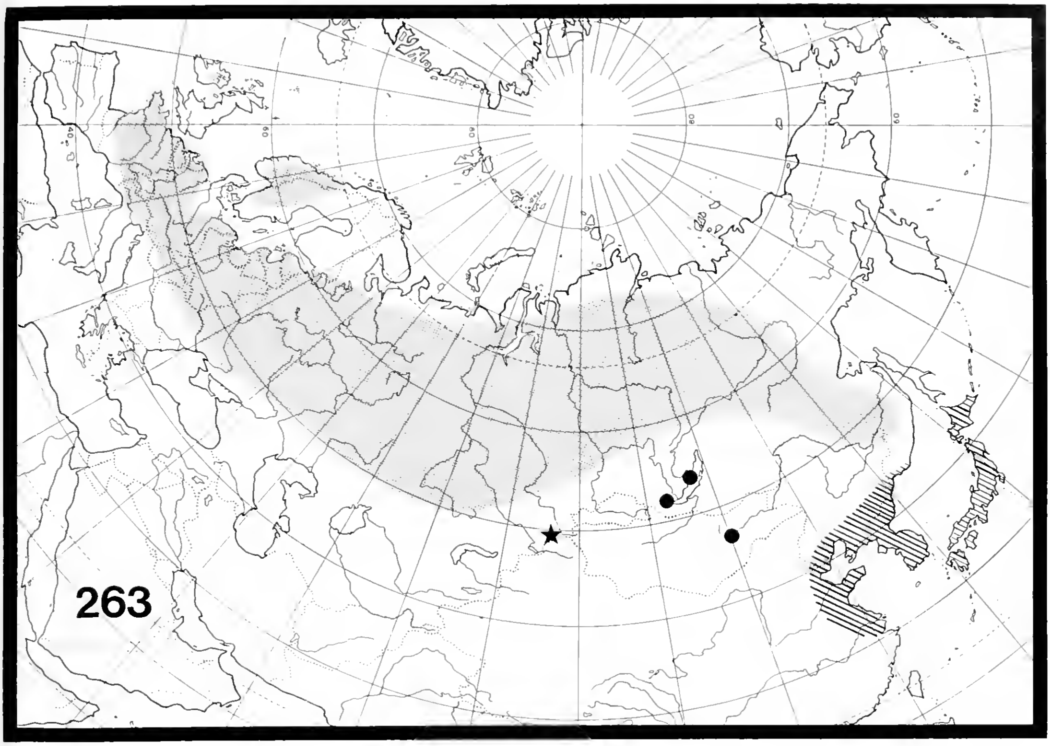
Figure 256. Ventral view of abdominal segment IX of first instar *B. carinula*. Same scale as Figure 255.

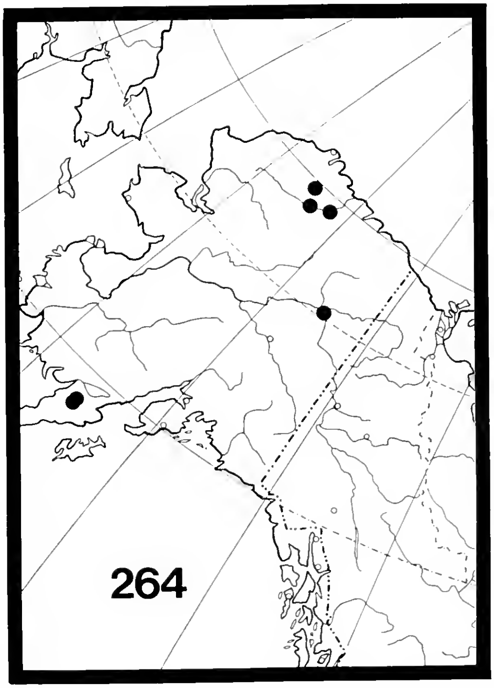
Figures 257. Urogomphi of first instar *B. balli*, dorsal view. Same scale as Figure 255.

Figures 258–260. Urogomphi of second instar *Bracteon*, dorsal view. Figures 258–260 at same scale; scale bar = 200 μm. 258. *B. balli*. 259. *B. lapponicum*. 260. *B. carinula*.

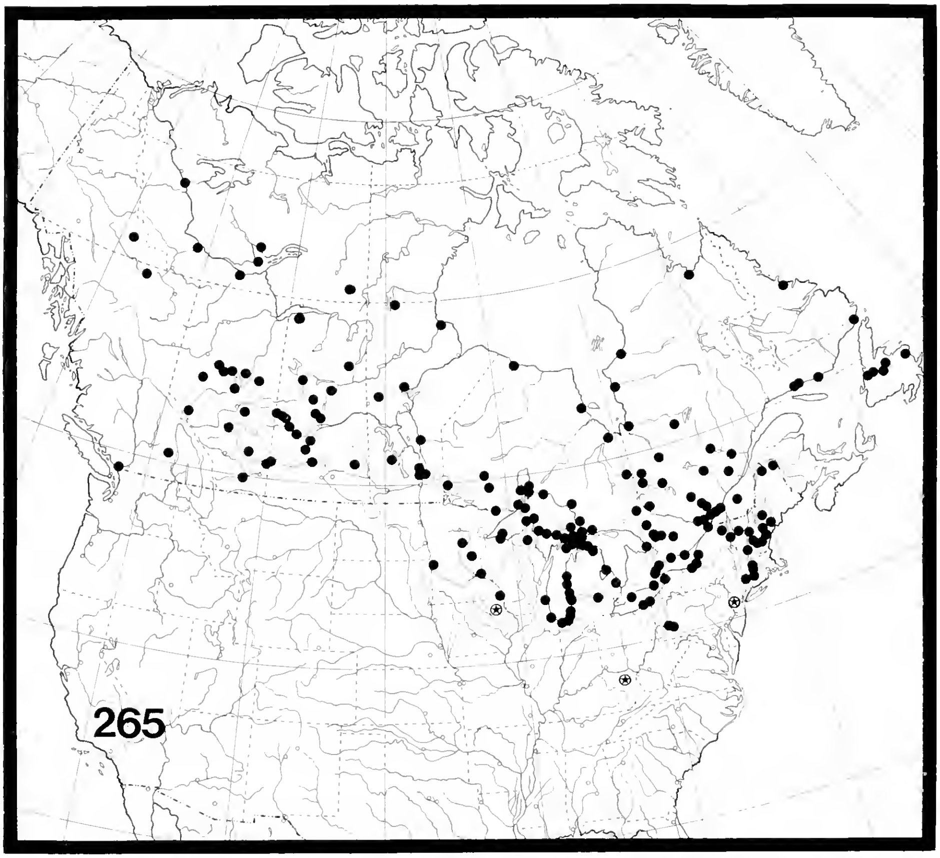


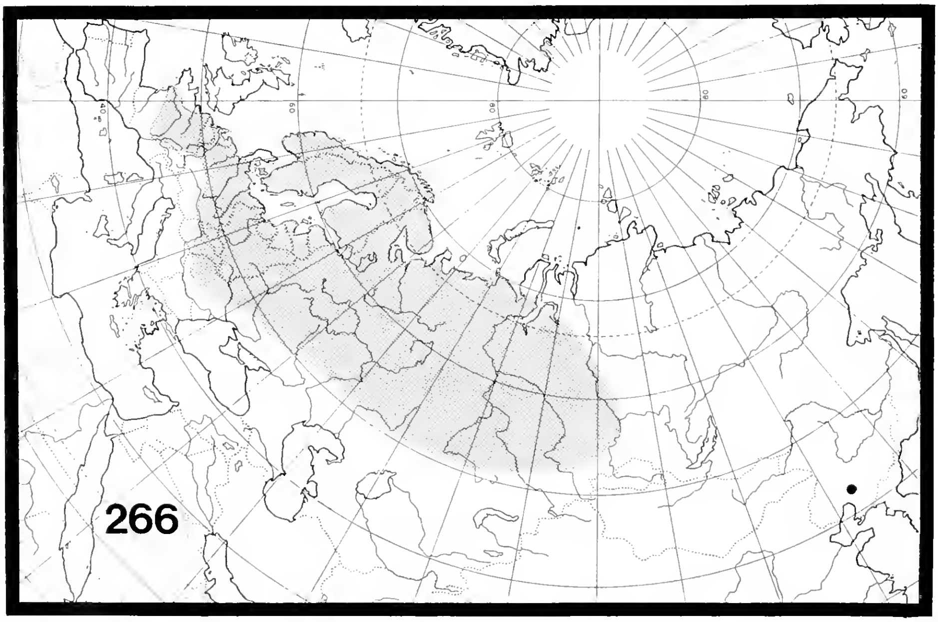
Figures 261, 262. Geographic distributions of species of *Bracteon*. 261. *B. balli*. 262. *B. foveum*. **a.** Nearctic distribution. It is also known from Churchill, Manitoba, off the eastern edge of the map. **b.** Approximate Palearctic distribution. Based on Lindroth (1962) and personal observations.





Figures 263, 264. Geographic distributions of species of *Bracteon*. 263. *B. argenteolum* (stippled), Palearctic *B. alaskense* (dots), *B. semenovi* (star), and *B. stenoderum* (striped). Approximate distributions of *B. argenteolum* and *B. stenoderum* based on Lindroth (1962), Netolitzky and Meyer (1933), Turin *et al.* (1977), and personal observations. 264. Nearctic distribution of *B. alaskense*.





Figures 265, 266. Geographic distributions of species of *Bracteon*. 265. *B. carinula;* circled stars represent state records. 266. *B. velox*. Based on Lindroth (1962), Netolitzky and Meyer (1939), Turin *et al.* (1977), Kirschenhofer (1984), and personal observations.

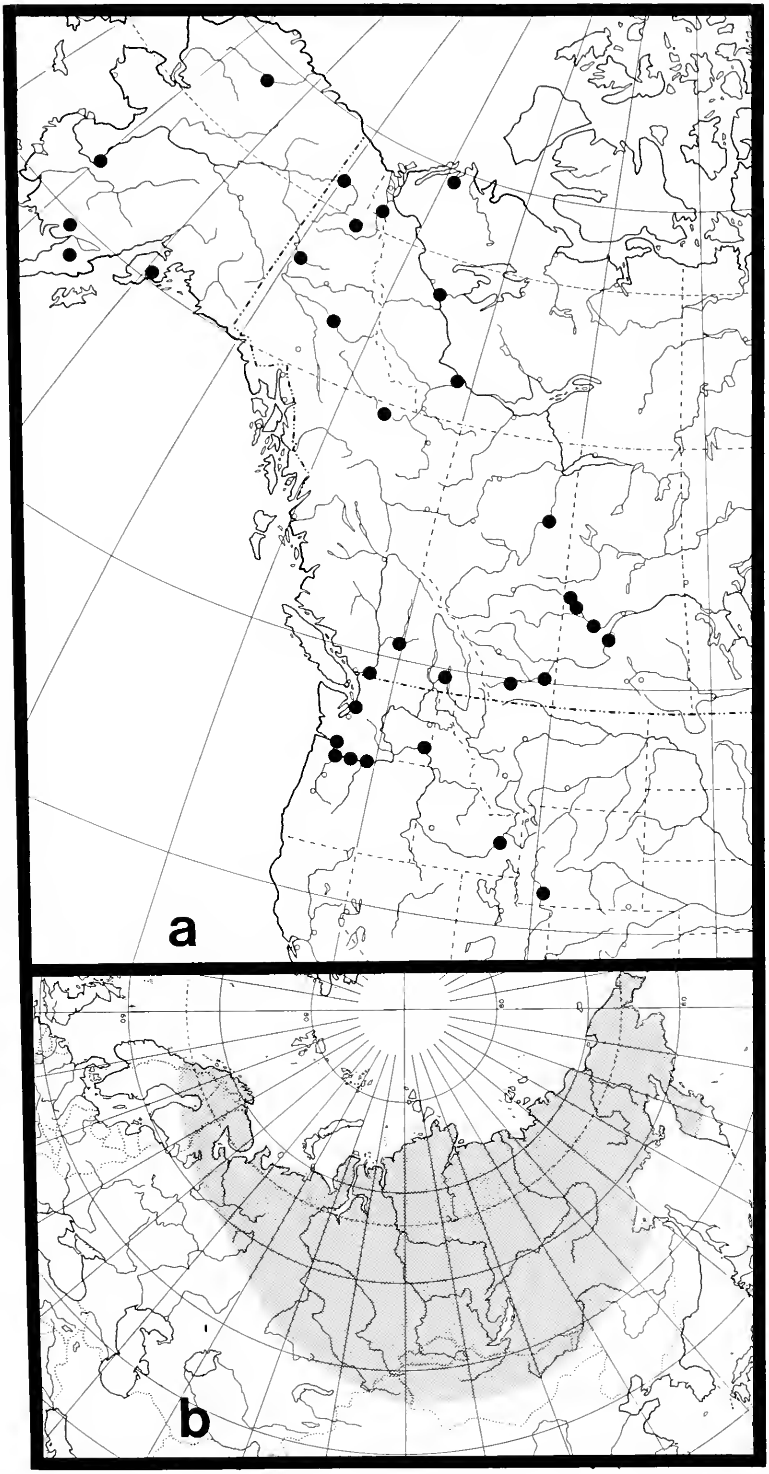
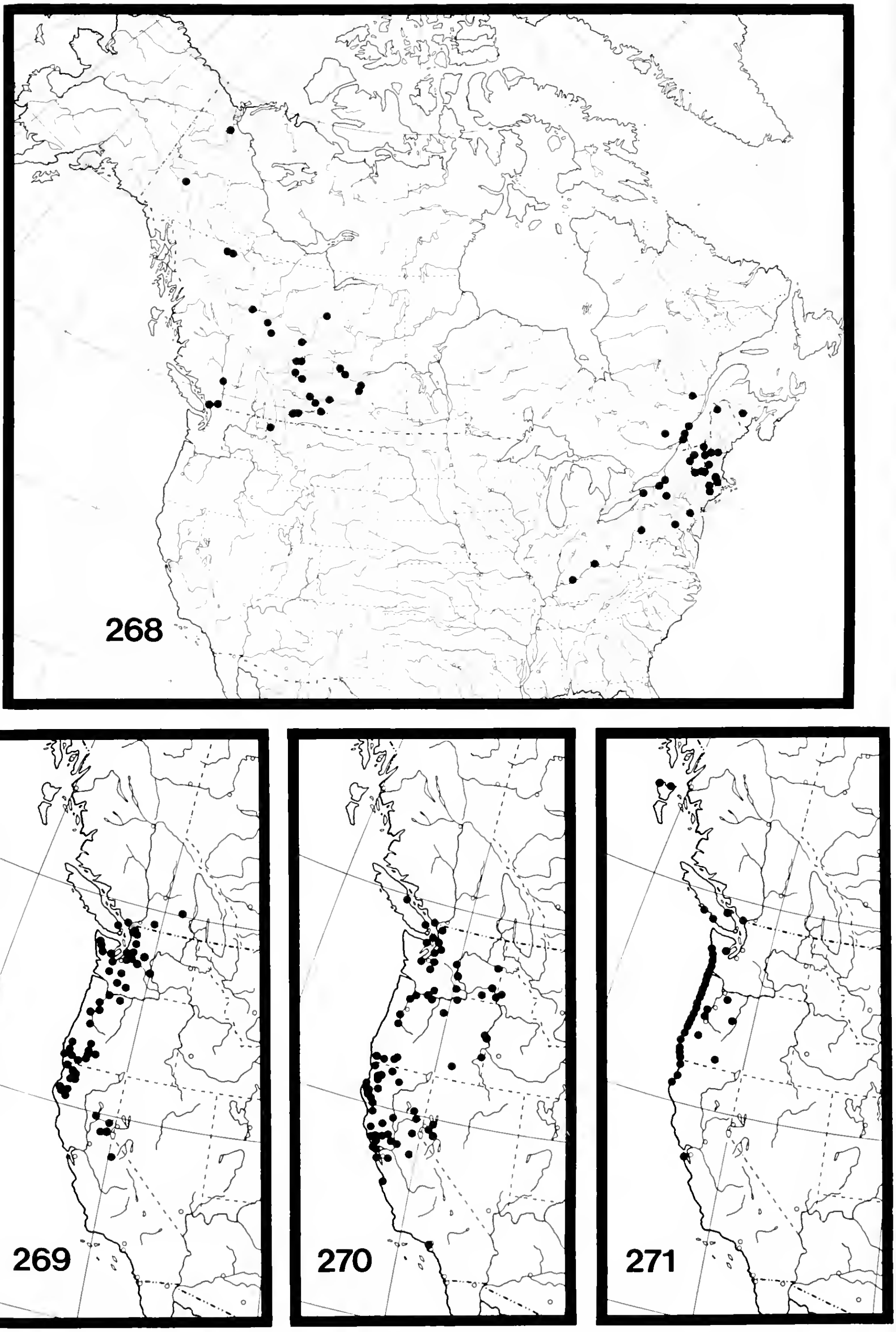


Figure 267. Geographic distribution of *B. lapponicum*. **a.** Nearctic distribution. **b.** Approximate Palearctic distribution. Based on Lindroth (1962) and personal observations.



Figures 268–271. Geographic distributions of species of *Bracteon*. 268. *B. punctatostriatum*. 269. *B. hesperium*. 270. *B. lorquinii*. 271. *B. zephyrum*.

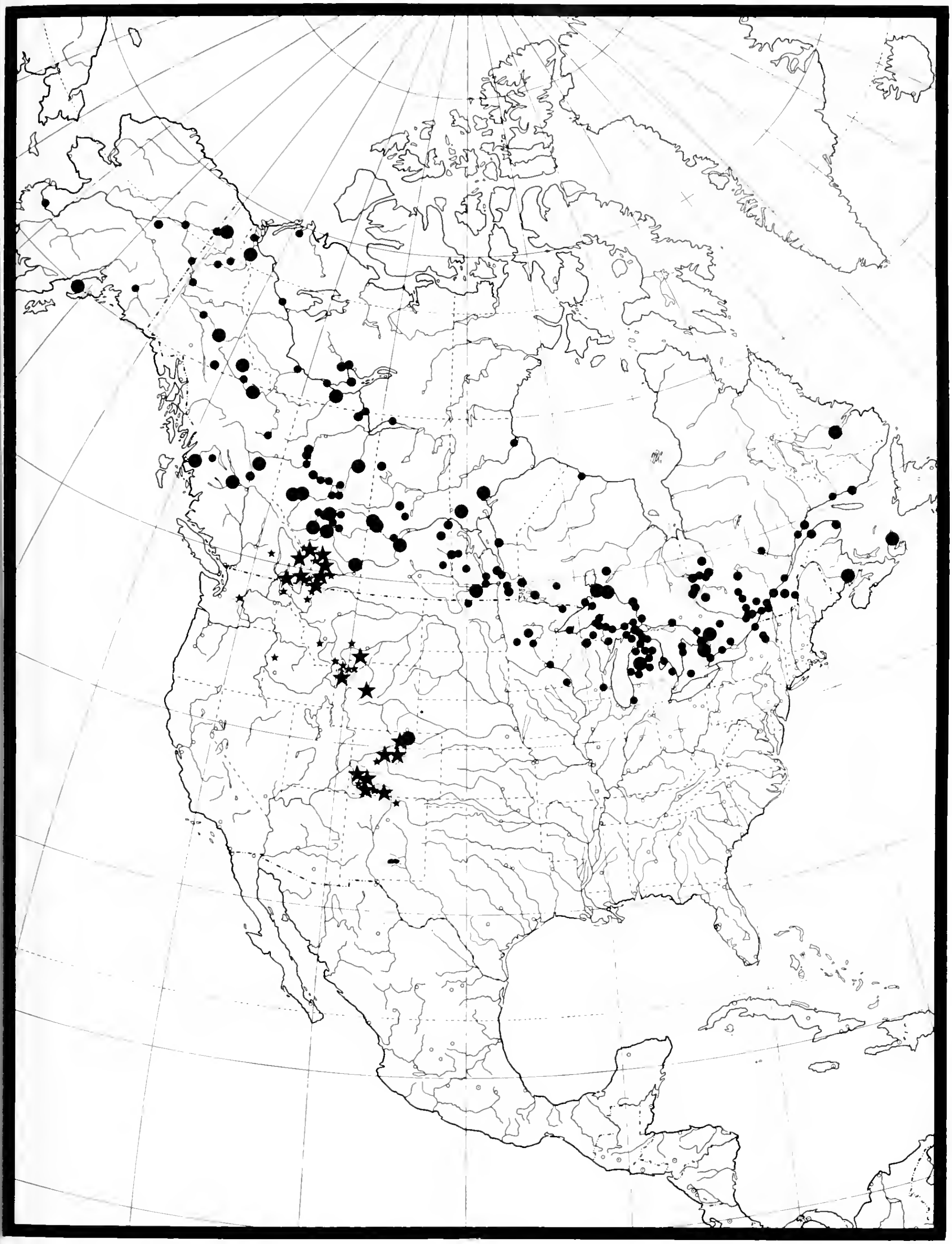
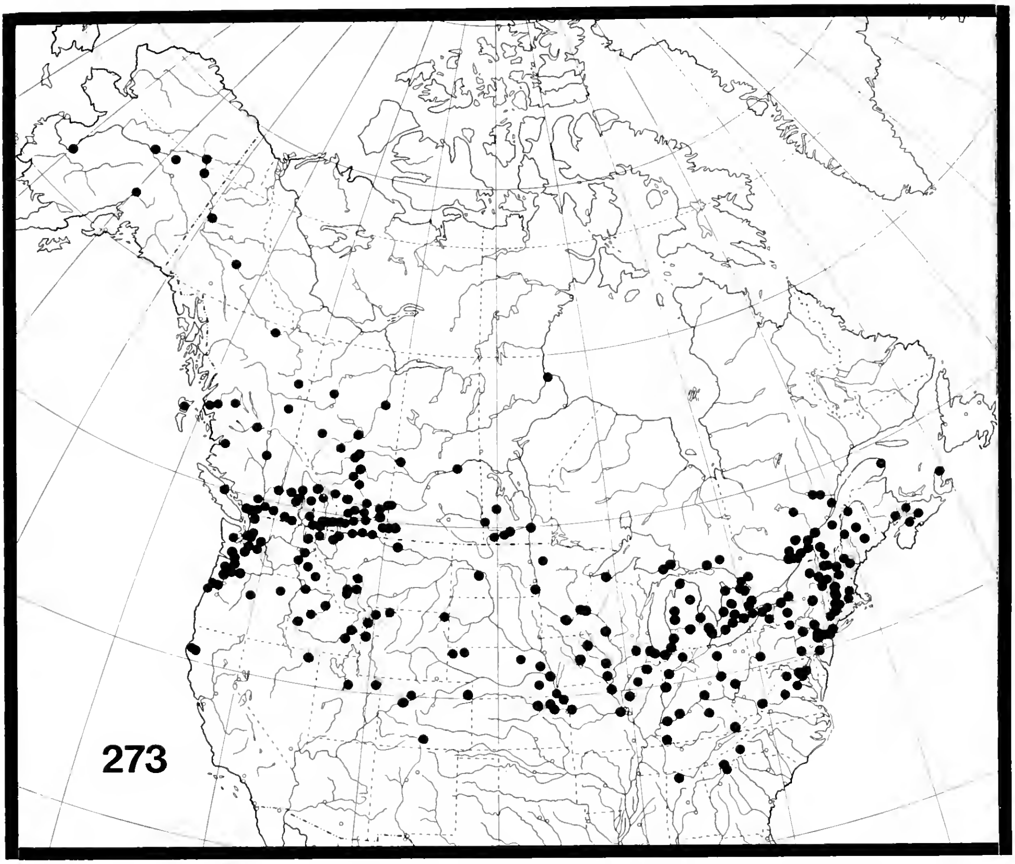
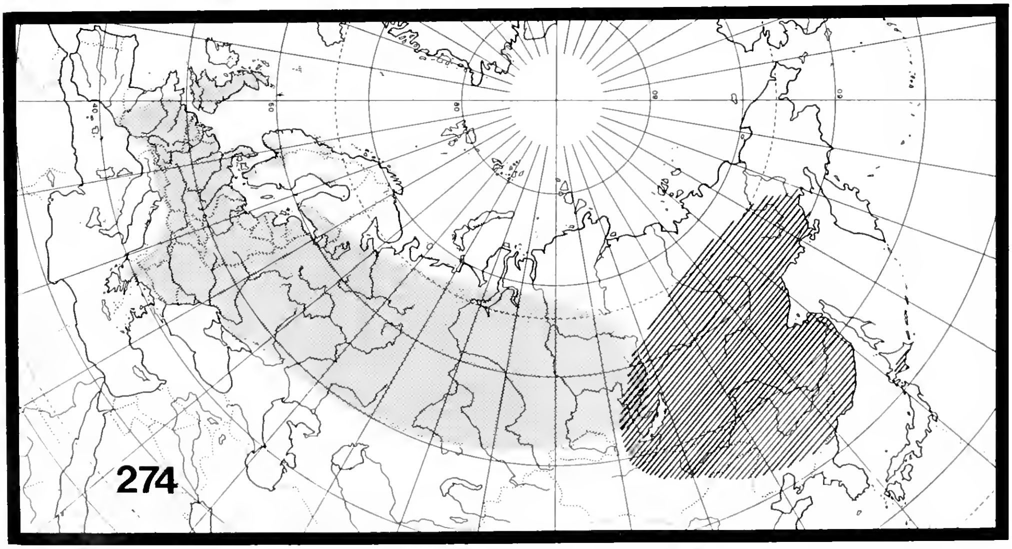


Figure 272. Geographic distribution of *B. levettei*. *B. levettei levettei* (stars) and *B. levettei carrianum* (dots). Localities of specimens identified using male genitalia indicated by larger symbols.





Figures 273, 274. Geographic distributions of species of *Bracteon*. 273. *B. inaequale*. 274. Approximate distributions of *B. litorale* (stippled) and *B. conicolle* (striped). Based on Lindroth (1962), Turin *et al.* (1977), and personal observations.

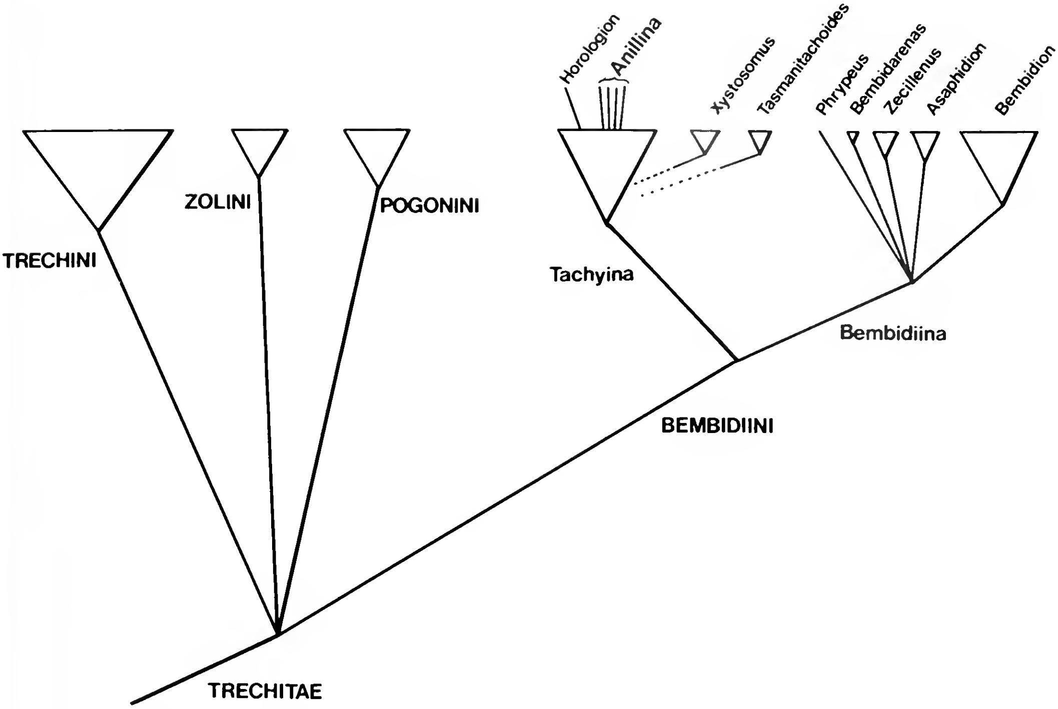
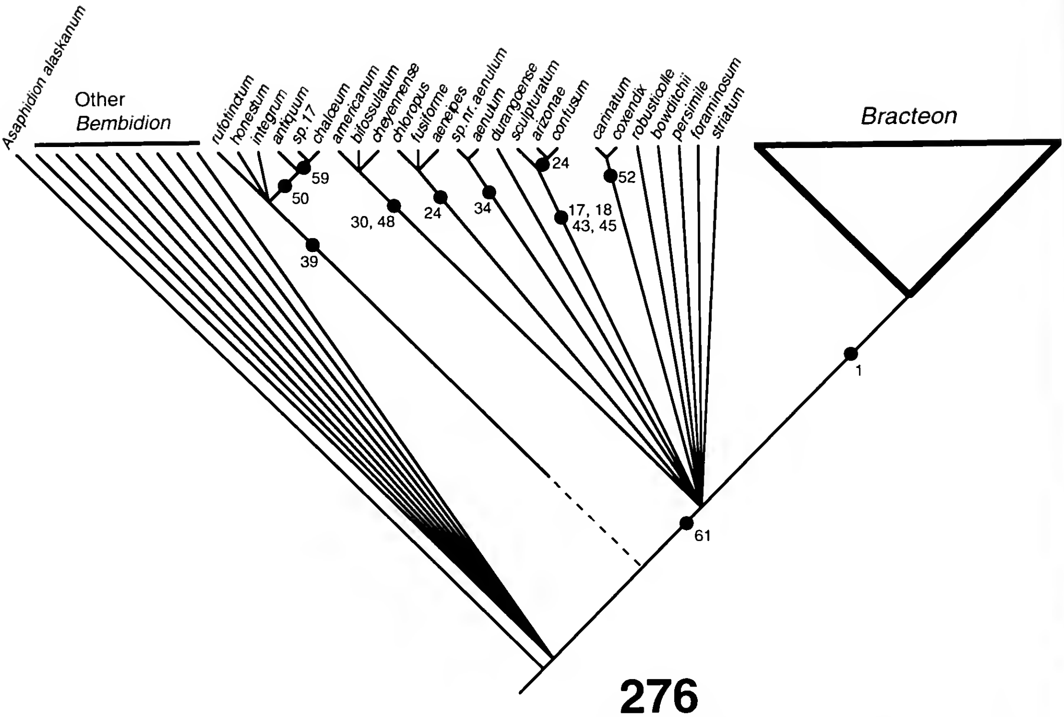
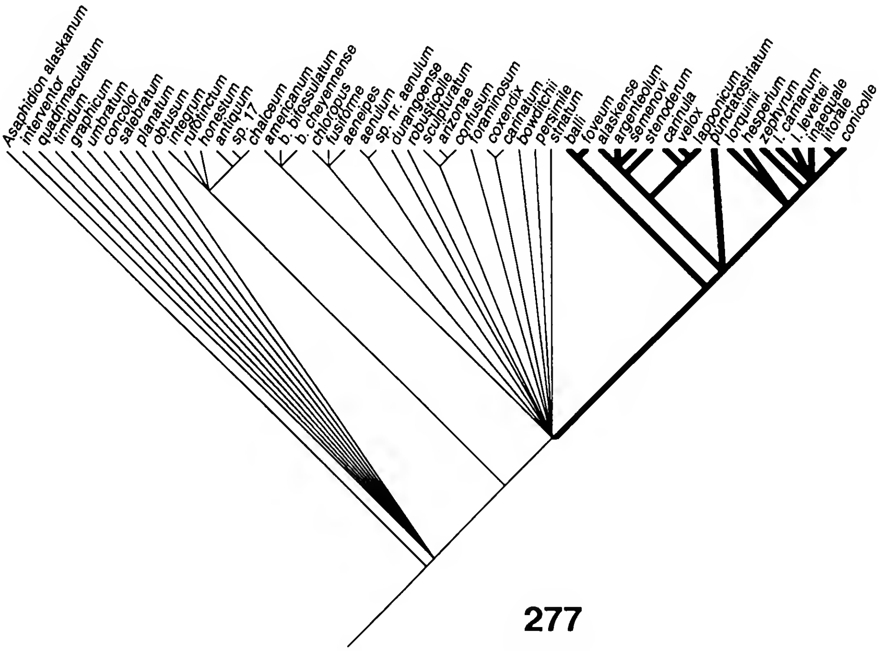


Figure 275. Proposed cladistic structure of Trechitae and genera of Bembidiina. Based mainly on Kryzhanovskij (1976) and Erwin (1972, 1982, and 1985).



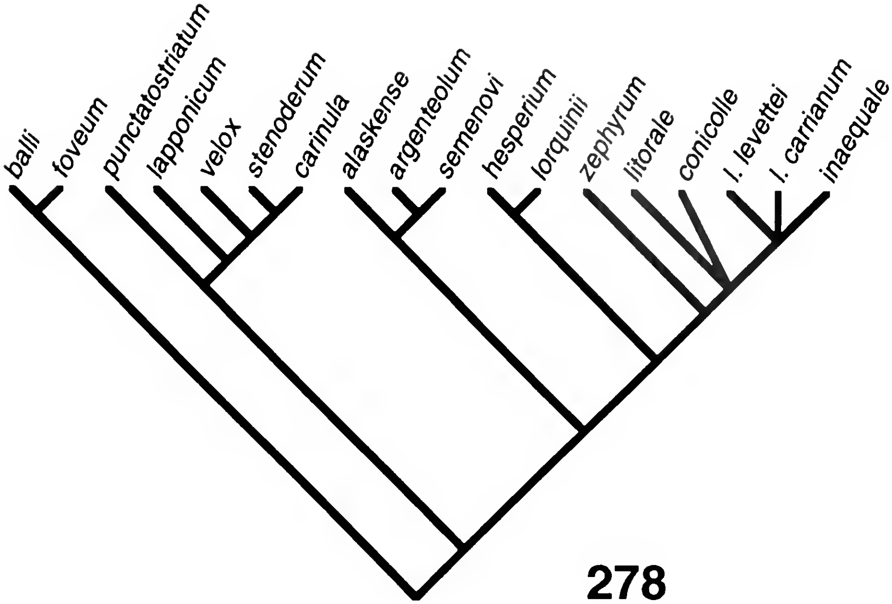
276

Figure 276. Cladistic structure of near relatives of *Bracteon*, based on traditional analysis. Numbers below a clade are the numbers of characters for which derived states support monophyly of the clade (see Tables 2, 4, and 5).

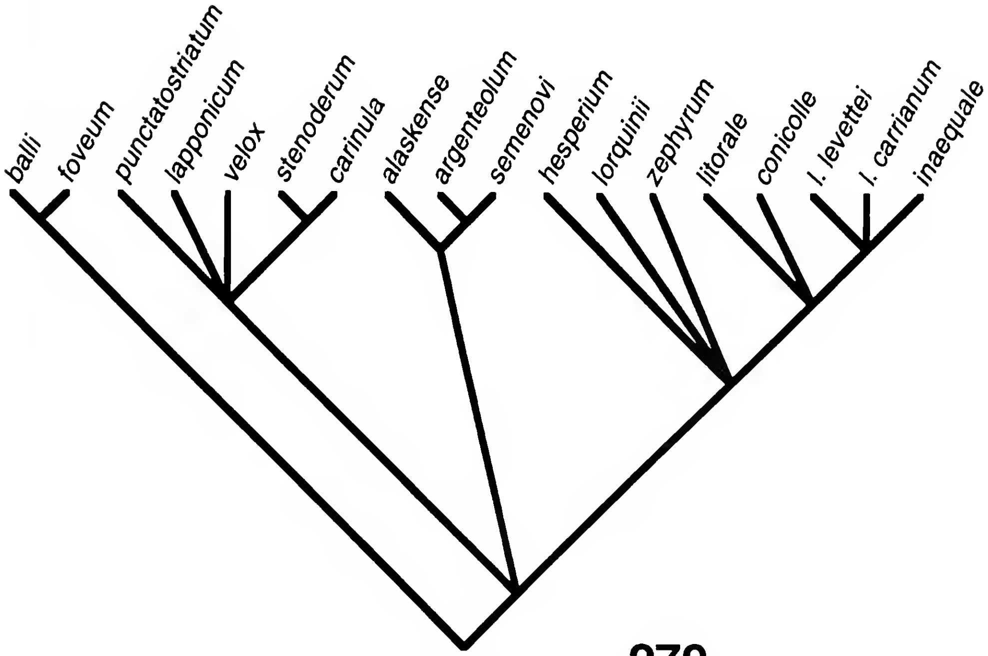


277

Figure 277. Phylogeny inferred from traditional analysis. *Bracteon* lineages are shown with thicker lines.

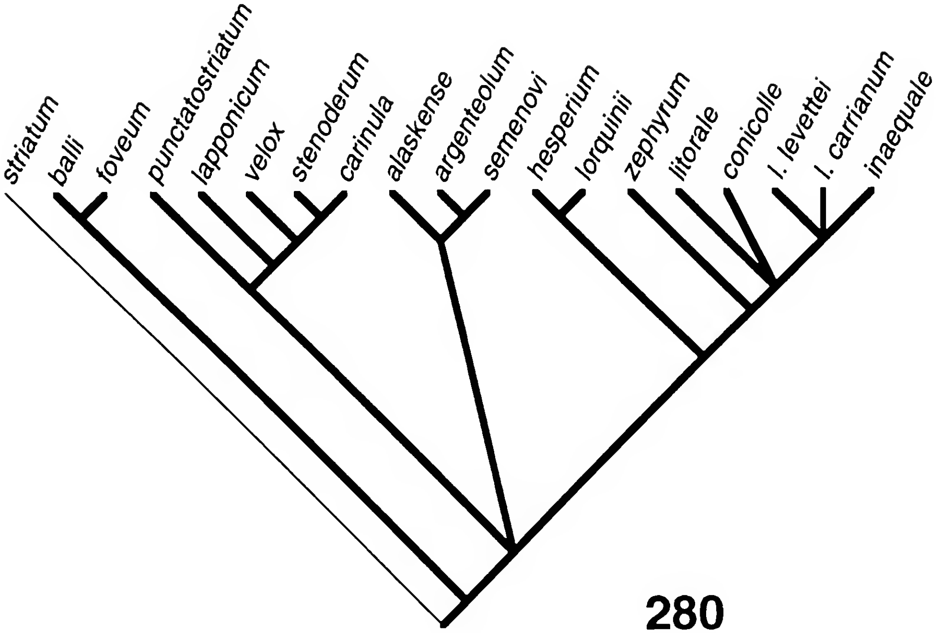


278

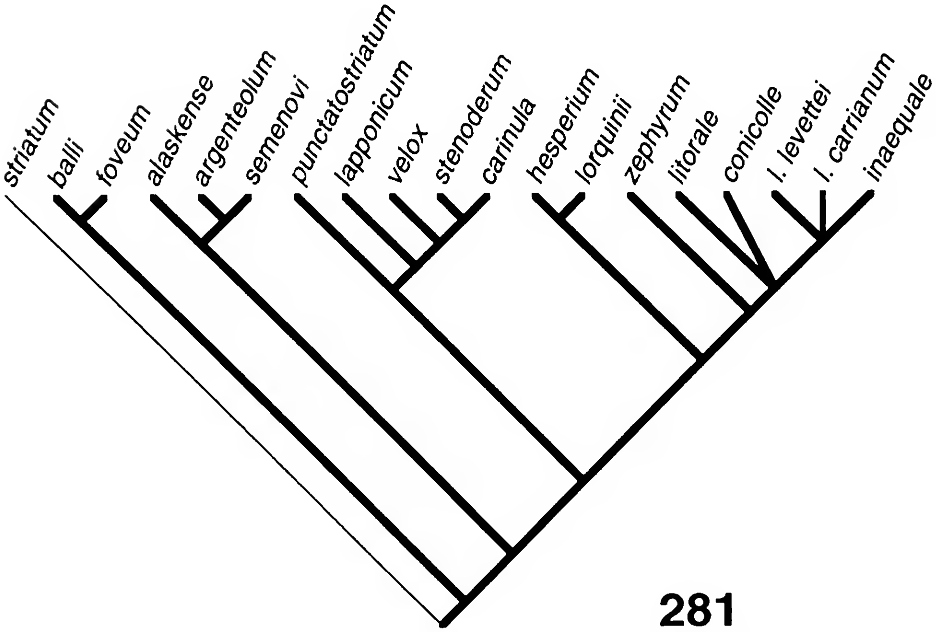


279

Figures 278, 279. Most-parsimonious trees of only the 18 *Bracteon* taxa. 278. Equal weighting. 279. Error-prone characters devalued.

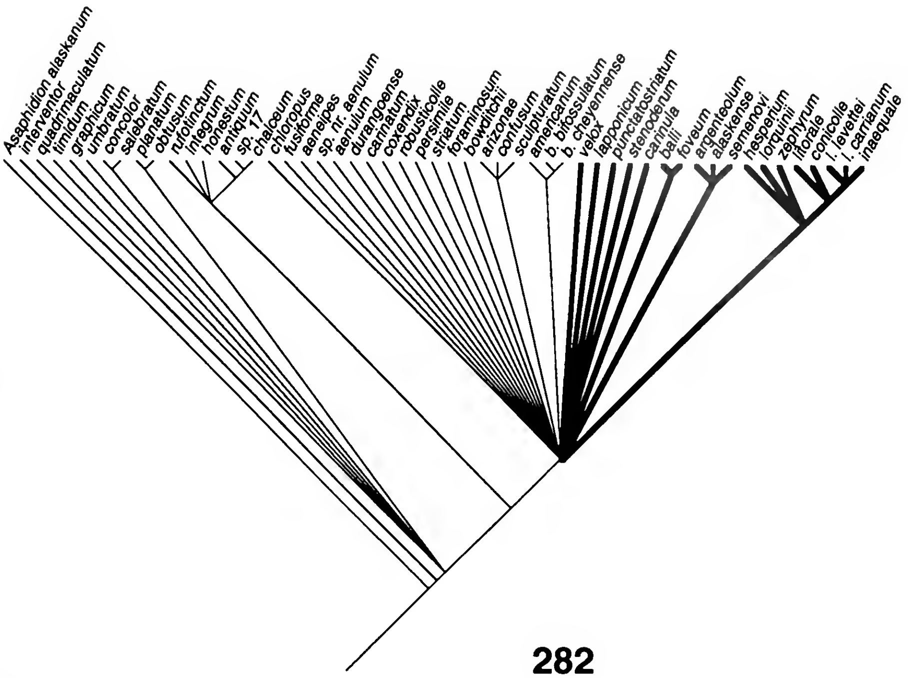


280



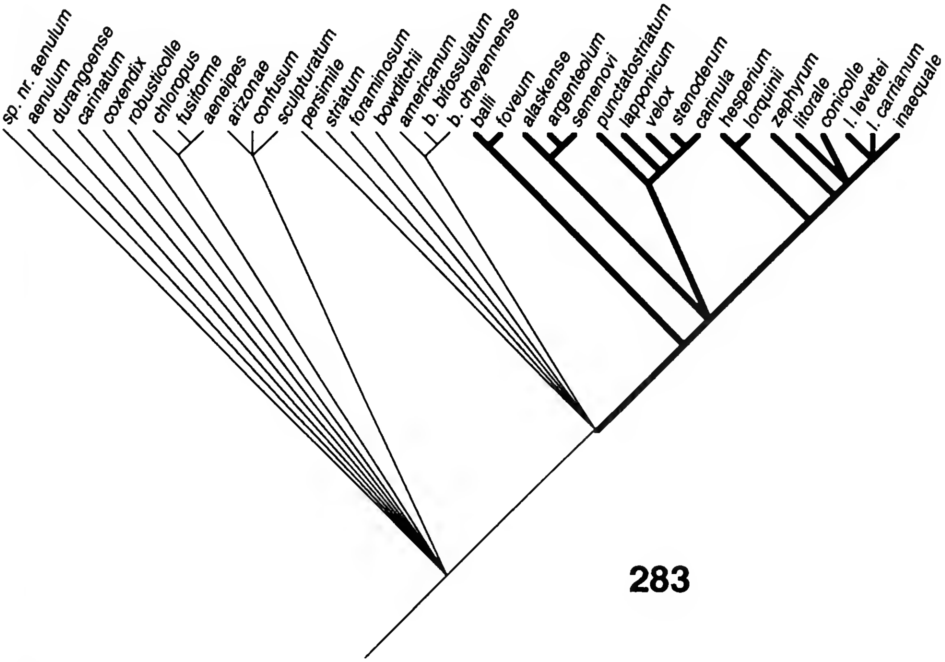
281

Figures 280, 281. Most-parsimonious trees of only the 18 *Bracteon* taxa plus *B. striatum*. 280. Equal weighting. 281. Error-prone characters devalued.



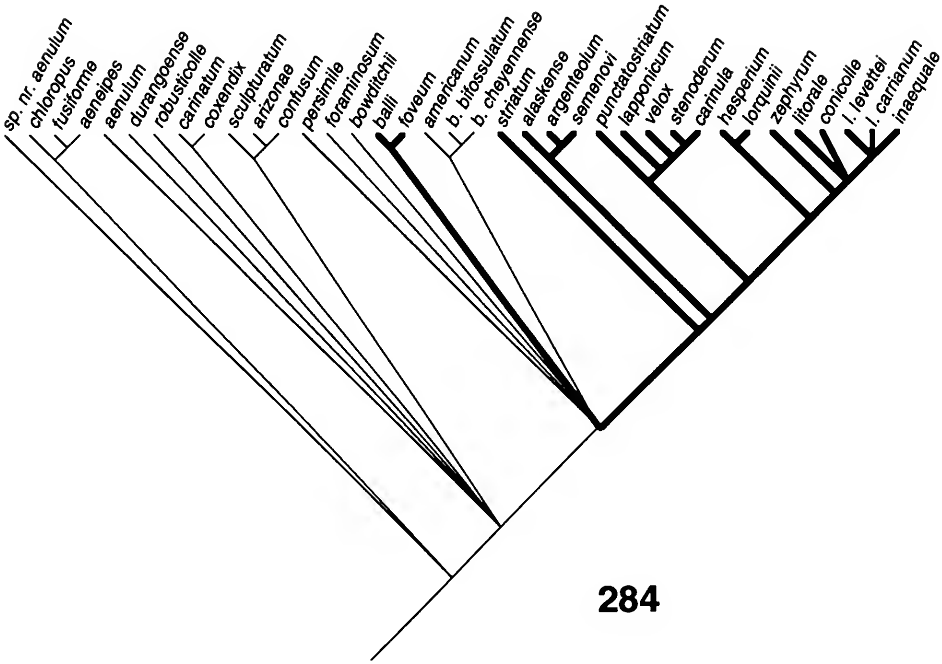
282

Figure 282. Strict consensus tree of all 545 most-parsimonious trees of length 653 found by PAUP; characters equally weighted.



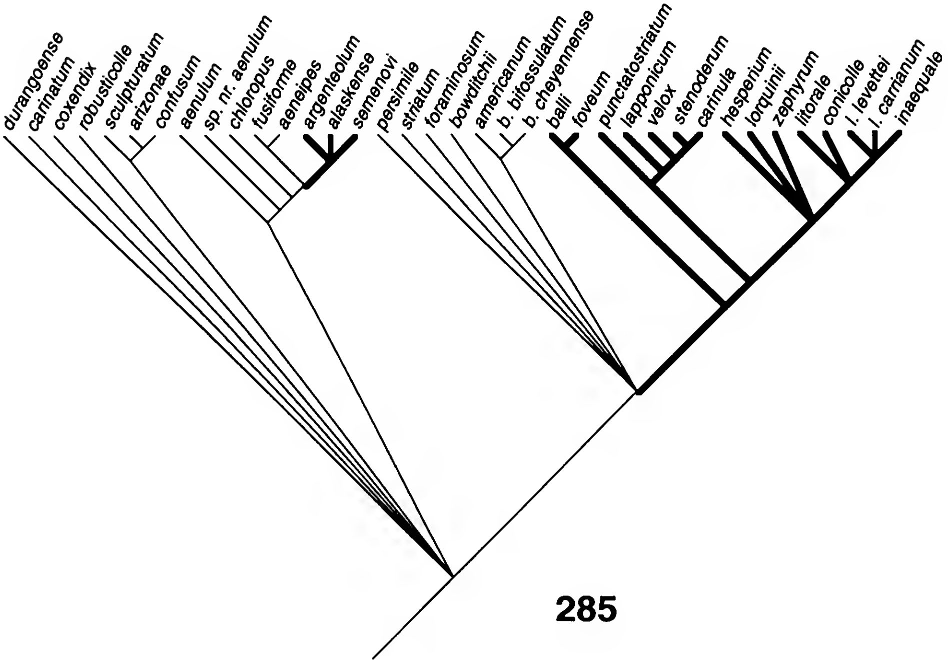
283

Figure 283. Part of the strict consensus tree of 140 trees of length 653 with *Bracteon* monophyletic.



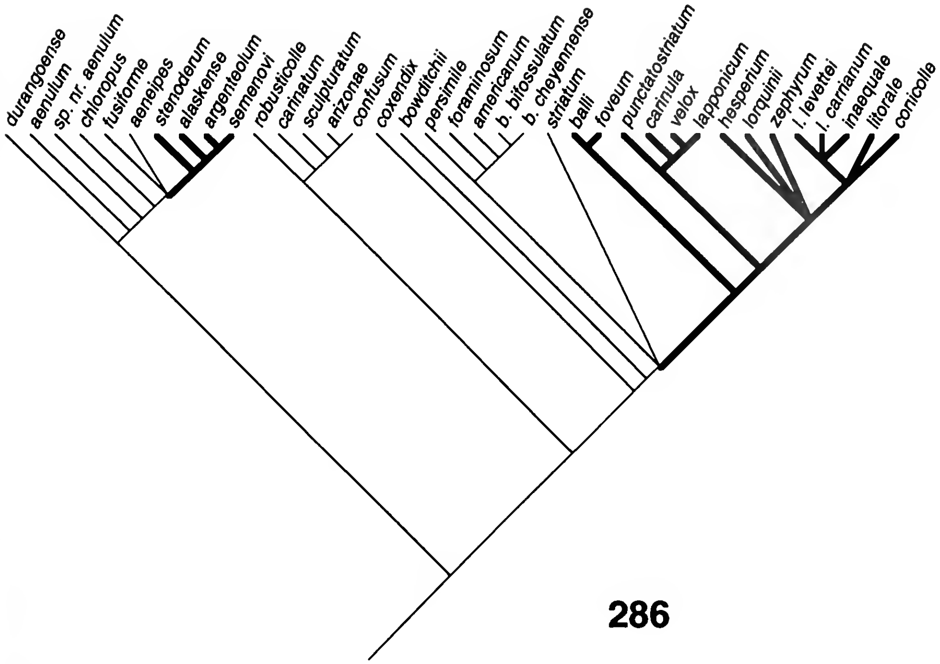
284

Figure 284. Part of the strict consensus tree of 88 trees of length 653 with *B. balli* and *B. foveum* excluded from *Bracteon*.



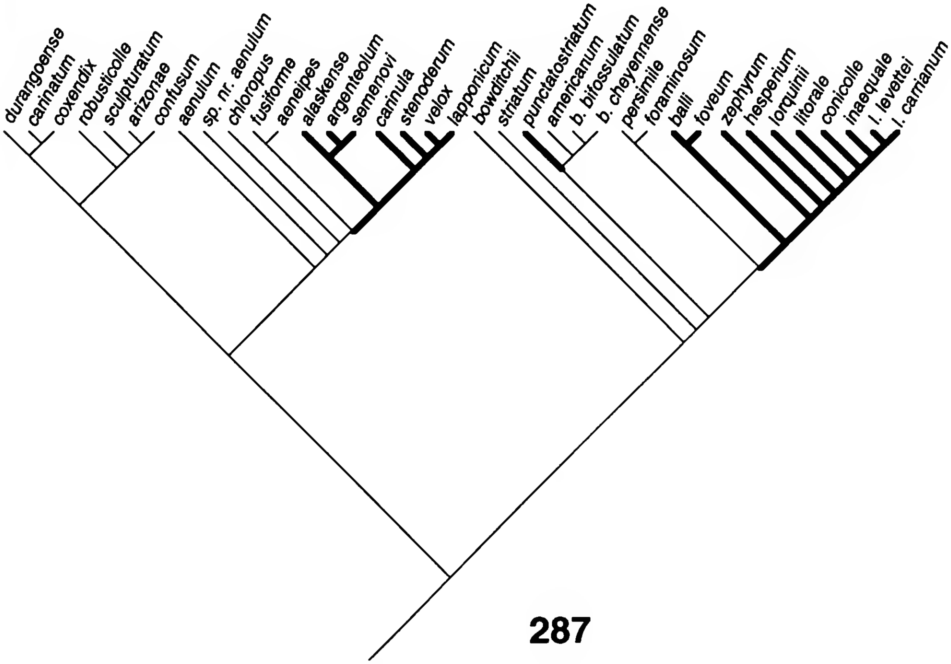
285

Figure 285. Part of the strict consensus tree of 268 trees of length 653 with the *B. argenteolum* group excluded from *Bracteon*.



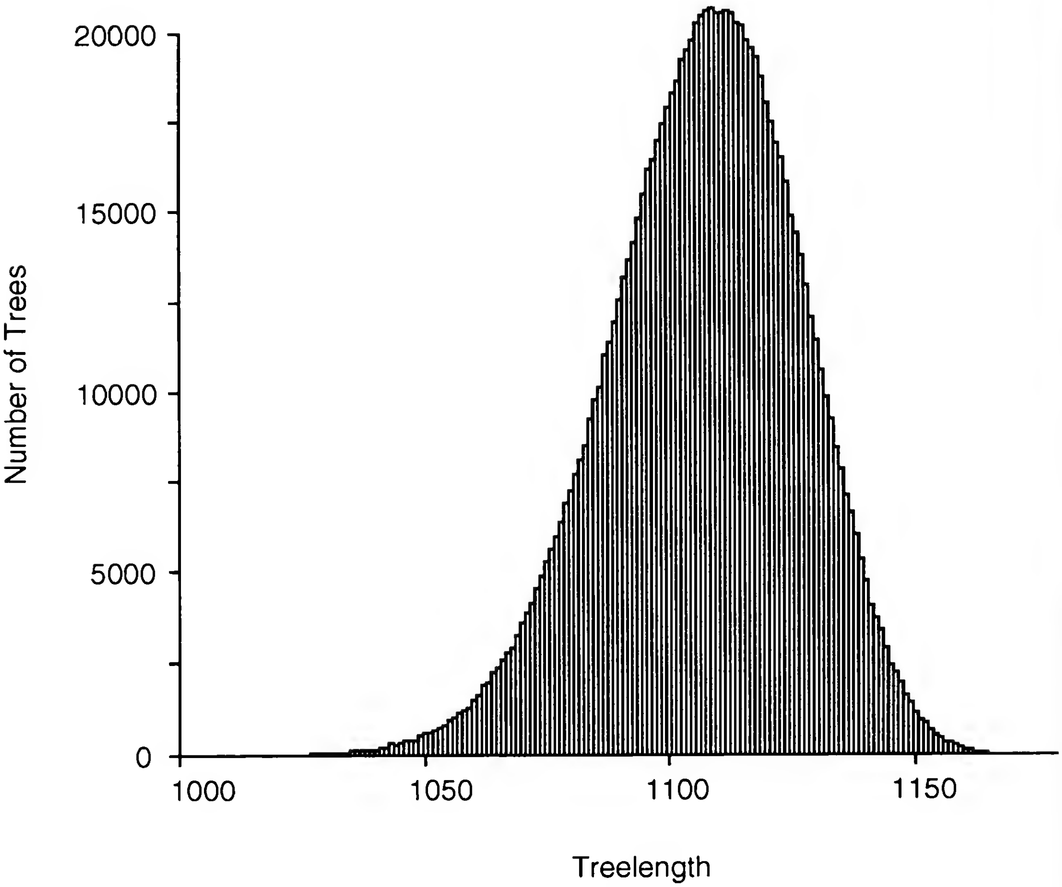
286

Figure 286. Part of the strict consensus tree of 48 trees of length 653 with the *B. argenteolum* and *B. stenoderum* group excluded from *Bracteon*.



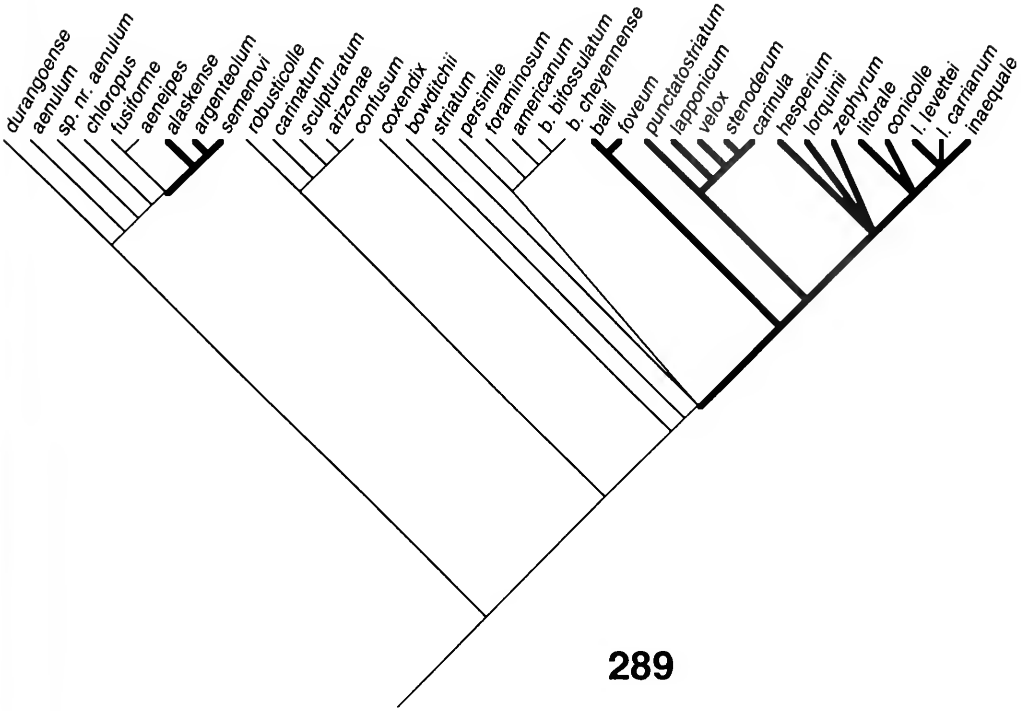
287

Figure 287. Part of the single tree of length 653 with *Bracteon* shattered into 3 clades.

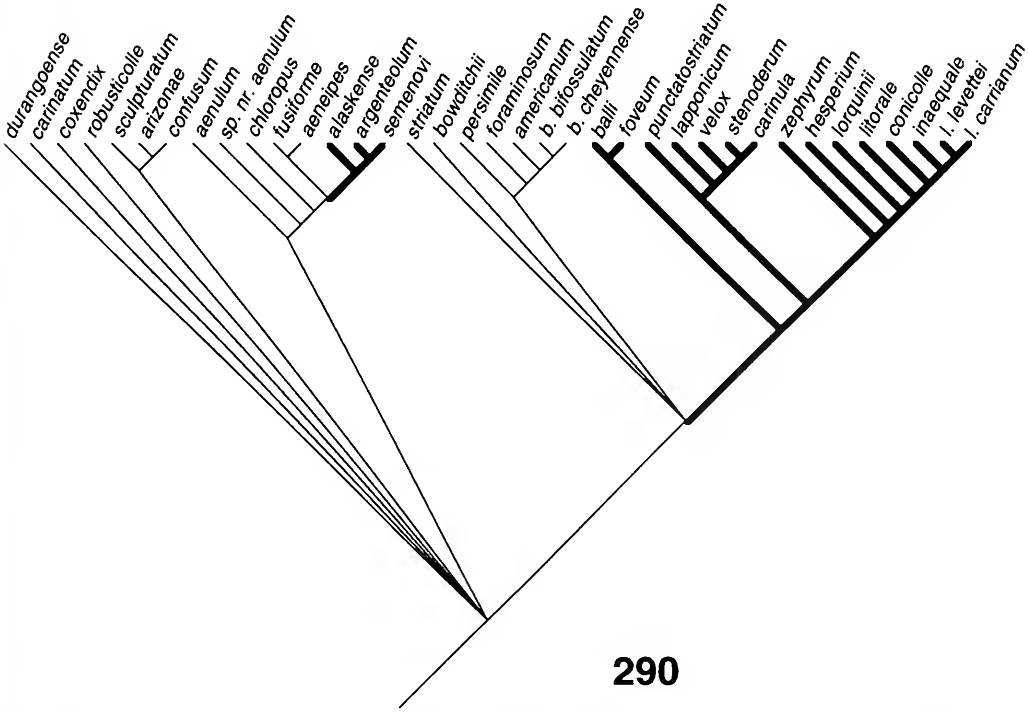


288

Figure 288. Distribution of random sample of 1,000,000 equiprobable trees from full, unrecoded data set; characters equally weighted.

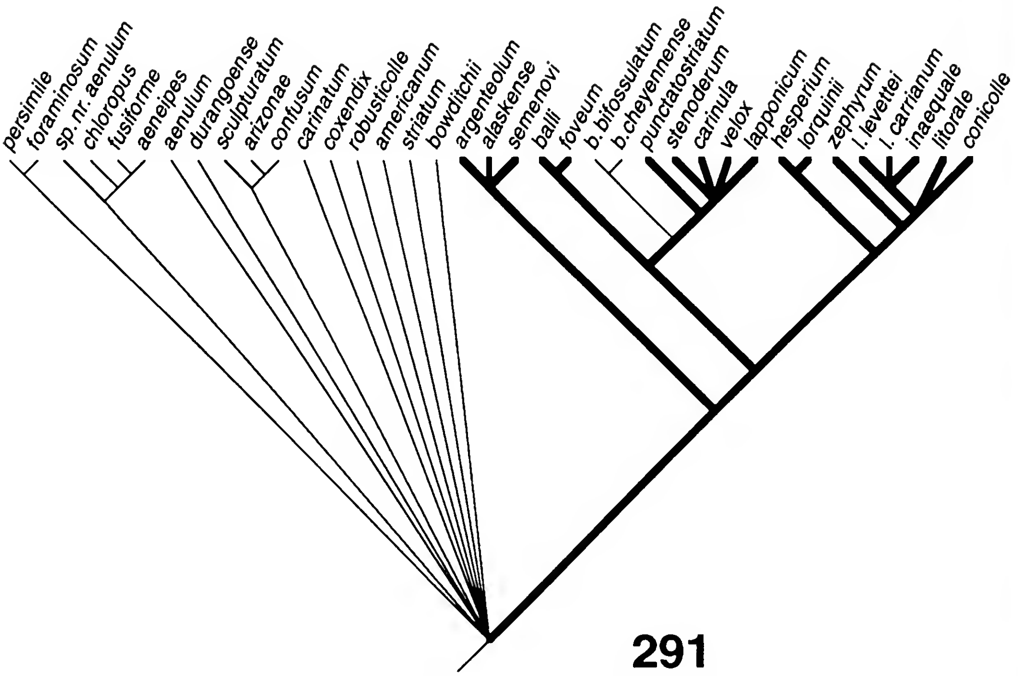


289



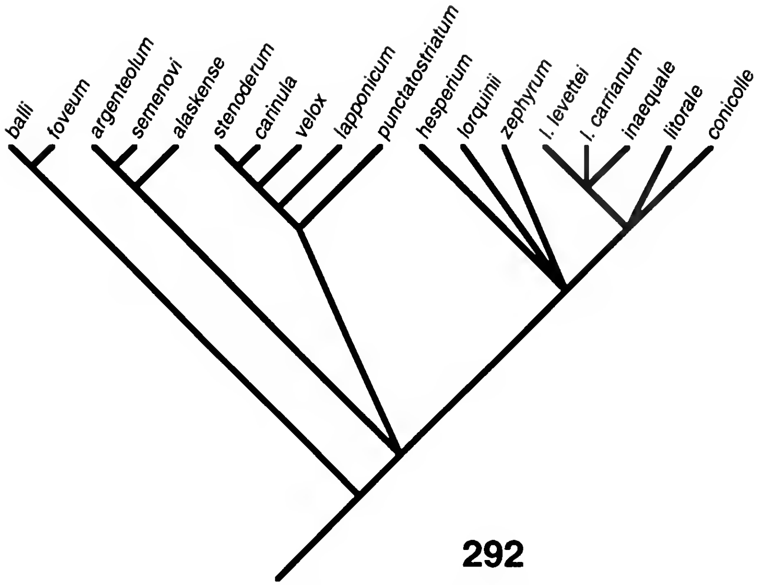
290

Figures 289, 290. Most-parsimonious trees under two weighting schemes. 289. Part of the strict consensus tree of 120 trees of length 1,086 with error-prone characters devalued. 290. Part of the strict consensus tree of 21 trees of length 1,406 with error-prone characters and extensively polymorphic characters devalued.



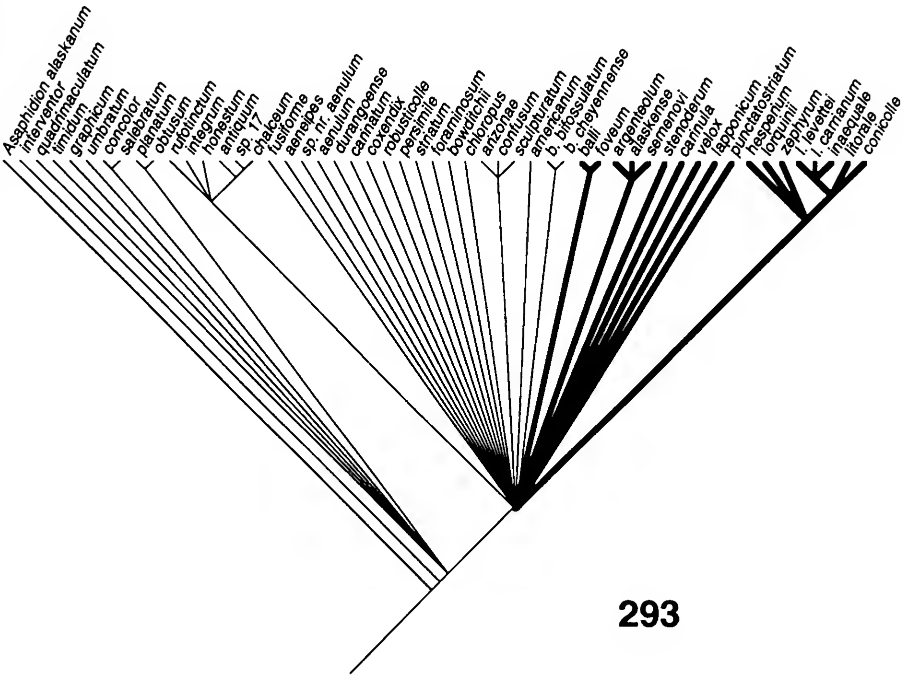
291

Figure 291. Part of the strict consensus tree of the island of 5,482 most-parsimonious trees for the matrix recoded so that inapplicable characters are not treated as missing data.



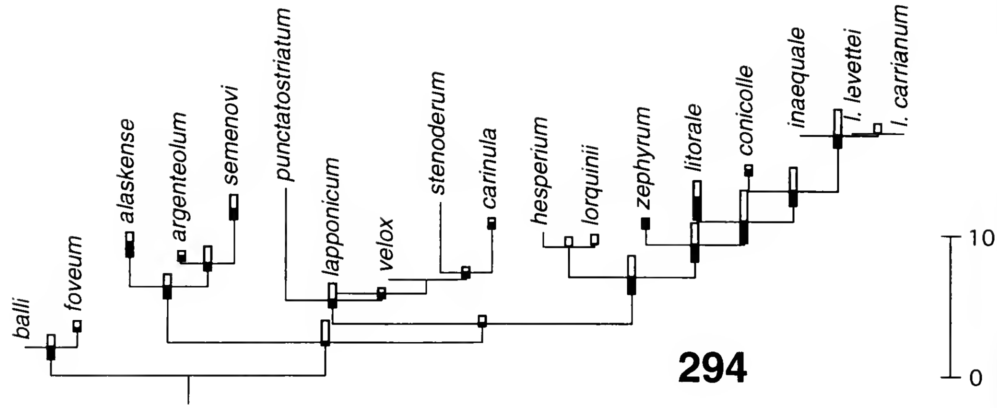
292

Figure 292. Part of the strict consensus tree of most-parsimonious trees under all three weighting schemes with the constraint enforced that *Bracteon* is monophyletic. Note that the structure shown here also matches that in Figures 278–281. This is the bold hypotheses of *Bracteon* relationships.

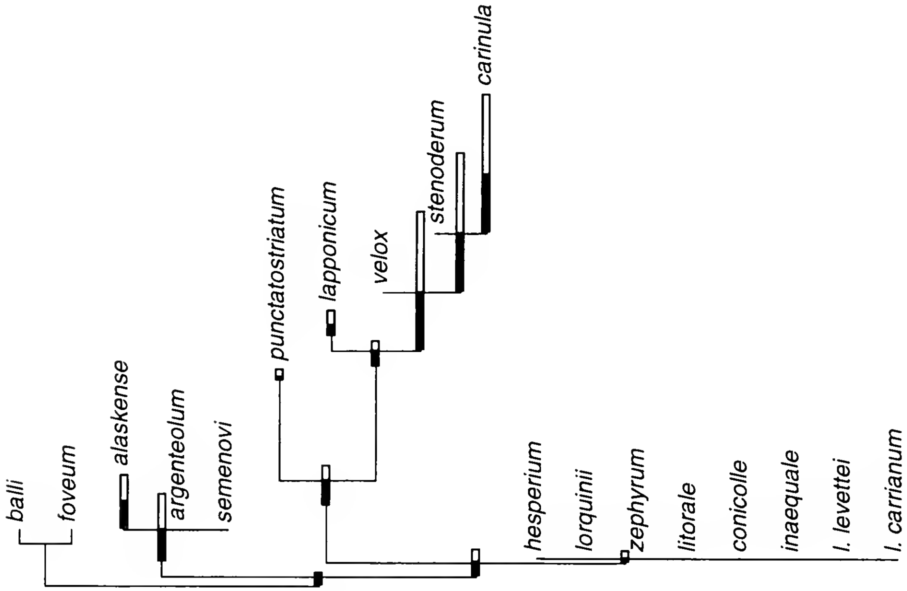


293

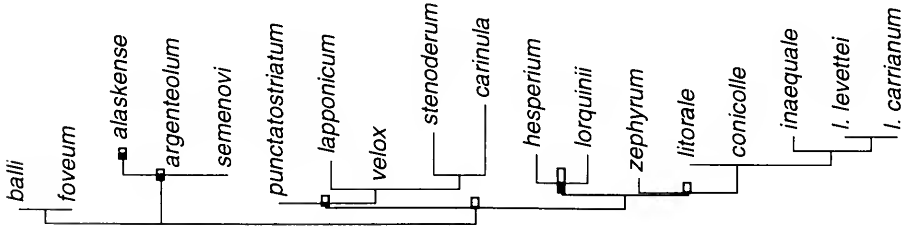
Figure 293. Strict consensus tree of most-parsimonious trees under all three weighting schemes, the most-parsimonious trees under the unequal weighting schemes in which *Bracteon* is forced to be monophyletic, and the most-parsimonious trees for the matrix recoded so that inapplicable characters are not treated as missing data. Under this cautious hypothesis, *Bracteon* is not presumed to be monophyletic.



294

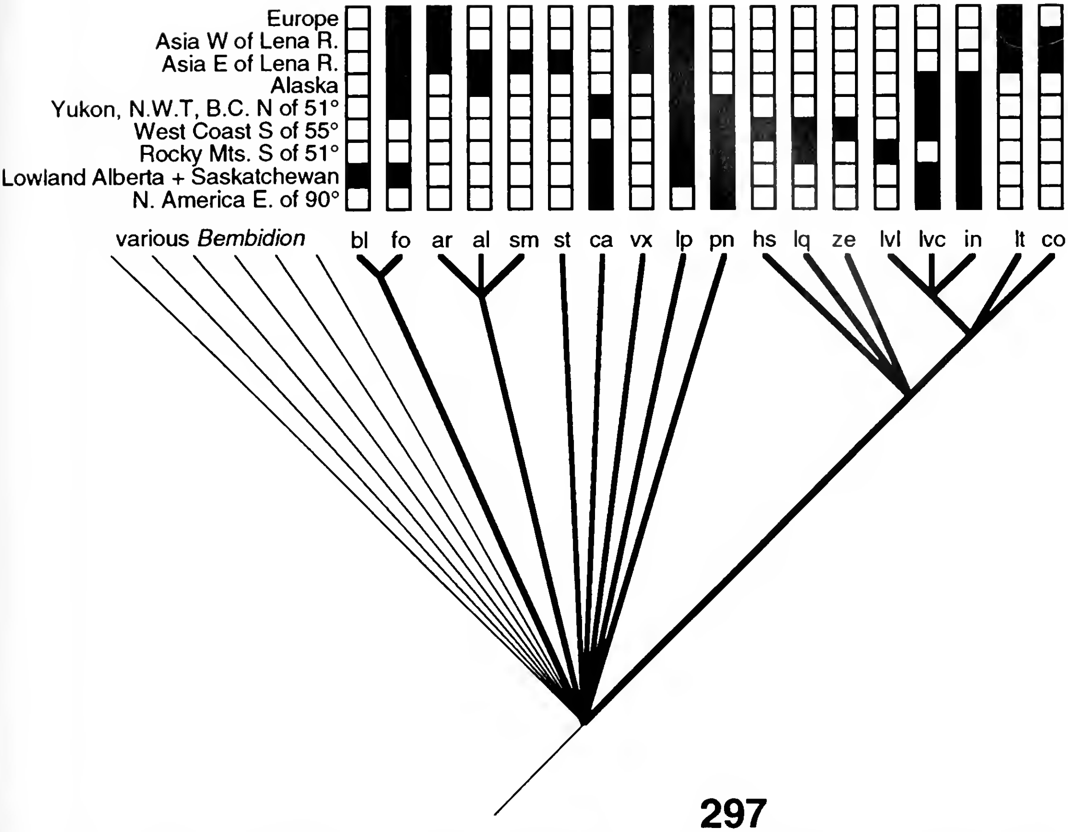


295



296

Figures 294–296. Distribution of evolutionary changes upon one of the four trees in common to the most-parsimonious trees for all three weighting schemes under the constraint that *Bracteon* is monophyletic. A dichotomous tree was chosen because of the difficulties in calculating branch lengths on polytomous trees (W. P. Maddison, 1989); this is thus a bolder hypothesis than is ideal. Branch length proportional to sum (over characters) of the average number of changes reconstructed by parsimony to occur on branch, where the average is taken over equally parsimonious reconstructions of character change for the character. The bottom of the black box on a branch indicates the sum (over characters) of the minimum number of changes reconstructed on that branch; the top of the white box indicates the sum (over characters) of the maximum number of changes reconstructed. 294. Adult external characters. 295. Larval characters. 296. Genitalic characters.



297

Figure 297. Geographic distributions of *Bracteon* species superimposed upon the cautious phylogeny. Abbreviations of taxon names as in Table 2.

US ISSN 0027-4100

Bulletin of the Museum of Comparative Zoology

Systematics of the Neotropical Moth Family Dalceridae (Lepidoptera)

SCOTT E. MILLER

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 153, NUMBER 4
29 JUNE 1994

(US ISSN 0027-4100)

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

Breviora 1952–
Bulletin 1863–
Memoirs 1865–1938
Johnsonia, Department of Mollusks, 1941–1974
Occasional Papers on Mollusks, 1945–

SPECIAL PUBLICATIONS.

1. Whittington, H. B., and W. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. 192 pp.
2. Turner, R. D., 1966. A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia). 265 pp.
3. Sprinkle, J., 1973. Morphology and Evolution of Blastozoan Echinoderms. 284 pp.
4. Eaton, R. J., 1974. A Flora of Concord from Thoreau's Time to the Present Day. 236 pp.
5. Rhodin, A. G. J., and K. Miyata (eds.), 1983. Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams. 725 pp.
6. Angelo, R., 1990. Concord Area Trees and Shrubs. 118 pp.

Other Publications.

Bigelow, H. B., and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprinted 1964.

Brues, C. T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects. (*Bulletin of the* M.C.Z., Vol. 108.) Reprinted 1971.

Creighton, W. S., 1950. The Ants of North America. Reprinted 1966.

Lyman, C. P., and A. R. Dawe (eds.), 1960. Proceedings of the First International Symposium on Natural Mammalian Hibernation. (*Bulletin of the* M.C.Z., Vol. 124.)

Ornithological Gazetteers of the Neotropics (1975–).

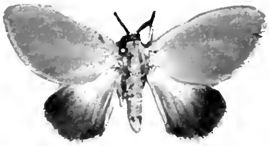
Peters' Check-list of Birds of the World, vols. 1–16.

Proceedings of the New England Zoological Club 1899–1947. (Complete sets only.)

Proceedings of the Boston Society of Natural History.

Price list and catalog of MCZ publications may be obtained from Publications Office, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A.

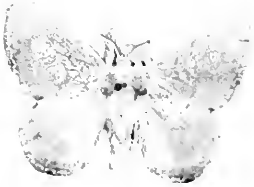
This publication has been printed on acid-free permanent paper stock.


1

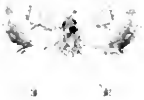

2

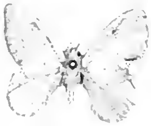

3


4


5


6


7


8


9


10


11


12


13


14


15


16


17


18


19


20

SYSTEMATICS OF THE NEOTROPICAL MOTH FAMILY DALCERIDAE (LEPIDOPTERA)

SCOTT E. MILLER[1]

TABLE OF CONTENTS

Left column, top to bottom:
Figure 1. *Dalcera semirufa*, male paralectotype, Colombia (BMNH).
Figure 2. *Dalcera abrasa*, male, Brazil (BMNH).
Figure 3. *Dalcera canescens*, male, Surinam (BMNH).
Figure 4. *Dalcerina tijucana*, male, Brazil (BMNH).
Figure 5. *Minacraga disconitens*, male, Trinidad (BMNH).
Figure 6. *Minacraga hyalina*, male holotype, Peru (BMNH).

Middle column, top to bottom:
Figure 7. *Dalcerides alba*, male, Mexico (USNM).
Figure 8. *Paracraga necoda*, male paralectotype, Colombia (USNM).
Figure 9. *Acraga flava*, male, Brazil (BMNH).
Figure 10. *Dalcerides dulciola*, male, Venezuela (BMNH).
Figure 11. *Oroya aurora*, male paratype, Peru (BMNH).
Figure 12. *Minacragides arnacis*, male, Peru (BMNH).
Figure 13. *Paracraga halophora*, male, Peru (USNM).

Right column, top to bottom:
Figure 14. *Acraga ria*, male, Brazil (BMNH).
Figure 15. *Acraga goes*, male, Venezuela (BMNH).
Figure 16. *Acraga ciliata*, male, Jamaica (USNM).
Figure 17. *Minonoa perbella*, female (holotype of *variegata*), Brazil (BMNH).
Figure 18. *Minonoa pachitea*, female holotype, Peru (ZSBS).
Figure 19. *Acraga puno*, male holotype, Peru (BMNH).
Figure 20. *Acraga leberna*, male, Brazil (USNM).

---

[1] Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, and Department of Entomology, Smithsonian Institution, Washington, D.C. 20560. Present address: Bishop Museum, Box 19000-A, Honolulu, Hawaii 96817.

Line drawings by L. Laszlo Meszoly, photographs by Victor Krantz, and color plate by Bernard D'Abrera.

Bull. Mus. Comp. Zool., 153(4): 301–495, June, 1994

ABSTRACT. The family Dalceridae is revised, and descriptions, keys, and illustrations are provided for all 84 species (except the *Acraga infusa* species complex). The family includes 11 genera: *Acraga* (=*Anacraga*, n. syn., *Dalargentina*, n. syn.), *Ca*, *Dalcera*, *Dalcerides* (=*Acragopsis*, n. syn.), *Dalcerina*, *Minacraga*, *Minacragides*, *Minonoa*, *Oroya*, n. gen., *Paracraga*, and *Zikanyrops*. These genera are retained in two subfamilies, Acraginae (*Acraga*, *Dalcerides*, and *Zikanyrops*) and Dalcerinae (all others). The status of *Zikanyrops* is uncertain because no males have been available. Cladistic relationships among the genera are discussed. Dalceridae is tentatively placed in a monophyletic group including Epipyropidae, Limacodidae, and Megalopygidae, but many problems exist in the higher classification of the families associated with Zygaenoidea and Cossoidea. Dalceridae is restricted to the Neotropical Region, except one species, *Dalcerides ingenita* (Hy. Edwards), which occurs as far north as Arizona. The geographical and ecological distributions of all species are reviewed, the latter via Holdridge Life Zones. The slug-shaped larvae, distinctive in their dorsal covering of gelatinous conical tubercules, appear to be general feeders on smooth-leaved trees and shrubs.

INTRODUCTION

Dalceridae is a small family of small to medium-sized moths, restricted to the Neotropical Region, with only one species reaching north of the Tropic of Cancer to Arizona. This is the first comprehensive revision of the family, most species of which were named between 1890 and 1930, usually in very short descriptions limited to gross color patterns. This work includes a revision of the species and a phylogenetic analysis of the genera, facilitating future studies of biology, ecology, biogeography, and relationships of the family.

Historical Review

Although the first species of Dalceridae described were placed in diverse and unrelated families, by the late 1800s they were generally placed in what is now Limacodidae. In 1898, Dyar recognized Dalceridae as a family separate from Limacodidae, albeit without adequate definition. Schaus (1905) and Dyar (1910c) provided keys to genera and characterized the family. Almost all subsequent authors have recognized Dalceridae as a distinct family, although without justifying familial status. Of the seven authors who treated the group as a subfamily of Limacodidae, probably only Hopp (1928a) was truly familiar with dalcerids.

Following a few early descriptions by Herrich-Schäffer (1854), Walker (1855a,b, 1865), Burmeister (1878), Edwards (1882), Jones and Moore (1882), and Druce (1887, 1890, 1901, 1910), most of the species and genera were described by Schaus (1892–1940) and Dyar (1898–1928). Dyar and Schaus worked at the Smithsonian Institution for most of their careers, and most of their specimens are deposited there. Dognin (1907–1923) proposed seven dalcerid species. Hopp (1921, 1922, 1924, 1928a) was the only other significant contributor of names.

The treatment of Dalceridae in Seitz' *Macrolepidoptera of the World* (Sick, 1939) is merely a compilation of translated original descriptions, with many errors in both text and plates. The authors in the United States and Europe often misidentified species proposed by their transatlantic colleagues because they did not see each other's types. An exception was Dognin, who sent his novelties to Schaus or Dyar for approval before description.

The only treatment of dalcerids in a modern context is Orfila's (1961) paper on five Argentinian species, which, however, suffered from lack of comparative material from Brazil.

Dalceridae is generally considered to belong to the superfamily Zygaenoidea, closely related to the Limacodidae and Megalopygidae (e.g., Munroe, 1982; Minet, 1986). However, superfamily affinities of the group of families including the Dalceridae, Epipyropidae, Limacodidae, and Megalopygidae are a major problem, and some authors, starting with Brock (1971), place them in Cossoidea.

Justification of Family Status

Based on the apomorphies discussed below, the Dalceridae is a monophyletic group. Although the sister group of the Dalceridae cannot presently be identified, the dalcerids must be given family rank because all the potential outgroups (e.g., Epipyropidae, Limacodidae, Megalopygidae) are families. Furthermore, dalcerids differ from all Lepidoptera at the level traditionally assigned family rank by moth workers. Thus, for stability in Lepidoptera higher classification, and lacking evidence to the contrary, Dalceridae is retained at family rank.

Apomorphies of the Dalceridae include the following: In forewing venation, the pairing of R_2 with R_3 and R_4 with R_5 is apomorphic within the zygaenoid and cossoid families. Although recognition of homologies in the male genitalia is difficult (see the discussion under Morphology), many (if not most) of the reductions and fusions of parts must be apomorphic, because they have not been found elsewhere in the Lepidoptera. The secondary "accessory glands" of the female genitalia are autapomorphic within the Lepidoptera. Dalcerid larvae possess a dorsal covering of translucent gelatinous tubercules, which is unique in the Lepidoptera. The presence of ventral crochets on abdominal segments 2 and 7 in dalcerid larvae is abnormal within Lepidoptera (see the discussion of Larvae, under Biology of Dalceridae).

Relationships of Dalceridae

Of New World Lepidoptera families, Dalceridae appears to be most closely related to Limacodidae, Megalopygidae, and Epipyropidae. The Limacodidae and Megalopygidae have long been associated with Dalceridae (e.g., Hampson, 1898: 12; Forbes, 1923: 99), and the closeness of Epipyropidae and Dalceridae was recognized by Jordan (1928: 137), Hopp (1928a: 283), and Heinrich (1931: 3). Adult characters that have been used to associate the families include the following: male antenna bipectinate (Bodine, 1896: 33), ocelli absent, maxillary palpi and proboscis reduced or absent (Philpott, 1926), thoracic sclerite morphology (Shepard, 1930: 244; Brock, 1971), foreleg epiphysis absent, tibial spurs reduced or absent, wing venation (Forbes, 1923: 99), and male genital structure (Eyer, 1924: 317; Heinrich, 1931: 3). The sculptured flange on the pupal eyepiece of Limacodidae and Megalopygidae (Chapman, 1894: 349; Mosher, 1916: 42–43; Holloway, 1986: 52) appears to be present in Dalceridae and may be a synapomorphy for the three families. There are also strong similarities in general adult habitus as well as in larval (Stehr and McFarland, 1985, 1987) and pupal (Mosher, 1916: 43; Heinrich, 1931: 3) morphology. Although these characters have not been adequately surveyed among families of Lepidoptera, many can be hypothesized to be apomorphic because of their apparent uniqueness. Thus, I suggest that Dalceridae, Limacodidae, Megalopygidae, and Epipyropidae form a monophyletic group (although family limits of Limacodidae and especially Megalopygidae have never been adequately defined). The Old World Chrysopolomidae (near Limacodidae) and Somabrachyidae (near Megalopygidae) apparently belong in this group as well, although they may not be worthy of family rank (see the Appendix).

The relationships among the families discussed above remain problematic, and available data do not support the relationships surmised by previous authors. Stehr and McFarland (1985: 36) suggested, based on larval characters, that ". . . the Megalopygidae . . . gave rise to the Dalceridae . . . and hence to the Limacodidae . . . . Another possibility is to derive . . . both the Megalopygidae and Limacodidae from the Dalceridae." Forbes (1942: 392) placed Dalceridae "intermediate between . . . [Limacodidae] and Megalopygidae, but more primitive than either." Many adult characters, especially in male genitalia, of Dalceridae are more derived than those of Limacodidae and Megalopygidae and, in an evolutionary context, could be derived from corresponding characters in one of them, but they do not suggest that the Dalceridae are basal. These relationships can only be resolved by revision of the family level classification of these groups.

Superfamily Placement

Although Dalceridae, Epipyropidae, Limacodidae, and Megalopygidae usually have been placed in Zygaenoidea, and I follow that placement here, that placement is not certain. None of the zygaenoid or cossoid families have ever been adequately defined in terms of apomorphic characters (except parts of Zygaenidae; e.g., Naumann, 1977; Tarmann, 1984). This section will review the families currently included in Zygaenoidea and Cossoidea, reasons that have been proposed for the placement of Dalceridae in each superfamily, and problems in the higher level relationships between Zygaenoidea and Cossoidea.

The Zygaenoidea of most recent authors includes Zygaenidae, Dalceridae, Epipyropidae, Limacodidae, Megalopygidae, and Somabrachyidae (often placed as a subunit of Megalopygidae) as well as the enigmatic Old World families Heterogynidae and Cyclotornidae. The relationships of the zygaenoid families have never been carefully analyzed, and all of them are, in general, poorly known both taxonomically and biologically. Evaluation of these families is outside the scope of this study, but a synopsis of the families is given in the Appendix.

In addition to the questionable placement of Limacodidae and related families in Cossoidea, the rest of the composition of the Cossoidea remains uncertain. The following families have been associated with Cossoidea in the traditional sense: Cossidae, Metarbelidae, Dudgeoneidae, Compsoctenidae, and Ratardidae. Metarbelidae (=Squamurinae of Roepke, 1957) is variously considered a subfamily of Cossidae (Janse, 1925a; Minet, 1986: 299) or placed as a family related to Cossidae (most recent authors, including Holloway, 1986: 42–43; Schoorl, 1990). Dudgeoneidae, traditionally placed in Cossoidea, was transferred to Pyraloidea by Minet (1982: 266; 1983: 182), but he has reversed his opinion (Minet, 1991: 84, 85). Compsoctenidae was placed near Cossidae (Dierl, 1970) but has subsequently been placed as a subfamily of Eriocottidae in Tineoidea (Nielsen, 1978; Robinson, 1988). The obscure Indo-Malayan family Ratardidae (Hering, 1925; Holloway, 1986: 41–42) has been placed by recent authors in Cossoidea (e.g., Brock, 1971; Holloway, 1986: 43; Owada, 1993), Geometroidea (*sensu lato*) (Heppner and Wang, 1987), Bombycoidea (e.g., Munroe, 1982; Minet, 1986), or Calliduloidea (Minet, 1987); Alberti (1954: 340) even suggested, with little evidence, placing Ratardidae in or near Zygaenidae. Thus, Cossoidea in the narrowest sense includes only Cossidae, but it has been used to include seven or more families.

Brock (1971), relying primarily on adult thoracic morphology, moved the Chrysopolomidae, Dalceridae, Limacodidae, and Megalopygidae from Zygaenoidea to Cossoidea, while placing (probably due to inaedequate representation) Epipyropidae, Heterogynidae, and Somabrachyidae in a diverse, polyphyletic "Tinaeoidea." However, Common (1975: 199), Kuznetsov and Stekol'nikov (1981: 64–65), and Minet (1986: 298, 300; 1991: 84, 91) argued against the placement of Limacodidae and related families in Cossoidea. On the basis of larval characters, Stehr (1987: 453–462) also placed the families related to Limacodidae in Zygaenoidea. Kuznetsov and Stekol'nikov pointed out that most of the similarities between Cossidae and Limacodidae in male genital morphology are symplesiomorphies, and they were unable to identify an apomorphy linking the two families. They listed differences in adult circulatory system morphology, larval morphology, and pupal abdominal morphology that contradict placement of Limacodidae in Cossoidea.

Kuznetsov and Stekol'nikov (1981: 70) concluded that "on the basis of the transfer of the aedoeagal retractor *M4* to the anellus, similarity of structure of the juxta, and . . . morphology of intermediate taxa [Chrysopolomidae], there is support for including the Limacodidae in the Zygaenoidea." Minet (1986) defined his Zygaenoidea on the basis of two apomorphies: (1) the larval head is clearly retractile at least in the last stages, and (2) pupae with stigmata of the second urite hidden by the pterotheca (when these are laid against the abdomen). These authors pointed out, however, that thorough character surveys are necessary to properly define these groups. Until further information is available, I prefer to be conservative and follow the recent reviews of Lepidoptera higher classification by Common (1970, 1975, 1990), Gomez Bustillo (1978), Holloway *et al.* (1987), Kuznetsov and Stekol'nikov (1981), Munroe (1982), Minet (1986, 1991), Nielsen (1989), Nielsen and Common (1991), and Scoble (1992) in retaining Limacodidae and related families in Zygaenoidea (although only Holloway *et al.*, Minet, Munroe, and Nielsen and Common specifically mentioned Dalceridae). Brock (1990: 212, table) appears to have changed his opinion in provisionally including "Eucleoidea" in Zygaeniformia rather than Cossiformia.

Although Heppner (1984: xxi) retained Megalopygidae in Zygaenoidea (along with Heterogynidae and Somabrachyidae), he placed Dalceridae (along with Epipyropidae, Limacodidae, Cyclotornidae, and Chrysopolomidae) in Cossoidea. This placement was apparently based on evidence from the circulatory system noted by Hessel (1969). However, I do not feel that there is evidence at present to place Megalopygidae in a different superfamily from Limacodidae and related families (Hessel, 1969: 365–366, himself agreed). The similarities, some of them unique similarities, among the families related to the Dalceridae already discussed strongly contradict their division based on this one character.

The relationships of Zygaenoidea and Cossoidea to each other and the rest of Lepidoptera are not clear. Most reviews of Lepidoptera higher classification have concentrated on either primitive Lepidoptera or selected superfamilies of "higher" Macrolepidoptera, ignoring relationships of groups that are usually considered "intermediate" (e.g., Castnioidea, Cossoidea, Tortricoidea, Zygaenoidea). Kuznetsov and Stekol'nikov (1981: 65, 69) found similarities among the Cossoidea, Tortricoidea, Sesioidea, Zygaenoidea, and Castnioidea, but they could find no apomorphies linking any of them together. Common and Edwards (1981) demonstrated an apparent relationship of Cossoidea to Castnioidea.

Historically, most authors have assumed relationships between Castnioidea or Cossoidea and butterflies, the Papilionoidea and Hesperioidea (e.g., Forbes, 1923: fig. 1; Brock, 1971: fig. 53; Heppner, 1977: fig. 1). However, Scott (1985: 244; 1986: 33–34) cast doubt on these relationships, concluding (Scott, 1986: 34) that ". . . the Cossoidea–Castnioidea–Zygaenoidea is a derived offshoot of the moth line which could not possibly have produced the butterflies or any other Macrolepidoptera." Scott's ideas need further testing, however, especially in light of new data on the taxonomic composition of the butterflies (Brock, 1989, 1990; Scoble, 1986).

Because of the lack of familial definitions based on apomorphic characters throughout the Lepidoptera, but especially in the zygaenoid and cossoid families, it is presently not possible to define relationships among these taxa. Proper definitions of the families and their relationships will require revisionary work on all their component parts, after they have been segregated into monophyletic units and their diversity has been sampled. My approach to resolving the phylogeny of these families has been to start by defining and revising a small monophyletic group, the Dalceridae.

Although I have examined all relevant published data and dissected members of many zygaenoid and cossoid families to examine critical characters, this effort has been cursory. The number of dissections required to sample, for example, the world diversity of Limacodidae alone (over 800 described species, with very few published illustrations) is outside the scope of the present revision. Thus, I offer these observations only as a starting point for future research.

Biology of Dalceridae

Very little is known about the immature stages of Dalceridae, and larval and pupal characters have not been utilized in this revision due to lack of representative material. The following generalizations are taken from the meager literature (especially Araujo, 1951; Dyar, 1925b; Genty *et al.*, 1978; Hopp, 1928a; Orlando and Ribeiro, 1955; Stehr and McFarland, 1985, 1987) and unpublished observations of A. Aiello, V. O. Becker, P. Genty, N. McFarland, and myself. The complete life histories of only four species (*Acraga* sp. near *A. infusa, Dalcera abrasa, Dalcerides ingenita,* and *Dalcerina tijucana*) are known, but larvae of 12 other species have been reared to adults (although for some the only data available are foodplant records on specimen labels). Adults of many species have been observed alive (especially by Becker). Although not enough is known yet about dalcerids to draw conclusions about their ecology, they appear to share many ecological traits with other heavy-bodied moths with nonfeeding adults (e.g., Saturniidae in Janzen, 1984). It is likely, however, that some of the rare dalcerids differ from these patterns.

Adults. Adult dalcerids usually are rare (at least rarely attracted to light), with several specimens per night being a "good catch" at blacklights. They live about a week and cannot feed. Females of most (but not all species) are much rarer than males at lights; sex ratios in nature are not known.

Dalcerids, especially the larger Dalcerinae, have a weak "fluttering," erratic and undulating, style of flight. When resting on a flat substrate, they hold the wings "tented" loosely over the body, with the plumose fore- and midlegs outstretched, the hindlegs hidden under the wings, and the antennae upright (Fig. 3). This posture is very distinctive and allows their easy recognition. The patterns of colored scales on the legs may even mimic the appearance of a spider in some species such as *Dalcera abrasa*.

Eggs. The small (about 1 mm long in large species), oblong, smooth, often yellow eggs are apparently laid singly and dispersed among vegetation. One female can lay several hundred eggs, which hatch in 8–10 days. When laid, the eggs are coated with a quickly drying fluid that forms a (protective?) layer surrounding them (Fig. 1).

Larvae. The distinctive slug-shaped larvae are oval in outline, flattened dorsoventrally, translucent, hyaline yellow or green, and often with blue, black, yellow, or green stripes (Fig. 2). The dorsal surface is covered with rows of translucent gelatinous conical tubercules, which can become detached when handled. The colors become dull and the tubercules may slough off before larval molts. (Hopp [1928a] describes molting by the fragmenting of the skin in *Acraga flava*, but this has not been observed in other species.) Larvae take 2–6 months to mature, reaching a length of 30 mm in large species.

This dorsal covering of translucent gelatinous tubercules appears to be unique in the Lepidoptera. A possible exception is the limacodid genus *Olona* Snellen (see Cock *et al.*, 1987: 109–110, pl. 30, fig. 4), but I have only seen illustrations, not specimens of *Olona*.

The legs are reduced and the venter is modified into a sluglike, mucus-covered pad. The larvae usually move in the wavelike fashion of a slug. Stehr and McFarland

(1985, 1987) reported that dalcerids are unique among Lepidoptera in having crochets on abdominal segments 2 and 7 in addition to those on segments 3–6. However, M. Epstein (personal communication, 1987) found a megalopygid larva (? *Megalopyge* sp. from Argentina in BMNH) that has crochets on A2 and A7 also.

The larvae are general herbivores and have been recorded from more than 20 plant families (Table 1), but they prefer trees and large shrubs with smooth leaves. They are almost always found on leaves (occasionally on fruits) and seem to prefer sheltered, older leaves toward the center of the plant. Young larvae tend to chew away the surface and skeletonize the leaf in patches, whereas older larvae will eat entire leaves. In the laboratory, larvae can be switched among hosts in several families.

Parasitic flies (Diptera: Tachnidae) and wasps (Hymenoptera: Braconidae and Chalcididae) (Table 2) as well as a fungus (*Beauveria* sp. (Deuteromycetes); Araujo, 1951) have been recorded from immature Dalceridae. Nothing is known of larval predators, which are presumably discouraged by the sluglike shape and gelatinous covering.

Pupae. The white or yellow silken cocoons are usually spun inside clusters of leaves on the hostplant and consist of a loose outer web enclosing a more or less fusiform inner cocoon. There is some diversity in cocoon design (e.g., Dyar, 1925b), perhaps at the generic level. Pupation lasts 1–3 weeks. The pupal shell is extruded from the cocoon during eclosion.

Economic Importance. Dalcerids occasionally are agricultural pests and have been reported damaging the following crops in South America (Table 1): African oil palm (Genty *et al.*, 1978), castor bean (Lourenção *et al.*, 1989), cocoa (Kirkpatrick, 1954), guava (Biezanko, 1961a), and especially coffee (Araujo, 1951, and others) and orange (Gomes and Reiniger, 1939, and others). The appearance of dalcerids as pests is sporadic and localized, but when larvae occur in large numbers they can cause severe defoliation. What is known of dalcerid biology suggests that most species can opportunistically become pests under the right circumstances. Circumstances that may promote expansion of dalcerid populations are not known, however.

Mimicry. Some adult dalcerids apparently avoid predation via one of two forms of mimicry. Many of the small orange species are very similar in appearance and behavior (both in flight and at rest) to several immaculate orange species of the geometrid moth genus *Eubaphe* (Fletcher, 1954). These small, orange, weak-flying moths apparently mimic lycid beetles, which are distasteful to predators. Such mimicry occurs throughout the range of Dalceridae, a good example being the mimetic complex based on *Lycus loripes* (Chevrolat) and *Lycus simulans* Schaeffer in Arizona (Linsley *et al.*, 1961) to which *Dalcerides ingenita* and *Eubaphe unicolor* (Robinson) apparently belong.

Some of the larger dalcerids, especially *Dalcera abrasa*, may mimic spiders when at rest. They rest with the dark, plumose antennae, forelegs, and midlegs outstretched and the wings "tented" back over the body; the resulting appearance is similar to that of a spider.

METHODS

General Taxonomic Philosophy. In the frequent occurrences of incomplete data for taxonomic decisions, I have been conservative and retained established names where possible, while still reflecting available data. Thus, I have generally chosen to leave established generic and specific names standing, unless there are strong data on which to reduce them to synonymy, and not to erect new names, unless there are strong data to support their differentiation. I do not feel that current knowledge of dalcerid distribution and variation allows the use of subspecific names. Whitehead (1972) discussed the practical problems of recognizing taxa, especially spe-

TABLE 1. FOODPLANTS OF DALCERIDAE.[a]

Anacardiaceae
Anacardium occidentale Linnaeus (cashew)—unidentified larva (Brazil, USNM)
Spondias purpurea Linnaeus—*Dalcera abrasa*

Combretaceae
Terminalia buceras Wright—*Paracraga argentea*
**Terminalia catappa* Linnaeus—*Acraga citrina*
Terminalia sp.—*Acraga coa*

Ericaceae
Arctostaphylos pungens Kunth—*Dalcerides ingenita*

Euphorbiaceae
Adelia triloba (Müller Argoviensis) Hemsley—*Paracraga argentea*
**Ricinus communis* Linnaeus (castor bean)—*Acraga citrinopsis, Acraga citrina*
**Ricinus* sp.—*Acraga citrina*

Fagaceae
Quercus emoryi Torrey—*Dalcerides ingenita*
Quercus oblongifolia Torrey—*Dalcerides ingenita*

Graminae
Echinochloa polystachia (Kunth) Hitchcock—*Dalcera abrasa*

Hippocrateaceae
Peritassa campestris Cambessèdes—*Acraga* sp. (orange female, CPAC Lot 5551)

Lauraceae
Nectandra sp.—*Acraga flava*

Mimosaceae
Inga sp.—unidentified larva (Venezuela, USNM)

Myrtaceae
**Eucalyptus robusta* Smith—*Dalcera abrasa*
**Eucalyptus saligna* Smith—*Dalcerina tijucana*
**Eucalyptus* sp.—*Dalcera abrasa*
Psidium guajava Linnaeus (guava)—*Acraga flava*

Ochnaceae
Ouratea sp.—*Dalcerina tijucana*

Olacaceae
Minquartia guianensis Aublet—*Minacraga* sp. (died as pupae, Costa Rica, S. Passoa, personal communication, 1989

Orchidaceae
"Orchid"—*Dalcerides sofia*

Palmae
**Elaeis guineensis* Jacquin (African oil palm)—*Acraga* sp. (*infusa* complex, misidentified by Genty *et al.*, 1978, as *A. ochracea*)

Polygonaceae
Triplaris felipensis Weddell—*Acraga* sp. (*infusa* complex)

Proteaceae
**Macadamia* sp., probably *M. integrifolia* Maiden & Betche (macadamia nut)—*Minacraga disconitens*

Rhamnaceae
Colubrina sp.—*Dalcerides alba*

TABLE 1. CONTINUED.

Rosaceae
***Eriobotrya japonica* (Thunberg) Lindley (loquat)—*Acraga moorei*
**Prunus cerasifera* Ehrhart var. *pissardii* Carrière (cherry plum)—*Paracraga argentea*
**Prunus domestica* Linnaeus (plum)—*Acraga flava*, *Acraga* sp. (*infusa* complex)
**Prunus salicina* Lindley (Japanese plum)—*Acraga* sp. (misidentified by Ballou, 1945, as *A. ochracea*)

Rubiaceae
Alibertia edulis (L. Richard) A. Richard—*Minacraga plata*
**Coffea arabica* Linnaeus (coffee)—*Acraga coa*, *A. moorei*, *Dalcera abrasa*
Uncaria tomentosa (Willdenow) DC—*Paracraga argentea*

Rutaceae
**Citrus sinensis* (Linnaeus) Osbeck (orange)—*Acraga sexquicentenaria*, *Dalcerina tijucana*
**Citrus* sp.—*Acraga coa*

Sapindaceae
Melicoccus bijugatus Jacquin—*Acraga citrina*
Paullinia bracteosa Radlkofer—*Dalcerides mesoa*

Sterculiaceae
Theobroma cacao Linnaeus (cocoa)—*Acraga* sp. (misidentified by Kirkpatrick, 1954 and Figueroa Potes, 1977, as *A. ochracea*)

Tiliaceae
Triumfetta sp.—unidentified larva (Ecuador, S. J. Weller Lot WE84-136, personal communication, 1986)

Ulmaceae
Trema micrantha (Linnaeus) Blume–*Paracraga argentea*

[a] Most plant identifications are as listed by the collectors; plant voucher specimens are available for only a few records. An asterisk (*) denotes species introduced in the region where collected.

cies, in insect groups for which the only data available are from adult morphology and distribution.

Generic Criteria. Genera recognized are monophyletic groups that are distinguished from related genera by (presumed) apomorphic characters of the following "magnitude":

1. Male genital "groundplan"—major differences in general structure of sociuncus, gnathos, vinculum and/or juxta and/or valvae (individually or in complex), aedoeagus, and any processes.
2. Wing venation branching pattern (especially forewing radial veins), but avoiding regions such as the branching of the medial veins from the forewing cell, as in *Dalcerina,* in which there is considerable individual variation.
3. In Dalcerinae, general habitus—major differences in wing coloration or pattern.

Species Criteria. Species generally are separated by consistent and concordant differences in the following:

1. Male genitalia. I have generally used only the presence of or differences in structure or configuration of a part. I have not used minor differences in proportions or relative degree of development of structures because insect genitalia can vary considerably resulting from environmental factors during

TABLE 2. INSECT PARASITES OF DALCERIDAE.[a]

Parasite	Host	Locality	Source
Order Diptera			
Family Tachinidae			
"*Euphorocera* sp."	*Dalcerina tijucana*	Brazil	Gonçalves and Gonçalves, 1973
Pararrhinactia parva Townsend	*Acraga* sp.	Trinidad	Kirkpatrick, 1954
Pararrhinactia sp.	*Acraga* sp.	Colombia (San Alberto)	USNM
Pararrhinactia sp.	*Acraga* sp.	Colombia (Turbo)	USNM
Pararrhinactia sp.	*Acraga coa*	Costa Rica	USNM
Family Sarcophagidae			
Sarcodexia sp.	*Acraga* sp.	Colombia	BMNH
Order Hymenoptera			
"Microhymenoptera"	*Dalcera abrasa*	Brazil	Araujo, 1951
Family Ichneumonidae			
**Isdromas monterai* (Lima)	*Acraga citrinopsis*	Brazil	Santis, 1987
Family Braconidae			
Glyptapanteles dalosoma Santis	*Acraga citrinopsis*	Brazil	Santis, 1987
Pelecystoma sp.	*Acraga* sp.	Colombia	USNM
Family Chalcididae			
Brachymeria sp.	*Acraga* sp.	Colombia	USNM
**Conura* (*Ceratosmicra*) *immaculata* (Cresson) [as *C. argentina*]	*Acraga citrinopsis*	Brazil	Santis, 1987
Conura (*Conura*) *acragae* Delvare	*Acraga* sp.	Colombia	Delvare, 1993
Family Perilampidae			
*cf. *Perilampus* sp.	*Dalcerides flavetta*	Ecuador	CMNH
*cf. *Perilampus* sp.	*Paracraga halophora*	Brazil	BMNH

[a] All records of *Acraga* sp. refer to species near *Acraga infusa*. Determinations of parasites by E. E. Grissell (Chalcidoidea), P. M. Marsh (Braconidae), and N. E. Woodley (Tachinidae), all Systematic Entomology Laboratory, U.S. Dept. of Agriculture, N. P. Wyatt (Sarcophagidae), BMNH, G. Delvare, CIRAD, France (Chalcididae), and D. C. Darling (Perilampidae), Royal Ontario Museum. An asterisk (*) denotes probable hyperparasites.

development (e.g., Shapiro, 1979); specimen preparation techniques and mounting angles also can cause apparent distortion.

2. Major differences in wing pattern or coloration. Minor color differences have generally been ignored because subtle colors are easily lost in damaged or old specimens.

In groups where external differences are not significant (especially *Acraga*), I have utilized genitalia alone to separate species. The same relative level of differentiation was used to separate species in such groups as in groups with both internal and external differences.

Specimen Preparation. Genital and other dissections were prepared in the standard way (Clarke, 1941; Robinson, 1976), stained with Chlorazol black and Safranin O, and either mounted on slides in balsam or kept in glycerin. Almost all drawings were made from specimens in glycerin, to avoid distortion. Slide mounting is not always satisfactory because of the thick, cylindrical nature of most dalcerid male genitalia, but when slide-mounted the lateral view usually shows the most characters. Wings were bleached and then stained with Eosin Y and mounted in balsam. Five-digit numbers refer to dissections deposited in the USNM, while numbers prefixed with 84-, 85-, 86-, or 87- are deposited in other collections.

Descriptions. The descriptions are generally composite and based largely on the best available specimens. Minor color shades are easily obscured in damaged or old specimens, so many color descriptions are necessarily vague. Many specimens are missing most of the colored body scales, especially those of the head and legs.

Identification Keys. The keys and diagnoses utilize the character states that are most convenient for identification purposes. The male uncus and other genital structures often can be seen adequately for identifications (at least to species-group) after removing the scales from the apex of the abdomen by brushing. All questionable identifications should be verified by dissection.

Locality Names. South American localities, except those in Brazil and the Guianas, generally follow the ornithological gazetteers published by the Bird Department of the MCZ (R. A. Paynter, Jr., and coauthors, 1975–1991). Other standard references are F. Brown (1941; Ecuador), K. Brown (1979), Lamas (1976; Peru), Selander and Vaurie (1962; Central America), Vanzolini and Papavero (1968; Brazil), and the U.S. Board on Geographic Names country gazetteers. In locality lists, added data that are not on the specimen labels (other than minor spelling corrections and expansions) are enclosed in square brackets. All months in dates have been converted to Roman numerals.

The distribution maps were computer-generated, using latitude and longitude coordinates from the gazetteers already cited or appropriate maps. The DI 3000 mapping system, as implemented on the Smithsonian Institution's Office of Information Resources Management IBM 4381 computer, was used.

Notes on Locality Names.

1. Specimens labeled only "Para, Brazil/ A. Miles Moss" (BMNH, via Rothschild Collection) were collected in the vicinity of Belém between 1911 and 1918 (Moss, 1920: 358–360).
2. Sitio, Costa Rica, an enigmatic locality of William Schaus, is located midway between Juan Viñas and Turrialba, at some 1,000–1,200 m (L. D. Gomez, personal communication, 1985).
3. I have seen several specimens from the MMU and BMNH labeled only "Colombia/Coll. by W. E. Pratt." I know nothing of the localities at which and dates when Pratt collected, but known distribution of several species (e.g., *Acraga hamata*) suggest that at least some were collected in the former part of Colombia that is now Panama. The MMU specimens were received in the C. H. Schill collection in 1893 (C. Johnson, personal communication, 1985), so they were collected before Panama became independent from Colombia.
4. Specimens collected by J. F. Zikan in southern Brazil are usually accurately dated, but they frequently bear incomplete locality data. Zikan's moths, with the exception of a trip to the Amazon from June 1927 to January 1928, were collected at four localities where he lived (butterflies, however, were also collected at other localities) (Mielke, 1971; W. Zikan, personal communication, 1985):
   - XI-1911 to 7-X-1915, Fazenda Jerusalem, Alegre, Espírito Santo;
   - 10-X-1915 to 27-I-1922, Fazenda dos Campos, 1,500 m, Minas Gerais (near Passa Quatro);
   - 28-I-1922 to 29-IX-1923, Passa Quatro, 950 m, Minas Gerais; and
   - 30-IX-1923 to 3-II-1949, Itatiaia (formerly Campo Bello), 400 m, Rio de Janeiro.

Completion Date. Most of the research reported here was completed in 1986. Specimen records seen through 1987 and literature seen through 1993 have been included. Additional specimens will be treated in future papers.

COLLECTIONS CONSULTED

The following collections were consulted during this study. Abbreviations generally follow Heppner and Lamas (1982). I personally visited the AMNH, BMNH, BPBM, CMNH, CNC, CPAC, FSCA, INPA, IOC, LACM, MCZ, MNRJ, PMY, SMEK, UMO, USNM, VOB, and ZSBS during this study, locating many specimens that were placed in incorrect families and would have been missed otherwise. The bulk of the material studied is in the BMNH, USNM, VOB, and ZSBS, and most species are represented in each of these collections. The most important secondary collections are the AMNH, CMNH, CU, LACM, and UCV. For simplicity, I have listed all of Janzen's Costa Rica material as USNM, but duplicates will be distributed to the BMNH and Costa Rica's Instituto Nacional de Biodiversidad.

AJW	Adolfo and Jorge White private collection, Mexico City
AMNH	American Museum of Natural History, New York (F. H. Rindge)
BMNH	British Museum (Natural History), London (D. Carter, M. Honey, A. Watson) [now Natural History Museum]
BPBM	Bishop Museum, Honolulu, Hawaii
CAS	California Academy of Sciences, San Francisco (P. H. Arnaud)
CIBC	Commonwealth Institute of Biological Control, Curepe, Trinidad (S. T. Murphy)
CMNH	Carnegie Museum of Natural History, Pittsburgh (J. Rawlins, C. Young)
CNC	Canadian National Collection, Agriculture Canada, Ottawa (J. D. Lafontaine)
CPAC	EMBRAPA–Centro de Pesquisa Agropecuaria dos Cerrados, Planaltina, Brazil (V. O. Becker)
CU	Cornell University, Ithaca, New York (J. K. Liebherr)
FSCA	Florida State Collection of Arthropods, Gainesville (J. B. Heppner)
IML	Fundacion e Instituto Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina (A. Willink) (no specimens seen)
INPA	Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil (V. Py-Daniel, J. Adis)
INTA	Departamento de Patología Vegetal, Instituto Nacional de Tecnología Agropecuaria, Castelar, Argentina (H. F. Rizzo) (no specimens seen)
IOC	Insituto Oswaldo Cruz, Rio de Janeiro, Brazil (O. V. Ferreira)
LACM	Natural History Museum of Los Angeles County, Los Angeles (J. P. Donahue, C. L. Hogue)
MBR	Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina (A. O. Bachmann) (no specimens seen)
MCML	Merseyside County Museum (formerly Free Public Museum), Liverpool, England (I. D. Wallace) (no specimens seen)
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
MHNP	Muséum National d'Historie Naturelle, Paris (G. Luquet)
MJWC	M. J. W. Cock private collection, Ascot, England
MLP	Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina (R. A. Ronderos) (no specimens seen)
MMU	Manchester Museum, Manches-

	ter University, Manchester, England (C. Johnson)
MPM	Milwaukee Public Museum, Milwaukee, Wisconsin (A. M. Young)
MNRJ	Museu Nacional, Rio de Janeiro, Brazil
NHMV	Naturhistorisches Museum, Vienna, Austria (F. Kasy)
NMVM	Museum of Victoria, Australia (K. Walker) (no specimens seen; checked for F. Walker types)
PMY	Peabody Museum, Yale University, New Haven, Connecticut (D. G. Furth)
RJM	Roberto and Javier de la Maza private collection, Mexico City
RNHL	Rijksmuseum van Natuurlijke Histoire, Leiden, The Netherlands (R. de Jong)
RT	Rafael Turrent private collection, Mexico City
SDNH	San Diego Natural History Museum, San Diego, California (D. K. Faulkner)
SMEK	Snow Museum of Entomology, University of Kansas, Lawrence (R. Brooks)
SMF	Senckenberg Museum, Frankfurt-am-Main, Germany (H. Schröder)
UCB	Essig Museum of Entomology, University of California, Berkeley (J. A. Powell)
UCR	University of California, Riverside (S. I. Frommer)
UCV	Instituto de Zoologia Agricola, Universidad Central de Venezuela, Maracay, Venezuela (F. Fernandez Yepez)
UMO	University Museum, Oxford University, Oxford, England (M. J. Scoble)
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C. (D. R. Davis)
UWIT	University of the West Indies, St. Augustine, Trinidad (Kirkpatrick voucher specimens) (P. D. Stiling)
VOB	V. O. Becker private collection, Brasilia, Brazil
ZMHB	Zoologisches Museum, Humboldt Universität, Berlin, Germany (H. J. Hannemann)
ZMUC	Zoologisk Museum, Universitets Copenhagen, Copenhagen, Denmark (N. P. Kristensen)
ZSBS	Zoologische Sammlungen des Bayerischen Staates, Munich, Germany (W. Dierl)

I have seen primary type material of all species names except the following—lost, but identifiable from original description: *Acraga boliviana* Hopp, *A. moorei* Dyar, *A. sexquicentenaria* (Orfila), *A. sulphurea* (Burmeister), and *Dalcera abrasa* Herrich-Schäffer; lost, not identifiable from original description: *Acraga luteola* (Hopp), *Dalcera haywardi* Orfila, and *Zikanyrops sparsa* Hopp; apparently destroyed, replaced here by neotypes: *Acraga ochracea* (Walker) and *Acraga concolor* (Walker).

MORPHOLOGY

External Morphology

Small to medium-sized moths, with heavy, hairy bodies and broadly rounded wings, usually white, yellow, or orange in ground color.

Head (Fig. 4). Small and densely scaled; lower frontoclypeus naked, covered by upturned labial palpi; ocelli and chaetosemata absent; proboscis vestigial and densely spinose (Fig. 5); maxillary palpi vestigial (Fig. 6); eyes large; labial palpi two-segmented, short and appressed to frontoclypeus; first palpal segment small, less than twice as long as wide; second palpal segment four to seven times as long as wide.

Antenna. Short, about as long as thorax, broadly bipectinate in males, narrowly bipectinate in females; antenna composed of scape, pedicel, and 18–45 bipectinate flagellar segments; shaft scaled, sometimes with scale tuft at apex. Pectinations bear three types of sensilla (following standard nomeclature based on external morphology [Callahan, 1975; Wirth and Navai, 1978], which may however lead to lumping of sensilla with different functions [Odendaal *et al.*, 1985]): common type, long, thin, sharp sensilla trichodea cover the pectinations (Fig. 8); less common sensilla chaetica are more stout and usually occur at the tips of pectinations (Fig. 8); and uncommon sensilla coeloconica are scattered among the other sensilla (Fig. 9). Dalcerid sensilla coeloconica are similar to those in other Lepidoptera but lack the normal "picket fence" of inward-pointing spines around the perimeter of the pit.

Thorax. Relatively large and densely scaled. Tympanal organs absent. Small fields of close-set microtrichia present on upper sides of metascutum (wing-locking device joining a field on ventral forewing and present in most Lepidoptera; see Common, 1969; Kuijten, 1974). The circulatory system is of "chamber dorsal–transverse" configuration (Hessel, 1969; only *Dalcerides ingenita* examined). Metathoracic furca (Fig. 48) varies somewhat in relative length and the shape of apophyses (nine species examined) but does not seem to be useful as a generic level character in Dalceridae. Although the metathoracic furca can be very useful at the generic level in some "lower" Lepidoptera, it is not in many "higher" Lepidoptera (e.g., Horak, 1984: 18). Legs densely scaled; tibial spurs and foretibial epiphysis absent.

Forewing. Somewhat ovate, long along base to apex axis, more broadly rounded in females than males. Veins Sc, R system, M_1, M_2, M_3, CuA_1, CuA_2, CuP, and 1A+2A are present (nomenclature follows Common, 1970). Most of M stem present in discal cell, and radial system forms an accessory cell in Acraginae. Anal loop present (except *Ca* and *Minacragides*). In the radial system, R_1 is either separate or stalked (fused in *Ca*) with the R_{2+3} stem. The stems of R_{2+3} and R_{4+5} are often stalked. R_2 and R_3 are always stalked or fused; R_4 and R_5 are always stalked or fused. The pairing of R_{2+3} and R_{4+5} is unique among the zygaenoid and cossoid families. Although this is considered the "Ditrysian archetype" by Brock (1971: 36–37), it is probably secondarily derived within the superfamily here (see also Holloway, 1986: 52). Subcostal retinaculum present in males that have a frenulum (except maybe *Zikanyrops*), as a narrow, elongate rolled flap arising from Sc, forming a tube through which the frenulum fits (Braun, 1924; Common, 1970: 769) (Figs. 10–12). A field of microtrichia present on ventral inner margin near base (wing-locking device) (Figs. 23, 24).

Hindwing. Generally same color as forewing, but paler and usually without maculation (except around anal angle). Veins Sc + R_1, Rs, M_1, M_2, M_3, CuA_1, CuA_2, CuP, 1A+2A, and 3A are present (3A apparently present in most preparations but difficult to distingish from adjacent folds). Most of M stem present in discal cell. Sc + R_1 and Rs free, fused, or connected by a small "bridge" in discal cell. Male frenulum present in most genera, a long bristle (Figs. 13, 14) formed by partial fusion of some 10–30 acanthae (Richards, 1981). In scanning electron microscope (SEM) photographs, 4–14 acanthae are visible from the dorsal side (thus more than half the acanthae; five genera examined). When male frenulum is absent, the humeral angle is somewhat produced (e.g., Fig. 51). Female frenulum (Fig. 15) a clump of long, narrow, unfused scales (more than 15 in dorsal view of *Dalcerides ingenita*). Campaniform sensilla like those described by Brown and Miller (1983: 276) are usually present on the base of the cubital stem of the hindwing (only dorsal sides examined) (Fig. 22).

Neither the Dalceridae nor the relationship of Cossoidea and Zygaenoidea were treated in the wing base study by Sharplin (1964); I have not examined wing base characters due to the specialized dissections required.

Wing Scales. The wing scales of dalcerids vary primarily in gross shape (outline) and the size and spacing of windows (seven genera examined with SEM). Terminology follows Ghiradella (1984) and Downey and Allyn (1975). General form of scales usually lamellar, mixed with piliform. Lamellar scales usually spatulate, sometimes lanceolate, the apex rounded or dentate (two to four teeth). Upper lamina of "normal" lepidopteran plan. Longitudinal ridges prominent, straight, parallel, composed of overlapping elongate scutes (=lamellae) with elongate basal arms (Fig. 19). Microribs dominate the "flats" between the ridges, virtually obliterating the windows (=areolae, =fenestrae). Windows usually present, small to very small, varying in size and spacing (Fig. 19). The extensive microribs form "ranks of chevron-shaped cuticular rodlets [which] give the scale a characteristically satiny texture" (Ghiradella, 1985: 252). This scale structure, found in most dalcerids, is the "microrib-satin" type of Ghiradella (1984: 643, fig. 6; 1985: 252). The lack of structural diversity agrees with observations by Ghiradella (1985) and Brown and Miller (1983) that there is generally little diversity among species in scale types of a given wing region within most (but not all) Lepidoptera families.

Abdomen. Length about equal to hindwing anal angles, densely scaled, usually the same color as dorsal hindwings. I have not found any useful taxonomic characters in the dalcerid abdominal surface, except the posterior hooklike processes of the eighth tergite of *Minacragides arnacis.*

Sexual Dimorphism. In species where both sexes are known, the sexes are very similar, differing only in the following: female antennal pectinations are short, yielding narrowly bipectinate antennae; female frenula are composed of many unfused bristles; females are larger—the smallest females are about the size of the largest males; and female wings, especially forewing angles, are more broadly rounded. Females are also much less commonly collected than males at lights (with the notable exceptions of *Acraga flava* and *Dalcerides ingenita*).

Male Genitalia (Fig. 25)

The male genitalia of dalcerids are marked by extensive reduction and fusion, especially of the valvae. Recognition of homologies of genital parts, both among dalcerids and in relation to other families, is difficult. Furthermore, the knowledge of Lepidoptera genital morphology and homology in general (e.g., Klots, 1970: 116; Razowski, 1976: 107–117; Zimmerman, 1978: 201–204, 210) is inadequate due to the enormous structural diversity within Lepidoptera, and so does not provide an adequate framework for resolution of difficult cases. I have assigned names primarily on the basis of position relative to "landmarks" such as the aedoeagus and anal tube. Names follow standard usage, but it should be emphasized that the parts designated by the same names are not necessarily homologous throughout the Lepidoptera (Klots, 1970).

Tegumen and *sociuncus* [sensu Sibatani (1972)] generally well developed, frequently fused into one complex. *Uncus* usually bilobed, sometimes with medial and/or lateral points or hooks (especially in *Acraga*). *Socii* sometimes developed as densely hairy pads (in *Minacraga*, *Dalcera*, *Dalcerina*, and *Oroya*); otherwise represented only as poorly defined lateral hairy areas on sociuncus. *Gnathos* generally well developed, but taking many forms; two-parted in many genera, with median process(es) in the middle of the genitalia ventral of anal tube, and free lateral arms extending outward near the tegumen/vinculum suture; median process(es) composed of two symmetrical structures, frequently touching but not attached to each other (most Acraginae), or fused into one solid structure (most Dalcerinae); median process and lateral lobes probably are the cochlear and brachia, respectively, of Ogata *et al.* (1957) and Sibatani (1972). *Vinculum* generally elongate and thin, usually extended anteriorly as long saccus. *Valvae* extremely reduced, immovable, usually only small processes, frequently fused with juxta, anellus, and/or vinculum; sometimes not recognizable. *Juxta* often present as independent rod; frequently juxta (independently or fused with other parts) forms an external support structure under the aedoeagus extending outward about same distance as aedoeagus (in pinned specimen); sometimes bifid externally; sometimes platelike internally; sometimes fused with valvae, anellus, and/or vinculum. *Anellus* usually cannot be differentiated from surrounding structures, but probably is represented in fused complexes with valvae, juxta, and/or vinculum. *Saccus* generally elongate, sometimes broad. *Aedoeagus* generally long and slender, but can be short and stout (e.g. *Minacraga*), hooked at tip (some *Dalcerides*), or with a single triangular spine externally (*Paracarga*); *vesica* with a small patch of cornuti in some species of *Acraga*.

Sibatani (1972) uses the term sociuncus (=scaphium of Ogata *et al.* [1957]) for the dorsal appendages of the tenth somite including uncus and socii. Ogata *et al.* (1957) discuss the problems in defining units within the sociuncus (see also Stekol'nikov and Kuznetsov, 1986: 139).

An alternative way of naming dalcerid structures would be to consider the socii absent, consider my socii to be gnathos, and my gnathos to be transtilla (compare for example *Minacraga* with Agonoxenidae [=Blastodacnidae] in Gelechioidea; Clarke, 1962; Bradley, 1966). However, because of the difficulties in defining units of the sociuncus, in general, and the homologies of valvae and anellus in Dalceridae (discussed below), I have not applied the term transtilla here.

Processes of the vinculum occur in *Dalcera*, *Dalcerina*, and *Minacraga*, the identity of which has not been resolved; they are probably not homologous with each other. In *Dalcerina*, the process is a semicircular, slender, flexible rod attached at the middle between the outside of the juxta and the inside of the outer wall of the saccus; it might be related to the bifid "anellus" attached to the vinculum in some Epipyropidae (see Heinrich, 1931: fig. 5). *Minacraga* have tusk- or bladelike processes arising adjacent to and below the rudimentary valvae; these are reminiscent of the furca described in Geometridae by Okagaki *et al.* (1956) and similar in appearance to processes that occur in some Mimallonidae (e.g. some *Cicinnus* spp.). *Dalcera* has two pairs of setose processes arising from the vinculum-saccus-juxta complex; both appear solidly fused with this complex—one may represent valvae, the other may be the bifid end of a fused juxta. The relationship of the processes discussed above to those in some Limacodidae (e.g., *Euclea cupostriga* Dyar) is unknown and awaits further study (see further comments in the *Minacraga* generic description later).

Throughout the Lepidoptera, the morphology and nomenclature of structures in the region around, and especially ventral to, the aedoeagus is a major problem (e.g. Klots, 1970: 120, 122). Apparently many structures have evolved in multiple ways to meet the general need of supporting the aedoeagus. The general confusion, together with the fusion and reduction in dalcerid genitalia, makes identification of the homology of these processes almost impossible with present knowledge.

Birket-Smith (1965, 1974) introduced several novel concepts to the morphology of male genitalia of Lepidoptera. Application of his ideas remains difficult, because he applied them to representatives of very few families, and subsequent authors have generally ignored his work (see Kanazawa, 1987; Kristensen, 1984: 172-173; Kuznetsov and Stekol'nikov, 1986; Stekol'nikov and Kuznetsov, 1986: 136; Udea, 1978, however). One of his concepts are "valvella," paired structures "mesad of the valvae and laterad or dorso-laterad of juxta . . . often displaced dorsad; they . . . form an independent ventral support for phallos . . . [or] an integrated part of phallos . . . or they may degenerate" (Birket-Smith, 1965: 6). In Birket-Smith's example in Cossidae, the "valvellae" have fused with the juxta as hollow dorsal lobes of it. These fused "valvellae" in *Xyleutes* (the American species formerly placed in *Xyleutes* are now in *Morpheis* [Donahue, 1980; Schoorl, 1990]) are somewhat reminiscent of the vinculum processes in Dalcerinae, but the juxta is a platelike structure well separated from the valvae and vinculum. This structure is well illustrated in the related *Psychonoctua masoni* (Schaus) by Blanchard and Knudson (1985: fig. 16). There is no agreement on the identity of these "valvellae" in the literature, and in *Xyleutes* they are usually considered "lobes" or "ligulae" of the juxta (e.g., Roepke, 1957), "juxta complex" (e.g., Razowski, 1981), or anellus (e.g., Arora, 1976). Until further evidence is available, I prefer not to use the "valvellae" concept.

Birket-Smith (1974: 20-21) also introduced the concept of pseudaedoeagus versus aedoeagus (the latter including the fused valvellae). However, without definitive means of distinguishing between the two, I continue to use "aedoeagus" in the traditional sense.

Eyer (1924: 318) suggested the valvae of some Megalopygidae are "characterized by a complete separation of the cucullus and sacculus." This suggestion has never been evaluated in detail, but the only subsequent authors to use names for these parts used "harpe" and "sacculus" (Hopp, 1927 and other years), "cucullus" and "sacculus" (Mehta, 1933: fig. 63; Lima, 1945: fig. 62), and "apendice da juxta?" and "saccullus da valva incompleta?" (Oiticica, 1946: 62). Eyer (1924: 318) extended this view to *Dalcerides ingenita* (compare his pl. XXXVIII, figs. 1 and 3), where he suggested the "cucullus is indistinguishably fused with the tegumen, forming a pair of dorsal ear-like lobes." While I cannot disprove this idea, I have not found anything to support it in the dalcerids and am not using it here. I would call Eyer's "ear-like lobes" the sociuncus. Split valvae are also present in some Limacodidae.

Study of the musculature and functional morphology of the genitalia might resolve these homology problems. However, the only related family that has been appropriately studied is Limacodidae (Kuznetsov and Stekol'nikov, 1981).

Female Genitalia (Fig. 26)

Bursa copulatrix. Sterigma usually a weakly differentiated invagination, sometimes a sclerotized plate, often with a depression or cleft in middle; ostium bursa narrow to broad; ductus bursae relatively long, narrow to broad, usually with one or two strong bends; corpus bursae medium to small, ovate or spherical, without signa. *Ductus seminalis* arising from first half of ductus bursae, usually near a bend. *Spermatheca* with long duct, a portion of which is tightly coiled, ending in a bilobed sac (the spermatheca is often broken or missing in specimens, and this is reflected in the illustrations). *Apophyses anteriores* absent. (The lateral lobes on the anterior edge of the eighth abdominal tergite of some Dalceridae [e.g., *Dalcerides ingenita*] are not apophyses anteriores, since these lobes occur together with apophyses anteriores in some Megalopygidae [e.g., *Megalopyge defoliata* (Walker)], *Apophyses posteriores* straight and narrow or wide at base, narrowing to apex, short to long. *Papillae anales* large, densely setose; divided by a cleft into upper and lower lobes; the duct from the "accessory glands" opens into the outside end of this cleft.

"*Accessory Glands*" (Miller, 1993). One on each side, closely anteriad of papillae anales; ovate or triangular in lateral view, flattened laterally, the outer surface usually covered with convoluted lobes and ridges. The two accessory glands are not connected to each other, only to the outside by short ducts that open onto the outer side of the papillae anales, into the cleft between the upper and lower lobes (Figs. 27–32).

Glands removed from pinned specimens, cleaned with KOH and ethanol and examined by light microscopy and SEM (following critical-point drying) show the following structure. The outer surface is covered with small regular pits (Fig. 27), which are presumably the bases of the inner structures. The inner surface is covered with regular polyplike structures (Fig. 28), consisting of a round, straight "trunk" topped with multiple small spinelike processes (Fig. 29).

The short ducts connecting the "accessory glands" to the outside of the body fuse with the outermost ventral portion of the bases of the apophyses posteriores (In *Acraga citrinopsis*, a lobe of the gland is fused with each apophysis, forming part of the inner wall of the apophysis [Fig. 242].) The ducts then empty into the cleft between the papillae anales (Figs. 30–32). Based on one observation of live *Dalcerina tijucana*, the glands appear to secrete a rapidly drying fluid onto the eggs as they are laid. This fluid completely covers the eggs and forms a smooth layer, which entraps loose scales and other debris as it dries (Fig. 1). The function of this layer is unknown—it could glue the eggs in place, strengthen the eggs, or protect the eggs from moisture loss or egg parasites. This layer appears to be thicker than that of most Lepidoptera eggs (see Downey and Allyn, 1981: 1–13).

The Epipyropidae have a single (not paired) gland that may be analogous or homologous (D. R. Davis, personal communication, 1986) to the glands of the Dalceridae. The Aidinae of Megalopygidae have glands that appear similar to those of Dalceridae, but they are less sclerotized and broadly connected to each other (thus lacking independent ducts to the outside). I have seen nothing similar in a limited sample of Limacodidae and other Megalopygidae.

The "Petersen's glands" of Zygaeninae (Bode and Naumann, 1988; Naumann, 1988) appear to not be homologous with dalcerid "accessory glands." I am not aware of similar "accessory glands" in any other Lepidoptera. The paired glands used in egg-laying in other Lepidoptera are usually connected to each other and/or the oviduct (e.g., Klots, 1970: 126). My use of the term "accessory glands" does not imply homology to "accessory glands" as used in other Lepidoptera to designate "colleterial glands" or "glandulae sebaceae" or a variety of poorly identified structures.

In addition to the zygaenoid families already discussed, secondary accessory glands are present in females of various unrelated taxa of Ditrysian Lepidoptera, including Nymphalidae, Hesperiidae, Noctuidae, and Geometridae (e.g., Bode and Naumann, 1988: 27–29; Burns, 1984: 21; Petersen, 1900: 100–102; Pierre, 1986; Urbahn, 1913: 339). However, dalcerid "accessory glands" differ from all these in having their external openings on the outside of the papillae anales (versus emptying into the genital tract or externally but between the papillae anales) and in the two members of the gland pair not being connected.

PHYLOGENETIC ANALYSIS

Phylogenetic analysis was undertaken to hypothesize the relationships among the genera of Dalceridae and to suggest the most appropriate generic placement of the species groups formerly placed in poorly diagnosed genera associated with *Acraga*. I chose to use cladistic methods because they are the most efficient for this type of study (Farris, 1980, 1983) and they standardize the reconstruction method, allowing future workers to test my results (Wiley, 1981). Cladistic procedures group taxa based on synapomorphies (shared derived character states), rather than overall similarity (Hennig, 1966).

Procedures

Terminal Taxa. The terminal taxa used were chosen in accord with the two purposes of the analysis (see the Introduction for discussion of generic and specific criteria used). In the Dalcerinae, genera were used as terminal taxa because the genera are well defined by both external and internal (genital) characters that provide clear apomorphies. Because it might represent a distinct genus, the *Minacraga aenea* species-group was included in the analysis, as well.

Due to paucity of external characters and apparent discordance of internal characters in species formerly placed in the genera *Acraga*, *Acragopsis*, *Anacraga*, *Dalargentina*, and *Dalcerides*, determination of appropriate generic limits was difficult. Therefore, all distinctive species groups (based primarily on male genitalia) were included in the analysis as terminal taxa. Thus, the phrase "terminal taxa" is used here to refer to both genera and distinctive species groups. The enigmatic genus *Zikanyrops* could not be included in the analysis because no males were available for study; it is probably near to or synonymous with *Dalcerides*.

Character Choice and Coding. The morphological characters to be coded were chosen, on the basis of the criteria discussed in the Introduction, as being appropriate to express relationships among genera or species groups. Some are simple presence or absence of a structure (e.g., frenulum); others, however, are three-dimensional shapes of complicated features, often of uncertain homology (e.g., sociuncus–tegumen complex, juxta–valval region). Optimal coding schemes for the latter kind of characters were hypothesized experimentally, using Transformation Series Analysis (TSA; see p. 320 and Mickevich, 1981, 1982; Mickevich and Weller, 1990; Mickevich and Lipscomb, 1991; Pogue and Mickevich, 1990; Lipscomb, 1990, for explanation).

Parallel data sets were prepared with features in question coded in several different ways. After completing TSA on each data set, the set with the highest character concordance was chosen as the optimal coding scheme. Character concordance (e.g., the best fit between that coding scheme and the rest of the data set) was measured by information content (e.g., resolution of the tree), transformational fits, and the equality of contribution to the cladogram across all characters (Mickevich and Lipscomb, 1991; Mickevich and Miller, in preparation). Only the coding schemes chosen as "best" are discussed here, and the details of this experimental approach will be published elsewhere (Mickevich and Miller, in preparation).

For example, the system of radial veins in the forewing was coded in parallel data sets as three characters (based on the individual branching points) and as one character (based on the overall pattern created by the branching). TSA of both data sets revealed that coding the radial system as one character was preferable to coding it as three characters. In more than 50 individual iterations on 20 data sets, similar experiments were made with the juxta–valval region (coding as one, two, or three characters), the gnathos (coding as one or two characters), and the sociuncus–tegumen complex (coding as one to four characters).

The great diversity in some characters of the male genitalia (especially the juxta–valval region and the sociuncus–tegumen complex) made it difficult to code character states to emphasize similarities (putative synapomorphies) rather than differences (autapomorphies for the various genera and species groups). In this study, I have excluded morphological features that vary within the terminal taxa. This was difficult, however, because the full range of variation within many terminal taxa is unknown due to lack of adequate material. The optimal coding schemes (chosen as already outlined) generally assessed the gross morphology of the largest appropriate region, rather than its component parts. For example, treating the entire sociuncus–tegumen complex as a unit emphasized similarities, while treating the various processes on different regions of the uncus separately emphasized differences.

As discussed by Weitzman and Fink (1985: 8–9), character choice is a subjective balance between describing perceived morphology and distinguishing evolutionary novelties. "A nonarbitrary way to divide the functional and morphological attributes of an organism into subunits appropriate for phylogenetic studies has not yet been found, because of the functional and structural unity of the whole organism" (Weitzman and Fink, 1985: 8). An example of this problem is the juxtavalval region, which has evolved morphologically in several apparently independent ways to fulfill the general functional need for supporting the aedoeagus.

Methods. Data analysis utilized most parsimonious Wagner trees constructed by the PHYSYS program package (Farris and Mickevich, 1985), as installed at the University of Maryland, College Park, using discrete Wagner analysis with local and global branch swapping. The basic assumption of Wagner analysis is that the best estimate of phylogenetic relationships is that estimate which requires the fewest character transformations and is therefore the shortest possible cladogram (Farris *et al.*, 1970; Wiley, 1981). Unlike other algorithms such as Weighted Invariant Step Strategy (Farris *et al.*, 1970) or Dollo's model, which restrict the direction of character change, the Wagner method allows any possible change in order to minimize the number of ad hoc statements (i.e., extra steps) concerning character information.

Polarities of Transformation Series. Half of the final characters were polarized by outgroup comparison, which is the most reliable method (Maddison *et al.*, 1984; Stevens, 1980). The characters polarized directly by outgroup comparison are frenulum, forewing accessory cell, forewing anal loop, apical scale tuft on antennae, socii, and vinculum processes. No ontogenetic data are available, and none of the relevant families have a known fossil record (Carpenter, 1992).

However, due to the highly derived condition of many characters of Dalceridae relative to the rest of the Lepidoptera, only half the characters include states that are shared between the putative outgroups and the ingroup (Dalceridae). Another complication is the large number of states in some of the multistate characters. These problems were addressed with TSA.

TSA is an iterative procedure that derives the most parsimonious interpretations of character change from successive cladograms, obtaining a better approximation with each iteration, until a final stable result is reached (Mickevich, 1981, 1982; Mickevich and Weller, 1990; Lipscomb, 1990; Pogue and Mickevich, 1990). The following example illustrates the use of TSA in a simple case. The first iteration of cladogram construction uses initial hypothesized transformation series, based on any available knowledge, or the transformation series may be unordered if necessary. The distribution of character states is plotted on the resultant cladogram and a simplified tree of states within each character is prepared, using Farris optimization and nearest neighbor associations (Mickevich, 1982: 462–466) to resolve ambiguous situations. The resultant character cladograms are reduced to transformation series that are used for the next iteration of cladogram construction. Character cladograms are again prepared from the next cladogram, and the process continues until both the cladogram and the transformation series stabilize. Mickevich (1982: 461) demonstrated that when TSA "gives results different from the original Wagner trees, the cladograms . . . [resulting from TSA] . . . show greater taxonomic congruence."

Outgroups. As discussed in the Introduction, the Epipyropidae, Limacodidae, and Megalopygidae appear to form a monophyletic group with the Dalceridae, but relationships among the four families are unknown. Use of these families as outgroups is hindered by three problems: the morphological diversity and homology of characters (especially of genitalia) of these families are poorly known; inability to choose a single sister group of the Dalceridae; and, most importantly, lack of shared character states (especially in genital structures) with the ingroup (Dalceridae). Lack of knowledge of the three families is a serious problem that may lead to overlooking character states that are shared with Dalceridae. This problem, however, is beyond the scope of this revision. Inability to resolve relationships among the potential outgroups is probably the least serious problem, because either they all share the same state (some external characters) or none share a state with the ingroup (genital characters).

Most of the genital characters of Dalceridae are highly derived, and many are not known to occur elsewhere in the Lepidoptera (see the discussion under Morphology). Recognition of the homology of many structures (especially in the genitalia) within the family is difficult, so extending homologies for these structures to the other families is almost impossible with present knowledge. Most of these structures of questionable homology appear to have arisen in the Dalceridae via reduction and fusion and, in some cases have resulted in the creation of apparently new structures (e.g., juxta–valval region), although this would be difficult to confirm. I agree with Weitzman and Fink (1985: 10) that "when such losses are associated with new, complex, and unique similarities among related taxa, . . . a hypothesis of homology (i.e., synapomorphy) may be proposed and then analyzed for parsimonious correlation with other shared derived characters."

As already discussed, half the characters were polarized directly by outgroup comparison, and the other characters were polarized by TSA. Thus, outgroup comparison was used to root the cladogram and the cladogram was used to polarize the characters for which outgroup comparison was not available.

For this analysis, I have chosen Epipyropidae as an outgroup, because their morphological diversity is better understood than the much more species-rich Limacodidae and Megalopygidae, and because the monophyly of the Limacodidae and Megalopygidae has not been demonstrated. The only practical difference in using Limacodidae or Megalopygidae is that these two families lack a forewing accessory cell, which makes no significant difference to the tree. Data for Epipyropidae have been taken from Heinrich (1931), Jordan (1928), Krampl and Dlabola (1983), Richards (1941), and D. R. Davis (personal communication, 1985).

Characters

The following are the final characters used, annotated listings of the states included, and the transformation series resulting from TSA on multistate characters. For detailed descriptions of the states, see the discussions of general morphology, genera, and illustrations. The transformation series derived from TSA are illustrated schematically for the six characters with more than three states. These transformation series are derived solely from the cladogram and are intended only as a hypothesis for further testing. The outgroup is designated as state A in the multistate characters. When more than one state is hypothesized to be derived from another state, each of these states is assumed to be independently derived (e.g., in the juxta–valval region, states H, I, J, and K are all considered to be derived independently from state B). Character states that are autapomorphic for terminal taxa were not deliberately included in the data set, although they are often included as unique states within characters included for other reasons. Females were excluded from the analysis due to incomplete data.

Wing Characters. Frenulum—Present or absent. *Forewing Radial System (Fig. 33)*—All radial veins free (A); R_1 free, $R_2 + R_3$ stalked, $R_4 + R_5$ stalked, R_{2+3} and R_{4+5} stems arising together (B); like B but R_{2+3} and R_{4+5} stems stalked (C); like B but R_{2+3} and R_{4+5} stems not arising together (D); R1 arising together with R_{2+3} stem, R_{2+3} stalked, R_4+R_5 stalked (E); R_1 free, R_{2+3} fused, R_{4+5} fused, R_{2+3} and R_{4+5} stems stalked (F); only two radial veins, apparently R_{1-3} fused, R_{4-5} fused (G); R_1 stalked with R_{2+3} stem, R_{2+3} fused, R_{4+5} fused (H). *Forewing Accessory Cell*—Present or absent. *Forewing Anal Loop*—Present or absent.

Head Character. Apical Scale Tuft on Antennae—Present or absent.

Genital Characters. Oval Pad Socii—Present or absent. *Juxta–Valval Region (Fig. 34)*—Normal valvae present (A); juxta fused complex partly surrounding and supporting aedoeagus, valval lobes dorsolateral of aedoeagus (B); juxta completely fused with vinculum, valvae tabs on vinculum (C); juxta unfused rod, valvae tabs (D); like G, but complex more strongly curved and sclerotized, encasing aedoeagus (E); like G, but complex less strongly scelerotized (F); juxta–valval complex forming sclerotized plate supporting aedoeagus, with weaker tube surrounding aedoeagus dorsally (G); external juxta rodlike, valval lobes partly or completely fused with base of juxta (H); juxta–valval complex around aedoeagus with hooklike valval tabs (I); juxta(?) conical complex encasing aedoeagus, valval lobes dorsolateral of aedoeagus (J); juxta–valval region very reduced (K). *Saccus (Fig. 35)*—Short, very broad (A); long, slender (B); reduced (C); short, slender (D); long, with bulbous apex (E); medium length, broad tapering to point (F); medium length, medium width (G); very reduced (H). *Aedoeagus (Fig. 36)*—Triangular (TRIANGULAR); long and slender (LONG); long and slender, end recurved (RECURVED); long with interior saclike (SAC); long and slender with exterior spine (SPINE); long with patch of cornuti on vesica or apex of aedoeagus (CORNUTI); medium length and stout (MEDIUM); reduced, encased in vinculum (ENCLOSED); long and slender, bent (BENT); internode hypothesized by TSA (?). *Gnathos (Fig. 37)*—Broad with ridges (A); unfused comblike (B); unfused triangular tabs (C); similar to C with strongly developed median process (D); developed as lateral arms (E); similar to C, but independent triangular tabs less well developed (F); fused (or near) into triangular plate (G); reduced unfused processes (H); single sclerotized ridged plate (I); like I with strong lateral arms (J); thin fused plate, conforming to ventral surface of sociuncus (K); thin fused plate (L). *Sociuncus–Tegumen Complex (Fig. 38)*—Tegumen laterally extended, sociuncus reduced (A); elongate, with at most small points or lobes on uncus (B); globular, flattened, gently rounded (C); elongate, with long paired arms on uncus (D); globular (E); elongate, with lateral lobes on uncus (F); globular, with lobes (G); elongate, with dorsal hoods or lobes on uncus (H). *Process of Vinculum*—Absent, semicircular, or tusk- or bladelike. Transformation series: ABSENT–CIRCULAR–TUSK.

Discussion of Cladogram

The cladogram indicating relationships among genera is presented in Figure 39. For simplicity, the cladogram of relationships among the species groups of *Acraga* is presented separately in Figure 40. For clarity of graphic presentation, the multistate characters are presented on the cladogram recoded as additive binary characters (Kluge and Farris, 1969), following the final transformation series obtained by TSA. Thus, the character states and transformation series already discussed under Characters are the same as those on the cladogram—they are just coded differently.

This cladogram shows excellent fit to the data set, with a total length of 61 steps. The minimum number of steps required for perfect fit would be 58 (number of steps for each character summed over all characters). The overall consistency index (Kluge and Farris, 1969: 7–8) is 95.082. The individual consistency indices for the characters are all 100, except aedoeagus (90.000), gnathos (91.667), and sociuncus–tegumen complex (87.500).

After the study was completed, the results were checked using the binary coded data set (Figs. 39, 40) in the HENNIG86 package (Farris, 1988). The HENNIG86 run resulted in one tree identical to Figures 39 and 40, with a length of 60 steps, a consistency index of 95, and a retention index of 97.

The ensuing discussion treats only major clades. Apomorphies uniting other clades may be found on the cladogram. Character state changes on the terminal stems are discussed in the treatments of those taxa and will not be elaborated here. Autapomorphic states for terminal taxa were not deliberately included in the cladogram; those that are included are unique states within multistate characters included for other reasons. Some stems remain poorly defined and some nodes are not fully resolved, resulting in multifurcations. It must be emphasized that this is a preliminary estimate of the phylogeny of Dalceridae, and that (as with most neotropical organisms) the cladogram will change as new data are gathered for both Dalceridae (especially characters of females and immature stages) and its outgroup(s).

The branching points of the cladogram are defined by apomorphic character states. As used here, a state is apomorphic when it and all the states derived from it are unique to the group it defines. A monophyletic group ". . . shares an ancestral stem [character state] common only to members of that group" (Mickevich, 1981: 212). Thus, all the taxa in a monophyletic group do not have to possess the apomorphic state that defines that group but must have either that state *or* a state uniquely derived from it.

Genera of Dalceridae (Fig. 39). The subfamily Dalcerinae is based on absence of the forewing accessory cell, gnathos shape H, and sociuncus–tegumen complex shape C. *Oroya* is quite different from other taxa of Dalcerinae and shares juxta–valval state B with *Acraga*. *Minacraga* and its aberrant *aenea* species-group are united by saccus shape F and tusklike vinculum processes. These two terminal taxa are clearly closest relatives and could be placed as one genus or as sister genera. Without further data, I prefer to retain them as the single genus *Minacraga*.

The subfamily Acraginae is based on gnathos shape B. The association of gnathos shape B (apomorphic for *Dalcerides*) with *Acraga* rather than with Dalcerinae is weak, but several other characters corroborate the monophyly of Acraginae. Forewing radial pattern B, although placed in the analysis as an apomorphy for Dalceridae, is a synapomorphy for members of Acraginae. If the polarity of the forewing accessory cell is reversed by use of an alternate outgroup (as already discussed), then the presence of the accessory cell becomes a synapomorphy for members of Acraginae.

Dalcerides includes an unresolved multifurcation of four species-groups. Although this clade is based here only on juxta–valval shape I, gnathos shape B of Acraginae is a synapomorphy for members of *Dalcerides*. Relationships among the four species-groups used in the analysis (the species formerly included in *Dalcerides* [*sensu stricto*], the species formerly included in *Acragopsis*, *Dalcerides alba*, and *Dalcerides nana*) are unresolved, so they are not included on the cladogram. The only difference among them in the final character set is possession of the bent aedoeagus shape by *D. alba*. The genus *Zikanyrops*, which could not be included in the analysis, probably belongs in or near *Dalcerides*.

Acraga, based on gnathos shape C and sociuncus–tegumen complex shape F, includes all the species-groups of Acraginae not placed in *Dalcerides*. The relationships of the species-groups of *Acraga* are discussed separately below.

Species-Groups of Acraga (Fig. 40). All these species-groups were previously placed in the poorly defined genera *Acraga*, *Anacraga*, and *Dalargentina*. Although some of the groups (e.g., *ampela* and *ochracea*) are clearly related, the relationships between most groups are weakly diagnosed. Although accumulation of further data may indicate that *Acraga* should be split into several genera, no strong groupings suitable for generic status are apparent in the cladogram. The relationships among the species-groups of *Acraga* are based here only on five multistate characters (juxta–valval complex, aedoeagus, sociuncus–tegumen complex, saccus, and gnathos), which were polarized by TSA. Therefore, some of the included homologies and polarities are based on weak evidence. Further indication of the weakness of postulated relationships within *Acraga* is that many clades changed relationships in different experimental data sets (although the terminal pairings were generally the same), while the relationships among genera within Dalcerinae remained stable in all data sets. The basal unresolved quadrichotomy within *Acraga* exemplifies the difficulties in splitting *Acraga* into meaningful subunits. The *Acraga ciliata* group possesses many autapomorphic states, making its placement especially difficult.

Subfamilies. The subfamilies Dalcerinae and Acraginae were first separated by Orfila (1961), primarily on the basis of absence and presence, respectively, of the forewing accessory cell. Although these subfamilies have been weakened by analysis of characters that Orfila did not see (especially those of *Oroya*), the cladogram confirms the split of Dalceridae into two subfamilies, albeit weakly diagnosed (for further characters, see the discussions of the two subfamilies under Key to Genera).

A Test of the Stability of the Generic Phylogeny (Fig. 39A)

TSA was the sole means used to order transformation series for multistate characters (the forewing radial vein system as well as the complex genital characters: juxta–valval region, saccus, aedoeagus, gnathos, sociuncus–tegumen complex, and vinculum processes). For these multistate characters (with the exception vinculum processes), no direct outgroup information was available (although the tree constructed with TSA was polarized using an outgroup, in these genital characters the ingroup generally did not share states with the outgroup).

While the relationships among species-groups within *Acraga* already postulated have no effect on nomenclature, the relationships and definitions of the genera are very important for the stability of dalcerid nomenclature. To test this, I removed the multistate genital characters from the data set and reanalyzed the remaining characters. This test is important to see whether TSA allowed maximal information extraction from the data or it produced results that are not concordant with the original data. Besides the important practical implications of this test, it has theoretical interest, as well. Is a phylogeny generated through a more conventional analysis (e.g., using only "traditional" characters with little or no use of TSA) concordant at the generic level with the phylogeny that used multistate genital characters ordered with TSA?

For the test, the multistate genital characters were removed from the data set. The remaining characters (frenulum, forewing radial system, forewing accessory cell, forewing anal loop, antennal tufts, and socii) were analyzed using PHYSYS. The same terminal taxa as in the full analysis were used (however, as in Fig. 39, species groups within *Acraga* and *Dalcerides* are not included in Fig. 39A for clarity).

The test data were analyzed in three ways, to evaluate the effects of ordering in the forewing radial system: (1) using the forewing radial system transformation series postulated by TSA (Fig. 33), (2) using the forewing radial system as unordered, and (3) applying TSA to the results of analysis 2. The results of the three analyses were similar, each producing either one (analyses 1 and 3) or two (analysis 2) trees of length 13, with consistency indices of either 92.308 (analysis 2) or 100 (analyses 1 and 3). All the trees had the same topology, except for one tree generated by analysis 2, which differed slightly in the placement of *Paracraga*. Only analysis 3, the stable result of new TSA on the forewing radial system, will be discussed further (as "test cladogram").

One further test was made to evaluate

the effect of outgroup choice. The data set from analysis I was used, reversing the polarity of the forewing cell (e.g., using Limacodidae or Megalopygidae as an outgroup). This analysis generated one tree with a length of 14, a consistency index of 92.857, and the same topology as the test cladogram.

The test cladogram (summarized in Fig. 39A) is concordant with the full cladogram (Fig. 39), but the test cladogram is less resolved. Because resolution of the species-groups within Acraginae (especially the species-groups of *Acraga*) is based on the five genital multistate characters, these cannot be resolved in the test cladogram. Likewise, as discussed previously, there are other conventional characters that support placement of *Acraga* and *Dalcerides* as monophyletic genera. The test data set does not include the apomorphies that resolve *Minacraga*, the *Minacraga aenea* group, and *Dalcerina*; however, the monophyly of *Minacraga* is evident from the tusklike processes of the vinculum (not included in the test data set, but included in Fig. 39A for clarity).

Thus, cladistic analysis of "traditional" characters of external morphology (socii of the genitalia were included in the test but show the same distribution as the forewing venation state C of Fig. 33) yields the same generic relationships as the analysis including multistate genital characters using TSA. The multistate genital characters, as ordered with TSA, allowed greater phylogenetic resolution within the groups of *Acraga* (Fig. 40).

BIOGEOGRAPHY

The following discussion attempts to draw preliminary conclusions about the ecological and historical biogeography of Dalceridae, via Holdridge Life Zones, current distribution patterns, and the composition of local faunas. Moths have great potential for use in biogeographic studies and also as indicators of environmental quality in areas undergoing rapid change in vegetation or climate (e.g., Holloway, 1983; Miller and Holloway, 1991), but such use requires a greater knowledge of distribution and biology than is currently available for Dalceridae.

Distribution by Life Zones

The ecological distribution of dalcerids is summarized according to the Holdridge Life Zone system, following the example of Becker (1982). This system has the advantages of being simple and readily available, because Life Zone maps are available for most neotropical countries (the important exception being Mexico). However, the system's application here is oversimplified. For instance, label data, especially for old collections, are sometimes vague or incorrect; because of this, and local ecological variation (e.g., gallery forest in savanna areas), specimens may have been collected in Life Zones different from those calculated from label data. In addition, the summaries include only Life Zones where a species has been collected, not all Life Zones where it may occur (i.e., many Life Zones have not been adequately sampled). However, the Life Zone system provides a good indication of where a species could be expected to occur.

My placement of localities in Life Zones follows Becker (1982), Tosi (1983), and references therein. I have seen published Life Zone maps (most cited by Tosi, 1983) for all relevant areas except Argentina, French Guiana, Guyana, Jamaica, Mexico, Surinam, Trinidad, and the United States (Arizona). Life Zones for northernmost Argentina and the Guianas were interpolated from maps of adjacent countries and climatic data. Life Zones for Arizona, Mexico, and Trinidad were calculated from climatic data (following Holdridge, 1978; Holdridge *et al.*, 1971). I follow Becker (1982) in citing localities such as Planaltina, Brazil, as "Tropical Premontane Moist Forest," and La Oroya, Peru, as "Tropical Premontane Wet Forest" rather than "Subtropical Moist Forest" (Tosi, 1983, etc.), because of their elevation.

Dalceridae have been recorded most

commonly (measured in species per Life Zone) from Tropical Moist and Tropical Premontane Wet Forest Life Zones, with fewer but significant numbers from Tropical Wet, Tropical Premontane Moist, Subtropical Moist and Wet, and Warm Temperate Moist Forest Life Zones. A few species are also recorded from Tropical Rain and Dry, Tropical Premontane Dry and Rain, Tropical Lower Montane Rain, Subtropical Dry, Subtropical Lower Montane Wet and Moist, and Warm Temperate Dry Forest Life Zones.

By examining the individual ecological components of the Life Zones (again by counting species per Life Zone), the following preliminary conclusions can be drawn (with the caveat that this may indicate more about the distribution of collectors than of moths and that marginal habitats are probably not adequately taken into account). Dalceridae are concentrated in the tropical and subtropical latitudinal regions, although a few species penetrate into the Warm Temperate region in Southeastern Brazil and adjacent areas. They occur primarily in the Basal and Premontane altitudinal belts, with some occurring in the Lower Montane belt and perhaps a few entering the Montane belt (Andean collecting localities are difficult to place accurately in Life Zones). Dalceridae occur mostly in the Moist and Wet humidity provinces, with some entering the Dry and Rain provinces (although the effect of local variations within Life Zones is hard to evaluate).

Dispersion and Dispersal

Although many species of Dalceridae are widely dispersed (*sensu* Platnick, 1976), their dispersal abilities appear to be limited. Some species range widely over most of tropical and subtropical South America, often occurring at elevations from sea level to over 1,000 m, even 1,500 m (e.g., *Acraga moorei, Dalcera abrasa*). Most species, however, appear to be more limited in distribution, and many are still known from very few localities. Dalcerids have been relatively unsuccessful at colonizing areas south of Peru, Bolivia, and Brazil and north of Costa Rica and are not known at all in the Old World. Like Limacodidae and Megalopygidae, dalcerids are very poor at colonizing islands (Epstein and Miller, 1990), the only known island occurrence (excepting Trinidad and the Tres Marías Islands) being the endemic species *Acraga ciliata* on Jamaica. Like many other neotropical insect groups (see Typical Neotropical Dispersal Pattern in Halffter, 1976), Dalceridae have not significantly penetrated the Mexican Plateau. While dalcerids appear to be generalists in habitat and foodplant choices, they are restricted by the limited mobility of the sluglike larvae and the short lifespan and poor flight abilities of the adults and perhaps also low population densities.

Geographical Distribution Patterns

Most dalcerid species fall into one of the following categories, although some species are known from too few localities to permit generalizations on their distribution, and several species fall into two categories:

1. Northern South America (to about the southern limit of the Amazon Basin), often extending north to Costa Rica.
2. Tropical and subtropical South America (to northernmost Argentina), often extending north to Costa Rica.
3. Andean–Guiana Shield Highlands, often following highlands into Costa Rica.
4. Southeastern Brazil and adjacent Argentina, Paraguay, and Uruguay.
5. Central America, with a few species penetrating north of southern Mexico and a few occurring in western Colombia and Ecuador.

Most of the genera (and species-groups in *Acraga*) are widely distributed in South America, below about 1,500 m. Only *Dalcerides*, *Paracraga*, and the *ciliata* and *infusa* groups of *Acraga* have penetrated north of Costa Rica; only *Dalcerides* has colonized north of Nayarit and Veracruz in Mexico. Only *Dalcerina*, two species of *Dalcerides, Minonoa perbella, Zikanyrops sparsa*, and the *ferruginea*, *flava*, and *ochracea* groups of *Acraga* are restricted to southeastern Brazil and adjacent areas. The *ampela, hamata*, and *melinda* groups of *Acraga* are concentrated in highland areas of the Andes (up to 2,800 m for *A. mariala*) and Costa Rica and Panama, although they include species that occur in the Amazon Basin lowlands.

The Pleistocene refuge hypothesis has become very popular for explaining distributional patterns and areas of endemism in tropical forest organisms (see reviews by Beven *et al.*, 1984; Mayr and O'Hara, 1986; Prance, 1982; Salo, 1987; Whitmore and Prance, 1987). The available data suggest that the lowland dalcerid species are widely distributed, and there are not enough data on the species restricted to the Andes and Guiana Shield to evaluate patterns. Thus, due to lack of data, Dalceridae cannot yet be utilized to critically evaluate the refugia and centers-of-origin postulated (e.g., Beven *et al.*, 1984: fig. 1) by this model for biological diversification in the tropics.

Occurrence at Selected Sites

The combination of poor sampling in the neotropics in general and the rarity of dalcerids in collections means that the local resident dalcerid fauna is known for very few sites. I have selected nine localities that have been sampled fairly intensively for moths during most months over a period of years. This approach is biased by differences among collecting methods and sums species across years, ignoring possible local habitat changes. With the exception of Saint-Jean, the sampling apparently represents relatively small areas. Although these localities are among the best sampled for moths in the neotropics, many dalcerids are known only from one or several specimens per site—illustrating the paucity of our knowledge.

The sites are Turrialba (Costa Rica), Barro Colorado Island (Panama), Rancho Grande (northern Venezuela), Kartabu (northern Guyana), Saint-Jean (northern French Guiana), Cerro de la Neblina Basecamp (0°50′N, 66°10′W, southern Venezuela), Planaltina (central Brazil), Nova Brémen (southeastern Brazil), and La Oroya (southern Peru). All numbers below count specimens of the *Acraga infusa* complex as one species (although several as yet unresolved species may be involved).

Each of these nine sites has between 6 and 12 dalcerid species, with an average of 8 species per site. A total of 40 species occur at the sites, but 25 of these are found only at one site. The 15 species that are common to several sites are *Acraga goes, A. leberna, A. moorei, A. ochracea, A.* species near *A. infusa, Dalcera abrasa, Dalcerides alba, D. dulciola, D. flavetta, D. mesoa, Dalcerina tijucana, Minacraga disconitens, Minacragides arnacis, Paracraga argentea*, and *P. innocens.*

SYSTEMATIC TREATMENT

Family Dalceridae

Dalceridae Dyar, 1898: 231; 1910c: 113.—Hampson, 1898: 12, 16, 19.—Schaus, 1905: 331.—Kuznetsov, 1910: 881, 887; 1967: 8, 11, 18.—Dyar and Strand, 1913b: 27.—Forbes, 1914: 58; 1923: 99; 1942: 392.—Hopp, 1921: 276.—Eyer, 1924: 318, 322.—Comstock, 1925: 605.—Kaye and Lamont, 1927: 121.—Jordan, 1928: 137.—Heinrich, 1931: 3.—Sick, 1939: 1303.—Lima, 1945: 180.—D'Almeida, 1945: 193.—Duarte, 1947: 188.—Orfila, 1961: 249.—Munroe, 1970: 7.—Brock, 1971: 31, 51.—Watson and Whalley, 1975: 188.—Fletcher and Nye, 1982: ix.—Munroe, 1982: 632.—Davis, 1983: 67.—Holloway, 1986: 10.—Stehr and McFarland, 1987: 460.—Holloway *et al.*, 1987: 48, 139.—Scoble, 1992: 269–270.

Acragidae Hampson, 1918: 385, 390.

Dalcerinae [of Limacodidae] Janse, 1925b: 321, 335.—Handlirsch, 1925: 896.—Hopp, 1928a: 283.—Zerny and Beier, 1936: 1696.—Bourgogne, 1951: 393.—Remington, 1954: 234.

Dalcerinae [of Megalopygidae] Tams, 1935: 174.

Type Genus. Dalcera Herrich-Schäffer, [1854].

Diagnosis. Small to medium-sized, white, yellow, or orange (occasionally brown) ground-colored moths with no proboscis and bipectinate antennae that taper evenly to the apex; distinguished from similar Limacodidae and Megalopygidae by the pairing of forewing veins R_2 with R_3 and R_4 with R_5 as well as genitalia; some small orange Geometridae (especially *Eubaphe* Hübner) are superficially similar, differing in having narrow antennae and a prominent proboscis; some small whitish Lasiocampidae (especially *Nesara* Walker) are superficially similar, differing in the broadly expanded hindwing humeral angle and well-developed humeral vein.

Discussion. All the genera, and the species-groups within *Acraga,* are arranged below according to cladistic analysis. Within these groups, the species are grouped according to apparent relationships (but cladistic analysis of species has *not* been made).

Taxa Incorrectly Described as Dalceridae

The genus *Protacraga* and the four species listed below were originally described in Dalceridae and have been moved to other families by subsequent authors. I have seen the types of the four species and confirm the placements outside of Dalceridae.

Dalcera? innoxia *Schaus, 1910: 415.* Based on a female holotype (USNM), this species was transferred to the new genus *Coamorpha* Dyar (as type species) in Megalopygidae by Dyar and Strand (1913a: 14). It was also placed in Megalopygidae (without generic assignment) by Schaus (1915: 501). *Vescoa glutina* Schaus (1920: 146), based on males only, was synonymized by Hopp (1929: 44; 1935: 1077) under *Coamorpha innoxia.* However, I have seen a Costa Rican male (VOB collection 30946), which appears to be the true male of *innoxia* and suggests that *glutina* is not the male of *innoxia.*

Dalcera nigerella *Dognin, 1923a: 24.* Based on a male holotype (USNM), this species was transferred to *Protacraga* by Dyar (1927: 551). The genus *Protacraga* was transferred to Epipyropidae by Hopp (1928a: 284).

Protacraga micans *Hopp, 1924: 553.* Based on a holotype female (ZMHB), this genus and species was transferred to Epipyropidae by Hopp (1928a: 283).

Dalcera laxta *Druce, 1890: 506.* Transferred to *Nesara* in Lasiocampidae by Draudt (1928: 620) and Collier (1936: 93), this placement in *Nesara* appears to be correct, based on examination of the unique holotype in BMNH (in poor condition, without an abdomen); it is not a dalcerid.

KEY TO GENERA OF DALCERIDAE

1\. Forewing without accessory cell (e.g., Fig. 55) .... (Dalcerinae) 2
Forewing with accessory cell (e.g., Fig. 41) .... (Acraginae) 9
2(1). Antenna with apical scale tufts; forewing R_4+R_5 stalked (e.g., Fig. 54); usually large, male forewing length $\geq$ 13 mm 3
Antenna without apical scale tufts; forewing R_4+R_5 fused or stalked (e.g., Fig. 51); small, male forewing length $\leq$ 20 mm 5
3(2). Wings brown, bronze, or gold, usually metallic (Figs. 139–146) .... *Minacraga*
Wings orange, never metallic 4
4(3). Forewing R_1 and R_{2+3} arising separately (Fig. 55); male forewing without submedial shading and curved inner half-band (Figs. 129, 131, 132) .... *Dalcera*
Forewing R_1 and R_{2+3} arise together on short stalk from cell (Fig. 56); male forewing with submedial shading and curved inner half-band (Fig. 133) .... *Dalcerina*
5(2). Wing ground color white or light brown, with brown pattern; male frenulum absent 6
Wing ground color fuscous with multicolored pattern, or orange; male frenulum present 8
6(5). Wing ground color white or tan, forewing pattern brown or metallic (Figs. 117–124); forewing R_1 arises separately from R_{2+3} (Fig. 51) .... *Paracraga*
Wing ground color light brown, not patterned (may have a few spots); forewing R_1 fused or stalked with R_{2+3} (Figs. 49, 52) 7
7(6). Forewing with 3 radial veins (Fig. 49); male forewing length ca. 9 mm .... *Minacragides*
Forewing with only 2 radial veins (Fig. 52); male forewing length ca. 6 mm .... *Ca*
8(5). Wings fuscous with pattern (Figs. 125–128); forewing R_{2+3} fused (Fig. 53) ......

.... *Minonoa*

Wings orange (Fig. 150); forewing R_2+R_3 stalked, but not fused (Fig. 47) .... *Oroya*

9(1). Forewing with accessory cell and especially upper half of discal cell retracted, distal ends of cells not in line (e.g., Figs. 43, 44) .... *Dalcerides*

Forewing cell normal, discal veins in line (e.g., Fig. 41) 10

10(9). Forewing accessory cell large, at least half length of discal cell (e.g., Fig. 41) . *Acraga*

Forewing accessory cell small, limited to apical tip of discal cell (Fig. 46) .... *Zikanyrops*

Subfamily Acraginae

Diagnosis. Distinguished from Dalcerinae by the presence of the forewing accessory cell (e.g., Figs. 41, 48).

Discussion. This subfamily includes *Acraga*, *Dalcerides*, and *Zikanyrops*. See Discussion of Cladogram for justification of subfamily status.

Acraga Walker

Acraga Walker, 1855a: 807.—Dyar, 1898: 232; 1910c: 115.—Dyar and Strand, 1913b: 28.—Sick, 1939: 1305.—Forbes, 1942: 393–394.—D'Almeida, 1945: 193.—Orfila, 1961: 255–256.—Fletcher and Nye, 1982: 3. Type species: *Acraga ciliata* Walker, 1855, by monotypy.

Aeruga [misspelling]. Pagenstecher, 1909: 439.

Pinconia Moore in Jones and Moore, 1882: 364.—Kirby, 1892: 543.—Druce, 1898: 441.—D'Almeida, 1945: 195.—Fletcher and Nye, 1982: 127. Type species: *Pinconia ochracea* Moore, 1882 [not Walker, 1855], by monotypy. [synonymized under *Acraga* by Dyar, 1898: 232]

Epipinconia Dyar, 1898: 231, 232.—Schaus, 1905: 331.—D'Almeida, 1945: 194.—Fletcher and Nye, 1982: 59. Type species: *Dalcera flava* Walker, 1855, by original designation. [synonymized under *Acraga* by Dyar, 1910c: 115]

Anacraga Dyar, 1905a: 176; 1910c: 119.—Dyar and Strand, 1913b: 29.—Hopp, 1921: 281.—Sick, 1939: 1307.—D'Almeida, 1945: 193.—Fletcher and Nye, 1982: 10. Type species: *Dalcera citrina* Schaus, 1896, by original designation. NEW SYN.

Dalargentina Orfila, 1961: 253–254.—Fletcher and Nye, 1982: 48. Type species: *Dalargentina sexquicentenaria* Orfila, 1961, by original designation. NEW SYN.

Diagnosis. Differs from *Dalcerides* in having forewing cell normal (discal veins in line) (e.g., Figs. 41, 42).

Adult Male. Small to large, forewing 7–18 mm. Ground color: usually orange or yellow, some species white, several species brown or brownish red; some species with maculation. Forewing: Accessory cell present; R_1 free, arising from accessory cell; $R_2 + R_3$ long-stalked; $R_4 + R_5$ short-stalked; retinaculum present. Hindwing: Rs fused *or* not fused with Sc + R_1 in cell; frenulum present. Genitalia: Tegumen and sociuncus fused; sociuncus with various lateral lobes and posterior hooks and/or lobes; socii not distinct, but lobes of sociuncus usually hairy; gnathos various, central portion usually pair of unfused rectangular or triangular tabs, lateral arms sometimes present; vinculum slender, elongate; valvae reduced, fused into complex around aedoeagus, or lobes dorsolateral of complex; juxta not distinct, fused into complex surrounding and supporting aedoeagus (very strongly developed in some species); anellus probably present as complex surrounding aedoeagus; saccus slender, short to very long; aedoeagus various, medium length and stout to long and slender.

Adult Female. Medium to large, forewing 14–26 mm. Genitalia: Sterigma broad, often well sclerotized; ostium bursae narrow to broad; ductus bursae usually broad to first bend, then narrowing; corpus bursae spherical to elongate ovate; ductus seminalis arising between bends in ductus bursae; apophyses posteriores short to long, usually wide at base, narrowing to apex; "accessory glands" ovate or triangular in lateral view.

Discussion. Cladistic analysis shows that almost all the species previously placed in *Acraga*, *Anacraga*, and *Dalargentina* should be placed in *Acraga* (the few exceptions are transferred to *Dalcerides*). For convenience, I have organized *Acraga* into 11 species-groups. In most cases, all the species placed in a species-group are clearly both monophyletic and closely related, but placement of a few species (e.g., *Acraga perbrunnea*, *Acraga ria*) is problematic. These informal species-group names are for convenience only, and I do not intend them as the "interpolated species group names" of the *International Code of Zoological Nomenclature* (ICZN, 1985, Article 6b).

Because the male holotype of *Acraga luteola* is lost, and *Acraga ingenescens* is known only from the female holotype without an associated male, proper assignment of these names is problematic, so I designate several species by letter only. Further material will be necessary to resolve the nomenclature and taxonomy of these lettered species.

The gender of *Acraga* Walker is taken to be feminine because its author described it with the included species *Acraga ciliata*.

To facilitate identification of species of *Acraga*, I provide two keys. The first is designed to sort all *Acraga* to species-group, but requires use of characters that may be difficult to see without dissection in some specimens. The second key is designed to sort immaculate orange and yellow *Acraga* to species or species-groups, using the shape of the sociuncus, which may usually be seen by gently brushing away the scales on a pinned specimen.

KEY TO SPECIES-GROUPS OF MALE *ACRAGA*

(Note that to allow use of simple characters in the key, *Acraga chicana* [Mexico] and *Acraga neblina* [southern Venezuela] will key incorrectly to the *melinda* and *ciliata* groups, respectively.)

1\. Wings orange with veins lighter *or* darker than ground color (Figs. 69, 70, 72) ...... *ciliata* group
Wings not as above 2
2(1). Wings white or pale yellow with pattern (Figs. 87–91, 115–116) ...... *ampela* group
Wings not as above 3
3(2). Hindwing Rs not fused with $Sc+R_1$ in discal cell (e.g., Fig. 41) 4
Hindwing Rs fused with $Sc+R_1$ in discal cell (e.g., Fig. 42) 9
4(3). Forewings slightly falcate (e.g., Fig. 60) 5
Forewings not falcate 8
5(4). Wings orange, orange-brown, or forewings brownish red with hindwings transparent yellow; highlands from Costa Rica to Peru, and the Amazon Basin ...... *melinda* group
Wings metallic yellow or brown; southeastern Brazil and adjacent areas 6
6(5). Wings metallic yellow ...... *flava* group (part)
Wings brown or brownish red 7
7(6). Genitalia with single median posterior point on sociuncus (Fig. 158) ...... *flava* group (part)
Genitalia with no *or* 2 posterior points on sociuncus (Figs. 176, 177) ...... *ferruginea* group
8(4). Aedoeagus very long, slender, flattened, and recurved externally (Figs. 157, 159–161); Central and South America ...... *infusa* group
Aedoeagus long and stout, pointed at apex (but not flattened), enclosed in strong spoutlike complex (Figs. 188–191); southeastern Brazil and adjacent areas ...... *ochracea* group
9(3). Wings yellow; forewing length 14–17 mm; highlands of Costa Rica through the Andes ...... *hamata* group
Wings yellow or whitish; forewing length under 14 mm; Central and South America 10
10(9). Wings yellow or orange; sociuncus with single pair of adjacent strong posterior-directed downward-sloping points (Figs. 151, 152); Central and South America ...... *goes* group
Wings yellow or whitish; sociuncus points, if present, not as above; South America 11
11(10). Sociuncus with long points or processes (Figs. 175, 198) ...... *citrina* group
Sociuncus with only short points or gentle lobes (Figs. 166–169) ...... *concolor* group

KEY TO SPECIES-GROUPS OF IMMACULATE YELLOW AND ORANGE MALE *ACRAGA*

(This key is designed for convenience in rough sorting specimens without dissecting genitalia. The characters used can be seen in most specimens by brushing the scales from the sociuncus. However, all identifications should be verified by comparison with the diagnoses and illustrations, including dissection if necessary. This key includes all *Acraga* with yellow or orange wings with no markings as well as a few other species that might appear similar if in poor condition. *Dalcerides nana* is also included, because it can easily be confused with *Acraga*; other species of *Dalcerides* as well as *Oroya aurora* may be easily separated by the forewing venation characters used in the key to genera.)

1\. Sharp points or hooks arising laterally from sociuncus, one on each side (*infusa* group) 2
Blunt or rounded points or lobes arising from middle or dorsum of sociuncus 3

2(1). Sharp points on sociuncus (Figs. 159, 161); aedoeagus long, flattened, and recurved at tip ..... *infusa* group (part)
Elongate, curved hooks on sociuncus (Fig. 157); aedoeagus long, relatively straight ..... *ria*
3(1). Sociuncus with 1, 2, or 4 sharp central points or tabular processes 4
Sociuncus with undulating lobes, points short or absent, no tabular processes (Figs. 166–168) ..... *concolor* group
4(3). Sharp points on sociuncus 5
Tabular lobes directed dorsally from dorsum of sociuncus (Figs. 170–173); wings orange or orange-brown ..... *melinda* group (part)
5(4). One central sharp point on sociuncus; southeastern Brazil and adjacent countries 6
Two or 4 central sharp points on sociuncus; Central and South America 8
6(5). Wings metallic yellow; sociuncus as in Figure 155 ..... *flava*
Wings brownish or golden yellow, not metallic 7
7(6). Wings brownish; sociuncus as in Figure 158 ..... *obscura*
Wings golden yellow, with pale line along end of forewing cell (often hardly visible); sociuncus as in Figure 202 ..... *Dalcerides nana*
8(5). Four long, strongly downturned, sharp central points on sociuncus (Fig. 175); wings whitish with yellow tint; northern South America ..... *citrina*
Two sharp central points; orange, yellow, or whitish 9
9(8). Sociuncus with dorsal hoods (Figs. 176, 188–191); aedoeagus stout; wings orange or red; southern Brazil, Uruguay, Paraguay, and northern Argentina 10
Sociuncus relatively smoothly tapered dorsally (Figs. 151–154, 174, 198); aedoeagus narrow; wings yellow or orange; Central and South America 11
10(9). Sociuncus as in Figures 188–191; wings orange; sociuncus often covered with dense, long hairs ..... *ochracea* group
Sociuncus as in Figure 176; wings brownish rusty red; sociuncus covered with normal hairs only ..... *ferruginea*
11(9). Sociuncus with 2 simple central points, sharp or rounded (Figs. 151–154); wings yellow or orange 12
Sociuncus with 2 large semicircular dorsal processes; yellow; Colombia and Ecuador ..... *hoppiana*
12(11). Sociuncus as in Figures 151 and 152 ..... *goes* group
Sociuncus as in Figures 153 and 154 ..... *hamata* group

Acraga goes Species-Group

Diagnosis. Distinguished from other yellow or orange *Acraga* by single pair of adjacent strong posterior-directed downward-sloping points on sociuncus (Figs. 151, 152).

Adult Male. Medium size, forewing 9–11 mm. Ground color: yellow or orange. Hindwing Rs fused with Sc + R_1 in cell. Genitalia: tegumen and sociuncus fused, elongate; sociuncus with bluntly pointed downward-directed lateral lobe on each side; uncus with one pair of posterior points; gnathos rectangular tabs; vinculum thin, elongate; valvae fused into complex with juxta, maybe represented by lobes dorsolateral of complex; juxta fused into complex with valvae; saccus slender, elongate; aedoeagus long, slender.

Adult Female. Medium size, forewing 14–17 mm. Genitalia: sterigma medium width; ostium bursae narrow; ductus bursae long, narrow, recurved; corpus bursae elongate ovate; ductus seminalis arising at second bend of ductus bursa; apophyses posteriores broad, long, pointed or rounded; "accessory glands" ovate in lateral view.

Discussion. *Acraga goes* is a common species with distinctive genitalia. The other three species are only provisionally placed in this species-group: *Acraga ingenescens* is known only from the unique female holotype, the male holotype of *Acraga luteola* is lost, and *Acraga* new species F is known only from one male in poor condition.

KEY TO *GOES* GROUP MALES

Wings yellow; paired sociuncus points touching (or almost) along entire length (Fig. 152); Central and South America; common ..... *goes*
Wings orange (?); paired sociuncus points divergent from one another (not touching) (Fig. 151); Colombia; rare ..... species F

Acraga goes Schaus, RESURRECTED COMB.

Figures 57, 152, 232; Map 1; Color Plate, Figure 15

Acraga goes Schaus, 1910: 415.

Anacraga goes:—Dyar and Strand, 1913b: 30.
Anacraga geos [sic]:—Sick, 1939: 1307.

Diagnosis. Distinguished from other yellow species by paired median points of sociuncus, which touch (or almost touch) each other along entire length (Fig. 152).

Adult Male (Fig. 57). Forewing length 9–11 mm.

Entirely light yellow. Forewing slightly darker than hindwing. Hindwing costal margin lighter than rest of hindwing. Genitalia as in Figure 152.

Adult Female. Forewing length 14–16 mm. Colored as in male, but anal angles of wings less produced. Genitalia as in Figure 232.

Type. Lectotype male, paralectotype male, here designated, USNM 11948.

Type Locality. Costa Rica, Guápiles, 850 feet [250 m].

Host. Unknown.

Immature Stages. Unknown.

Flight Period. Year-round.

Distribution (Map 1). Costa Rica, Ecuador, Venezuela, Trinidad, Guyana, Surinam, French Guiana, Colombia, Peru, and Brazil, in Tropical Wet, Tropical Moist, Tropical Dry, Tropical Premontane Wet, Tropical Premontane Moist, and Subtropical Dry (Maricá) Forest Life Zones.

Material Examined. 227 males and 3 females. BRAZIL: *Amazonas:* Codajás, IV-1907, S. M. Klages (BMNH); Fonte Boa, V–VIII-1906, Klages (BMNH); São Paulo de Olivença, XI–XII-[no year], A. H. Fassl (USNM), [no date], Fassl (ZSBS); Hyatanahan [=Huitanaã], Rio Purus, II–III, VI-1922, Klages (CMNH, USNM); Monte Cristo, [no date], Fassl (USNM); Nova Olinda, Rio Purus, V-1922, Klages (CMNH); Tefé, IX-[no year], Fassl (USNM); Tonantins, XI-1921 (USNM); Amazon between Tefé and Tonantins, XI-1921 (USNM); *Bahia:* Ipaiú, I-1967, V. O. Becker (VOB); *Espírito Santo:* "Esp. Sto.," [no date] (ZSBS); *Goiás:* Ilha do Bananal, Rio Javare, 200 m, 4–8-IX-1977, 7-IX-1983, 14–18-IX-1985, Becker (VOB); *Pará:* Belém, 20 m, I-1984, Becker (VOB); Marabá, 50 m, 9-I-1977, Becker (VOB); Pará [=Belém], [no date], A. M. Moss (BMNH); Prainha, 14-XI-1873 (BMNH); Rio Xingu Camp, 52°22′W, 5°39′S, ca. 60 km S Altamira, P. J. Spangler & O. S. Flint (USNM); *Rio de Janeiro:* "Rio," [no date] (BMNH); 10 km SW Maricá, 11–12-X-1985, S. E. Miller & Becker (USNM); *Rondônia:* Calama, Rio Madeira, VIII–X-1907, W. Hoffmanns (BMNH); COLOMBIA: *Valle del Cauca:* Juntas, Río Dagua, 300 m, V-1909, Fassl (USNM); *Cauca:* Río [San Juan de] Micay, [no date], W. Hopp (ZSBS); *Not located:* Cauca Valley, [no date], F. C. Nicholas (AMNH); COSTA RICA: "am [=on the slopes of Mount] Turrialba," 1-VI-1929, F. Nevermann (ZSBS); Guápiles, 850 feet [250 m], [no date] (lectotype), VI-[no year] (paralectotype), XI-1909, W. Schaus (USNM); Hacienda La Suerte/Tapezco, 29 air km W Tortuguero, 40 m, 13–31-VIII-1979, Donahue *et al.* (LACM); Sirena, Corcovado National Park, 19–27-III-1981, 10–19-VIII-1980, D. H. Janzen & W. Hallwachs (USNM); Sixaola River, III-1909, Schaus (BMNH, USNM); Peninsula de Osa, 20 m, 15-XI-1972, Becker (VOB); Tuis, 2,500 feet [750 m], III-[no year], Schaus (BMNH); 1.8 miles [3 km] W Rincón, Osa Peninsula, 5-II-1971, J. P Donahue & C. L. Hogue (LACM); Corcovado National Park, Osa Peninsula, 13–22-III-1980, Janzen & Hallwachs (USNM); 9.4 km W Bribri, Suretka, 200 m, 9–11-VI-1983, Janzen & Hallwachs (USNM); ECUADOR: Sarayacu, [no date], C. Buckley (BMNH) [locality may not be accurate]; FRENCH GUIANA: La Forestière, IV-[no year] (BMNH), VII-[no year] (ZSBS); Mana River, V-1917 (CMNH, USNM); Nouveau Chantier, II-[no year] (BMNH); Pied Saut, XII-1917, Klages (CMNH); Saint-Jean, IV–V-1904, Schaus (USNM), VII–VIII-1904 (BMNH), [no date] (BMNH, USNM); Saint-Laurent, I, II, IV, VI, VIII, X–XII-[various years] (BMNH, MNHP, USNM); 60 miles [100 km] up Maroni River, VIII-1904, Schaus (USNM); GUYANA: Kartabu, VI-1925 (CMNH), X-1920 (CU), [no date]-1920 (AMNH); MacKenzie, 24-VI-1927, [W. T. M. Forbes] (CU); Malali, [no date] (USNM); Moraballi Creek, Essequibo River, 2-XI-1929 (BMNH); Omai, VI-1908, Klages (BMNH); Rockstone, IX-1904, Schaus (USNM); Tumatumari, 28–29-VI-1927, [Forbes] (CU, USNM), XII-1907, Klages (BMNH); Takutu Mountains, 6°15′N, 59°5′W, 11-XII-1983, Spangler & W. E. Steiner (USNM); Wineperu, 18–24-III-1969, Duckworth & Dietz (USNM); PERU: *Loreto:* [Contamana], Middle Río Ucayali, 16-XI-1927, H. Bassler F6039 (AMNH); Río Ampiyacu, [no date] (BMNH); SURINAM: Aroewarwa Creek, Maroewym Valley, III–VI-1905, Klages (BMNH); Paramaribo, [no date] (USNM); TRINIDAD: Arima Valley, VIII-1906 (AMNH); Caparo, XI-1905, [no date], Klages (BMNH); Valencia Forest, 5-VIII-1981, M. J. W. Cock (MJWC); VENEZUELA: *Amazonas:* Cerro de la Neblina Basecamp, 0°50′N, 66°9′44″W, 140 m, 4–12-II-1984, D. Davis & T. McCabe, 24-XI–1-XII-1984, R. L. Brown (USNM); Río Baria, 140 m, 0°55′N, 66°10′W, 25-XI–4-XII-1984, E. Osuna (UCV); San Pedro de Cataniapo, 100 m, 23–31-VIII-1981, J. L. Garcia (UCV); 6 km E San Carlos de Río Negro, 23-XI-1984, Brown (USNM); *Bolívar:* El Bochinche Res. Forestal Imataca, 200 m, 16–18-V-1985, 6–13-XII-1974 (UCV); El Dorado to Santa Elena road, Km 88, 160 m, 28-IX-1967, C. J. Rosales (UCV); Río Surukum, Carretera Santa Elena Icabaru, 850 m, 19–31-I-1985, F. Fernandez Y. *et al.* (UCV); *Carabobo:* Las Quiguas, Esteban Valley, XI–III-[no year] (CMNH), 5–8-XI-1974, J. Salcedo (UCV); San Esteban, VI, VIII-1909, Klages (BMNH); Valencia, [no date] (BMNH); *Falcón:* Palma Sola, [no date] (BMNH); Yaracal, 120 m, 1-VI-1982, J. A. Clavijo & A. Chacon (UCV); *Lara:* "Sanare and Baraquasimeto [sic], 6000 ft.," [no date] (BMNH); *Trujillo:* Valera, [no date], E. P. de Bellard (USNM).

Discussion. The female from the type locality is not mentioned in the original description, so it is not a paralectotype. The record of *Acraga goes* from Minas Gerais, Brazil (Hambleton and Forbes, 1935: 218) may refer to *Acraga citrinopsis*. *Acraga luteola* Hopp may be a synonym of *A. goes*, as discussed under *A. luteola*.

Acraga ingenescens (Dyar), NEW COMB.
Figures 58, 231; Map 2

Anacraga ingenescens Dyar, 1927: 551.—Sick, 1939: 1308.

Diagnosis. Similar to *Acraga goes*, but apices and anal angles of wings more produced (Fig. 58).

Adult Male. Unknown.

Adult Female (Fig. 58). Forewing length 17 mm. Body rubbed, probably golden yellow. Forewing golden yellow. Hindwing pale yellow. Genitalia as in Figure 231.

Type. Holotype female, USNM 40716.

Type Locality. Venezuela, Mérida, "Terra temperee."

Host. Unknown.

Immature Stages. Unknown.

Flight Period. Unknown.

Distribution (Map 2). Venezuela, probably in Tropical Lower Montane Moist Forest.

Discussion. Known only from the female holotype, which is in poor condition. This species is close to *Acraga goes*, but the wing angles are more produced and the female genitalia of *A. ingenescens* have a smaller corpus bursa, blunt-tipped apophyses posteriores, and more ovate "accessory glands" (the sterigma is damaged in the unique holotype).

Acraga luteola (Hopp), NEW COMB.
Figure 59; Map 2

Anacraga luteola Hopp, 1921: 281.—Sick, 1939: 1308.

Adult Male (Fig. 59). Expanse 22 mm. *Head:* Yellow. *Thorax:* Yellow ochre. Forewings golden yellow, the basal halves of the broad inner margin and the narrow costal margin bright yellow ochre. Hindwings a little paler but darker yellow at the anal angle. Ventral wings somewhat paler than dorsal. Legs yellow. *Abdomen:* Yellow ochre. Genitalia unknown.

Adult Female. Unknown.

Type. Holotype male, lost.

Type Locality. Brazil, Pará, [Belém].

Host. Unknown.

Immature Stages. Unknown.

Flight Period. Unknown.

Distribution (Map 2). Northern Brazil (Amazon Basin), presumably collected in Tropical Moist Forest Life Zone.

Discussion. *Acraga luteola* was described from a single male collected by Sieber from "Pará," probably refering to Belém. The holotype is supposed to be in ZMHB, but it is not (H. J. Hannemann, personal communication, 1984). ZSBS has a poor-quality black and white photograph of the holotype, upon which my treatment is based. Dyar (1927: 551) treated *Acraga luteola* as a synonym of *A. ria* Dyar (without documentation), but the size and wing shape of the two disagree. I suspect that *A. luteola* is a synonym of *A. goes*, but I do not want to synonymize it formally without seeing the genitalia. The preceding color description is a translation of the original description.

Acraga new species F
Figure 151; Map 2

Diagnosis. Similar to *Acraga goes*, differing in male genitalia (Fig. 151) and probably in coloration.

Adult Male. Forewing length ca. 9 mm. Single male rubbed and damaged by fungus. Body probably orange dorsally, pale yellow ventrally. Forewing orange. Hindwing pale yellow or whitish. Ventral wings pale yellow or whitish. Genitalia as in Figure 151.

Adult Female. Unknown.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. June.

Distribution (Map 2). Known only from Pacific slope of western Andes of Colombia.

Material Examined. 1 male. COLOMBIA: *Valle del Cauca:* "Naranjito," Río Dagua, 3,900 feet [1,200 m], VI-1908, [M. G. Palmer] (BMNH).

Discussion. Although the male genitalia are somewhat similar to *Oroya aurora,* this species appears to be most closely related to *Acraga goes.* The male genitalia of this species differ from those of *Acraga goes* as follows: paired points of sociuncus shorter and divergent (not touching); gnathos reduced; lateral saclike process on each side at sociuncus–tegumen articulation; and single hairy bulbous-ended process arising from vinculum under aedoeagus, protruding externally almost as far as aedoeagus. I refrain from naming this genitally distinctive species due to the poor condition of the single available specimen. The locality Naranjito has not been located.

Acraga hamata Species-Group

Diagnosis. Differs from *Acraga melinda* group and *Acraga flava* group in yellow coloration (Figs. 60–62), hindwing venation (Rs fused with Sc + R_1 in cell), and genitalia (see below and Figs. 153, 154, 156).

Adult Male. Medium size, forewing 14–17 mm. Ground color: yellow, without maculation. Forewing somewhat falcate. Hindwing Rs fused with Sc + R_1 in cell. Genitalia: tegumen and sociuncus fused, elongate; sociuncus with bluntly pointed downward-directed lateral lobe on each side; uncus with two median downwardly directed processes; gnathos rectangular tabs, as in *Acraga goes*; vinculum thin, elongate; long cylindrical complex (=anellus?) encasing aedoeagus; valvae reduced to lobes dorsolateral of cone; juxta not distinct; saccus slender, elongate; aedoeagus long, slender, slightly bent, with fine barbs on external end.

Adult Female. Medium size, forewing 19–21 mm. Genitalia: sterigma large, weakly sclerotized; ostium bursae broad, saclike; ductus bursae short, medium width, recurved; corpus bursae spherical; ductus seminalis arising about middle of ductus bursae; apophyses posteriores broad, shallow, rounded; "accessory glands" ovate in lateral view.

KEY TO *HAMATA* GROUP MALES

Central America; genitalia as in Figure 153	*hamata*
South America; genitalia as in Figure 154	*andina*

Acraga hamata Schaus
Figures 60, 61, 153, 230; Map 3

Acraga hamata Schaus, 1910: 414.—Dyar and Strand, 1913b: 29.—Sick, 1939: 1306, pl. 168a.

Diagnosis. Similar to the sympatric *Acraga melinda,* but pale yellow, not deep orange; differing from the Andean *A. andina* only in male genitalia (Fig. 153).

Adult Male (Fig. 60). Forewing length 14–16 mm. *Head:* Yellow. *Thorax:* Dorsum deep yellow; venter pale yellow. Forewings somewhat falcate, slightly produced and rounded below M_3, bright light yellow. Hindwings incurved below apex, the anal angle produced, yellow (lighter than forewing) with costal margin whitish. Ventral wings pale yellow. Legs yellow. *Abdomen:* Pale yellow. Genitalia as in Figure 153.

Adult Female (Fig. 61). Forewing length 21 mm. Colored as in male, wings more rounded. Genitalia as in Figure 230.

Type. Lectotype male, 2 male paralectotypes, here designated, USNM 4947.

Type Locality. Costa Rica, Cartago, Juan Viñas.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. May to February.

Distribution (Map 3). Costa Rica, Panama, and maybe Colombia, in Tropical Premontane Wet and Rain Forest Life Zones.

Material Examined. 48 males and 1 female. COLOMBIA: "Colombia" [no further data], W. E. Pratt (MMU); COSTA RICA: Braulio Carrillo, 1,100 m, VII-1981, V. O. Becker (VOB); Cachí, VIII–X-1912, C. H. Lankester (BMNH); "Costa Rica," [no date], A. H. Fassl (ZSBS); Juan Viñas, [1,000 m], II, V–VI, XI-[no year], W. Schaus & J. Barnes (USNM, including lectotype and paralectotype; BMNH); La Fuente, Turrialba, I-1940, A. Alfaro (USNM); La Montura, Braulio Carrillo Nat. Park, 1,100 m, 17-XII-1981, D. Janzen & W. Hallwachs (USNM); Monteverde, 1,400 m, 15–16-V-1980, Janzen & Hallwachs (USNM), 11–18-VIII-1976, E. M. Fisher (LACM), 15-IX-1982, C. Nagano & M. Hayes (LACM); Moravia de Chirripó, 1,000 m, 10-V-1983, Janzen & Hallwachs (USNM); Orosí, 1,200 m, [no date], Fassl (BMNH); Sitio, V–VI-[no year], Schaus (BMNH, CMNH, UMO, USNM); Tuis, 28-V–4-VI-[no year], Schaus & Barnes (BMNH, UMO, USNM); Volcán de Turrialba, 1,800 m, 13-VIII-1972, Becker (VOB); 3 km S Casa Mata, 16 km S San Isidro de Tejar, 1,800 m, 4-XII-1983, Janzen & Hallwachs (USNM); PANAMA: Lino, 800 m, [no date], Fassl (NHMV, USNM, ZSBS).

Discussion. Acraga hamata is apparently restricted to elevations above 800 m. The "Colombia" record probably refers to that portion of Colombia that is now Panama (see under *Acraga coa*).

Acraga andina, new species
Figures 62, 154, 229; Map 3

Diagnosis. Similar to the Central American *Acraga hamata,* differing in male genitalia (Fig. 154), especially uncus points and wider complex around aedoeagus.

Adult Male (Fig. 62). Forewing length 14–17 mm. Colored as in *Acraga hamata,* although forewing slightly darker. Genitalia as in Figure 154.

Adult Female. Forewing length 19 mm. Colored as in male, wings more rounded. Genitalia as in Figure 229.

Type. Holotype male, USNM 103444.

Type Locality. Peru, Huánuco, "near Leonpampa."

Host. Unknown.

Immature Stages. Unknown.

Flight Period. February, July, and December.

Distribution (Map 3). Andes of Venezuela, Colombia, Ecuador, and Peru, in Tropical Wet, Tropical Premontane Wet, Tropical Premontane Moist, and probably Tropical Montane Wet Forest Life Zones.

Material Examined. 10 males and 1 female. COLOMBIA: *Guainía:* "Ob. [upper] Río Negro," 800 m, [no date], A. H. Fassl (BMNH); ECUADOR: *Tungurahua:* Baños, 1,800–2,000 m, 10-VII-1936, W. Clark-Macintyre (NHMV, 1 female); PERU: *Huánuco:* near Leonpampa, [no date], F. Woytkowski (USNM, holotype); *Puno:* Oconeque, 7,000 feet [2,100 m], VII-1904, G. R. Ockenden (BMNH, USNM, 4 paratypes); Santo Domingo, 6,500 feet [1,900 m], XII-1902, Ockenden (BMNH, paratype); VENEZUELA: *Barinas:* San Isidro, 14 km S La Soledad, 1,500 m, 30–31-V-1975, R. E. Dietz (UCV); *Mérida:* El Valle, 2,400 m, 15–16-II-1983, J. Demarmels *et al.* (UCV); Mucuy Fish Hatchery, 7 km E Tabay, 6,600 feet [2,000 m], 10–13-II-1978, J. B. Heppner (USNM).

Discussion. The species name refers to the Andes Mountains, where the species occurs.

The type series is restricted to the Peru specimens, because the other specimens vary slightly in male genitalia and might represent a different species. The Venezuela specimens vary in the sociuncus having the posterior points straight (not curved) and the lateral lobes differently curved (Fig. 156). The single Colombia male is like the Venezuela specimens, but the posterior points are somewhat longer.

If the males discussed here represent two species, then the identity of the single female is unknown (because there are no males known from Ecuador).

Acraga flava Species-Group

Diagnosis. Species in southern Brazil and adjacent regions with forewings slightly falcate (Figs. 63–65), gnathos rectangular tabs, and aedoeagus encased in conical "anellus" (Figs. 155, 158).

Adult Male. Medium size, forewing 9–13 mm. Ground color: metallic yellow or brown, without maculation. Forewing somewhat falcate. Hindwing Rs not fused with $Sc + R_1$ in cell. Genitalia: tegumen and sociuncus fused, elongate; sociuncus with bluntly pointed downward-directed lateral lobe on each side; uncus with one median hooklike process; gnathos rectangular tabs, as in *Acraga goes*; vinculum thin, elongate; long conical complex (=anellus?) encasing aedoeagus; valvae lobes dorsolateral of cone; juxta not distinct; saccus slender, elongate; aedoeagus long, slender, bent, external end pointed.

Adult Female. Medium size, forewing

14–19 mm. Genitalia: sterigma broad; ostium bursae broad; ductus bursae wide to first bend, narrowing and recurved again to corpus bursae; corpus bursae spherical; ductus seminalis arising between bends; apophyses posteriores very short; "accessory glands" irregularly ovate in lateral view.

Discussion. The name *Epipinconia* Dyar, 1898 (type species: *Acraga flava*) is available for this group, although I prefer to regard it as an informal species-group only. *Epipinconia* was originally separated from *Acraga* on the basis of forewing $R_2 + R_3$ being coincident, but they are not completely fused. *Epipinconia* was synonymized under *Acraga* by Dyar (1910c: 115).

KEY TO *FLAVA* GROUP MALES

Wings metallic yellow (Fig. 63) .... *flava*
Wings dark brown to golden brown (Fig. 65) .... *obscura*

Acraga flava (Walker)

Figures 63, 64, 155, 234; Map 4

Dalcera flava Walker, 1855b: 1107.—Kirby, 1892: 542.—Burmeister, 1879: 53, pl. XXIV, fig. 3.—Koehler, 1924: 25; 1928: 9.
Caviria sulphurea Burmeister, 1878: 517.—Kirby, 1892: 434. [synonymized by Burmeister, 1879: 53]
Epipinconia flava:—Dyar, 1898: 233.
Acraga flava:—Dyar, 1910c: 118.—Dyar and Strand, 1913b: 29.—Hopp, 1921: 280; 1928a: 284–286.—Sick, 1939: 1306, pl. 168e.—Duarte, 1947: 189.—Orfila, 1961: 249.—Biezanko, 1961a: 3; 1961b: 4.—Biezanko *et al.*, 1966: 5; 1974: 124; 1978: 57.—Ruffinelli Rey, 1967: 20.—Silva *et al.*, 1968: 295.

Diagnosis. Wings golden yellow with metallic luster; distinguished from *Dalcerides radians* by larger size, wing venation, and male genitalia (Fig. 155).

Adult Male (Fig. 63). Forewing length 12–13 mm. *Head:* Pale yellow. *Thorax:* Yellow. Forewings bright golden yellow with metallic luster; the scales patterned to appear as undulating transverse bands; very slightly falcate. Hindwings pale yellow. Ventral wings pale yellow. Legs pale yellow. *Abdomen:* Pale yellow. Genitalia as in Figure 155.

Adult Female (Fig. 64). Forewing length 14–19 mm. Colored as in male. Anal angles of wings less developed. Genitalia as in Figure 234.

Types. Holotype (?) male, BMNH (*flava*); lost? (*sulphurea*).

Type Localities. Brazil, Rio de Janeiro (*flava*); Argentina, Prov. Buenos Aires, Las Conchas [now Tigre] (*sulphurea*).

Hosts. Nectandra sp. (as "canellinha-busches") (Lauraceae) (Hopp, 1928); *Psidium guajava* Linnaeus (Myrtaceae) (Biezanko, 1961a, 1961b; Biezanko *et al.*, 1966); *Prunus domestica* Linnaeus (Rosaceae) (Biezanko *et al.*, 1974: 124).

Immature Stages. Described by Burmeister (1879), Dyar (1910c), and Hopp (1928a).

Flight Period. Year-round.

Distribution (Map 4). Southern Brazil and northern Argentina, in Tropical Premontane Moist, Subtropical Wet, Subtropical Moist, Subtropical Lower Montane Wet, Subtropical Lower Montane Moist, and Warm Temperate Moist Forest Life Zones.

Material Examined. 46 males and 36 females. ARGENTINA: *Misiones:* Posadas, 26-IX-1921 (BMNH); BRAZIL: *Espírito Santo:* "Espírito Santo" (USNM); Santa Teresa, 400 m, 1920, F. H. Hoffmann (NHMV); *Goiás:* Vianópolis, XII-1931, R. Spitz (BMNH); *Minas Gerais:* Bergland um [=hilly country about] Ouro Preto, Fazenda Barcellos, 1,100–1,200 m, 10–14-IX-1952, H. Ebert (CMNH); "Capela Nova do Betim," III-1916 (IOC); [Fazenda dos Campos, 1,500 m], reared from "canellinho," I-1921, J. F. Zikan (IOC); "Minas Geraes" [Fazenda dos Campos], I-1922, VI-1921, Zikan (BMNH); Nova Lima, I-I-1985, V. O. Becker (VOB); "Passa Quatro" [Fazenda dos Campos], I-1921, II-1918, XII-1920, Zikan (ZSBS); Sete Lagoas, 720 m, 20-III-1968, Becker (VOB); *Paraná:* Banhado, Quatro Barras, 800 m, 26-III-1971, 30-X-1970, Becker & Laroca (VOB); Castro, [no date] (USNM), 950 m, [no date], E. D. Jones (BMNH); *Rio de Janeiro:* Cachoeiros de Macacu, 800 m, 15-X-1985, S. E. Miller & Becker (USNM); "Campo Bello" [Itatiaia, 400 m], II-1927, IX-1924, XII-1924, XII-1926, Zikan (ZSBS); Independencia, Petrópolis, XII-1932, L. Travassos (IOC); [Itatiaia, 400 m], 23-II-1928, 28-II-1930, 8-IX-1934, 14-X-1927, 18-XII-1948, 22-XII-1924, Zikan (IOC); Maromba [1,100 m], Itatiaia, 28-VII-1952, Travassos (IOC); Nova Friburgo, [no date] (MNHP); Petrópolis, [no date] (BMNH, USNM), 13-X-1910, J. G. Foetterle (NHMV); "Prov. Rio" [Itatiaia, 400 m], Zikan (USNM); "Rio Janeiro," [no date] (BMNH, probably Walker's type); Teresópolis, [no date] (USNM), 13–22-III-1958,

H. B. D. Kettlewell (BMNH), 1,000 m, 15–16-I-1985, Becker (VOB); *Rio Grande do Sul:* Pelotas, 15-III-1966, Becker (VOB), 9-III-1953, 14-VI-1950, C. M. Biezanko (CU); Rio Grande do Sul, 1921, V. Wernicke (ZSBS); *Santa Catarina:* Hills between Hansa [=Corupá] and Jaraguá, 400 m, II-1935, A. Maller (BMNH); Jaraguá do Sul, VII-1935, Hoffmann (BMNH); Joinvile, 7-VIII-1953, Biezanko (MCZ); Nova Teutonia, F. Plaumann (USNM); Santa Catarina, [no date] (BMNH); *São Paulo:* Ipiranga, 16-VII-1922, R. Spitz (NHMV); São Paulo, [no date], Jones (BMNH).

Discussion. Orfila (1961: 249) doubts the Argentina record of Burmeister (1878, 1879). Although Burmeister's locality, "Las Conchas," may be wrong, the country record is confirmed by a Misiones specimen (BMNH).

The type of *Caviria sulfurea* is lost, but based on the original description, the synonymy appears to be correct. The Burmeister collection is at MBR, but the type is apparently not there. "Under the heading of '*Dalcera flava* Wlkr., Buenos Aires,' handwritten by Burmeister himself, there are two specimens without any label, which we assume cannot be the types of *sulfurea*" (A. O. Bachmann, personal communication, 1986).

Acraga obscura (Schaus)
Figures 65, 158; Map 5

Dalcera obscura Schaus, 1896a: 57.—Dyar, 1898: 231.
Acraga obscura:—Dyar, 1910c: 117.—Dyar and Strand, 1913b: 29.—Sick, 1939: 1306.
"*Acraga*" *obscura:* Biezanko, 1961a: 3.

Diagnosis. Similar to *Acraga meridensis* but darker; similar to *A. sexquicentenaria,* differing in slightly falcate forewing (Fig. 65), and usually darker color and smaller size; differs from *A. ferruginea* and *A. brunnea* in median point of sociuncus (Fig. 158), size, and coloration.

Adult Male (Fig. 65). Forewing length 9–12 mm. *Head:* Tan with light brown antennae. *Thorax:* Dorsum brown, venter tan. Forewings dark to golden brown; slightly falcate. Hindwings golden brown, lighter than forewing, especially at costal margin. Ventral wings light brown except distal half of forewing and costal margin of hindwing, which are brown. Legs tan. *Abdomen:* Dorsum light brown, venter tan. Genitalia as in Figure 158.

Adult Female. Unknown.

Type. Lectotype male, here designated, USNM 12550.

Type Locality. Brazil, São Paulo.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. January, March, May to July, October, and December.

Distribution (Map 5). Southern Brazil and Uruguay, in Warm Temperate Moist, Subtropical Wet, and Subtropical Moist Forest Life Zones.

Material Examined. 14 males. BRAZIL: *Paraná:* Antonina, 1,000 m, 21-I-1970, V. O. Becker (VOB); Curitiba, 920 m, 19-X-1974, Becker (VOB); *Rio Grande do Sul:* Pelotas, 9-III-1953, 14-III-1953, 20-V-1957, 4-VI-1958, C. Biezanko (CMNH, MCZ, USNM); "Rio Grande du Sul," [no date] (BMNH); *Santa Catarina:* Brusque, 28-XII-1969, Becker (VOB); Nova Teutonia, 2-VI-1963, F. Plaumann (MCZ), [no date], Plaumann (USNM); *São Paulo:* Ipiranga, 9-VII-1922, R. Spitz (NHMV); São Paulo, [no date], (USNM, lectotype); São Paulo, 2,300 feet [700 m], [no date], E. D. Jones (BMNH); URUGUAY: *Treinta y Tres:* Quebrada de los Cuervos, 16-XII-1952, C. S. Carbonell (MCZ).

Acraga infusa Species-Group

Diagnosis. Differs from other orange *Acraga* in male genitalia, especially sociuncus shape and narrow, elongate aedoeagus and saccus (Figs. 157, 159–161).

Adult Male. Medium size, forewing 9–14 mm. Ground color: orange, usually without maculation. Hindwing Rs not fused with Sc + R_1 in cell. Genitalia: tegumen and sociuncus fused, relatively compact, one strong pointed or hooked process on each dorsolateral, external, posterior surface of sociuncus; gnathos two unfused tabs, somewhat triangular in posterior view (not rectangular as in *Acraga flava* group), connected across bases; vinculum thin, elongate; valvae apparently lobes dorsolateral of aedoeagus (developed into hooks in *Acraga ria* and arms in *A. serrata*); juxta fused into complex surrounding and supporting aedoeagus; saccus long and slender; aedoeagus long, slender, flattened, and recurved externally.

Adult Female. Medium size, forewing 15–19 mm. Genitalia: sterigma broad and well sclerotized; ostium bursae broad; ductus bursae long and narrow, with two bends; corpus bursae elongate ovate; ductus seminalis arising from second bend in ductus bursae; apophyses posteriores medium length, wide at base, narrowing to apex; "accessory glands" ovate in lateral view.

KEY TO *INFUSA* GROUP MALES

1. Forewing concolorous orange (Figs. 67, 68, 75) 2
   Forewing deep orange with pale veins (Fig. 66) .... *neblina*
2(1). Forewing apex sharply angled (Fig. 75); genitalia with curved lateral hooks on sociuncus (Fig. 157) .... *ria*
   Forewing apex rounded (Figs. 67, 68); genitalia with only short points on sociuncus (Figs. 159, 161) 3
3(2). Apex of aedoeagus with serrate edges (Fig. 161); valvae developed as long arms arising dorsally from complex around aedoeagus (Fig. 161) .... *serrata*
   Apex of aedoeagus with smooth edges (Fig. 159); valvae not as above (Fig. 159) .... *infusa complex*

Acraga ria (Dyar), NEW COMB.
Figures 75, 157; Map 6

Anacraga ria Dyar, 1910c: 119.—Dyar and Strand, 1913b: 30.—Sick, 1939: 1307, pl. 168b.

Diagnosis. Differs from other orange *Acraga* in forewing shape (Fig. 75) and male genitalia, especially hook (apparently valve) arising from each side of sociuncus (Fig. 157).

Adult Male (Fig. 75). Forewing length 8–10 mm. Entirely ocher yellow, with hindwings, abdomen, and ventral wings pale yellow. Forewing triangular, less rounded than most species. Genitalia as in Figure 157.

Adult Female. Unknown.

Type. Holotype male, USNM 13058.

Type Locality. Brazil, Rio de Janeiro.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. November to February.

Distribution (Map 6). Southern Brazil and Peru, in Subtropical Moist Forest Life Zone.

Material Examined. 17 males. BRAZIL: *Rio de Janeiro:* [Itatiaia, 400 m], 17-I-1929, J. F. Zikan (IOC); "Rio Janeiro," [no date] (USNM, holotype); *Santa Catarina:* Hansa Humbolt [=Corupá], XII-1932, A. Maller (BMNH); Nova Brémen, 250 m, 20-II-1937, F. Hoffmann (NHMV); PERU: *Madre de Dios:* Río Tambopata Reserve, 30 air km SW Puerto Maldonado, 290 m, 6–30-XI-1979, J. B. Heppner (FSCA, USNM).

Discussion. Holotype in very poor condition. Dyar and Strand (1913b: 30) recorded *Acraga ria* from Panama; I have seen no specimens to support this record and consider it a misidentification.

Acraga neblina, new species
Figures 66, 160; Map 7

Diagnosis. Similar to *Acraga coa*, differing in more falcate forewing (Fig. 66) and male genitalia (Fig. 160).

Adult Male (Fig. 66). Forewing length 14–17 mm. Entirely light orange except dorsal forewing, which is deep orange with light orange veins. Genitalia as in Figure 160.

Adult Female. Unknown.

Type. Holotype male, USNM 103445.

Type Locality. Venezuela, Amazonas, Cerro de Neblina, Camp VII, 1,850 m, 0°51′N, 65°58′W.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. May, August, and December.

Distribution (Map 7). High altitudes of southern Venezuela, in Tropical Premontane(?) Wet and Tropical Lower Montane Rain Forest Life Zones.

Material Examined. 3 males. VENEZUELA: *Amazonas:* Cerro de Neblina, Camp VII, 1,850 m, 0°51′N, 65°58′W, 2–4-XII-1984, R. L. Brown (USNM, holotype); *Bolívar:* El Dorado to Santa Elena road, Km 155, 1,280 m, 19–21-V-1985, J. Clavijo & A. Chacon (UCV, paratype); Ptari-tepuí, 30 miles [50 km] N Kavanayen, 1,800 m, 17–19-VIII-1970, R. E. Dietz IV (USNM, paratype).

Discussion. The species name is a noun in apposition.

Acraga serrata, new species
Figure 161; Map 7

Diagnosis. Differs from other orange *Acraga*, except *Acraga infusa* complex, in configuration of sociuncus (Fig. 161); differs from *Acraga infusa* complex in valvae developed as long arms arising dorsally from complex around aedoeagus and serrate edges of external end of aedoeagus (Fig. 161).

Adult Male. Forewing length 11–13 mm. Entirely orange. Dorsal hindwing slightly lighter colored than forewing. Ventral surfaces paler than dorsal surfaces. Genitalia as in Figure 161.

Adult Female. Unknown.

Type. Holotype male, USNM 103446.

Type Locality. Brazil, Amazonas, Tefé.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. January, September, November, and December.

Distribution (Map 7). Amazon Basin in Brazil and Peru, in Tropical Moist Forest Life Zone.

Material Examined. 5 males. BRAZIL: *Amazonas:* Hyutanahan [now Huitanaã], Rio Purus, 1-1922, S. M. Klages (CMNH, paratype); São Paulo de Olivença, XI–XII-[no year], A. H. Fassl (USNM, paratypes); Tefé, IX-[no year], Fassl (USNM, holotype); PERU: *Loreto:* Callicebus Research Station, Mishana, Río Nanay, 25 km SW Iquitos, 120 m, 10–17-I-1980, J. B. Heppner (USNM, paratype).

Discussion. Although this species is very close to the *Acraga infusa* complex, I am describing it now because the male genitalia are so distinctive, and particularly because the form of the apparent valvae provides clues to the homology of the valvae of related species. I have seen many specimens in the *A. infusa* complex from the Amazon Basin but have found only five specimens of this species. The species name refers to the edges of the apex of the aedoeagus, which are toothed like a saw.

Acraga infusa complex
Figures 67, 68, 159, 236

Diagnosis. Differs from other orange *Acraga* in male genitalia, especially sociuncus and narrow, elongate aedoeagus and saccus (Fig. 159).

This may represent one variable species or could be a complex of closely related species, but resolution of the problem is beyond the scope of the present work. All the specimens are entirely orange (paler ventrally), varying considerably in size and somewhat in apparent wing shape and color tone (perhaps due to wear) (Figs. 67, 68). The male genitalia are alike except for the configuration of the structures around the aedoeagus (juxta and valvae) and extreme variation in the length of the saccus and aedoeagus, from medium length (for a dalcerid) to very long (almost the length of the abdomen). Further analysis of the variation in length is necessary.

Three names are available: *Acraga infusa* Schaus (1905: 332), *A. philetera* (Schaus, 1910: 415), and *A. conda* Dyar (1910c: 116). Lectotypes need to be designated for the latter two. Literature records cannot be trusted, because this complex has been frequently misidentified as *Acraga ochracea*.

I have seen specimens in this complex from Guatemala, Belize, Costa Rica, Panama, Colombia, Venezuela, Trinidad, Guyana, Surinam, French Guiana, Ecuador, Brazil, Peru, Bolivia, and Paraguay.

Acraga ciliata Species-Group

Diagnosis. Orange species with the wing veins lighter (Figs. 72, 73) *or* darker (Figs. 69–71) than ground color (except *Acraga chicana*; Fig. 74), and recurved structure encasing aedoeagus (Figs. 162–165).

Adult Male. Medium to large, forewing 10–18 mm. Ground color: orange with veins distinctly lighter *or* darker than ground color (except *Acraga chicana*, which has concolorous veins). Hindwing Rs not fused with Sc + R_1 in cell. Genitalia: tegumen and sociuncus fused, somewhat globose, posterior end developed as lateral lobes with split between them, paired lateral lobes along sides also; gnathos two elongate rectangular processes fused at base, adjacent but free above base; vinculum slender, elongate, extended, forming loop, encasing aedoeagus—very narrow at articulation with tegumen–sociuncus, membranous portion connecting overlapping distal and proximal sclerotized portions (in vicinity of aedoeagus opening), proximal portion very elongate to saccus, where vinculum fuses into one structure, which turns sharply to become posterior-directed, ending externally, with long narrow spines on apex; valvae and juxta not identified; saccus presumably small saclike process at bend in vinculum; aedoeagus very slender elongate tube, encased in recurved portion of vinculum, free of vinculum only at ends.

Adult Female. Medium to large, forewing 14–26 mm. Genitalia: sterigma broad; ostium bursae narrow; ductus bursae broadened near outlet, remainder narrow; corpus bursae ovate; ductus seminalis arising from ductus bursae midway between broadened section and corpus bursae; apophyses posteriores narrow, long; "accessory glands" triangular in lateral view.

Discussion. This group contains four species that are different from all other dalcerids in coloration and male genitalia. The recurved structure that encases the aedoeagus is apparently unique among Lepidoptera; this structure is probably the vinculum (as already described) but may include the fused valvae and juxta.

KEY TO *CILIATA* GROUP MALES

1\. Forewing veins darker than ground color (Figs. 69, 70) 2
Forewing veins lighter than or same color as ground color (Figs. 72, 74); Central America 3
2(1). Larger, forewing 15–18 mm; South America .... *moorei*
Smaller, forewing 10–11 mm; Jamaica *ciliata*
3(1). Forewing veins lighter than ground color (Fig. 72) .... *coa*
Forewing veins same color as ground color (Fig. 74) .... *chicana*

Acraga ciliata Walker
Figures 41, 69, 162, 233; Map 8; Color Plate, Figure 16

Acraga ciliata Walker, 1855a: 807.—Kirby, 1892: 542.—Dyar, 1898: 232; 1910c: 116–117.—Dyar and Strand, 1913b: 28.—Sick, 1939: 1305.

Diagnosis. Jamaican species similar to *Acraga moorei* but much smaller; somewhat similar to *A. infusa*, but the wing veins are darkened (Fig. 69) and genitalia have a looped vinculum encasing aedoeagus (Fig. 162).

Adult Male (Fig. 69). Forewing length 9.5–12 mm. *Head:* Pale luteous. *Thorax:* Pale luteous. Forewings pale luteous, darker along veins, especially at end of cell, and along outer and inner margins. Hindwings pale luteous, slightly lighter than forewing. Ventral wings pale luteous. Legs pale luteous. *Abdomen:* Pale luteous. Genitalia as in Figure 162.

Adult Female. Forewing length 14 mm. Colored as in male. Genitalia as in Figure 233.

Type. Holotype female [not male as stated in original description], BMNH.

Type Locality. Jamaica.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. Year-round.

Distribution (Map 8). Jamaica, widely distributed through many habitats from rather dry to wet, and sea level to 1,300 m.

Material Examined. 41 males and 1 female. JAMAICA: "Jamaica," [no date] (BMNH, CMNH, USNM), [1844–1846], E. H. Gosse (BMNH, holotype), [no date], Taylor (BMNH); Baron Hill, X-1931, L. Perkins (CMNH); Claremont, 10-V, 8-VI-1936, Perkins (CMNH), 1955, B. Heineman (AMNH); Clarendon, about 3,000 feet [ca. 900 m], 15–18-XII-1919 (AMNH); Falmouth, 19-VII-1960, C. & P. Vaurie (AMNH); Hardwar Gap, I-1937, IV, VI, VIII-1936, VIII-1938, IX-1939, X-1934, XII-1933, E. Paine (CMNH); Highgate, 25-VII-1936, A. Avinoff & N. Shoumatoff (CMNH); Mandeville, 2,000 feet [600 m], 13-IV-1937, Avinoff & Shoumatoff (CMNH); Port Antonio, 4-1-1959, 3-II-1962, 16-II-1961, Heineman (AMNH), 21-III-1957, S. A. Hessel (PMY); 1 mile [1.6 km] N Hardwar Gap, 12–20-XI-1966, E. L. Todd (USNM, BMNH); 4 miles [6.5 km] S Hartford, 850 feet [250 m], 26–27-IV-1973, D. & M. Davis (USNM); 3.2 miles [5 km] NE Kellits, near Pedro River, 1,600 feet [480 m], 18-IV-1973, Davis (USNM).

Discussion. This species is endemic to Jamaica and is the only dalcerid known from the West Indies (excluding Trinidad). It is not uncommon among insects for families to be represented in the West

Indies only by Jamaican endemics (Buskirk, 1985). No dependable Life Zone map is available for Jamaica (G. R. Proctor, personal communication, 1986).

Acraga moorei Dyar
Figures 4–6, 70, 71, 163, 235; Map 9

Pinconia ochracea Moore in Jones and Moore, 1882: 364–365.—Jones in Jones and Moore, 1882: 365.—Kirby, 1892: 543.—Holloway, 1986: 9, fig. 13. [preoccupied by *Acraga ochracea* Walker, 1855]

Acraga moorei Dyar, 1898: 232; 1910c: 116.—Dyar and Strand, 1913b: 28.—Handlirsch, 1925: 896.—Sick, 1939: 1305, pl. 168d.—Orfila, 1961: 257–258, figs. 7, 8, pl. 1, figs. 5, 6.—Silva *et al.*, 1968: 295—Scoble, 1992: 349, fig. 248.

Diagnosis. Readily distinguished by dark forewing veins (Fig. 70); *Acraga coa* is similar but has light veins.

Adult Male (Fig. 70). Forewing length 15–18 mm. *Head:* Ochreous. *Thorax:* Ochreous. Forewings ochreous with veins (except costa) dark. Hindwings ochreous, slightly brighter than forewings, veins slightly darkened near margins. Ventral wings ochreous. Legs ochreous. *Abdomen:* Ochreous. Genitalia as in Figure 163.

Adult Female (Fig. 71). Forewing length 23–26 mm. Colored as in male. Genitalia as in Figure 235.

Types. Two male syntypes, apparently destroyed during World War II in a fire at MCML (I. D. Wallace, personal communication, 1982).

Type Locality. Brazil, São Paulo.

Hosts. Eriobotrya japonica (Thunberg) Lindley (Rosaceae) (Jones in Jones and Moore, 1882); *Coffea arabica* Linnaeus (Rubiaceae) (Silva *et al.*, 1968: 295 and CPAC).

Immature Stages. Discussed by Jones in Jones and Moore (1882).

Flight Period. Year-round.

Distribution (Map 9). Venezuela, Colombia, Brazil, Ecuador, Peru, Bolivia, Paraguay, and northern Argentina. Recorded from Tropical Wet, Tropical Moist, Tropical Premontane Wet, Tropical Premontane Moist, Tropical Lower Montane Wet, Tropical Lower Montane Moist, Subtropical Wet, Subtropical Moist, Subtropical Lower Montane Moist, Subtropical (Lower?) Montane Wet or Rain, and Warm Temperate Moist Forest Life Zones.

Material Examined. 137 males and 37 females. ARGENTINA: *Misiones:* Misiones, [no date], P. Koehler (ZSBS); *Salta:* San Andrés, Río Zenta, 31-V-1935, J. P. de Verteuil (BMNH); BOLIVIA: *Cochabamba:* Cochabamba, [no date], J. Steinbach (CMNH); Incachaca, [no date], Steinbach (USNM); Yungas de Incachaca, 2,100 m, 10-II-1959, R. Zischka (ZSBS); *La Paz:* Yungas de Coroico, 1,900 m, 18-V-1950, W. Forster (ZSBS); Río Zongo, 750 m, [no date], A. H. Fassl (BMNH, NHMV, USNM, ZSBS); BRAZIL: *Distrito Federal:* Brasilia Airport, 23-III-1972, Munroes (CNC); Planaltina, 1,000 m, 18-III-1977, 20-III-1982, 2-IV-1976, V. O. Becker (VOB, CPAC), 5-VIII-1978, Santos (CPAC), larva on coffee, 21-VI-1985, pupated 15-VII-1985, emerged 2-VIII-1985, C. Braga (CPAC); *Goiás:* Leopoldo de Bulhões, XII-1933, R. Spitz (BMNH); 20 km N São João da Aliança, 15-IV-1956, F. S. Truxal (LACM); *Mato Grosso do Sul:* Salobra, 1-9-III-1940 (IOC); *Minas Gerais:* [Fazenda dos Campos, 1,500 m], 27-V-1920, J. F. Zikan (IOC); [Passa Quatro, 950 m], 18-V-1922, Zikan (IOC); Sete Lagoas, 720 m, 14-III-1974, Becker (VOB); Teófilo Otoni, Rio São Jacinto, XII-1907, F. Birch (BMNH); *Paraná:* Castro, [no date], E. D. Jones (BMNH); Curitiba, 920 m, 28-XII-1974, 27–28-IV-1975, 10-I-1975, Becker (VOB); Guarapuava, II-1950, F. Justus (CU); Iguaçu, 25-XI-1921 (BMNH); *Rio de Janeiro:* "Campo Bello" [Itatiaia, 400 m], III-1927, IV, XII-1926 (ZSBS), 19-V-1933, 21-VI-1928, 6-XII-1926, 6-XII-1933, 17-XII-1935, 17-XII-1937, Zikan (IOC); Itatiaia, 12-IX-1933, Travassos & H. S. Lopes (IOC), 800 m, 20-IV-1965, H. Ebert (ZSBS), 800–1,200 m, 31-III-1965, Ebert (ZSBS); [probably] Nova Friburgo, I-1913, J. Arp (USNM); *Santa Catarina:* Blumenau, [no date] (MCZ); "Joinville?", [no date], E. & A. Boettcher (ZSBS); Nova Brémen, Rio Laeiss, IV-1936, F. H. Hoffmann (BMNH); Rio Vermelho, near São Bento, 850 m, IV-1936, A. Maller (NHMV); Santa Catarina, IV-1922, E. D. Jones (LACM); *São Paulo:* Alto da Serra, I, III, VI–VIII, XI–XII, 1922–1929, Spitz (BMNH); Boracéia, Salesópolis, 22-V-1947, Travassos (IOC); Cantareira, XI-1920, Pohl (USNM); "Faxina," [no date] (ZSBS); Ipiranga, I-1926, III-1923, Spitz (BMNH); Mato do Governo, I, IV-1921, XII-1920, Pohl (ZSBS); São Paulo, [no date] (BMNH, USNM, ZSBS), [no date], Von Ihering (USNM), Pohl (CMNH), IV-1917, V-1918 (ZSBS); São Paulo, 750 m, IV-1913, Jones (BMNH); COLOMBIA: *Antioquia:* Medellín, La Estrella, 1,700 m, II-1960, P. B. Schneble (ZSBS); *Cauca:* Popayán, 1897 (USNM), [no date], W. Hopp (ZSBS), [no date], Lehmann (BMNH); *Cundinamarca:* Monterredondo, 1,420 m, 24-IX-1961, Schneble, 2-IV-1961, J. Foerster (ZSBS); *Guainía:* Ob. [=Upper] Río Negro, 800 m, [no date], Fassl (BMNH); *Valle del Cauca:* San Antonio, 1,800 m, VI-1909, Fassl (USNM); 4 km NW San Antonio, 6,500 feet [2,000 m], 15-IV-1958, 5-I-1959, A. H. Miller (UCB); Ulloa, "4-II-1976," R. Cardenas, reared from coffee foliage (USNM); *Not located:* "Colombie," [no date], Reigner (BMNH); ECUADOR: *Imbabura:* "Otavalo/Apuela," 2,200 m, 8–9-IX-1977, L. E. Peña G. (LACM); *Pastaza:* La Victoria, Río Pastaza, 3,500 feet [1,000 m], [no date], M. G. Palmer (BMNH); *Tungurahua:* El Rosario, Río Pastaza, 4,900 feet [1,500 m], [no date], Palmer (BMNH); PARAGUAY: "Paraguay," [no date], C. Jorgensen (ZMUC), "Dr. Bohls" (BMNH); *Guairá:* Villarrica, 24-V-1921, Jorgensen (USNM), 15-III-1938, O. Kaeser (BMNH), 1, III, IX, XII-1922–1924, F. Schade (BMNH), "4/2 1926 . . . Modt. 2/10 1926 af," Schade (ZMUC), [no date], Jorgensen (BMNH); *Paraguarí:* Sapucaí, XI-1901, XI-1903, W. Foster (BMNH); PERU: *Cajamarca:* Hacienda Taulís, III-1955, N. Bismarck (ZSBS); *Madre de Dios:* Avispas, 400 m, 20–30-IX-1962, L. Pena (CNC); *Pasco:* Huancabamba, Cerro de Pasco, 6,000–10,000 feet [1,800–3,000 m], E. Boettger (BMNH); *Puno:* La Oroya, Río Inambari, 3,000 feet [900 m], V-1905, G. R. Ockenden (USNM), XI–XII-1905, X-1904, Ockenden (BMNH); Oconeque, 7,000 feet [2,100 m], VII-1904, Ockenden (BMNH); Quintun, 5,000 feet [1,500 m], I-1905, Ockenden (BMNH); Río Huacamayo, 3,100 feet [900 m], VI-1904, Ockenden (BMNH); Santo Domingo, 6,000 feet [1,800 m], XI-1904, XII-1901, Ockenden, 6,500 feet [2,000 m], XII-1902, Ockenden (BMNH); VENEZUELA: *Aragua:* La Victoria, 1,700 m, VII–VIII-1963, XII-1961, W. Gatz (ZSBS); Rancho Grande, 1,100 m, 15-VII–31-VIII-1967, R. W. Poole, 1–20-I-1978, J. B. Heppner (USNM), 23-VII-1946, 2-IX-1946 (AMNH), [no date], Vogelsang (ZSBS), VI–VII-1974, A. Watson (BMNH), 16-XI-1955, F. Fernandez Y. (UCV); *Distrito Federal:* Los Venados, Caracas, [no date], P. C. Vogl (ZSBS); *Lara:* Parque Nacional Yacambú, 6–8-IV-1981, A. S. Menke & L. Hollenberg (USNM).

Discussion. I have seen one male (ZSBS), which was once sold by a dealer, labeled Orizaba, Mexico; I consider it mislabeled.

Acraga coa (Schaus)
Figures 27–32, 72, 73, 164, 237; Map 8

Pinconia coa Schaus, 1892: 322.—Druce, 1898: 441, pl. LXXXVII, fig. 23.—Holland, 1903: 369–370, pl. VIII, fig. 6.—Comstock, 1925: 606.

Acraga coa:—Dyar, 1898: 232; 1910c: 116; 1914: 252; 1925b: 44–46.—Dyar and Strand, 1913b: 28.—Hoffmann, 1933: 295.—Sick, 1939: 1305, pl. 168d.—Forbes, 1942: 394.—Schröder, 1963: 493.—Stehr and McFarland, 1985: 36; 1987: 460.—Beutelspacher, 1992: 144.—Miller, 1993: 180, figs. 2–5.

Acraga moribunda Schaus, 1920: 150.—Sick, 1939: 1307. NEW SYN.

Acraga canaquitam Dyar, 1925a: 18.—Sick, 1939: 1305. [synonymized under *coa* by Dyar, 1925b: 44]

Diagnosis. Distinguished from all other orange dalcerids (except *Acraga neblina*) by wing veins lighter than ground color (Fig. 72); differs from *A. neblina* in more rounded wings (Fig. 72) and male genitalia (Fig. 164).

Adult Male (Fig. 72). Forewing length 12–18 mm. *Head:* Orange. *Thorax:* Orange. Forewings yellow-orange to red-brown, with veins yellow. Hindwings yellow-orange, paler than forewings. Ventral wings yellow-orange. Legs orange. *Abdomen:* Orange. Genitalia as in Figure 164.

Adult Female (Fig. 73). Forewing length 19–25 mm. Colored as in male, but forewing veins do not contrast as much with ground color. Forewing anal angle not as developed. Genitalia as in Figures 27–32 and 237.

Types. Lectotype male, and 5 male and 3 female paralectotypes, here designated, USNM 12548 (*coa*); lectotype male, and 2 paralectotype males, here designated, USNM 22497 (*moribunda*) (also 2 male paralectotypes at CMNH and 1 male at BMNH); lectotype female, and paralectotype female, here designated, USNM 27866 (*canaquitam*).

Type localities. Mexico, Veracruz, Jalapa (*coa*); Guatemala, Volcán de Santa María (*moribunda*); Mexico, Quintana Roo, Payo Obispo [now Chetumal] (*canaquitam*).

Hosts. "Almond" (Dyar, 1925a,b), determined as *Terminalia* sp. (Combretaceae) by L. D. Gomez; *Coffea* sp. (Rubiaceae) (USNM); *Citrus* spp. (Rutaceae) (USNM); *Citrus* sp. (S. Passoa, personal communication, 1985).

Immature Stages. Described by Dyar (1925b: 44–46) and Stehr and McFarland (1985: 36).

Flight Period. Year-round.

Distribution (Map 8). Southern Mexico, Belize, Honduras, Guatemala, El Salvador, Costa Rica, Panama. Recorded from Tropical Wet, Tropical Moist, Tropical Premontane Wet, Tropical Premontane Rain, Tropical Lower Montane Moist, Subtropical Wet, Subtropical Moist, Subtropical

Dry, and Warm Temperate Wet Forest Life Zones.

Material Examined. 189 males and 68 females. BELIZE: Belize [city], [no date] (BMNH); Corozal, I-1925, XI-1925, [no date] (USNM, AMNH); Punta Gorda, IV, VII-1933, VII–VIII-1934, J. J. White (BMNH); Río Grande, VII-1935, White (BMNH); COSTA RICA [localities only]: Braulio Carrillo, 700 m (USNM), 1,100 m (VOB); Buenos Aires, 200 m (VOB); Cachí (BMNH, USNM); Cariblanco (BMNH); "Costa Rica" (BMNH, USNM, ZSBS); Hacienda La Suerte, Tapezco, 29 air km W Tortuguero, 40 m (LACM); Hamburg Farm, Reventazón, 25 m (ZSBS); Juan Viñas (BMNH, CMNH, UMO); Orosí, 1,200 m (BMNH); Río La Vieja, near Lagarto (USNM); San José (BMNH, CMNH); San Pedro de Montes de Oca, larva 19-II-1934, emerged, 17-IV-1934, "on coffee and *Citrus* spp.," C. H. Ballou (USNM); Santa Rosa Nat. Park, 300 m (USNM); Sitio (CMNH); Sixaola River (BMNH, CMNH, USNM); Tuis (USNM); "am [=on Mount] Turrialba" (ZSBS); 1.5 miles [2.5 km] S Potrerillos (USNM); 4 km E Casetilla, Rincón Nat. Park (USNM); 9.4 km W Bribri, Suretka, 200 m (USNM); EL SALVADOR: San Salvador, 600 m, 19-VI-1960, B. Bechyne (ZSBS); GUATEMALA: Antigua, 1,500 m, 7-IX-1969 (USNM); Cayuga, III, VI, X-[no year] (BMNH, CMNH); Chichicastenango, 6,000 feet [1,800 m], VI-1947, H. G. Pulsifer (AMNH); Guatemala City, [no date], Rodriguez (BMNH); "La Naranja," [no date] (ZSBS); Machaquila, 8-VII-1972, V. O. Becker (VOB); Purulhá, VII-[no year], W. Schaus & J. Barnes (BMNH, USNM); "Qeuriflia," V-[no year] (BMNH); Quiriguá, III, VI-[no year], Schaus & Barnes (BMNH, USNM); San Sebastián, Retalhuleu, [no date] (USNM); Sayaxché, Petén, 8-VII-1972, Becker (VOB); Volcán de Santa María, [no date], Schaus & Barnes (lectotype of *moribunda*) (USNM), XI-[no year] (paralectotypes of *moribunda*) (USNM, CMNH, BMNH); HONDURAS: El Zamorano, larva on citrus 11-IX-1981, S. Passoa (died as pupa, genitalia examined); La Lima, "10-8-1971," H. E. Ostmark (USNM); Lancetilla, Tela, 25–26-II-1935, 30-IV-1935, M. Bates (MCZ); San Pedro Sula, 700 m, 25-VI-1979, R. D. Lehman (USNM); MEXICO [localities only]: *Campeche:* La Lucha (USNM); *Chiapas:* Chiapas (BMNH, USNM); Esmeralda (USNM); "Hamburgo," [1,150 m] (AMNH); "La Granja," [600 m] (AMNH); Ocozocoautla, 823 m (CAS); Palenque (RT); San Jeronimo, Tacana (BMNH); "Santa Anita," [720 m] (AMNH); Tapachula (ZSBS); Teopisca, 1,900 m (VOB); 20–25 miles [32–40 km] N Huixtla (CNC); *Colima:* Colima (BMNH); *Hidalgo:* Chapulhuacan (LACM); Jacala, 4,500 feet [1,350 m] (MCZ); Santa Ana (AMNH); 2 miles [3 km] N Chapulhuacan (LACM); *Jalisco:* Jalisco (BMNH); *Nayarit:* San Blas (AMNH); *Oaxaca:* Candelaria Loxicha (BMNH); Metates (RJD); Oaxaca (BMNH); Tuxtepec (USNM); 5 miles [8 km] W Santos Reyes Pápalo (LACM); *Puebla:* Cuetzalán (RT); Villa Juárez, 1,000–1,100 m (ZSBS); *Quintana Roo:* Payo Obispo [now Chetumal] (USNM, types of *canaquitam*); X-Can Nuevo (BMNH); *San Luis Potosi:* Tamazunchale, 300 feet [90 m] (AMNH, UCB); Xilitla, Vencidor Station (AMNH); *Tabasco:* Tabasco (BMNH); *Veracruz:* Coatepec (USNM, paralectotypes of *coa*; AMNH; NHMV); Córdoba (USNM, CU); Fortín de Las Flores (RJD, UCB); Huatusco (BMNH); Jalapa (USNM, types of *coa*; AMNH; BMNH; ZSBS); Misantla (AMNH, NHMV, USNM, ZSBS); Orizaba (AMNH, BMNH, USNM, ZSBS); Presidio (AMNH); Santiago Tuxtla, 800 m (VOB); Zacualpan (BMNH); *Yucatán:* Colonia Yucatán (AMNH); Mérida (AMNH); PANAMA: Ancón, [no date], E. Celestine & G. Ireneo (USNM); Bugaba, [no date], Schaus (USNM); Chiriquí, 18-II-1960, K. Brown & D. Veirs (PMY); Corozal, XI-1912, C. P. Crafts (USNM); Lino, 800 m, [no date], A. H. Fassl (USNM).

Discussion. Holland (1903: 369) recorded *Acraga coa* as "a straggler" in Arizona and is apparently responsible for modern citations of two dalcerid species in Arizona (e.g., Borror *et al.*, 1981: 519). The specimen Holland illustrated (CMNH) bears a label "caught in Coch. Co. Ariz.," but "North. Mex." appears elsewhere on the label. I have seen an additional male (SMEK) labeled "Cochise Co./June Ariz." and "U. of K./Lot 734" but no further data is available for Lot 734. Because I have seen only two old specimens, I do not trust the Arizona record and consider the specimens mislabeled.

A male (BMNH) labeled only "Colombia/Coll. by/W. E. Pratt" probably refers to that former part of Colombia that is now Panama.

Dyar (1925a: 18; 1925b: 44) recorded this "common on shade trees, especially on almond [*Terminalia*]" and "defoliating . . . almond trees" at Payo Obispo [Chetumal], Mexico.

Acraga chicana, new species
Figures 74, 165; Map 8

Diagnosis. Similar to *Acraga coa*, differing in darker forewing, without pale veins (Fig. 74); differs from *Acraga melinda* group in narrower forewing (from apex to anal angle).

Adult Male (Fig. 74). Forewing length 13 mm. *Head:* Brownish orange. *Thorax:* Dorsum brownish orange, venter orange.

Forewings brownish orange. Hindwings orange. Ventral wings orange. Legs orange with brownish orange tufts. *Abdomen:* Orange. Genitalia as in Figure 165.

Adult Female. Unknown.

Type. Holotype male, AMNH.

Type Locality. Mexico, Campeche, near Xpujil, Chicana Ruins.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. January.

Distribution (Map 8). Southern Mexico, apparently in Subtropical Moist Forest Life Zone.

Material Examined. Known only from unique holotype, collected 6-I-1980 by R. Holland at ultraviolet light.

Discussion. The species name is a noun in apposition honoring the type locality.

Acraga concolor Species-Group

Diagnosis. Distinguished from other medium-sized whitish or yellow *Acraga* by having only short points or gentle lobes on the sociuncus (Figs. 166–169).

Adult Male. Medium size, 8–11 mm. Ground color: whitish or yellow. Hindwing Rs fused with Sc + R_1 in cell. Genitalia: tegumen and sociuncus fused, elongate; sociuncus with short points or gentle lobes; gnathos unfused tabs with strong median process; vinculum thin, elongate; valvae fused with juxta into cylindrical complex surrounding aedoeagus; saccus slender, elongate; aedoeagus long, slender.

Adult Female. Medium size, forewing 14 mm. Genitalia: sterigma broad; ostium bursae wide; ductus bursae long, wide; corpus bursae ovate; ductus seminalis arising at middle of ductus bursa; apophyses posteriores broad, pointed; "accessory glands" ovate in lateral view.

KEY TO *CONCOLOR* GROUP MALES

1. Wings yellow or whitish; upper *and* lower lobes of posterior sociuncus developed as points with strongly sclerotized tips (Figs. 166, 168, 169) 2
   Wings yellow; sociuncus upper lobe gently rounded, with no point (Fig. 167) .... *concolor*
2(1). Wings whitish; forewing length 8–10 mm; sociuncus lobes with upper *and* lower points developed (Fig. 169) .... *citrinopsis*
   Wings yellow; forewing length 10–11 mm; sociuncus lobes with upper points developed less strongly than in *citrinopsis*, lower points strongly developed and slightly downturned (Figs. 166, 168) 3
3(2). Sociuncus lobes as in Figure 168; Venezuela .... *beebei*
   Sociuncus lobes as in Figure 166; Colombia .... species C

Acraga concolor (Walker), NEW COMB.
Figures 76, 167; Map 10

Limacodes concolor Walker, 1865: 487.—Schaus, 1896b: 647 ("Not identified").—Dyar, 1905b: 396 (". . . unable to identify . . . probably . . . Dalceridae").

Diagnosis. Similar to *Acraga citrinopsis*, differing in light yellow (not whitish) coloration and less developed lobes of sociuncus (Fig. 167).

Adult Male (Fig. 76). Forewing length 9–10 mm. Entirely light yellow (similar to *Acraga goes*), dorsal forewing darker than hindwing. Genitalia as in Figure 167.

Adult Female. Unknown.

Type. Neotype male, here designated, BMNH.

Type Locality. Brazil, Amazonas, Santo Antônio de Javari (based on neotype).

Host. Unknown.

Immature Stages. Unknown.

Flight Period. Year-round.

Distribution (Map 10). Venezuela, Surinam, French Guiana, northern Brazil (Amazon Basin), Ecuador, Peru, and Bolivia. Most records are from Tropical Moist Forest, with several from Tropical Wet, Tropical Premontane Rain, Tropical Premontane Wet, and Subtropical Moist (?) Forest Life Zones.

Material Examined. 108 males. BOLIVIA: *La Paz:* Sarampiuni, San Carlos, 1,000 m, 2-IV, 8-IX-1950, W. Forster (ZSBS); *Santa Cruz:* "Prov. del Sara" [now Gutiérrez], 450 m, VII-1909, J. Steinbach (CMNH); BRAZIL: *Amazonas:* Canal Maturaca, Mission Cauaburi, 70 m, 14-I-1963, C. Lindemann (ZSBS); Fonte Boa, V, VI-1906, S. M. Klages (BMNH); Hyutanahan [=Huitanaã], Rio Purus, II-1922, Klages (CMNH); Manaus, 26-XI-1919, H. S. Parish (CU); Santo Antônio de Javari, VI-1907, Klages (BMNH, neotype); São Paulo de Olivença, [no date], A. H. Fassl (ZSBS); Tefé, VIII-1935, A. M. Moss (BMNH), IX-[no year], Fassl (USNM), VII-[no year], Fassl (ZSBS); "Uypiranga," VI-1931, W. Hopp (ZSBS); *Pará:* Belém, 20 m, I-1984, V. O. Becker (VOB); Marabá, 50 m, 9-I-1977, Becker (VOB); Ponte Nova, Rio Xingu, [no date] (USNM); ECUADOR: *Pastaza:* Alpayacu, Río Pastaza, 3,600 feet [1,100 m], [no date], M. G. Palmer (BMNH); *Tungurahua:* El Topo, Río Pastaza, 4,200 feet [1,250 m], [no date], Palmer (BMNH); *Not located:* Cashaureu[?], 4,600 feet [1,400 m], [no date], Palmer (BMNH); FRENCH GUIANA: Pied Saut, Oyapock River, II-1918, XII-1917, Klages (CMNH); Saint-Jean, III-1904, W. Schaus (USNM), [no date] (BMNH), VII–VIII-1904 (BMNH); PERU: *Loreto:* "Below Arica [Colombia]," 13-VIII-1920 (CU); Caballococha, V–VII-1884, M. de Mathan (ZSBS); Contamana, Río Ucayali, X–XII-[no year] (BMNH); [Puerto Limon], Middle Río Marañon, 22-X-1928, H. Bassler F6076 (AMNH); [Puerto Melendez], Middle Río Marañon, 27-VIII-1924, Bassler F6091 (AMNH); Río Pacaya, VII-1912, VIII-IX-1912 (BMNH); *Madre de Dios:* Río Tambopata Reserve, 30 air km SW Puerto Maldonado, 290 m, 6–20-XI-1979, J. B. Heppner (FSCA, USNM); *Puno:* La Oroya, Río Inambari, 3,100 feet [900 m], [no date] (BMNH, USNM), III-1905, wet season, G. R. Ockenden (BMNH, CMNH, USNM), IX-1904, IX-1905, dry season, Ockenden (BMNH), XI-XII-1905, Ockenden (BMNH, USNM); La Union, 2,000 feet [600 m], XII-1904, Ockenden (BMNH); Río Huacamayo, 3,100 feet [900 m], VI-1904, dry season, Ockenden (BMNH); Santo Domingo, 6,000 feet [1,800 m], XI-1904, 6,500 feet [1,950 m], IV-1902, dry season, XII-1902, wet season, Ockenden (BMNH); Tincuri, 3,400 feet [1,000 m], I-1905, wet season, VIII-1904, dry season, Ockenden (BMNH); Yahuarmayo, 1,200 feet [360 m], II–III-1912, H. & C. Watkins (BMNH); SURINAM: Moengo, Boven, Upper Cottica River, 20–27-V-1927, [W. T. M. Forbes] (CU); VENEZUELA: *Amazonas:* Cerro de la Neblina Basecamp, 0°50′N, 66°9′44″W, 140 m, 4–12-II-1984, D. Davis & T. McCabe (USNM); Río Baria, 140 m, 0°55′N, 66°10′W, 14–19-III-1984, J. A. Clavijo & J. Demarmels (UCV); 6 km E San Carlos de Río Negro, 23-XI-1984, R. L. Brown (USNM); *Bolívar:* El Dorado to Santa Elena road, Km 107, 520 m, 15-VIII-1957, F. Fernandez Y. & C. J. Rosales (UCV); Kanarakuni, 450 m, 31-I–4-II-1967, Fernandez & A. D. Ascoll (UCV, USNM); Río Surukum, Carretera Santa Elena Icabaru, 850 m, 19–31-I-1985, Fernandez *et al.* (UCV).

Discussion. "*Limacodes*" *concolor* was described (Walker, 1865: 487) from a yellow male, expanse "9 lines" [19 mm], from the "Amazon Region" in "Mr. Saunders' Collection." The type was lost in the early part of this century according to Dyar (1905b: 359) and an unpublished handwritten note by Hampson in his personal copy (now in BMNH) of Walker (1865). Although there is enough information in the original description to indicate that the type was a dalcerid, there is not enough to place it accurately in a genus or species. The name *concolor* has, therefore, remained unidentified since the original description. To end this confusion, I am fixing the identity of *concolor* as this species by designating a neotype. There is no reason why the original type could not have been this species, because it is common in the "Amazon Region" and is the correct size and color. My proposed neotype designation has been discussed with other specialists on neotropical Lepidoptera who agree with this action.

I have also seen the following specimens, which differ slightly from typical *concolor* in the shape of the sociuncus lobes but are probably this species: 37 males and 1 female from COLOMBIA: *Cundinamarca:* Monterredondo, 1,420 m, III–X, XII-1961, J. Foerster & P. B. Schneble (ZSBS, USNM); 1 male from ECUADOR: *Zamora-Chinchipe:* Cumbaratza, 3-4-III-1965, L. E. Peña (AMNH); and 2 males from VENEZUELA: *Tachira:* Río Frio, 600 m, 2–10-IX-1981, Fernandez *et al.* (UCV, USNM).

Acraga citrinopsis (Dyar)

Figures 77, 78, 169, 242; Map 11

Anacraga citrinopsis Dyar, 1927: 550.—Sick, 1939: 1307.—Lourenção *et al.*, 1989: 109.
Anacraga sp.:—Santis, 1987: 97.
Acraga citrinopsis:—Miller, 1993: 179.

Diagnosis. Similar to *Acraga concolor*, differing in whitish (not light yellow) coloration and more strongly developed lobes of sociuncus (Fig. 169); similar to *A. citrina*, differing in not having strongly pointed sociuncus processes (Fig. 169).

Adult Male (Fig. 77). Forewing length 8–10 mm. Entirely whitish with yellow tint (similar to *Acraga citrina*), dorsal forewing slightly more yellow than pale hindwing. Genitalia as in Figure 169.

Adult Female (Fig. 78). Forewing length

14 mm. Colored as in male. Anal angles less produced. Genitalia as in Figure 242.

Type. Holotype female [not male as stated by Dyar], USNM 40715.

Type Locality. Peru, Lima, "Callao."

Host. Ricinus communis Linnaeus (Euphorbiaceae) (Lourenção *et al.*, 1989).

Immature Stages. Lourenção *et al.*, 1989.

Flight Period. Year-round.

Distribution (Map 11). Venezuela, Brazil, Peru, and Bolivia, in Tropical Moist, Tropical Dry, Tropical Premontane Moist, Subtropical Moist, and Warm Temperate Moist or Dry Forest Life Zones.

Material Examined. 62 males and 6 females. BOLIVIA: *Santa Cruz:* Buena Vista, 750 m, VIII-1906–IV-1907, Steinbach (BMNH); "Prov. del Sara" [now Gutiérrez], 450 m, VII-1909, J. Steinbach (CMNH); BRAZIL: *Amazonas:* Fonte Boa, V–VI-1906, S. M. Klages (BMNH, USNM), [no date], A. H. Fassl (USNM); Hyatanahan [=Huitanaã], Rio Purus, I–II-1922, Klages (CMNH); São Paulo de Olivença, [no date], Fassl (ZSBS); Tefé, 20-I-1920, 22-XII-1919 (CMNH), X-1907, M. de Mathan (BMNH); *Goiás:* Formosa, 800 m, 19-III-1977, V. O. Becker (VOB); Ilha do Bananal, Rio Javare, 200 m, 4–8-IX-1977, 7-IX-1983, Becker (VOB); 24 km E Formoso, [ca. 900 m], 8-VI-1956, F. S. Truxal (LACM); *Mato Grosso do Sul:* Corumbá, 19–25-IV-1985, Becker (VOB); Rio Brilhante, 23–27-X-1970, Becker (VOB); *Minas Gerais:* Sete Lagoas, 720 m, 20-V-1974, Becker (VOB); *Pará:* Marabá, 50 m, 9-I-1977, Becker (VOB); Ponte Nova, Rio Xingu, [no date] (USNM); Rio Xingu Camp, 52°22′W, 3°39′S, ca. 60 km S Altamira, P. J. Spangler & O. S. Flint (USNM); Taperinha, 11–20-VI-1927, Zerny (NHMV); *São Paulo:* Junqueirópolis, VI-1984, A. L. Lourenção, reared from mamona (VOB); PERU: *Lima:* "Callao," [no date], Mrs. M. J. Pusey (USNM, holotype, data may be incorrect); *Loreto:* Middle Río Ucayali, 15-VIII-1923, H. Bassler F6191 (AMNH); Río Napo, 6-VI-1920 (CMNH); Río Ucayali, 3-XII-1926, Bassler F6165 (AMNH); [Roaboya], Middle Río Ucayali, 4-I-1927, Bassler F6131 (AMNH); Yurimaguas, Río Huallaga, 15–17-IV-1920 (CMNH); VENEZUELA: *Amazonas:* Cerro de la Neblina Basecamp, 0°50′N, 66°9′44″W, 140 m, 20-II-1985, P. & P. Spangler *et al.* (USNM); *Barinas:* Reserva Forestal de Ticoporo, 230 m, 26–29-III-1968, F. Fernandez Y. & C. J. Rosales (UCV); *Bolívar:* Kanarakuni, 450 m, 2-II-1967, Fernandez & A. D. Ascoll (USNM); Río Surukum, Carretera Santa Elena Icabaru, 850 m, 19–31-I-1985, Fernandez *et al.* (UCV); *Carabobo:* San Esteban, VII-1909, Klages (BMNH); *Falcón:* Palma Sola, 1896, Whytman (BMNH).

Discussion. The unique female holotype of *Acraga citrinopsis* is in poor condition, but it matches reared females from São Paulo that are associated with males like those described here. The type locality may be incorrect; specimens from Callao "are probably mislabelled as this locality is a desert area" (Becker, 1982: 231).

This species "caused considerable damage" to leaves of the crop "mamona" (*Ricinus communis*) in São Paulo, Brazil (V. O. Becker, personal communication, 1985; Lourenção *et al.*, 1989). Santis (1987) recorded parasites from this species under the name *Anacraga* sp., which was provided by me early in the present study.

Acraga species C
Figure 166; Map 12

Diagnosis. Similar to other light yellow *Acraga*, differing in strongly developed sociuncus lobes (Fig. 166); very similar to *Acraga beebei*, differing in development of sociuncus lobes (Fig. 166).

Adult Male. Forewing length 10–11 mm. Forewing yellowish dorsally (like *Acraga concolor*); dorsal hindwing and ventral wings pale yellow or whitish. Sociuncus lobes with upper points developed (but not quite as strongly as in *A. citrinopsis*), bottom points strongly developed and slightly downturned (Fig. 166).

Adult Female. Unknown.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. August.

Distribution (Map 12). Colombia, in Tropical Premontane and Lower Montane Wet Forest Life Zones.

Material Examined. 2 worn males. COLOMBIA: *Cundinamarca:* Pacho, 2,200 m, [no date], A. H. Fassl (NHMV, genitalia 85-60); *Risaralda:* "Pueblo Rico [Pueblorrico], [Río] San Juan, Choco," 5,200 feet [1,550 m], VIII-1909, [probably collected by M. G. Palmer] (BMNH, genitalia 85-7).

Discussion. This species may be an Andean variant of *Acraga beebei*, but examination of more material is necessary to resolve its status.

Acraga beebei, new species
Figures 79, 168; Map 2

Diagnosis. Differing from other light yellow *Acraga* in strongly developed sociuncus lobes (Fig. 168); very similar to *Acraga* species C, differing in development of sociuncus lobes (see later and Fig. 168).

Adult Male (Fig. 79). Forewing length 10 mm. *Head:* Light yellow. *Thorax:* Dorsum light yellow; venter whitish. Forewings light yellow. Hindwings whitish. Ventral wings whitish. Forelegs yellow; other legs whitish. *Abdomen:* Whitish. Genitalia as in Figure 168.

Adult Female. Unknown.

Type. Holotype male, USNM 103447.

Type Locality. Venezuela, Aragua, Rancho Grande.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. January, June, August, September, and November.

Distribution (Map 2). Northern Venezuela, in Tropical Premontane Moist Forest Life Zone.

Material Examined. 7 males (all paratypes). VENEZUELA: *Aragua:* Rancho Grande, 1,100 m, 17–20-I-1978, J. B. Heppner (USNM), 18-VI-1946 (AMNH), 8–21-VIII-1967, R. W. Poole (USNM, including holotype), 2-IX-1980, F. Fernandez Y. & J. L. Garcia (UCV), 8-XI-1955, Fernandez & C. J. Rosales (UCV).

Discussion. This species differs as follows in male genitalia from *Acraga* species C (lateral view): sociuncus–tegumen complex more rounded at top of slope down to lobes, upper lobe shape differs (especially in development of posterior point), and lower lobe turns down more quickly. The species name honors William Beebe, who opened the field stations that contributed greatly to our knowledge of Dalceridae of Guyana, Trinidad, and Venezuela.

Acraga melinda Species-Group

Diagnosis. Differs from *Acraga flava* group and *Acraga hamata* group in coloration (orange, orange-brown, or forewings brownish red with hindwings transparent yellow), and genitalia (Figs. 170–174).

Adult Male. Medium size, forewing 11–17 mm. Ground color: both wings orange or orange-brown, or forewings brownish red with hindwings transparent yellow. Male forewing somewhat falcate. Hindwing Rs not fused with $Sc + R_1$ in cell. Genitalia: tegumen and sociuncus fused, elongate; sociuncus with bluntly pointed downward-directed lateral lobes; uncus with two dorsal processes; gnathos nearly rectangular tabs; vinculum thin, elongate; complex (=anellus?), sometimes well sclerotized, encasing aedoeagus; valvae reduced to lobes on complex encasing aedoeagus; aedoeagus long, slender, slightly bent, external end with fine barbs.

Adult Female. Medium to large, forewing 16–23 mm. Genitalia: sterigma broad, usually strongly sclerotized; ostium bursae broad, usually strongly sclerotized; ductus bursae long; corpus bursae elongate ovate; ductus seminalis arising about middle of ductus bursae; apophysyes posteriores short to medium length, medium width at base, narrowing to apex; "accessory glands" ovate in lateral view.

KEY TO *MELINDA* GROUP MALES

1. Wings orange or orange-brown (Figs. 83, 85) 2
Forewings brownish red, hindwings transparent yellow (Fig. 80); Andes .... *perbrunnea*
2(1). Gnathos tabs bent sharply laterally near tips (Fig. 170); Central America .... *melinda*
Gnathos tabs gently curved (Figs. 171–173); South America 3
3(2). Complex surrounding aedoeagus forming a strong shelf ventral to aedoeagus (Figs. 172, 173); shelf ends in 2 lobes but without lobes on ventral surface; "valley" between dorsal uncus points narrow; Andes 4
Complex surrounding aedoeagus not forming a strong shelf; 2 small lobes on ventral surface of complex; "valley" between dorsal uncus points broad (Fig. 171); Amazon Basin .... *amazonica*
4(3). Dorsal points of uncus much narrower (in lateral view) than high (Fig. 172) .... *meridensis*

Dorsal points of uncus about as wide (in lateral view) as high (Fig. 173) .... *mariala*

Acraga melinda (Druce)
Figures 83, 84, 170, 241; Map 13

Pinconia melinda Druce, 1898: 441, pl. LXXXVII, fig. 24.

Acraga melinda:—Dyar, 1898: 232.—Dyar and Strand, 1913b: 28.—Hopp, 1921: 279.—Sick, 1939: 1305.

Diagnosis. Similar to the sympatric *Acraga hamata* but orange, not yellow; similar to *A. coa* but without pale veins on forewing; differs from related Andean species in genitalia (Figs. 170, 241).

Adult Male (Fig. 83). Forewing length 14–17 mm. Entirely orange-yellow, hindwing lighter than forewing, ventral body and wings pale. Wing shape as in *A. hamata*. Genitalia as in Figure 170.

Adult Female (Fig. 84). Forewing length 20–23 mm. Colored as in male. Wing angles less developed than those of male. Genitalia as in Figure 241.

Type. Holotype female, ZMHB.

Type Locality. Panama, Volcán de Chiriquí.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. February to March, May to September, and December.

Distribution (Map 13). Costa Rica and Panama, in Tropical Premontane Wet and Rain Forest Life Zones.

Material Examined. 30 males and 4 females. COSTA RICA: "Costa Rica," "1 1/2 1928," O. Bogh (ZMUC); "Costa Rica," [no date], A. H. Fassl (ZSBS); Estacion Carrillo, Parque Nacional Braulio Carrillo, 700 m, V-1985, IX-1984, J. & A. Chacon (USNM); Juan Viñas, VI-[no year], W. Schaus & J. Barnes (BMNH, USNM); La Fuente, Turrialba, III-1940, A. Alfaro (USNM); Monteverde, 1,400 m, 6-IX-1982, C. Nagano & M. Hayes (LACM), 1,300–1,400 m, 20–21-VII-1982, D. H. Janzen & W. Hallwachs (USNM); Moravia de Chirripó, 1,000 m, 10-V-1983, Janzen & Hallwachs (USNM); Orosí, 1,200 m, [no date], Fassl (BMNH); Sitio, VI-[no year], Schaus (BMNH, CMNH); Tuis, 28-V–4-VI-[no year], Schaus (USNM); Turrialba, 600 m, 20-VIII-1971, V. O. Becker (VOB), 7-VI-1986, S. Passoa (USNM); Volcán de Turrialba, 1,800 m, 13-VIII-1972, Becker (VOB); 3 km S Casa Mata, 16 km S San Isidro de Tejar, 1,800 m, 4-XII-1983, Janzen & Hallwachs (USNM); PANAMA: Lino, 800 m, [no date], Fassl (USNM, ZSBS); Volcán de Chiriquí [now Baru], [no date], Troetsch (ZMHB, holotype), 16–17-II-1936, F. E. Lutz & W. J. Gertsch (AMNH).

Discussion. The Brazilian records of *Acraga melinda* (Bertels and Baucke, 1966: 40; Biezanko, 1961a: 3; 1961b: 4; Mariconi and Soubihe Sobrinho, 1961: 38; Silva *et al.*, 1968: 295; Duarte, 1947: 189; Lima, 1936: 279) probably apply to *A. ochracea*. *Acraga melinda* is apparently restricted to elevations above 600 m.

The following specimens from Ecuador are very close to *Acraga melinda* but differ slightly in the shape of the dorsal uncus points: *Cañar:* 20 km SE La Troncal, 2,200 feet [660 m], 25-VI–21-VII-1984, S. J. Weller & N. L. Jacobson (USNM, 4 males, 1 female); *Pichincha:* Tinalandia, 700 m, 21-VII-1985, C. V. Covell (USNM, 1 male).

Acraga amazonica, new species
Figure 171; Map 14

Diagnosis. Similar to *Acraga melinda*, differing in less developed sociuncus points, shape of gnathos, and complex around aedoeagus (Fig. 171).

Adult Male. Forewing length 11–13 mm. Entirely orange brown. Hindwing slightly paler than forewing. Genitalia as in Figure 171.

Adult Female. Unknown.

Type. Holotype male, BMNH.

Type Locality. Brazil, Amazonas, Fonte Boa.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. February, May to September, November, and December.

Distribution (Map 14). Northern Brazil (Amazon Basin), in Tropical Moist Forest Life Zone.

Material Examined. 14 males (all paratypes). BRAZIL: *Amazonas:* Fonte Boa, V, VII–IX-1906, S. M. Klages (BMNH, including holotype); Nova Olinda, Rio Purus, VI-1922, Klages (CMNH); Remate de Males [now Atalaia do Norte], Rio Javari, 21-II-1920, H. S. Parish (CU); São Paulo de Olivença, V-1907, Klages (BMNH), VI–VII-1935, A. M. Moss (BMNH), VII-

1933, S. Waehner (BMNH), XI–XII-[no year], A. H. Fassl (USNM), [no date], Fassl (ZSBS).

Discussion. The species name refers to the distribution of this species in the Amazon Basin.

Acraga meridensis Dognin
Figures 85, 172, 240; Map 13

Acraga meridensis Dognin, 1907: 23.—Dyar, 1910c: 117.—Dyar and Strand, 1913b: 28.—Sick, 1939: 1305.

Diagnosis. An Andean species similar to *Acraga mariala*, differing in male genitalia, especially the points on sociuncus being narrow in lateral view (Fig. 172) and female genitalia, especially the larger ductus bursae (Fig. 240).

Adult Male (Fig. 85). Forewing length 11–13 mm. Entirely orange-brown. Hindwing slightly paler than forewing. Genitalia as in Figure 172.

Adult Female. Forewing length 17–19 mm. Colored as in male. Anal angles less developed. Genitalia as in Figure 240.

Type. Lectotype male, paralectotype male, here designated, USNM 29812.

Type Locality. Venezuela, Mérida.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. April to November.

Distribution (Map 13). Andes of Venezuela and Colombia, probably in Tropical Premontane and Lower Montane Moist (Wet?) Forest Life Zones.

Material Examined. 22 males and 2 females. COLOMBIA: *Cundinamarca:* Monterredondo, 1,420 m, IV-1961, XI-1956, J. Foerster, VI-1959, various dates IV–X-1961, P. B. Schneble (ZSBS); VENEZUELA: *Mérida:* Mérida, [no date] (USNM), [no date] (ZSBS); Mérida, XI-1898, S. Briceno (BMNH), [no date], Briceno (BMNH, USNM).

Discussion. One male from PERU: *Puno:* La Oroya, Río Inambari, 3,100 feet [900 m], IX-1904, G. R. Ockenden (BMNH) is very close to *Acraga meridensis* but varies in genitalia in the more delicately proportioned sociuncus lobes and more shallow medial cleft in the plate below the aedoeagus.

Acraga mariala Dognin
Figures 173, 239; Map 14

Acraga mariala Dognin, 1923b: 17.—Sick, 1939: 1306.

Diagnosis. An Andean species similar to *Acraga meridensis*, differing male genitalia, especially the points on sociuncus being wide in lateral view (Fig. 173), and female genitalia, especially smaller ductus bursae (Fig. 239).

Adult Male. Forewing length 13 mm. Superficially like *Acraga meridensis*, differing in male genitalia (Fig. 173).

Adult Female. Forewing length 16 mm. Colored as in male. Anal angles less developed. Genitalia as in Figure 239.

Type. Holotype female, USNM 29813.

Type Locality. Colombia, Cundinamarca, Bogotá, Insitut de la Salle.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. July and August.

Distribution (Map 14). Colombia, apparently in Tropical Lower Montane or Premontane Wet, and Tropical Lower Montane Moist Forest Life Zones.

Material Examined. 1 male and 2 females. COLOMBIA: *Cundinamarca:* Bogotá, Insitut de la Salle, 8-VII-1919, Brother Apollinaire-Marie (USNM, holotype); Bogotá, 2,800–3,200 m, [no date], A. H. Fassl (USNM); Finca San Pablo, 1,800 m, 3 km N Albán, 1–12-VIII-1967, P. & B. Wygodzinsky (AMNH).

Discussion. The association of the Colombia male with the female holotype of *Acraga mariala* is tentative. The male genitalia of a unique specimen from ECUADOR: *Pastaza:* Alpayacu, Río Pastaza, 3,600 feet [1,100 m], [no date], M. G. Palmer (BMNH) differ from the Colombia male in having the dorsal lobes of the sociuncus pointed anteriorly (not posteriorly), the "shoulder" of the sociuncus more strongly produced dorsally, and the tabs of the gnathos shorter. The Ecuador male may be a variant of *Acraga melinda* or may represent a distinct species.

Acraga perbrunnea Dyar
Figures 80, 174; Map 7

Acraga perbrunnea Dyar, 1927: 550.—Sick, 1939: 1307.

Diagnosis. Distinctive in thinly scaled brownish red forewings and transparent yellow hindwings (Fig. 80).

Adult Male (Fig. 80). Forewing length 14 mm. *Head:* Pale orange. *Thorax:* Dorsum light orange, venter pale orange. Forewings brownish red, thinly scaled. Hindwings transparent yellow with pale orange fringe, especially around anal angle. Ventral wings as dorsal. Legs pale orange. *Abdomen:* Pale orange. Genitalia as in Figure 174.

Adult Female. Unknown.

Type. Holotype male, USNM 40714.

Type Locality. Peru, Pasco, Oxapampa, 2,000 m.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. Unknown.

Distribution (Map 7). Colombia and Peru, in Tropical Lower Montane Moist (maybe also Dry) and Tropical Premontane (or Lower Montane) Wet Forest Life Zones.

Material Examined. 8 males. COLOMBIA: *Cundinamarca:* "Pueblo Guasca, Bogotá," [no date] (USNM, BMNH, CU); *Quindío:* Río Nabarco, [no date] (BMNH); PERU: *Pasco:* Oxapampa, 2,000 m, [no date] (USNM, holotype).

Discussion. The holotype is badly rubbed and missing its abdomen. I tentatively place *Acraga perbrunnea* here, but it may belong to the *Acraga infusa* group (especially based on aedoeagus shape).

Acraga citrina Species-Group

Diagnosis. Distinguished from other whitish or yellow *Acraga* in northern South America by the long processes of the male sociuncus (Figs. 175, 198).

Adult Male. Medium size, forewing 9–11 mm. Ground color: whitish or pale yellow. Hindwing Rs fused with Sc + R_1 in cell. Genitalia: tegumen and sociuncus fused, elongate; sociuncus with long processes; gnathos a median hairy lobe or tabs, with lateral arms; vinculum thin, elongate; valvae fused into complex with juxta; saccus slender, elongate; aedoeagus long, slender.

Adult Female. Medium size, forewing 14–15 mm. Genitalia: sterigma broad; ostium bursae medium width; ductus bursae long, medium width; corpus bursae spherical; ductus seminalis arising in middle of ductus bursa; apophyses posteriores broad, pointed; "accessory glands" elongate ovate in lateral view.

Discussion. Acraga citrina is a common, genitally distinctive species. *Acraga hoppiana,* known only from four males, is provisionally placed here.

KEY TO *CITRINA* GROUP MALES

Wings whitish; sociuncus with 2 pairs of elongate ventral-directed processes (total of 4 closely grouped points) (Fig. 175); northern South America .... *citrina*

Forewings yellow, hindwings whitish; sociuncus with long paired semicircular processes arising from dorsal surface, curving dorsally and then back posterolaterally (Fig. 198); Colombia and Ecuador .... *hoppiana*

Acraga citrina (Schaus), RESURRECTED COMB.
Figures 12, 20, 22, 42, 81, 82, 175, 246; Map 12

Dalcera citrina Schaus, 1896a: 57.—Dyar, 1896: 57.
Epipinconia citrina:—Dyar, 1898: 233.
Anacraga citrina:—Dyar, 1910c: 119.—Dyar and Strand, 1913b: 29.—Sick, 1939: 1307.
Acraga citrina:—Kaye and Lamont, 1927: 121.
Anacraga albescens Hopp, 1928a: 286.—Sick, 1939: 1308. NEW SYN., NEW COMB.

Diagnosis. Differs from *Acraga citrinopsis* (a more southern species) only in male genitalia (Fig. 175); distinguished from *A. concolor* by whitish coloration and male genitalia (Fig. 175).

Adult Male (Fig. 81). Forewing length 9–11 mm. Entirely whitish with yellow tint, with whitish hindwing. Genitalia as in Figure 175.

Adult Female (Fig. 82). Forewing length 14–15 mm. Colored as in male, anal angles of wings less developed. Genitalia as in Figure 246.

Types. Lectotype male, here designated, USNM 12549 (*citrina*); holotype male, ZSBS (*albescens*).

Type Localities. Trinidad (*citrina*); Venezuela, Aragua, Maracay (*albescens*).

Hosts. Melicoccus bijugatus Jacquin (UCV, as mamon) (Sapindaceae); *Ricinus* sp. (USNM) and *Ricinus communis* Linnaeus (UCV, as tartago) (Euphorbiaceae); *Terminalia catappa* Linnaeus (UCV, as almendron) (Combretaceae).

Immature Stages. Undescribed.

Flight Period. Year-round.

Distribution (Map 12). Trinidad, Venezuela, Guyana, Surinam, French Guiana, and northern Brazil, in Tropical Moist, Tropical Dry, Tropical Premontane Moist, and Tropical Premontane Dry Forest Life Zones.

Material Examined. 108 males and 19 females. BRAZIL: *Pará:* Amazon between Gurupá and Almeirim, 29-V-1927, Zerny (NHMV); Belém, 20 m, I-1984, V. O. Becker (USNM); Capitão Poço, 19–22-XI-1984, Becker (VOB); Pará [=Belém], [no date], A. M. Moss (BMNH); Prata [S of Igarapé Açu], 1920, A. H. Fassl (USNM); *Pernambuco:* Pernambuco [=Recife], 31-VII-1928, "s/ *Ricinus*," D. B. Pickel (USNM); Tapera, [no date], Pickel (USNM); FRENCH GUIANA: Mana River, V-1917 (CMNH); Pied Saut, Oyapock River, II-1918, S. M. Klages (CMNH); Saint-Jean, VII-1904, W. Schaus (USNM), III-1904, Schaus (BMNH), VII–VIII-1904, [no date] (BMNH); Saint-Laurent, IV-[no year] (USNM, female only), IV-1906, IX–X-1905 (BMNH), [no date] (MNHP); 60 miles [100 km] up Maroni River, VIII-1904, Schaus (USNM); GUIANA: Potaro, I, II, IV-1908, Klages (BMNH); Takutu Mtns., 6°15′N, 59°5′W, 14-XII-1983, P. Spangler & W. Steiner (USNM); Tumatumari, Potaro River, 27-VI-1927, [W. T. M. Forbes] (CU); "bought at Georgetown by Mr. Whitford" (BMNH); SURINAM: Aroewarwa Creek, Maroewym Valley, III–VI-1905, Klages (BMNH); Geldersland, Surinam River, [no date] (USNM); Moengo, Boven, Upper Cottica River, 18–22-V-1927, [Forbes] (CU, USNM); TRINIDAD: "Trinidad," [no date] (USNM, including lectotype of *citrina*), 28-I-1929 (AMNH); Arima Valley, 6-II-1950, 29-II-1952, 19-V-1951 (AMNH); Caparo, XI–XII-1905, Klages (BMNH); Curepe, 11–20-I-1982, 28-IX–4-X-1981, M. J. W. Cock (CIBC); Palmiste, 29-II-1932, 15-I-1947[?] (UWIT); Parrylands Oilfield, La Brea Ward, 13-XI-1980, Cock (CIBC); San Fernando[?], 22-II-1922 (UWIT); Textel Installation, Moune Bleu, 1-III-1981, 29-III-1979, Cock (CIBC, MJWC); Valencia Forest, 2.5 miles [4 km] SE Valencia, IV-1980, Cock (CIBC); [no locality] (UWIT); VENEZUELA: *Aragua:* El Limon, 450 m, 7-I-1964, C. J. Rosales, "ex larva en tartago," 25-VII-1962, F. Fernandez Y., 29-IX-1958, "ex larva en mamon," 19-I-1959, "ex larva en almendron," M. Gelvez (UCV); Maracay, [no date], P. Vogl (ZSBS, holotype and paratype of *albescens*), IV–V-1934, Vogl (BMNH), IV, VI, VIII-1936, Vogl (ZSBS); Maracay, 450 m, 1–10-VIII-1962, J. R. Reguena, "ex larva en almendron" (UCV); *Bolívar:* El Bochincha Res. Forestal Imataca, 200 m, 16–18-V-1985, 6–13-XII-1974 (UCV); *Delta Amacuro:* La Horqueta, 0–100 m, 30-VIII-1975, R. E. Dietz (UCV); *Miranda:* Valle Río Cuira, 280 m, SW Panaquire, ca. 10°12′N, 66°17′W, 18–21-IX-1979, Fernandez (UCV); *Monagas:* "N. Morichal Largo (Puente)," 2–3-IX-1975, Dietz (UCV).

Discussion. Kaye and Lamont (1927: 121) incorrectly recorded *Acraga citrina* from Costa Rica and Peru.

Acraga hoppiana, new species

Figure 198; Map 11

Diagnosis. Differs from other yellow *Acraga* in possessing large, semicircular dorsal processes of sociunucus (Fig. 198).

Adult Male. Forewing length 9–10 mm. *Head:* Pale yellow. *Thorax:* Dorsum yellow; venter pale yellow. Forewings yellow. Hindwings whitish. Ventral wings whitish. *Abdomen:* Whitish. Genitalia as in Figure 198.

Adult Female. Unknown.

Type. Holotype male, ZSBS.

Type Locality. Colombia, Cauca, Río [San Juan de] Micay.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. July and August.

Distribution (Map 11). Colombia, probably in Tropical Wet Forest and perhaps in Tropical Premontane Rain Forest Life Zones; Ecuador, probably in Tropical Lower Montane Dry Forest Life Zone.

Material Examined. 4 males. COLOMBIA: *Cauca:* Río [San Juan de] Micay, [no date], W. Hopp (ZSBS holotype, USNM paratype); ECUADOR: *Cañar:* 20 km SE La Troncal, 2,200 feet [660 m], 29-VII–3-VIII-1984, S. J. Weller & N. L. Jacobson (BMNH, USNM, paratypes).

Discussion. Differing in male genitalia from other *Acraga* in having upper processes of sociuncus large, semicircular, with tips pointing ventrally; lower processes as small points; median lobe of gnathos paired diverging flattened plates, lateral arms long and strong, extending along vinculum almost to saccus. The species name honors the Hopp brothers, Werner for his collections of dalcerids, and Walter for his studies of them.

Acraga ferruginea Species-Group

Diagnosis. Differs from all *Acraga* in southern Brazil and adjacent areas (except *Acraga obscura*) in dark coloration (Figs. 147–149); differs from *A. obscura* in coloration and male genitalia.

Adult Male. Medium size, forewing 9–12 mm. Ground color: Brown or brownish red. Hindwing Rs not fused with Sc + R_1 in cell. Genitalia: tegumen and sociuncus fused, elongate; sociuncus with hoodlike lobes or a pair of long points; gnathos a median lobe with lateral arms; vinculum thin, elongate; valvae fused with juxta into complex surrounding aedoeagus; saccus medium length, medium width; aedoeagus long, slender.

Adult Female. Medium size, forewing 16–17 mm. Genitalia: sterigma broad and strongly sclerotized; ostium bursae wide and sclerotized; ductus bursae medium width; corpus bursae damaged in available specimens; ductus seminalis arising at first bend in ductus bursae; apophyses posteriores short, narrow, bluntly pointed; "accessory glands" ovate in lateral view.

Discussion. The association of these two poorly known species with each other is provisional.

KEY TO *FERRUGINEA* GROUP MALES

Wings brown (Fig. 149); forewing ca. 9 mm .... *brunnea*
Wings brownish rusty red (Fig. 147); forewing ca. 12 mm .... *ferruginea*

Acraga ferruginea Hopp
Figures 45, 147, 148, 176, 238;
Map 15

Acraga ferruginea Hopp, 1922: 430.—Sick, 1939: 1306.

Diagnosis. Males differ from *Acraga obscura* in longer forewing and darker coloration (especially of hindwing) and from *Acraga brunnea* in larger size and lighter, more reddish coloration.

Adult Male (Fig. 147). Forewing 12 mm. *Head:* Brownish ochreous. *Thorax:* Brownish ochreous, venter paler than dorsum. Forewing brownish rusty red. Hindwing brownish rusty red, paler along costal margin. Legs brownish ochreous. *Abdomen:* Rusty red. Genitalia as in Figure 176.

Adult Female (Fig. 148). Forewing 16–17 mm. Colored as in male, but somewhat lighter. Wings more elongate and rounded. Genitalia as in Figure 238.

Type. Holotype female (missing abdomen), ZSBS.

Type Locality. Brazil, Espírito Santo, [Alegre], Fazenda Jerusalem.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. March, June, July, September, and October.

Distribution (Map 15). Southern Brazil, in Subtropical Wet and Moist Forest Life Zones.

Material Examined. 1 male, 4 females. BRAZIL: *Espírito Santo:* [Alegre], Fazenda Jerusalem, 19-IX-1913, J. F. Zikan (ZSBS, holotype); *Rio de Janeiro:* [Itatiaia, 400 m], 9-III-1925, 27-VI-1933, 25-VII-1926, 11-X-1934, Zikan (IOC).

Discussion. Sick (1939: 1306) incorrectly cited the type locality of *Acraga ferruginea* as Pachitea, Peru.

Acraga brunnea, new species
Figures 149, 177; Map 15

Diagnosis. Distinguished from all *Acraga* by dark brown color (Fig. 149); smaller and darker than both *Acraga ferruginea* and *Acraga obscura*.

Adult Male (Fig. 149). Forewing length 9 mm. *Head:* Light brown. *Thorax:* Dorsum deep brown, venter tan. Forewings dark brown. Hindwings dark brown, lighter than forewings, especially at costal margin. Ventral wings color of dorsal hindwings. Forelegs light brown, other legs tan. *Abdomen:* Dorsum color of dorsal hindwing, venter tan. Genitalia as in Figure 177.

Adult Female. Unknown.

Type. Holotype male, MNRJ.

Type Locality. Brazil, Rio de Janeiro, Petrópolis, 600 m.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. October and December.

Distribution (Map 15). Southern Brazil, in Subtropical Moist and Subtropical Lower Montane Wet Forest Life Zones.

Material Examined. 2 males. BRAZIL: *Espírito Santo:* "Esp. St.o" [Baixo Guandú], XII-1920, [F. Hoffmann] (ZSBS, paratype); *Rio de Janeiro:* Petrópolis, 600 m, 10-X-1985, S. E. Miller & V. O. Becker (MNRJ, holotype).

Discussion. The sociuncus of this species is divided into two lobes widely separated by the anal area, each lobe having one long, pointed, slightly curved, posteriorly directed process. The gnathos is similar to that of *Acraga goes* but with two long arms fused most of their length.

The specimen from Espírito Santo, although from the J. Arp collection, must have been collected by Hoffmann at Baixo Guandú (V. O. Becker, personal communication, 1985). The species name refers to its dark brown color.

Acraga ampela Species-Group

Diagnosis. Differ from other *Acraga* in white or yellow ground color, with brown pattern (Figs. 87–92, 115, 116).

Adult Male. Medium size, forewing 11–17 mm. Ground color: White or yellow, with brown pattern. Hindwing Rs not fused with Sc + R_1 in cell. Genitalia: sociuncus and tegumen fused, elongate; sociuncus terminating in small paired dorsal lobes and/or ventral points; gnathos usually strongly developed as two rectangular tabs, with lateral arms rudimentary or of several pairs of slender short to long hooklike processes; vinculum of medium thickness; valvae reduced into complex with juxta; juxta fused into strong curved platelike complex ventral to and supporting aedoeagus; saccus medium length, medium diameter throughout length; aedoeagus long and stout, with a small patch of cornuti on the vesica.

Adult Female. Medium size, forewing 16–19 mm. Genitalia: sterigma broad, with concave sclerotized ventral lip; ostium bursae wide; ductus bursae wide and well sclerotized, then narrowing, bending and becoming membranous; corpus bursae spherical; ductus seminalis arising from bend; apophyses posteriores medium length, narrow; "accessory glands" ovate in lateral view.

KEY TO *AMPELA* GROUP MALES

(Undescribed new species near *leberna* not included; identifications of worn specimens should be confirmed by examination of genitalia.)

1. Forewing ground color yellow 2
   Forewing ground color whitish 4
2(1). Forewing with well-defined subterminal and postmedial bands (Fig. 89); hindwing white; Bolivia and western Brazil .... *boliviana*
   Forewing without well-defined subterminal and postmedial bands (Figs. 90, 91); hindwing yellow 3
3(2). Forewing with brown angled line at end of discal cell (Fig. 90); smaller, forewing 11–12 mm; Guianas and Trinidad .... *angulifera*
   Forewing without angled line at end of cell (Fig. 91); larger, 11–15 mm; Panama and northern South America .... *leberna*
4(1). Forewings mostly white with patterning of mostly well-defined dark brown lines (Fig. 87); larger, forewing 14–17 mm; Colombia, Bolivia, and Peru .... *ampela*
   Forewings suffused with brown and/or any brown lines poorly defined (Figs. 88, 115, 116); smaller, forewing 11–14 mm 5
5(4). Most of outer half of forewing (including anal angle) suffused with brown (Fig. 115); Costa Rica and Panama .... *isothea*
   Forewing brown suffusion less extensive, anal angles whitish (Figs. 88, 116) 6
6(5). Smaller, forewing 11–12 mm (Fig. 116); French Guiana .... *umbrifera*
   Larger, forewing 14 mm (Fig. 88); Peru .... *puno*

Acraga ampela (Druce), NEW COMB.
Figures 87, 178–180; Map 16

Dalcera ampela Druce, 1890: 505.—Kirby, 1892: 542.—Dyar, 1898: 231.—Hopp, 1921: 280.

Dalcera? ampela:—Dyar and Strand, 1913b: 27.—Sick, 1939: 1304.

Acraga cosmia Dognin, 1911: 63.—Dyar and Strand, 1913b: 29.—Sick, 1939: 1306. NEW SYN.

Diagnosis. Similar to *Dalcerides alba*, but larger and without brown forewing anal angle (Fig. 87); similar to *Acraga puno*, differing in more clearly defined wing pattern (Fig. 87) and male genitalia (Figs. 178–180).

Adult Male (Fig. 87). Forewing length 14–17 mm. *Head:* Light brown. *Thorax:* Brown and white. Forewings white; brown suffusion from base to middle of inner margin, then up to CuA_2 to outer margin, then subterminally to M_2, bending inward to R_4; veins CuA_2 to M_2 brown between subterminal line and margin; margin brown between CuP and M_2; brown spot at apex. Hindwings white with brown anal angle. Ventral wings white with brown anal angles. Legs: forelegs brown, others white. *Abdomen:* Dorsum brown, venter white. Genitalia as in Figures 178–180.

Adult Female. Unknown.

Types. Holotype male, BMNH (*ampela*); holotype male, USNM 29811 (*cosmia*).

Type Localities. "Bolivia" (*ampela*); Colombia, Valle del Cauca, near Cali, San Antonio, 2,000 m (*cosmia*).

Host. Unknown.

Immature Stages. Unknown.

Flight Period. Year-round.

Distribution (Map 16). Colombia, Peru, and Bolivia, in Tropical Wet, Tropical Moist, Tropical Premontane Wet, and Tropical Lower Montane Wet Forest Life Zones.

Material Examined. 23 males. BOLIVIA: [no further data], Buckley (BMNH, holotype of *ampela*); COLOMBIA: *Chocó:* La Selva, San Juan, 4,600 feet [1,400 m], IX-1909 (BMNH); *Cundinamarca:* Pacho, 2,200 m, Fassl (USNM); *Guainía:* Ob. [=Upper] Río Negro, 800 m, [no date], A. H. Fassl (BMNH); *Valle del Cauca:* San Antonio, 2,000 m, IV-1909, Fassl (USNM, holotype of *cosmia*); PERU: *Puno:* La Oroya, Río Inambari, 3,000 feet [900 m], V-1905, IX-1904, dry season, G. R. Ockenden (BMNH, ZSBS), I, III, XI–XII-1905, I-1906, wet season, Ockenden (BMNH); Río Huacamayo, 3,100 feet [900 m], VI-1904, dry season, Ockenden (BMNH); Santo Domingo, 6,000 feet [1,800 m], XI-1904, Ockenden (BMNH); Tincuri, 3,400 feet [1,000 m], I-1905, wet season, VIII-1904, dry season, Ockenden (BMNH); *San Martín:* Pumayacu, [no further data] (USNM).

Discussion. The male genitalia of this species varies somewhat in the shapes of the sociuncus lobes, diaphragma ridges, and complex ventral to the aedoeagus (e.g., Figs. 178–180).

Acraga puno, new species
Figures 88, 184; Map 17;
Color Plate, Figure 19

Diagnosis. Similar to *Acraga ampela*, but wing pattern less clearly defined (Fig. 88); similar to *A. umbrifera*, but larger and wing pattern is more clearly defined.

Adult Male (Fig. 88). Forewing length 14 mm. Very similar to *Acraga ampela*, differing in forewing pattern, which is lighter brown (reddish?), in lines that are not as fine; brown patch along hindwing anal angle longer, extending forward almost to M_2; wing angles (especially hindwing) more rounded; lateral processes of gnathos well developed; and hooklike processes dorsolateral of aedoeagus. Genitalia as in Figure 184.

Adult Female. Unknown.

Type. Holotype male, BMNH.

Type Locality. Peru, Puno, La Union, 600 m.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. March and November.

Distribution (Map 17). Southern Peru, in Tropical Moist and Tropical Premontane Wet Forest Life Zones.

Material Examined. 2 males. PERU: *Puno:* La Oroya, Río Inambari, 3,100 feet [900 m], III-1905, G. R. Ockenden, wet season (USNM, paratype); La Union, Río Huacamayo, 2,000 feet [600 m], XI-1904, Ockenden, wet season (BMNH, holotype).

Discussion. The species name is a noun in apposition referring to the type locality. I have seen one female (forewing 16 mm) that might be this species (the wing pattern is similar but more diffuse, and there is no associated male) from BRAZIL: *Amazonas:* "Iucaby" [Iucai], Rio Negro, 12-VIII-1927, J. F. Zikan (IOC).

Acraga boliviana Hopp, NEW STATUS
Figures 89, 181; Map 17

Acraga cosmia var. *boliviana* Hopp, 1921: 280.—Sick, 1939: 1306.

Diagnosis. Differs from *Acraga ampela* and *A. puno* in coloration and proportions of wings (Fig. 89), and male gnathos (especially lack of development of hooklike lateral arms) (Fig. 181).

Adult Male (Fig. 89). Forewing length 14 mm. *Head:* Yellowish (worn). *Thorax:* Yellowish (worn). Forewings pale yellow with light brown subterminal (inner margin to R_5) and postmedial (inner margin to R_4) lines; veins CuA_2 to M_2 brown between subterminal line and margin; brown spot near base of inner margin. Hindwings white, margin yellowish brown around anal angle. Ventral wings white. *Abdomen:* Dorsum yellowish, venter whitish. Genitalia as in Figure 181.

Adult Female. Unknown.

Type. Holotype male, lost.

Type Locality. Bolivia, La Paz, Río Songo [Zongo], 1,200 m, Garlepp.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. July.

Distribution (Map 17). Bolivia and western Brazil, in Subtropical Moist Forest Life Zone.

Material Examined. 1 male. BRAZIL: *Amazonas:* Fonte Boa, VII-1906, S. M. Klages (BMNH).

Discussion. The holotype of *Acraga boliviana* should be at ZMHB but is not (H. J. Hannemann, personal communication, 1984). A single male (BMNH) seems to match the superficial original description, but it might not be conspecific with the lost holotype. My concept of the species is based on the BMNH male.

Acraga angulifera Schaus
Figures 90, 183; Map 17

Acraga angulifera Schaus, 1905: 332–333.—Dyar, 1910c: 117.—Dyar and Strand, 1913b: 28.—Sick, 1939: 1305.

Diagnosis. Similar to *Acraga leberna*, readily distinguished by wing coloration (especially the angled line at the end of the cell; Fig. 90), more delicate build, and male genitalia (Fig. 183).

Adult Male (Fig. 90). Forewing length 11–12 mm. *Head:* Pale yellow. *Thorax:* Pale yellow. Forewings pale yellow; dark brown inwardly curved line along end of cell; subterminal brownish shade from R_5, curved inward between CuA_2 and CuP, then out to anal angle. Hindwings pale yellow; whitish toward costal margin; brown at anal angle. Ventral wings: forewing pale yellow, hindwing white with brown anal angle. Legs pale yellow. *Abdomen:* Pale yellow. Genitalia as in Figure 183.

Adult Female. Unknown.

Type. Lectotype male, and paralectotype male, here designated, USNM 8909.

Type Locality. French Guiana, Maroni River, Saint-Jean.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. Year-round.

Distribution (Map 17). Trinidad, Venezuela, Surinam, and French Guiana, in Tropical Moist Forest Life Zone.

Material Examined. 18 males. FRENCH GUIANA: Mana River, VI-1917 (CMNH); Pied Saut, Oyapock River, III-1918, XII-1917, S. M. Klages (CMNH); Saint-Jean, VII-1904, W. Schaus (USNM, lectotype and paralectotype), [no date] (BMNH); Saint-Laurent, IX-1904, Schaus (USNM); [no further data], C. Bar (ZSBS); SURINAM: Aroewarwa Creek, Maroewym Valley, IV-1905, Klages (BMNH); TRINIDAD: Arima Valley, 19–21-I-1961, B. Heineman, 10–22-II-1964, Rozen & Wygodzinsky, III-1956, N.Y. Zool. Soc. (all AMNH); Morne Bleu, Textel Installation, 9-XI-1978, M. J. W. Cock (MJWC); VENEZUELA: *Bolívar:* Río Surukum, Carretera Santa Elena Icabaru, 850 m, 19–31-I-1985, F. Fernandez Y. *et al.* (UCV).

Acraga isothea Dognin
Figures 115, 182; Map 16

Acraga isothea Dognin, 1914: 100–101.—Sick, 1939: 1306, pl. 168f.

Diagnosis. Similar to *Acraga umbrifera*, distinguished by brown forewing anal angles (Fig. 115).

Adult Male (Fig. 115). Forewing length 12–14 mm. *Head:* Pale reddish brown. *Thorax:* Dorsum reddish brown with patches of white; venter white. Forewings white; reddish brown suffusion over inner margin (except near base), outer margin from anal angle to M_1 (except white crescents at margins between veins from CuA_2 to M_1), and postmedial area; reddish brown spot at apex. Hindwings white with reddish brown anal angle. Ventral wings white with hindwing anal angle reddish brown. Legs: forelegs reddish brown, others white. *Abdomen:* Dorsum reddish brown, venter whitish. Genitalia as in Figure 182.

Adult Female. Unknown.

Type. Lectotype male, and paralectotype male, here designated, USNM 29810.

Type Locality. Panama, Lino, 800 m.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. July.

Distribution (Map 16). Costa Rica and Panama, in Tropical Premontane Wet and Rain Forest Life Zones.

Material Examined. 5 males. COSTA RICA: Braulio Carrillo, 1,100 m, VII-1981, V. O. Becker (VOB); "Costa Rica" [no further data] (ZSBS); PANAMA: Lino, 800 m, [no date], A. H. Fassl (USNM, types; ZSBS).

Acraga leberna (Druce)
Figures 91, 92, 186, 247; Map 18; Color Plate, Figure 20

Dalcera leberna Druce, 1890: 505.—Kirby, 1892: 542.—Dyar, 1898: 231.

Acraga leberna:—Dyar, 1910c: 117.—Dyar and Strand, 1913b: 28.—Hopp, 1921: 280.—Sick, 1939: 1305.

Acraga arcifera Dyar, 1910c: 117.—Dyar and Strand, 1913b: 29.—Sick, 1939: 1306. NEW SYN.

Diagnosis. Similar to *Acraga angulifera*, but larger and without angled line at end of forewing discal cell (Fig. 91).

Adult Male (Fig. 91). Forewing length 11–15 mm. *Head:* Pale yellow. *Thorax:* Dorsum pale yellow with reddish brown stripe on each side behind head; venter whitish. Forewings pale yellow with wide submarginal reddish brown band, faint from R_5 to CuA_1, darker and curved inward to inner margin near anal angle; inner margin dark basally; discal spot small; outer margin darkened, especially where submarginal band is close to, sometimes connected with, outer margin. Hindwings pale yellow with reddish brown anal angle. Ventral wings yellowish white with hindwing anal angle brown. Legs yellowish white with touches of reddish brown on foreleg. *Abdomen:* Dorsum yellow, venter whitish. Genitalia as in Figure 186.

Adult Female (Fig. 92). Forewing length 16–19 mm. Colored as in male. Genitalia as in Figure 247.

Types. Holotype female, BMNH (*leberna*); lectotype male, and paralectotype male, here designated, USNM 13057 (*arcifera*).

Type Localities. Ecuador, Pastaza, Sarayacu (Brown [1941: 849] cautions that all Buckley's material was not collected in the immediate vicinity of Sarayacu and some may have come from as far west as the Andean foothills) (*leberna*); French Guiana, Maroni River, Saint-Jean (*arcifera*).

Host. Unknown.

Immature Stages. Unknown.

Flight Period. Year-round.

Distribution (Map 18). Panama, Colombia, Venezuela, Guiana, Surinam, French Guiana, Ecuador, northern Brazil (Amazon Basin), Peru, and Bolivia, in Tropical Wet, Tropical Moist, and Tropical Premontane Wet Forest Life Zones.

Material Examined. 112 males and 8 females. BOLIVIA: *Cochabamba:* Chaparé-Gebiet oberer Río Chipiriri, 400 m, 27-X-1953, W. Forster (ZSBS); BRAZIL: *Amazonas:* Amazon between Tefé and Tonantins, XI-1921 (USNM); Fonte Boa, V, VII–IX-1906, S. M. Klages (BMNH); Monte Cristo, A. H. Fassl (USNM); Reserva Ducke, Km 26 Manaus-Itacoatiara Highway, 21-IV-1972, E. G. Munroe (CNC); Rio Madeira, VII–VIII-[no year], Fassl (USNM); Santo Antônio de Javari, VI-1907, Klages (BMNH); São Paulo de Olivença, VIII, XI–XII-[no year], Fassl (USNM, ZSBS), I-1933, S. Waehner (BMNH), XII-1931–I-1932, F. Wucherpfennig (BMNH); *Pará:* Belém, 20 m, I-1984, V. O. Becker (VOB); Marabá, 50 m, 9-I-1977, Becker (VOB); Pará [=Belém], [no date], A. M. Moss (BMNH); Ponte Nova, Rio Xingu (USNM); Taperinha, 11–20-VI-1927, Zerny (NHMV); Utinga, Belém, 10-III-1964, O. H. H. Mielke (MNRJ); COLOMBIA: *Guainía:* Ob. [=Upper] Río Negro, 800 m, [no date], Fassl (BMNH); *Meta:* Villavicencio, 400 m, [no date], Fassl (BMNH); ECUADOR: "Sarayacu" [see preceding Type Localities] (BMNH, holotype of *leberna*); FRENCH GUIANA: Nouveau Chantier, [no date] (USNM), VI–VII-[no year] (BMNH); Pied Saut, Oyapock River, III-1918, XII-1917, Klages (CMNH); Saint-Jean, III-1904 (lectotype of *arcifera*), IV-1904 (paralectotype of *arcifera*), W. Schaus (USNM), VII–VIII-1904 (BMNH); Saint-Laurent, II, VI, X, XII-[no year] (BMNH, USNM); GUYANA: Kartabu, 1-IV-1922, 18-VII-1922 (AMNH, USNM); Kartabu Point, secondary forest, 24-XII-1983, W. E. Steiner (USNM); Malali, 28-I-1913 [?], H. S. Parish (CU); Potaro, V-1908, Klages (BMNH); Rockstone, 25-VI-1934, A. S. Pinkus (AMNH); Tumatumari, Potaro River, XII-1907, Klages (BMNH), 28–29-VI-1927, [W. T. M. Forbes] (CU); PANAMA: Barro Colorado Island, 11-III-1936, W. Gertsch *et al.* (AMNH); PERU: *Loreto:* [Contamana], Middle Río Ucayali, 12-II-1928, H. Bassler F6039 (AMNH); *Puno:* La Union, Río Huacamayo, 2,000 feet [600 m], XI-1904, wet season, G. R. Ockenden (BMNH); San Gaban, 2,500 feet [750 m], III–IV-1913, [H. & C. Watkins] (BMNH); Yahuarmayo, 1,200 feet [350 m], III-1911, V–VII-1912, Watkins (BMNH); *San Martín:* Jepelacio (USNM); SURINAM: Aroewarwa Creek, Maroewym Valley, IV, VI, VII-1905, Klages (BMNH); VENEZUELA: *Amazonas:* San Carlos de Río Negro, 65 m, 4–14-III-1984, 21–23-X-1984, 125 m, 19–31-VIII-1976 (UCV); *Bolívar:* El Bochinche Res. Forestal Imataca, 200 m, 6–13-XII-1974 (UCV); Río Grande Research Station, 26 km E El Palmar, 700 feet [200 m], 24–25-III-1978, J. B. Heppner (USNM).

Discussion. Worn individuals, such as Druce's type, appear whitish, due to removal of yellow scales.

I have seen two very worn males, which appear to be a new species near *Acraga leberna*. The wings are whitish with a brown pattern probably similar to that of *A. leberna*; the forewing length 12–13 mm; the genitalia are similar, differing most in shape and thickness of "gnathos" processes (Fig. 187). Both specimens are from Uberaba, Minas Gerais, Brazil, [no date], purchased from E. LeMoult by W. Hopp (USNM, ZSBS). The area around Uberaba is Subtropical Moist Forest.

Acraga umbrifera (Schaus)
Figures 116, 185; Map 16

Epipinconia umbrifera Schaus, 1905: 333.
Acraga umbrifera:—Dyar, 1910c: 117.—Dyar and Strand, 1913b: 29.—Sick, 1939: 1306.

Diagnosis. Both wing pattern and male genitalia very similar to *Acraga leberna*, but easily distinguished by white not yellow ground color; wing pattern similar to *A. isothea*, distinguished by white not brown forewing anal angle (Fig. 116).

Adult Male (Fig. 116). Forewing length 11–12 mm. *Head:* Light brown. *Thorax:* Dorsum light brown mottled with white; venter white. Forewings white with broad light brown postmedian shade, extended to fringe between M_1 and M_3; inner margin shaded; discal spot indistinct. Hindwings white with pale brown at anal angle. Ventral wings white. Legs white with light brown suffusion. *Abdomen:* Dorsum light brown, venter whitish. Genitalia as in Figure 185.

Adult Female. Unknown.

Type. Holotype male, USNM 8910.

Type Locality. French Guiana, Maroni River, Saint-Jean.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. March and June.

Distribution (Map 16). French Guiana, in Tropical Moist Forest Life Zone.

Material Examined. 3 males. FRENCH GUIANA: Saint-Jean, VI-1904, W. Schaus (holotype), III-[no year] (USNM); Saint-Laurent, [no date] (USNM).

Acraga ochracea Species-Group

Diagnosis. Differs from other orange *Acraga* in male genitalia, especially sociuncus and complex supporting aedoeagus (Figs. 188–191).

Adult Male. Medium size, forewing 9–14 mm. Ground color: orange, without maculation. Hindwing Rs not fused with Sc + R_1 in cell. Genitalia: tegumen elongate; sociuncus elongate, wider and higher than tegumen, sides developed posteriorly as blunt lateral lobes; uncus pair of hook-like down-curved processes in middle of posterior surface of sociuncus; gnathos median lobe split into upper and lower arms or fused, triangular in cross section, with or without a split in lower portion (gnathos without lateral arms); vinculum thin, elongate; valvae reduced into complex with juxta; juxta fused with valvae into complex surrounding and supporting aedoeagus, best developed ventrally, terminating ventrally in down-curved strongly sclerotized spoutlike process; saccus of medium length and thickness; aedoeagus long, stout, curved dorsally at ends, external end sclerotized, pointed, and covered with fine hairs (vesica may also have a patch of setae).

Adult Female. Medium size, 15–17 mm. Genitalia: sterigma broad with rounded tab on each side; ostium bursae broad; ductus bursae wide to first bend, narrowing and recurved again to corpus bursae; corpus bursae ovate; ductus seminalis arising between bends; apophyses posteriores long, wide at base, narrowing to apex; "accessory glands" ovate in lateral view.

Discussion. I recognize four closely related species in this group, from southern Brazil, Uruguay, Paraguay, and northern Argentina. *Acraga ochracea* Walker was one of the first dalcerids to be named and has been frequently misidentified; a neotype is designated here to fix its identity. Orfila (1961) described the genus and species *Dalargentina sexquicentenaria,* which is here placed in the *Acraga ochracea* group. I describe two new species similar to *Acraga sexquicentenaria.*

Orfila (1961) separated *Dalargentina sexquicentenaria* from *Acraga ochracea* as different genera, largely on the basis of the branching of the forewing radial veins. However, the species are closely related, based on the very similar male genitalia. The venation character is quite variable, and I have seen two extreme examples: *A. parana,* in which R_{2+3} and R_{4+5} are stalked on the right side, but not on the left side (BMNH, slide 85-10); and *A. ochracea,* in which R_{2+3} does not split off until just before R_4 and R_5 fork, almost forming a triple split (VOB).

KEY TO *OCHRACEA* GROUP MALES

1. Forewing angles, especially apex, rounded (as in most *Acraga*) (Fig. 93); usually with dense, long hairs covering dorsal portion of genitalia; gnathos strongly bifid, with short upper arm well separated from longer lower arm (Fig. 188) .... *ochracea*

Forewing angles, especially apex, more sharply angled (Figs. 95, 97, 98); with short *or* long hairs covering genitalia; gnathos somewhat triangular in lateral view, if split then no wide separation of parts (Figs. 189–191) 2

2(1). Forewing orange brown; gnathos split; pair of points on dorsal surface of sociuncus at articulation with tegumen (Fig. 189); with tuft of long hairs covering genitalia .... *victoria*

Forewing orange; gnathos split *or* solid; no dorsal pair of points at base of sociuncus (Figs. 190, 191); with only short hairs covering genitalia 3

3(2). Gnathos split; paired posterior spines on uncus of medium length and thickness (Fig. 190); forewing orange slightly darker and duller .... *sexquicentenaria*

Gnathos solid; paired posterior spines on uncus long and thick (Fig. 191); forewing orange slightly lighter and brighter ... *parana*

Acraga ochracea (Walker)
Figures 93, 94, 188, 245; Map 19

Dalcera ochracea Walker, 1855b: 1107.—Kirby, 1892: 542.

Acraga ochracea:—Dyar, 1898: 232; 1910c: 116.—Dyar and Strand, 1913b: 28.—Hopp, 1921: 279.—Sick, 1939: 1305.—Orfila, 1961: 256–257, figs. 2, 6, pl. 1, figs. 3, 4.

Diagnosis. Differs from related species in male genitalia: usually with dense, long hairs covering dorsal portion of genitalia; gnathos strongly bifid, with short upper arm well separated from longer lower arm (Fig. 188).

Adult Male (Fig. 93). Forewing length 9–13 mm. Entirely orange; dorsal forewing darker than hindwing. *Abdomen:* Orange, usually with dense tuft of long hairs extending over apex of abdomen. Genitalia as in Figure 188.

Adult Female (Fig. 94). Forewing length 16–17 mm. Colored as in male, wings more elongate and rounded. Genitalia as in Figure 245.

Type. Neotype male, here designated, BMNH.

Type Locality. Brazil, Rio de Janeiro, Corcovado Forest (based on neotype).

Host. Unknown.

Immature Stages. Unknown.

Flight Period. Year-round.

Distribution (Map 19). Southern Brazil, Paraguay, and northern Argentina. Recorded from Tropical Premontane Moist, Subtropical Wet, Subtropical Moist, Subtropical Dry, and Warm Temperate Moist Forest Life Zones.

Material Examined. 105 males and 3 females. ARGENTINA: *Misiones:* Iguazú, II-1934, F. Bourquin (BMNH), 30-I–13-III-1945, Hayward *et al.* (ZMUC); BRAZIL: *Distrito Federal:* Planaltina, 1,000 m, III-1976, III-1977, VII-1978, V. O. Becker (CPAC, VOB); *Espírito Santo:* "Espírito Santo," [no date], F. Johnson (USNM); *Mato Grosso do Sul:* Rio Brilhante, 25-I-1971, 23–27-X-1970, Becker (VOB); *Minas Gerais:* Sete Lagoas, 720 m, 12-III-1974, Becker (VOB); Viçosa, [no date], E. J. Hambleton (CU); *Paraná:* Banhado, 800 m, 12-II-1973, Munroes (CNC); Castro, [no date] (USNM); Castro, 950 m, [no date], E. D. Jones (BMNH); Foz do Iguaçu, 28-I-1971, Laroca & Jansen (VOB); Guaraqueçaba, 9-XII-1970, Becker (VOB); Iguaçu, 20–30-X-1921, X–XII-1922 (BMNH); *Rio de Janeiro:* "Campo Bello" [Itatiaia, 400 m], III-1927, IV-1931, XI, XII-1926, J. F. Zikan (ZSBS); Corcovado Forest, 1958, H. B. D. Kettlewell (BMNH, neotype; USNM); Imbarié, 50 m, 5-I-1956, H. Ebert (ZSBS); [Itatiaia, 400 m], 4-I-1927, 18-III-1928, 1-IV-1930, 17-V-1925, 28-VI-1929, 14-IX-1926, 4-XI-1929, Zikan (IOC); Itatiaia, 800–1,200 m, 31-III-1965, Ebert (ZSBS); 10 km SW Maricá, 5 m, 12–13-I-1985, V. O. Becker (VOB), VI-1985, R. F. Monteiro (USNM), 11–12-X-1985, S. E. Miller & Becker (USNM); Petrópolis, 23-XI-1913, J. G. Foetterle (NHMV); "Prov. Rio" [Itatiaia, 400 m], 6-XII-1928, Zikan (USNM); Rio de Janeiro, 7-V-1952, Ebert (ZSBS), XI-[no year] (CMNH); *Rio Grande do Sul:* Guaraní, 11-VI-1932, C. Biezanko (CU); Rio Grande do Sul, [no date] (ZSBS); *Santa Catarina:* Brusque, 100 m, 8-VII-1970, 13-VII-1966, 28-XII-1969, I-1983, Becker (VOB); Hansa Humbolt [=Corupá], [no date] (USNM); Joinvile, [no date] (USNM), 10 m, 6-XII-1969, Becker (VOB); Nova Brémen, Rio Laeiss, III-1936, F. H. Hoffmann (BMNH); Nova Teutonia, V-1938, 7-X-1939, F. Plaumann (CMNH, USNM); Santa Catarina, [no date], Hoffmann (USNM), 1921, v. Wernicke (ZSBS), [no date] (BMNH); *São Paulo:* Boracéia, Salesópolis, 800 m, 21–25-X-1963, Oliveira & Wygodzinsky (AMNH); PARAGUAY: *Guairá:* Villarrica, 21-II-1923, J. Schade (BMNH).

Discussion. Walker described *Acraga ochracea* from (apparently) one male from "Rio Janeiro. In Mr. Fry's collection" (Walker, 1855b: 1107). I have been unable to locate the type, and it has apparently been lost since at least Hampson's time. Apparently many of the species described by Walker as being in the Fry collection "were in such condition that their acceptance was refused" when they were returned to Fry (Dyar, 1905b: 359; also unpublished notes by Hampson in BMNH). Some type specimens from the Fry collection are now at UMO, but *A. ochracea* is not among them. Therefore, I am designating a neotype that is in keeping with the established use of *A. ochracea* (especially Orfila, 1961). A BMNH specimen has been selected as neotype because most other Walker types are at BMNH. A specimen from the type locality is also deposited in USNM.

Throughout most of its range, *Acraga ochracea* has two forms of the male genitalia: (1) valvae complex tip thin, pointed, and down-turned, and the paired posterior spines of the uncus short and stout (Fig. 188); and (2) valvae complex tip stout and blunt, and the uncus spines longer and more slender (Fig. 188, inset). It is possible that these are sibling species, but without information on females, immatures, and ecology, I prefer to recognize them as one species. The neotype has the first genitalic form.

The name *Acraga ochracea* has been frequently misidentified. The Costa Rica records of Druce (1887: 213) and Pittier and Biolley (1897: 29) apply to *Dalcerides* new species. The Mexico record of Druce (1898: 441) is *Dalcerides ingenita.* The Trinidad records of Kaye and Lamont (1927: 121) and Kirkpatrick (1954: 68) and the Colombia record of Genty *et al.* (1978: 354) apply to the *Acraga infusa* complex. I have seen no voucher specimens from the Venezuela records of Ballou (1945: 60, 104), Colombia record of Figueroa Potes (1977: 5), and the Ecuador records of Campos (1921: 54; 1931: 139). *Acraga ochracea* "race" *conda* (Dyar, 1910c: 116) is not related to *A. ochracea* but belongs in the *A. infusa* complex.

Acraga victoria, new species

Figures 97, 189; Map 20

Diagnosis. Appears somewhat intermediate between *Acraga ochracea* and *A. sexquicentenaria*, distinguished from both by darker forewing color and gnathos shape (Fig. 189).

Adult Male (Fig. 97). Forewing length 11.5–12 mm. Entirely dull orange, with dorsal forewing orange-brown (darker than in any other *ochracea* group species). Genitalia as in Figure 189.

Adult Female. Unknown.

Type. Holotype male, MNRJ.

Type Locality. Brazil, Santa Catarina, São Joaquim, 1,400 m.

Host. Unknown.

Immatures. Unknown.

Flight Period. January.

Distribution (Map 20). Southern Brazil (known only from the type locality), in Warm Temperate Wet Forest Life Zone.

Material Examined. 5 males from type locality, 22–24-I-1983, V. O. Becker (holotype and paratypes, MNRJ, VOB, USNM, BMNH).

Discussion. The species name honors Vitor O. Becker, who collected this and many other new and interesting species of Dalceridae.

Acraga sexquicentenaria (Orfila), NEW COMB.

Figures 95, 96, 190, 244; Map 20

Acraga sp. n. Biezanko, 1961a: 3.

Dalargentina sexquicentenaria Orfila, 1961: 254–255, figs. 1, 5, pl. 1, figs. 1, 2.—Biezanko *et al.*, 1966: 5; 1974: 124; 1978: 58.

Diagnosis. Differs from related species in male genitalia; gnathos split *and* paired posterior spines on uncus of medium length and thickness (Fig. 190).

Adult Male (Fig. 95). Forewing length 9–13 (usually 11–12) mm. Entirely orange. Dorsal forewing slightly darker than hindwing; slightly darker than forewing of *Acraga parana*, lighter than forewing of *A. victoria*. Genitalia as in Figure 190.

Adult Female (Fig. 96). Forewing length 15 mm. Colored as in male. Genitalia as in Figure 244.

Type. Holotype male, lost.

Type Locality. Argentina, Misiones, Parque Nacional Iguazú.

Host. Citrus sinensis (Linnaeus) Osbeck (Rutaceae) (Biezanko *et al.*, 1974: 124).

Immature Stages. Unknown.

Flight Period. January to May, August, October, and November.

Distribution (Map 20). Southern Brazil, northern Uruguay (Biezanko *et al.*, 1966), and northern Argentina (Orfila, 1961), in Subtropical Moist, Subtropical Lower Montane Moist, and Warm Temperate Moist Forest Life Zones.

Material Examined. 26 males and 2 females. BRAZIL: *Minas Gerais:* Fazenda dos Campos, [1,500 m], 16-I-1918, J. F. Zikan (IOC, 1 male); "Passa Quatro," 1-II-1922, Zikan (ZSBS, 1 male); *Rio Grande do Sul:* Hamburgo Velho, [no date], C. Ertl (ZSBS, 1 male only); Pelotas, various dates 1951–1964, C. Biezanko (AMNH, BMNH, CMNH, CU, MCZ, USNM, ZSBS), 21-V-1939, R. Figueiredo (CU).

Discussion. As in the case of *Dalcera haywardi* Orfila, inquiries to MBR, MLP, IML, and INTA failed to locate any type material of *Acraga sexquicentenaria*. However, the original description is adequate to identify the species, which is almost entirely known from specimens collected by Biezanko at Pelotas. The year on the specimen in ZSBS from "Passa Quatro" is illegible: if it is 1921, then it was collected at Fazenda dos Campos; if 1922, then from Passa Quatro at 950 m.

Acraga parana, new species

Figures 98, 191; Map 20

Diagnosis. Very similar to *Acraga sexquicentenaria*, differing in lighter and brighter orange forewings, solid (not bifid) gnathos, and stout paired posterior spines on the uncus (Fig. 191).

Adult Male (Fig. 98). Forewing length 11.5–14 mm. Entirely orange. Dorsal forewing slightly darker than hindwing; slightly lighter and "brighter" than forewing of *Acraga sexquicentenaria*. Genitalia as in Figure 191.

Adult Female. Unknown.

Type. Holotype male, MNRJ.

Type Locality. Brazil, Paraná, Curitiba, 920 m.

Host. Unknown.

Immatures. Unknown.

Flight Period. April to June, September, and November to February.

Distribution (Map 20). Southern Brazil and Paraguay, in Subtropical Wet, Subtropical Moist, and Warm Temperate Moist Forest Life Zones.

Material Examined. 18 males (all paratypes). BRAZIL: *Paraná:* Banhado, Quatro Barras, 800 m, 27-XI-1971, 28-XI-1970, V. O. Becker (VOB, USNM); Curitiba, 920 m, 6–14-I-1975, 28-XII-1974 (holotype), Becker (MNRJ, VOB, USNM); *Santa Catarina:* Jaraguá do Sul, IX-1932, F. H. Hoffmann (BMNH, USNM); Santa Catarina, 4-IV-1922, E. D. Jones (USNM); *São Paulo:* Alto da Serra, IV-1936, V-1927, V-1929, R. Spitz (BMNH, USNM); Ipiranga, V-1924, VI-1934, Spitz (BMNH); São Paulo, 2,300 feet [700 m], [no date], Jones (BMNH); PARAGUAY: *Alto Paraná:* Bella Vista, II-1938, Gassner (NHMV).

Discussion. The species name is a noun in apposition referring to the type locality.

Dalcerides Neumoegen and Dyar

Dalcerides Neumoegen and Dyar, 1893a: 121; 1893b: 98; 1894: 109, 111.—Dyar, 1895a: 14; 1898: 232; 1910c: 119.—Dyar and Strand, 1913b: 29.—Hopp, 1921: 282.—Sick, 1939: 1307.—D'Almeida, 1945: 194.—Fletcher and Nye, 1982: 48.—Davis, 1983: 67. Type species: *Artaxa ingenita* Hy. Edwards, 1882, by original designation.

Acragopsis Dyar, 1905: 176–177; 1910c: 120.—Dyar and Strand, 1913b: 30.—Hopp, 1921: 281.—Sick, 1939: 1308.—Forbes, 1942: 395.—D'Almeida, 1945: 193.—Fletcher and Nye, 1982: 3. Type species: *Acragopsis flavetta* Schaus, 1905, by original designation. NEW SYN.

Diagnosis. Forewing accessory cell and upper half of discal cell retracted (distal ends of cells not in line) (e.g., Figs. 43, 44); gnathos comblike (Figs. 192–197, 199–203).

Adult Male. Small to medium size, forewing 6–13 mm. Ground color: yellow, orange, or white, with maculation. Forewing: accessory cell present; accessory cell and especially upper half of discal cell retracted (i.e., distal ends of cells not in line); R_{2+3} and R_{4+5} arising from accessory cell or short-stalked; $R_2 + R_3$ very long-stalked or fused; $R_4 + R_3$ short-stalked; retinaculum present. Hindwing: Rs fused with, or free but running very close to, $Sc + R_1$ in cell; frenulum present. Genitalia: tegumen and sociuncus fused complex; sociuncus developed as two lobes with no processes; socii not distinct, posterior lobes of sociuncus hairy; gnathos paired comblike sclerotized structures; vinculum elongate and narrow; valvae tab- or hooklike, fused into complex with juxta and vinculum; juxta not distinct; saccus medium to long in length and slender to medium in thickness; aedoeagus long and slender, external end sometimes pointed, bent, almost hooklike, and/or with minute spine near apex.

Adult Female. Medium size, forewing 8–16 mm. Genitalia: sterigma medium width; ostium bursae narrow to medium width; ductus bursae long, narrow to medium width, straight or with bends; corpus bursae ovate; ductus seminalis arising about middle of ductus bursae; apophyses posteriores medium to wide, short to medium length, narrowing to apex; "accessory glands" ovate in lateral view.

Discussion. As constituted here, *Dalcerides* includes several common small yellow species and the only North American species of Dalceridae. The smaller species placed here have traditionally been placed in *Acragopsis*, the larger species in *Dalcerides*. Although the two groups of species differ somewhat in size, fusion of the hindwing Rs with $Sc + R_{1,}$ and male genitalia (development of uncus, gnathos, valvae complex, and aedoeagus tip), I do not consider these differences sufficient for generic status. *Zikanyrops* probably should be placed here also, but I do not want to synonymize it without seeing the male genitalia.

Dalcerides nana does not fit the preceding description because it has a large median point on the sociuncus and usually has the venation of *Acraga*. I tentatively place it here on the basis of other male genital structures.

The gnathos appears to be composed of both median processes and lateral arms; the median processes being comblike sclerotized structures connected by membrane, and the lateral arms also being comblike, either almost continuous with median processes or free with larger "teeth." As discussed previously, an alternative interpretation of the fusion of valvae was presented by Eyer (1924: 318).

KEY TO MALE *DALCERIDES*

(Male of *bicolor* unknown; new species from Costa Rica not included.)

1. Larger, forewing length ≥9 mm; hindwing Rs free, running close to, but not fused with, Sc + R_1 (e.g., Fig. 43) 1
Smaller, forewing length ≤9 mm; hindwing Rs fused with Sc + R_1 in cell (Fig. 44) 4
2(1). Wings entirely orange (or shade thereof) (Fig. 111); Arizona and Mexico .... *ingenita*
Wings not entirely orange 3
3(2). Forewing orange red, hindwing fuscous (Fig. 110); Costa Rica .... *bicolor*
Wings white with maculation (Fig. 113); Central America .... *alba*
4(1). Forewing entirely yellow or orange, without maculation darker than ground color 7
Forewing not entirely yellow or orange 5
5(4). Forewing dominated by dark shade or spot that is surrounded or bordered with yellow 6
Forewing whitish with light brown pattern (Fig. 107) .... *sofia*
6(5). Forewing with yellow limited to base and inner margin (Fig. 102) .... *dulciola*
Borders around all or most of forewing shading into yellow (Fig. 105) .... *mesoa*
7(4). Forewing with pale line along end of discal cell (Fig. 109); sociuncus with strong median point (Fig. 202) .... *nana*
Forewing entirely yellow or orange; sociuncus without median point 8
8(7). Forewing ground color yellow-orange *without* silky luster and appearance of transverse bands 10
Forewing ground color yellow, yellow-orange, or golden yellow *with* silky luster and appearance of transverse bands 9
9(8). Forewing golden yellow; Mexico and Guatemala .... *chirma*
Forewing pale golden yellow; Brazil .... *radians*
10(8). Valvae developed in long hooks (Fig. 192); northern South America .... *flavetta*
Valvae weakly developed (Fig. 193); Costa Rica and Ecuador .... *rebella*

Dalcerides flavetta Species-Group

See discussion under *Dalcerides*, earlier.

Dalcerides flavetta (Schaus), NEW COMB.
Figures 44, 99, 100, 192, 249; Map 21

Acragopsis flavetta Schaus, 1905: 332.—Dyar, 1910c: 120.—Dyar and Strand, 1913b: 30.—Hopp, 1921: 281.
Acragopsis flavetta Dyar [sic]:—Sick, 1939: 1308.

Diagnosis. Small yellow-orange species, wings lacking silky luster, distinguished from *Dalcerides rebella* by valvae developed as long hooks (Fig. 192).

Adult Male (Fig. 99). Forewing length 7–8.5 mm. Entirely yellow-orange, with forewing veins and dorsal body slightly darker than the rest. Genitalia as in Figure 192.

Adult Female (Fig. 100). Forewing length 10 mm. Colored as in male. Genitalia as in Figure 249.

Type. Holotype male, USNM 8908.

Type Locality. French Guiana, Maroni River, Saint-Jean.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. Year-round.

Distribution (Map 21). Venezuela, Guyana, Surinam, French Guiana, Colombia, Ecuador, Peru, Bolivia, and northern Brazil. Recorded from Tropical Wet, Tropical Moist, Tropical Premontane Wet, Tropical Premontane Moist, Subtropical Moist Forest, Tropical Dry Forest transitional to Subtropical, Warm Temperate Dry transitional to Moist (Corumbá, Brazil), and maybe Tropical Lower Montane Moist Forest Life Zones.

Material Examined. 196 males and 3 females. BOLIVIA: *Cochabamba:* Chaparé-Gebiet Oberer Río Chipiriri, 400 m, 6-IX–27-X-1953, W. Forster (ZSBS); Yungas del Espíritu Santo, 1888–1889, P. Germain (ZSBS); *Santa Cruz:* Buena Vista, VIII-1906–IV-1907, Steinbach (BMNH); "P. del Sara" [now Gutiérrez], XI-1912, XI-1913, J. Steinbach (CMNH); BRAZIL: *Amazonas:* Fonte Boa, V-VI-1906, S. M. Klages (BMNH); Manicoré, Rio Madeira, X–XI-[no year] (USNM); Reserva Ducke, Km 26 Manaus-Itacoatiara Highway, 17-V-1972, E. G. Munroe (CNC); Rio Cauaburi, ca. 60 m, 14-XII-1962, C. Lindemann (ZSBS); Rio Madeira, [no date], A. M. Moss (BMNH); Santo Antônio de Javari, VI-1907, Klages (BMNH); São Paulo de Olivença, IX-[no year], A. H. Fassl (ZSBS); Tefé, 23-XII-1919 (CMNH), IX-[no year], Fassl (USNM); *Goiás:* Formosa, 800 m, 19-III-1977, V. O. Becker (VOB); Goiás Velho, 500 m, 13–15-X-1984, Becker (VOB); 20 km N São João da Aliança, [ca. 1,000 m], 15-IV-1956, F. S. Truxal (LACM); *Mato Grosso do Sul:* Corumbá, 19–25-IV-1985, Becker (VOB); Rio Brilhante, 25-I-1971, 23–27-X-1970, Becker (VOB); *Minas Gerais:* Sete Lagoas, 720 m, 20-V-1974, Becker (VOB); Unaí, 700 m, 7-XI-1982, Becker (VOB); *Pará:* Belém, 20 m, I-1984, Becker (VOB); Capitão Poço, 19–22-XI-1984, Becker (VOB); Marabá, 50 m, 9-I-1977, Becker (VOB); Pará [=Belém], [no date], Moss (BMNH); Rio Guamá, 27-I-1914 (BMNH); Rio Iriri Camp, 52°40′W, 3°50′S, ca. 100 km S Altamira, 17–18-X-1986, P. J. Spangler & O. S. Flint (USNM); Rio Xingu Camp, 52°22′W, 3°39′S, ca. 60 km S Altamira, 1–21-X-1986, Spangler & Flint (USNM); Taperinha, 1–10-VII-1927, Zerny (NHMV); COLOMBIA: *Putumayo:* Mocoa, 530 m, 20–30-V-1922, W. Hopp (ZSBS); *Cauca:* Río [San Juan de] Micay, [no date], Hopp (ZSBS); ECUADOR: *Morona-Santiago:* 40 km NNE Macas, 1,020 m, 13-VI-1983, J. Rawlins & S. Thompson (CMNH); FRENCH GUIANA: Cayenne, VI-1904, W. Schaus (USNM); Godebert-Maroni, VI-[no year] (BMNH); Kourou River, II-1906 (BMNH); Pied Saut, II-1918, Klages (CMNH); Piste de la Montagne des Singes, Km 10, 150 m, 8-I-1985, J. F. Landry (USNM); Piste Nancibo, Km 6, 11-I-1985, Landry (USNM); Saint-Jean, VII-1904, Schaus (USNM, holotype), VII–VIII-1904 [and no date] (BMNH); Saint-Laurent, XII-[no year] (BMNH); 60 miles [100 km] up Maroni River, VIII-1904, Schaus (USNM); GUYANA: "Brit. Guiana," [no date], J. Rodway (BMNH); confluence of Oronoque & New Rivers, 650 feet [200 m], XI–XII-1937 (BMNH); Kartabu, 5-I-1921 (AMNH), VI-1925 (CMNH); New River, 750 feet [220 m], 20-I–23-III-1938, C. A. Hudson (BMNH); Rockstone, IX-1904, Schaus (USNM); PERU: *Amazonas:* [mouth of Río Cenipa], Upper Río Marañon, 21-IX-1929, H. Bassler F6030 (AMNH, 1 female only); *Cuzco:* Pilcopata, 600 m, 8–14-XII-1979, J. B. Heppner (FSCA, USNM); *Junín:* Río Colorado, 2,500 feet [750 m], VIII–IX-1902, Watkins (BMNH); Utcuyacu, 5,000 feet [1,500 m], XII-1919–II-1920, C. Watkins (BMNH); *Lima:* Callao, [no date], Mrs. M. J. Pusey (USNM) [locality probably incorrect]; *Loreto:* Lower Río Putumayo, 28-VIII-1920 (USNM); [Puerto Limon], Middle Río Marañon, 22-X-1928, Bassler F6076 (AMNH); Río Napo, 6-VI-1920 (CMNH); Río Pacaya, VII–IX-1912 (BMNH); *Madre de Dios:* Río Tambopata Reserve, 30 air km SW Puerto Maldonado, 290 m, 6–10-XI-1979, Heppner (USNM); *Puno:* La Oroya, Río Inambari, 3,100 feet [900 m], XI–XII-1905, G. R. Ockenden (BMNH); Tincuri, 3,400 feet [1,000 m], I-1905, Ockenden (BMNH); Yahuarmayo, 1,200 feet [350 m], II–III-1912, H. & C. Watkins (BMNH); SURINAM: Aroewarwa Creek, Maroewym Valley, III–V-1905, Klages (BMNH); Moengo, Boven, Upper Cottica River, 16–27-V-1927, [W. T. M. Forbes] (CU, USNM); Paramaribo, VIII-1892, C. W. Ellacombe (BMNH); VENEZUELA: *Aragua:* Rancho Grande, 1,100 m, 4-VII, 7-IX, 23-X-1967, 21-VII-1976 (UCV), 18-VI-1949, 17-VII-1946 (AMNH), 25-V-1967, L. Rodriguez (USNM), 15–31-VIII-1967, R. W. Poole (USNM); *Amazonas:* Cerro de la Neblina basecamp, 0°50′N, 66°9′44″ W, 140 m, 21-II, 10-III-1984, D. R. Davis & T. McCabe (USNM); Culebra, 250 m, 9–13-III-1985 (UCV); Ocamo, 13-XI-1982, F. Guanchez (UCV); San Carlos de Río Negro, 25-VIII-1982, 7–13-XI-1982 (UCV); 6 km E San Carlos de Río Negro, 23-XI-1984, R. L. Brown (USNM); *Barinas:* Reserva Forestal de Ticoporo, 230 m, 3–10-IV-1966, 26–29-II-1968, F. Fernandez Y. & L. J. Joly (UCV, USNM); *Bolívar:* Río Surukum, Carretara Santa Elena-Icabaru, 850 m, 19–31-I-1985, Fernandez *et al.* (UCV).

Dalcerides rebella (Schaus), NEW COMB.

Figure 193; Map 22

Anacraga rebella Schaus, 1911: 627–628.—Dyar and Strand, 1913b: 29.—Sick, 1939: 1307.

Diagnosis. Similar to *Dalcerides flavetta*, differing in more weakly developed valvae (Fig. 193).

Adult Male. Forewing length 7 mm. Dorsal forewing and thorax yellow orange, remainder of moth pale yellow. Genitalia as in Figure 193.

Adult Female. Unknown.

Type. Holotype male, USNM 17300.

Type Locality. Costa Rica, Banana River [Río Banano].

Host. Unknown.

Immature Stages. Unknown.

Flight Period. February, March, May, and July.

Distribution (Map 22). Costa Rica and Ecuador, in Tropical Wet and Premontane Wet Forest Life Zones (the Life Zones of Banana River and "am Turrialba" are unknown).

Material Examined. 5 males. COSTA RICA: Banana River, III-1907, W. Schaus (USNM, holotype); La Selva, 2 km SW Puerto Viejo, 29-V-1971, P. A. Opler (UCB); "am [=on Mount] Turrialba," 6-II-1934, F. Nevermann (ZSBS); ECUADOR: *Carchi:* Chical, 1-VII-1983, J. E. Rawlins (CMNH).

Dalcerides chirma (Schaus), NEW COMB.

Figure 194; Map 23

Acragopsis chirma Schaus, 1920: 150.—Hopp, 1921: 282.—Sick, 1939: 1308, pl. 168b.

Diagnosis. Similar to *Dalcerides radians*, but forewing color lighter, usually smaller, and shape of valvae differ (Fig. 194).

Adult Male. Forewing length 7–9 mm. *Head:* Pale yellow. *Thorax:* Dorsum golden yellow; venter pale yellow. Forewings golden yellow with silky sheen; scales arranged to give appearance of transverse undulating bands. Hindwings pale yellow. Ventral wings pale yellow. Legs pale yellow. *Abdomen:* Dorsum golden yellow, venter pale yellow. Genitalia as in Figure 194.

Adult Female. Unknown.

Type. Lectotype male, and 5 paralectotype males, here designated, USNM 22499.

Type Locality. Guatemala, Cayuga.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. May, June, and August.

Distribution (Map 23). Southern Mexico and Guatemala, in Tropical Moist and Subtropical Wet(?) Forest Life Zones.

Material Examined. 8 males. GUATEMALA: Cayuga, VI-[no year] (paralectotype), VIII-[no year] (lectotype and paralectotype), [no date] (3 paralectotypes), W. Schaus & J. Barnes (USNM); MEXICO: *Veracruz:* Huatusco, 1,300 m, 19–23-VIII-1981, V. O. Becker (VOB); Zacualpan, 29-V-1903 (ZSBS).

Dalcerides new species
Figures 101, 195; Map 23

Dalcera ochracea? of Druce, 1887: 213; Pittier and Biolley, 1897: 29 [misidentification].

Diagnosis. Similar to *Dalcerides chirma* but larger and male genitalia differ, especially in shape of valvae (Fig. 195).

Adult Male (Fig. 101). Forewing length 9–10 mm. Both specimens badly denuded. Forewings golden yellow dorsally, all other body surfaces apparently lighter yellow. Genitalia as in Figure 195.

Adult Female. Unknown.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. Unknown.

Distribution (Map 23). Costa Rica.

Material Examined. 2 males. COSTA RICA: Irazú, 6,000–7,000 feet [1,800–2,100 m], [no date], H. Rogers (BMNH); Orosí, 1,200 m, [no date], A.H. Fassl (BMNH).

Discussion. Known only from two badly rubbed males.

Dalcerides radians (Hopp), NEW COMB.
Figures 103, 104, 196, 251; Map 24

Acragopsis radians Hopp, 1921: 281.—Sick, 1939: 1308, pl. 168b.

Diagnosis. A southern Brazilian species with golden yellow wings with a silky luster; differs from *Acraga flava* in smaller size, wing venation, and male genitalia (Fig. 196).

Adult Male (Fig. 103). Forewing length 7–10 mm. *Head:* Pale yellow. *Thorax:* Dorsum pale golden yellow; venter pale yellow. Forewings pale golden yellow with silky luster; scales arranged to give appearance of transverse undulating bands. Hindwings pale yellow. Ventral wings pale yellow. Legs pale yellow. *Abdomen:* Dorsum pale golden yellow, venter pale yellow. Genitalia as in Figure 196.

Adult Female (Fig. 104). Forewing length 10–11 mm. Colored as in male. Genitalia as in Figure 251.

Type. Lectotype male, here designated, ZMHB. Paralectotype male and female, not seen, ZMHB.

Type Locality. Brazil, Santa Catarina.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. September to May.

Distribution (Map 24). Southern Brazil, in Subtropical Wet, Subtropical Moist, and Warm Temperate Moist Forest Life Zones.

Material Examined. 59 males and 5 females. BRAZIL: *Espírito Santo:* [Baixo] Guandú, F. H. Hoffmann, I-1921 (ZSBS), X-1920 (NHMV); *Paraná:* Banhado, Quatro Barras, 800 m, 26-III-1971, 28-XII-1970, V. O. Becker & Laroca (VOB); Castelhanos, Guaratuba, 22-III-1970, Becker (VOB); Castro, 950 m, [no date], E. D. Jones (BMNH); Guaraqueçaba, 9-XII-1970, Becker (VOB); *Rio de Janeiro:* Cachoeiras de Macacu, 400–800 m, 13–15-X-1985, S. E. Miller & Becker (USNM); "Campo Bello" [Itatiaia, 400 m], I, III-1927, III-1928, XII-1926, J. F. Zikan (BMNH, ZSBS); Imbarié, 50 m, 5-I-1956, H. Ebert (ZSBS); Itatiaia, 400 m, 13–15-III-1928, Zikan (ZSBS); [Itatiaia, 400 m], various dates I–V, X, XII-1926–1941, Zikan (IOC); Nova Friburgo, 1,000 m, 14-X-1985, Miller & Becker (USNM); "Rio de Janeiro," XI, H. H. Smith (CMNH); *Rio Grande do Sul:* Rio Grande do Sul, [no date] (BMNH); *Santa Catarina:* Brusque, 100 m, 15–20-I-1983, Becker (VOB); Joinvile, 100 m, 6-XII-1969, Becker (VOB); Nova Brémen, 8-III-1937, IV-1936, IV-1938, 12–18-V-1936, Hoffmann (BMNH, CU, NHMV, USNM); Nova Teutonia, [no date], F. Plaumann (USNM); "Sta. Catharina," 8-III-1907 [and no date], Hoffmann (USNM); "Sta Catharina," [no date], J. G. Scheidemantel (ZMHB, lectotype); *São Paulo:* Alto da Serra, II-1928, III-1925, IX-1929, XII-1922, R. Spitz (BMNH); Alto da Serra, Santos, 800 m, 26-II-1913, Jones (BMNH).

Dalcerides dulciola (Dyar), NEW COMB.

Figures 102, 197; Map 25;
Color Plate, Figure 10

Anacraga dulciola Dyar, 1914: 252.—Sick, 1939: 1307, pl. 168f.—Biezanko, 1961a: 3.
Acragopsis dulciola:—Forbes, 1942: 395, fig. 126.

Diagnosis. Distinguished by brown wings, yellowish along forewing inner margin and hindwing costal area (Fig. 102).

Adult Male (Fig. 102). Forewing length 6–9 mm. *Head:* Pale yellowish brown. *Thorax:* Dorsum pale yellowish brown; venter whitish. Forewings brown with yellowish patch from base along inner margin, not reaching anal angle. Hindwings yellowish brown shading to brown on the margins (brown coverage varies, sometimes leaving yellow only along costal third). Ventral wings as dorsal, but duller. Legs whitish. *Abdomen:* Dorsum pale yellowish brown, venter whitish. Genitalia as in Figure 197.

Adult Female. Unknown.

Type. Holotype male, USNM 16099.

Type Locality. Panama, La Chorrera.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. Year-round.

Distribution (Map 25). Southern Mexico, Costa Rica, Panama, northern Ecuador, and northern Venezuela. Recorded from Tropical Wet, Tropical Moist, Tropical Premontane Wet, and Tropical Premontane Rain Forest Life Zones. Palma Sola, Venezuela, is in Tropical Dry Forest Life Zone, but includes gallery forests (Becker, 1982: 235).

Material Examined. 94 males. COSTA RICA: Fila Esquinas, 35 km S Palmar Norte, 150 m, 7–8-VI-1983, D. H. Janzen & W. Hallwachs (USNM); Finca San Gabriel, 650 m, 8-II, 11-XI-1983, Janzen & Hallwachs (USNM); Golfito, 1948, P. & D. Allen (MCZ); 2.8 miles [4.5 km] E Golfito, 3–4-VII-1967, O. Flint & Ortiz (USNM); Hamburg Farm, III, C. P. Dodge (MCZ); "am [on Mount] Turrialba," X-1929, III, IV-1932, F. Nevermann (ZSBS); Orosí, 1,200 m, [no date], A. H. Fassl (BMNH); 1.8 miles [3 km] W Rincón, Osa Peninsula, 19–21-II-1971, J. P. Donahue & C. L. Hogue (LACM); 4 km E Casetilla, Rincón Nat. Park, 750 m, 11-IV-1983, 14-VIII-1981, 18-X-1982, Janzen & Hallwachs (USNM); Rincón de Osa, 20 m, 10–14-XI-1972, V. O. Becker (VOB); Río Sarapiqui, 6 air km S San Miguel, 800 m, 27-V-1985, J. A. Powell & J. T. Doyen (UCB); Sirena, Corcovado Nat. Park, Osa Peninsula, 5–11-I-1981, Janzen & Hallwachs (USNM); Turrialba, 600 m, 17-II–17-III-1965, W. D. & S. S. Duckworth (USNM), 10-III-1973, VII-1981, 2-VII, 5-VIII, 20-IX-1971, Becker (VOB), 13-V-1985, Powell (UCB); ECUADOR: *Esmeraldas:* Río Cayapas, [no date], G. Flemming & R. Miketta (BMNH); Salinero, 350 feet [100 m], III-1901, Flemming & Miketta (BMNH); Zapallo Grande, Río Cayapas, 20-III-1968, R. W. Hodges (USNM); *Imbabura:* Paramba, 3,500 feet [1,000 m], II-1897, dry season, W. Rosenberg (BMNH) [Bristow, 1979, doubts the accuracy of this locality]; MEXICO: *Veracruz:* Est. Biol. Tuxtlas, 11–16-VI-1981, Becker (VOB); PANAMA: Barro Colorado Island, 21-III-1941, 2-VII-1941, J. Zetek, 18–28-IV-1964, Duckworth (USNM), 12-II–12-III-1936, W. C. Wood (AMNH), 11-IV-1935, A. Friedman (CU), 26-I-[no year], 10-X–29-XI-1934, M. Bates (MCZ, CU), 8–25-VIII-1940, N. S. Scrimshaw (MCZ), 13–18-VII-1958, N. McFarland (LACM); Fort Clayton, 3-VII-1951, F. S. Blanton (USNM); La Chorrera, V-1912, A. Busck (USNM, holotype); Lino, 800 m, [no date], Fassl (USNM); Portobelo, XII-1912, G. F. Cleveland (USNM); VENEZUELA: *Barinas:* Reserva Forestal de Ticoporo, 230 m, 26–29-III-1968, F. Fernandez Y. & C. J. Rosales (UCV); *Carabobo:* Las Quiguas, Esteban Valley, [no date] (CMNH); *Falcón:* Palma Sola, 1896, Whytman (BMNH).

Discussion. I have seen no specimens to document Biezanko's (1961a: 3) record from Rio Grande do Sul, Brazil, and consider it a misidentification.

Dalcerides mesoa (Druce), RESURRECTED COMB.

Figures 105, 106, 199, 250;
Map 26

Dalcera mesoa Druce, 1887: 213.—Kirby, 1892: 542.
Dalcerides mesoa:—Dyar, 1898: 232.

Anacraga mesoa:—Dyar, 1910c: 119.—Dyar and Strand, 1913b: 30.—Hopp, 1921: 281.—Sick, 1939: 1308, pl. 168b.

Acragopsis mesoa:—Forbes, 1942: 395.

Anacraga gugelmanni Dyar, 1916: 34.—Hoffmann, 1932: 146.—Beutelspacher, 1992: 145. NEW COMB., NEW SYN.

Diagnosis. Distinguished by large brown spot in middle of orange-yellow forewings (Fig. 105).

Adult Male (Fig. 105). Forewing length 6–8 mm. *Head:* Pale yellow. *Thorax:* Dorsum orange-yellow; venter pale yellow. Forewings orange-yellow with large brown spot (of varying size) covering most of middle of wing. Hindwings yellow-orange. Ventral wings as dorsal, but duller. Legs pale yellow. *Abdomen:* Dorsum yellow-orange, venter pale yellow. Genitalia as in Figure 199.

Adult Female (Fig. 106). Forewing length 8–11 mm. Colored as in male. Genitalia as in Figure 250.

Types. Lectotype female, here designated, BMNH, and paralectotype female, ZMHB (*mesoa*); holotype male, USNM 19278 (*gugelmanni*).

Type Localities. Panama, Bugaba, 800–1,500 feet [250–450 m] (*mesoa*); Mexico, Tabasco, Teapa (*gugelmanni*).

Host. Paullinia bracteosa Radlkofer (Sapindaceae) (Aiello lot 82-12).

Immature Stages. Undescribed.

Flight Period. Year-round.

Distribution (Map 26). Southern Mexico, Guatemala, Costa Rica, Panama, Colombia, Venezuela, and Ecuador, in Tropical Wet, Tropical Moist, Tropical Dry, Tropical Premontane Wet, (probably Tropical Premontane Rain), Subtropical Wet (?), and Subtropical Dry Forest Life Zones.

Material Examined. 27 males and 19 females. COLOMBIA: *Magdalena:* Onaca, Sierra Nevada de Santa Marta, 2,000 feet [600 m], [IX–X-1901], Engelke (BMNH); COSTA RICA: Finca Campana, 5 km NW Dos Rios, 750 m, 21-III-1985, D. H. Janzen & W. Hallwachs (USNM); Hacienda Tapezco, 29 km W Tortuguero, 40 m, 8–13-III-1978, J. P. Donahue *et al.* (LACM); Sirena, Corcovado Nat. Park, Osa Peninsula, 5–11-I-1981, Janzen & Hallwachs (USNM); Turrialba, 600 m, 2-VII, 5-VIII, 10-20-IX-1971, 20-X-1972, V. O. Becker (VOB), 2–5-XI-1967, E. L. Todd (USNM); ECUADOR: *Esmeraldas:* Carondelet, [no date], G. Flemming & R. Miketta (BMNH); San Javier, Río Cachabí, 60 feet [20 m], [no date], Flemming & Miketta (BMNH); GUATEMALA: Cayuga, [no date] (USNM); Quiriguá, III-[no year], W. Schaus & J. Barnes (USNM); Volcán de Santa María, IV-[no year], Schaus & Barnes (USNM); MEXICO: *Campeche:* Escárcega, 85 m, 17–21-VI-1981, Becker (VOB); *Tabasco:* Tabasco, II-1912 (ZSBS); Teapa, III-1914, W. Gugelmann (USNM, holotype; AMNH); *Veracruz:* Córdoba, 13–25-VII-1966, J. S. Buckett (UCB), 12-VIII-1965, 14-X-1965, A. B. Lau (USNM); Est. Biol. Tuxtlas, 11–16-VI-1981, Becker (VOB); Huatusco, [no date] (BMNH); Jalapa, [no date] (USNM); Los Tuxtlas area, seeps at "Las Cabanas," 8–15-V-1981, C. M. & O. S. Flint (USNM); Misantla, XI-1920 (ZSBS); Orizaba, [no date] (USNM); Zacualpan, 12-III-1903 (ZSBS); *Yucatán:* Chichén Itzá, 20-II-1954, E. C. Welling (CMNH), 16-IX-1952, J. & D. Pallister (AMNH); PANAMA: Barro Colorado Island, 17-VI-1935, A. Friedman (MCZ), 26-III-1982 as larva, pupated 7-IV-1982, eclosed 14-IV-1982, A. Aiello lot 82-12 (USNM); Bugaba, 800–1,500 feet [250–450 m], [1881–1883], G. C. Champion (BMNH, lectotype of *mesoa*); Volcán de Chiriquí, [no date], H. Ribbe (ZMHB, paralectotype of *mesoa*); VENEZUELA: *Tachira:* Río Frio, 600 m, 2–10-IX-1981, F. Fernandez Y. *et al.* (UCV).

Discussion. A very dark female from Cerro de la Neblina Basecamp, 0°50′N, 66°9′44″W, 140 m, Amazonas, Venezuela (4–12-II-1984, D. R. Davis & T. McCabe, USNM) is probably this species.

Dalcerides nana (Dognin), NEW COMB.

Figures 109, 202; Map 21

Anacraga nana Dognin, 1920: 13.—Sick, 1939: 1308.

Diagnosis. Distinguished from other orange Acraginae by small size, pale line along end of forewing cell (Fig. 109), and single medial point of sociuncus (Fig. 202).

Adult Male (Fig. 109). Forewing length 7–8 mm. Entirely golden yellow, with hindwing lighter yellow. Pale line along end of forewing cell. Ventral wings lighter than dorsal. Genitalia as in Figure 202.

Adult Female. Unknown.

Type. Holotype male, USNM 103448.

Type Locality. Brazil, São Paulo.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. January, March, May, and December.

Distribution (Map 21). Southern Brazil, in Subtropical Wet and Subtropical Moist Forest Life Zones.

Material Examined. 22 males. BRAZIL: *Paraná:* Guaraqueçaba, 9-XII-1970, V. O. Becker (VOB); "Paraná," [no date], F. Johnson (USNM); *Santa Catarina:* Blumenau, [no date] (ZSBS); Brusque, 28-XII-1969, Becker (VOB); Hansa Humbolt [now Corupá], XII-1932, A. Maller (BMNH); Nova Brémen, Rio Laeiss, III-1936, XII-1935, 3-I-1937, 12–18-V-1936, 19-XII-1936, F. H. Hoffmann (BMNH, CU, USNM); Santa Catarina, 1-1-1937, Hoffmann (USNM); *São Paulo:* Anhangabaú, XI–XII-1926, R. Spitz (BMNH); "São Paulo," [no date] (USNM, holotype).

Discussion. Most specimens have the venation of *Acraga*, but one specimen (Nova Brémen, USNM) has the hindwing Sc + R_1 fused with Rs in the cell. The male genitalia differ from other *Dalcerides* in the strong posterior hooklike medial point of the sociuncus. The species may not belong in *Dalcerides*, but this seems to be the best place for it given current knowledge.

Dalcerides sofia (Dyar), NEW COMB.

Figures 107, 108, 200, 248; Map 27

Dalcera alba Druce, 1887: 213. [misidentification] (male only).

Anacraga sofia Dyar, 1910b: 268; 1910c: 120.—Dyar and Strand, 1913b: 30.—Sick, 1939: 1307.—Beutelspacher, 1992: 145.

Anacraga sororcula Dyar, 1927: 551.—Sick, 1939: 1307. NEW COMB., NEW SYN.

Anacraga phasma Dyar, 1927: 551.—Sick, 1939: 1308. NEW COMB., NEW SYN.

Diagnosis. Distinguished from other *Dalcerides* by whitish wings with light brown pattern (Fig. 107).

Adult Male (Fig. 107). Forewing length 6–9 mm. *Head:* Cream. *Thorax:* Dorsum cream with light brown; venter white. Forewings cream-colored with light brown suffusion, especially posterior half of wing (including inner margin), postmedially and subterminally; large medium brown spot distal to upper half of discal cell; tuft of white scales distal to lower half of discal cell. Hindwings white. Ventral wings white with brown forewing discal spot. Legs white. *Abdomen:* White. Genitalia as in Figure 200.

Adult Female (Fig. 108). Forewing length 9–11 mm. Colored as in male. Forewing anal angle less developed. Genitalia as in Figure 248.

Types. Holotype female, USNM 13036 (*sofia*); lectotype male, 3 male and 2 female paralectotypes, here designated, USNM 40717 (*sororcula*); holotype female, USNM 40718 (*phasma*).

Type Localities. Mexico, Morelos, Cuernavaca (*sofia*); Guatemala, Cayuga (*sororcula*); Mexico, Sinaloa, "Venadio" (*phasma*).

Host. "Orchid" (USNM).

Immature Stages. Undescribed.

Flight Period. Year-round.

Distribution (Map 27). Southern Mexico, Guatemala, El Salvador, Nicaragua, and Costa Rica, in Tropical Moist, Tropical Dry, Tropical Premontane Wet, Subtropical Moist, Subtropical Dry, and Warm Temperate Wet Forest Life Zones.

Material Examined. 89 males and 17 females. COSTA RICA: Puntarenas, 5-XII-1972, V. O. Becker (VOB); Santa Rosa Nat. Park, various dates I, III, V–VII, XI, XII-1979–1985, D. H. Janzen & W. Hallwachs (USNM); Turrialba, 600 m, 10-IX-1971, Becker (VOB); "Costa Rica," 18-VIII-1929, F. Nevermann (ZSBS); EL SALVADOR: Lago Ilopango, near Apulo, 4–5-VII-1966, O. S. Flint & Ortiz (USNM); San Salvador, 600 m, I, VI-1960, X-1959, B. Bechyne (ZSBS); 13 km N San Salvador, 4-II-1965, W. D. Duckworth (USNM); GUATEMALA: Cayuga, IX (lectotype of *sororcula*), V, VI, VIII, IX, X-[no year], W. Schaus & J. Barnes (USNM, CMNH, includes paralectotypes of *sororcula*); Laguna Nisquaya, near Pijije, 4-VIII-1965, P. J. Spangler (USNM); MEXICO: *Campeche:* "Campeche," VII-1935, C. C. Hoffmann (USNM); "Champich," 24-VII-1935 (AMNH); Escárcega, 85 m, 17–21-VI-1981, Becker (VOB); *Chiapas:* El Sumidero, 15 miles [24 km] NW Tuxtla Gutiérrez, 1-VIII-1957, J. A. Chemsak (UCB); El Zapotal, 2 miles [3 km] S Tuxtla Gutiérrez, 1-VII-1957, Chemsak (UCB); Teopisca, 1,900 m, 23–26-VI-1981, Becker (VOB); Villa las Rosas, 1,300 m, 27-VI-1981, Becker (VOB); *Morelos:* Chiconcuae, 26-X-1974, J. White (AJW); Cuernavaca, VIII-1906, Schaus (USNM, holotype of *sofia*), VI, X-1914 (ZSBS); *Nayarit:* 1 mile [1.6 km] S Huajicori, 22-VII-1984, Bloomfield & Faulkner (SDNH);

San Luis Potosí: El Pujal, VII-18-1939, R. Haag (MCZ); 2 miles [3 km] N Tamazunchale, 16–18-VII, 2-VIII-1963, D. R. Davis & Duckworth (USNM); 25 miles [40 km] N Tamazunchale, 26-VI-1965, Flint (USNM); *Sinaloa:* Presidio de Mazatlán, [no date], Forrer (BMNH, misidentified syntype of *alba*); "Venadio," [1918], [J. A. Kusche] (USNM, holotype of *phasma*); 5 miles [8 km] W Concordia, 2-XI-1961 (CMNH, USNM); 5 miles [8 km] N Mazatlán, 24, 28-VII-1964, J. A. Powell (UCB, USNM); 10 miles [16 km] S Rosario, 22-VI-1957, Chemsak (UCB); 18 miles [29 km] N Mazatlán, 29-X-1961 (CMNH); 27 miles [40 km] E Villa Unión, 800 feet [250 m], 26-VII-1964, Powell (UCB); *Veracruz:* Misantla, IX-1910, R. Müller (USNM, paralectotype of *sororcula*); Fortín [de las Flores], "Rf. orchid leaf," "29-XII-1954," Cary (USNM); 7 miles [11 km] SW Poza Rica, 200 feet [60 m], Davis & Duckworth (USNM); Puente Nacional, 6 miles [10 km] SE Rinconada, 29-IX-1975, Powell (UCB); Zacualpan, VIII-1916 (AMNH); *Yucatán:* Chichén Itzá, 11-I-1954, E. C. Welling (CMNH); *Not located:* "Mexico," C. H. T. Townsend (CMNH); NICARAGUA: Puerto Cabezas, 30-VI-1972, Becker (VOB).

Discussion. The male syntype of *Dalcerides alba* (Druce) (from Presidio de Mazatlán, Sinaloa, Mexico) is not conspecific with the lectotype of *D. alba* but is with *D. sofia*.

Although the unique holotype of *D. phasma* is in very poor condition, I am provisionally synonymizing *D. phasma* under *D. sofia*, because I can find no significant differences between the holotype of *D. phasma* and *D. sofia*. The apophyses posteriores of the *D. phasma* holotype are broader and blunter (Fig. 248, inset) than those of the other four female *D. sofia* dissected, but there is considerable variation in the apophyses posteriores of those specimens. "Venadio," the type locality of *D. phasma*, refers to El Venadillo, a town some 6.5 km north of Mazatlán airport (Cohn, 1965: 43; Nutting and Gurney, 1961: 52).

Dalcerides ingenita Species-Group

See discussion under *Dalcerides*, earlier.

Dalcerides ingenita (Hy. Edwards)
Figures 8–11, 14–16, 23, 24, 43, 48, 111, 112, 203, 253; Map 28

Artaxa ingenita Hy. Edwards, 1882: 12.—Grote, 1882: 18.

Dalcerides ingenita:—Neumoegen and Dyar, 1893a: 121; 1894: 111.—Holland, 1903: 369–370.—Smith, 1903: 83.—Dyar, 1903: 359; 1910c: 119; 1925: 46.—Bureau of Entomology, 1907: 515.—Dyar and Strand, 1913b: 29.—Barnes and McDunnough, 1917: 127.—Hopp, 1921: 282.—Eyer, 1924: 318, pl. XXXVIII, fig. 3.—Comstock, 1925: 606.—Sick, 1939: 1307, pl. 168a.—McDunnough, 1939: 7.—Comstock, 1959: 53.—Davis, 1983: 67.—Papp and Swan, 1984: 119.—Arnett, 1985: 563, fig. 27.163.—Stehr and McFarland, 1985: 35–36; 1987: 460–462, fig. 26.185.—Beutelspacher, 1988: 328, fig. 1; 1992: 145.—McFarland, 1993: 2.

Dalcera ochracea of Druce, 1898: 441 [misidentification].

Diagnosis. Distinguished from other *Dalcerides* by larger size and orange coloration (Figs. 111, 112); distinguished from orange *Acraga* by wing venation (Fig. 43) and genitalia (Figs. 203, 253).

Adult Male (Fig. 111). Forewing length 9–13 mm. Entirely orange. Hindwing sometimes slightly richer in color than forewing. Genitalia as in Figure 203.

Adult Female (Fig. 112). Forewing length 12–16 mm. Colored as in male, but lighter and less rich (more yellowish) in shade. Genitalia as in Figure 253.

Type. Holotype female [not male as cited by Edwards], USNM 34165.

Type Locality. United States, Arizona, Yavapai County, Prescott.

Host. Arctostaphylos pungens HBK (Ericaceae) (USNM, foodplant cited but not identified by Dyar; Stehr and McFarland, 1987); *Quercus emoryi* Torrey and *Quercus oblongifolia* Torrey (Fagaceae) (N. McFarland, personal communication, 1985). In the laboratory it can be reared on some other Ericaceae, such as blueberry (*Vaccinium* sp.; Stehr and McFarland, 1987).

Immature Stages. Dyar (1910c: 119; 1925: 46), Comstock (1959: 53), Stehr and McFarland (1985, 1987).

Flight Period. Late April to September (Arizona) and July to December (Mexico).

Distribution (Map 28). Arizona (southeastern Arizona north through the mountains to Flagstaff), southwestern Texas, and Mexico. Life Zone maps are not available for the range of *D. ingenita*, but it apparently occurs in Subtropical Moist (?), Subtropical Dry, Warm Temperate Moist (?), Warm Temperate Dry, and Warm Temperate Thorn Steppe Life Zones.

Material Examined. Over 70 males and 160 females. UNITED STATES: *Arizona* [only localities listed here, based on AMNH, BMNH, CAS, LACM, MCZ, PMY, UCR, USNM, ZSBS]: Cochise County: Ash Canyon, Huachuca Mtns., 1,500 m; Carr Canyon, Huachuca Mtns.; Cave Creek Ranch, Portal; Cochise Stronghold Campground, Dragoon Mtns.; Copper Canyon, ca. 900 m; Fort Huachuca; Garden Canyon, Huachuca Mtns.; Hereford; Palmerlee; Paradise; Ramsey Canyon, Huachuca Mtns.; Sierra Vista; Southwest Research Station, Chiricahua Mtns.; Yaqui Canyon area, 1,600–1,700 m; 1.6 km S Portal; Coconino County: Miller Canyon; Sycamore Rim; Todd's Lodge, Oak Creek Canyon; Gila County: "Gila Co."; Globe; Kohls Ranch; Payson; Mohave County: "Mohave Co."; Pima County: Babaquivera Mtns.; Brown's Canyon, east slope Babaquivera Mtns., 1,140 m; Mount Lemmon, Molino, Tucson; Pinal County: Oracle; Santa Cruz County: Box Canyon, Santa Rita Mtns.; Canelo; Madera Canyon, Santa Rita Mtns., 1,500 m and no elevation; Pena Blanca, 1,200 m; 6.5 km N Nogales; Yavapai County: Dewey; Granite Dells, 6.5 km N Prescott; Mayer; Prescott; Rio Verde Mtns., Phoenix; Not located: "Arizona"; "So. Arizona"; *Texas:* Brewster County: Alpine, 1–7-VIII-1926, O. C. Poling (USNM, 2 females only); MEXICO: *Colima:* Colima, VIII-1919 (ZSBS), 9-XII-1915 (AMNH); *Guerrero:* Aguas de Obispo, 21–22-X-1973, V. O. Becker (VOB); Balsas, 1,500 feet [450 m], VIII-1906, W. Schaus (USNM); "Guerrero," XII-1913, XII-1915 (ZSBS), XII-1924 [?], Draudt (USNM); "Sierra de [=mountains of] Guerrero," VIII-1911, R. Müller (USNM); Tierra Colorada, 2,000 feet [600 m], [no date], H. H. Smith (BMNH); Zihuatenejo, 28-XI-1939, S. H. & A. H. Rindge (AMNH); *Jalisco:* Guadalajara (USNM); Volcán de Colima, IX-1916, IX-1924, X-1923, X-1928, XI-1918, XII-1928, Müller (ZSBS); *México:* San Nicolas, 1-IX-1962 (RJM); *Nayarit:* Maria Magdalena Island, Tres Marías Islands, 15-XII-1939, Rindges (AMNH); 5.7 miles [9 km] N Huajicori, 26-VII-1984, Bloomfield & Faulkner (SDNH); 8 miles [13 km] E San Blas, 29-VIII-1961, D. Verity (LACM); 24 miles [38 km] SE Tepic, 4,100 feet [1,200 m], 27-VII-1971, E. M. Fisher (LACM); *Oaxaca:* Tangola, 8-XII-1937 (AMNH); *Puebla:* 2 miles [3 km] SW Tehuacán, 5,300 feet [1,600 m], 4-X-1975, J. A. Powell (UCB); *Sinaloa:* "Venadio," [no date] (BMNH, USNM); 5 miles [8 km] W Concordia, 2-XI-1961 (CMNH); 5 miles [8 km] N Mazatlán, 27-VII-1964, Powell (UCB); *Veracruz:* Zacualpan, IX-1915 (AMNH), X-1919 (ZSBS); *Not located:* "Mexico," 22-IX-1917 [and no date] (ZSBS); "Southern Mexico," Townsend (CMNH).

Discussion. This species is extremely variable in size; the smallest I have seen is one male from Maria Magdalena Island, Tres Marías Islands, Mexico, with a 7.5-mm forewing.

Noel McFarland has observed this species since 1979 at his home in Ash Canyon, southeastern Huachuca Mountains, Cochise County, Arizona (1,500 m, oak woodland and manzanita scrub). He reports (pers. comm., 1985) that *Dalcerides ingenita* is common every year in Ash Canyon, with two flights per year: a smaller brood from mid-May to mid-June and a larger brood from late July to the end of September (peak abundance mid-August to early September). Females are strictly nocturnal and come readily to blacklight throughout the night. Males come to blacklight primarily after midnight and fly actively until about an hour after sunrise.

In Arizona *Dalcerides ingenita*, along with the superficially similar geometrid *Eubaphe unicolor* (Robinson), is part of a mimetic complex modeled on *Lycus loripes* (Chevrolat) and *Lycus simulans* Schaeffer (Coleoptera: Lycidae) (Linsley *et al.*, 1961). Although *D. ingenita* was not discussed by Linsley *et al.* (1961), McFarland (personal communication, 1986) confirmed that *D. ingenita* fits the complex in behavior as well as appearance.

Dalcerides bicolor Schaus
Figures 110, 252; Map 22

Dalcerides bicolor Schaus, 1910: 415.—Dyar and Strand, 1913b: 29.—Sick, 1939: 1307.

Diagnosis. Easily distinguished by striking color pattern with forewing lighter than hindwing (Fig. 110).

Adult Male. Unknown.

Adult Female (Fig. 110). Forewing length 15 mm. *Head:* Orange red. *Thorax:* Orange red. Forewings orange-red, with veins slightly darker; narrow, with apex produced. Hindwings fuscous, thinly scaled. Ventral wings as dorsal. Legs orange-red. *Abdomen:* Dorsum fuscous, venter orange-red. Genitalia as in Figure 252.

Type. Holotype female, USNM 16952.

Type Locality. Costa Rica, Mount Poás [Volcán de Poás].

Host. Unknown.

Immature Stages. Unknown.

Flight Period. May.

Distribution (Map 22). Costa Rica.

Discussion. Dalcerides bicolor is known only from the unique holotype.

Dalcerides alba (Druce), NEW COMB.
Figures 113, 114, 201, 243; Map 29; Color Plate, Figure 7

Dalcera alba Druce, 1887: 213.—Kirby, 1892: 542.—Dyar, 1898: 231.

Dalcera? *alba:*—Dyar and Strand, 1913b: 27.—Sick, 1939: 1304.—Hopp, 1921: 280.

Acraga caretta Dyar, 1910b: 268; 1910c: 118; 1914: 252.—Dyar and Strand, 1913b: 29.—Hoffmann, 1932: 146; 1933: 295.—Sick, 1939: 1306.—Forbes, 1942: 394.—Beutelspacher, 1992: 145. NEW COMB., NEW SYN.

Diagnosis. Similar to *Acraga ampela*, distinguished by smaller size and brown forewing anal angle (Fig. 113).

Adult Male (Fig. 113). Forewing length 9–11 mm. *Head:* White. *Thorax:* Dorsum white with light brown stripes along wing bases; venter white. Forewings white; brown submarginal shading, well developed (including outer margin) near anal angle, becoming faint and finally lost toward apex; cross veins of discal cell and origins of CuA_1 and CuA_2 brown. Hindwings white with brown anal angle. Ventral wings white with brown anal angles. Legs white. *Abdomen:* White. Genitalia as in Figure 201.

Adult Female (Fig. 114). Forewing length 13–16 mm. Colored as in male, although generally lighter. Brown very reduced at hindwing anal angle. Genitalia as in Figure 243.

Types. Lectotype female, here designated, BMNH (*alba*) [male syntype is *Dalcerides sofia* (Dyar)]; Lectotype male, and paralectotype female, here designated, USNM 13037 (*caretta*).

Type Localities. Guatemala, Volcán de Atitlán, 2,500–3,500 feet [750–1,000 m] (*alba*); Panama, Chiriquicito (*caretta*).

Host. Colubrina sp. (Rhamnaceae) (USNM).

Immature Stages. Undescribed.

Flight Period. Year-round.

Distribution (Map 29). Southern Mexico, Guatemala, Honduras, Belize, Costa Rica, Panama, Colombia, and Ecuador, in Tropical Wet, Tropical Moist, Tropical Dry, Tropical Lower Montane Wet or Moist, Tropical Premontane Wet, Tropical Premontane Moist, Subtropical Wet, and Subtropical Moist Forest Life Zones.

Material Examined. 117 males and 27 females. BELIZE: Punta Gorda, VI, VII, IX-1933, VIII-1934, IX, X, XII-1935, J. J. White (BMNH); COLOMBIA: *Cauca:* Río [San Juan de] Micay, [no date], W. Hopp (ZSBS); COSTA RICA: Fila Esquinas, 35 km S Palmar Norte, 150 m, 7–8-I-1983, D. Janzen & W. Hallwachs (USNM); Finca San Gabriel, 650 m, 11-XI-1983, Janzen & Hallwachs (USNM); Guápiles, XI-[no year] (BMNH, CMNH); Hacienda La Suerte/Tepezco, 29 km W Tortuguero, 40 m, 13–31-VIII-1979, J. P. Donahue *et al.* (LACM); Hamburg Farm, III-[no year], C. P. Dodge (MCZ); Hamburg Farm, Reventazon, 25 m, II, V-1923, VI-1932, VII-1924, F. Nevermann (NHMV, ZSBS); La Selva, 2 km SW Puerto Viejo, 29-V-1971, P. A. Opler (UCB); San José, II–III-1926, Nevermann (ZSBS), VI-1923, H. Schmidt (BMNH); Sirena, Corcovado Nat. Park, 5–11-I-1981, Janzen & Hallwachs (USNM); Sixaola River, III-[no year], W. Schaus (BMNH); Tuis, VI-[no year], Schaus & J. Barnes (USNM); Turrialba, on *Colubrina* sp., pupated 12-I-1970, emerged 14-I-1970 (USNM); Turrialba, 600 m, many specimens, IV–X-1971–1973 and VII-1981, V. O. Becker (VOB); "am [=on Mount] Turrialba," I–II, IV–VIII-1929–1934, Nevermann (ZSBS); ECUADOR: *Cañar:* 20 km SE La Troncal, 2,200 feet [660 m], 8–21-VII-1984, S. J. Weller & N. L. Jacobson (USNM); *Esmeraldas:* Salinero, 350 feet [100 m], II-1901, G. Flemming & Miketta (BMNH); GUATEMALA: Cayuga, II–X, XII-[no year], Schaus & Barnes (BMNH, CMNH, USNM); "La Naranja," [no date] (ZSBS); Machaquila, Petén, 9-VII-1972, Becker (VOB); "Queriflia," IV-[no year] (BMNH); San Sebastián, Retalnuleu, [no date] (USNM); Volcán de Atitlán, 2,500–3,500 feet [750–1,000 m], [XII-1880], G. C. Champion (BMNH, lectotype of *alba*); HONDURAS: La Cumbre, 3–25-II-1922, J. Lienhart (BMNH); MEXICO: *Campeche:* Escárcega, 85 m, 17–21-VI-1981, Becker (VOB); *Chiapas:* Chiapas, V-1915 (ZSBS); "La Granja," [600 m], VI-1930 (AMNH); Maravillas, 30-IX-1929 (AMNH); *Distrito Federal:* Mexico City, II-1922, R. Müller (BMNH); *Veracruz:* El Palmar, 29-VI-1948, A. C. Smith (USNM); Est. Biol. Tuxtlas, 11–16-VI-1981, Becker (VOB); Fortín de las Flores, 1,010 m, 7–16-VII-1974, J. A. Powell *et al.* (UCB); Huatusco, [no date] (BMNH); Jalapa, XI-1910 (ZSBS); Misantla, VI-1909, Müller (USNM, paralectotype of *caretta*), VII-1911, Gugelmann (AMNH), IX-1914 (USNM), VI-1912 (ZSBS), VII-[no year] (BMNH); Orizaba, IX-1912, IX-1913, XI-1911 (ZSBS); Veracruz, I-1883, H. H. Smith (BMNH); *Yucatán:* Chichén Itzá, 26-X-1954, E. C. Welling (CMNH); PANAMA: Barro Colorado Island, 20-II-1935, 9-IV-1935, A. Friedman, 20-VII-1940, N. S. Scrimshaw, 23-XI-1934, 9-XII-1934, M. Bates (MCZ); Chiriquicito, III-[no year], Schaus & Barnes (USNM, lectotype of *caretta*); Portobelo, 7–24-IV-1912, A. Busck (USNM).

Discussion. The brown coloration on the forewing varies from dark fuscous to light brown. A specimen from Veracruz (I-1883, H. H. Smith) bears a *Dalcera alba* "cotype" label, but it was not mentioned in the original description, so it is not a type.

Zikanyrops Hopp

Zikanyrops Hopp, 1928a: 286.—Sick, 1939: 1310.—Fletcher and Nye, 1982: 172. Type species: *Zikanyrops sparsa* Hopp, 1928a, by original designation.

Diagnosis. Very close to *Dalcerides*, differing in wing venation (Fig. 46); male genitalia unknown.

Adult Male. (Modified from Original Description). Small, forewing 8.5 mm. Frons scarcely as broad as one eye. Labial palpi narrow, slightly upturned. Forewing with 1A + 2A and CuP arising from base; CuA_2 from middle of vein of cell; CuA_1 from a little before the cell angle; M_3 from the cell angle; M_2 from a little in front of the media; M_1 from close behind the media; R_5 from the accessory cell; R_4 absent [not in *dubiosa*]; R_3 from accessory cell; R_2 absent; R_1 from costal margin of accessory cell; Sc free from base; discal cell rather broad, divided by the media into almost equal halves of which the outer margin is slightly indented; accessory cell small and (in *sparsa*) of rhombic shape, half of it projecting toward the outer margin; retinaculum absent. Hindwing with anals and CuP arising from base; CuA_2 from the discal third of cell; CuA_1 and M_3 from cell angle and nearly pedunculate [not in *dubiosa*]; M_2 a little in front of M_1 which is behind the media; Rs from anterior cell angle; Sc close beside Rs, from the cell [Sc and Rs fused in cell in *dubiosa*].

Adult Female. Medium size, forewing 12 mm. As in male, but see earlier and description of *Zikanyrops dubiosa* for differences. Genitalia: sterigma Y-shaped, broad, and sclerotized; ostium bursae narrow; ductus bursae narrow, long, with bend at about first third; corpus bursae elongate ovate; ductus seminalis arising near bend in ductus bursae; apophyses posteriores very wide at base, narrowing to apex, short; "accessory glands" ovate.

Discussion. This genus is known only from two species, *Zikanyrops sparsa* known from a single male (now lost) and *Z. dubiosa* from a single female. The male genitalia and details of the male frenulum and retinaculum are unavailable.

Zikanyrops dubiosa Hopp
Figures 46, 86, 254; Map 30

Zikanyrops dubiosa Hopp, 1928a: 287.—Sick, 1939: 1310–1311.

Diagnosis. Coloration distinctive; ground color yellow ochre, with anterior portion of forewings pink with fuscous touch (Fig. 86).

Adult Male. Unknown.

Adult Female (Fig. 86). Forewing length 12 mm. *Head:* Yellow ochre (labial palpi missing). *Thorax:* Yellow ochre. Forewings yellow ochre posterior of cell and CuA_1, anterior pink with fuscous touch; slightly falcate. Hindwings yellow ochre. Ventral wings colored as dorsal, but duller. Legs yellow ochre. *Abdomen:* Yellow ochre. Genitalia as in Figure 254.

Type. Holotype female, ZMHB.

Type Locality. Bolivia, Cochabamba, Yungas del Espíritu Santo, 1888–1889, P. Germain.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. Unknown.

Distribution (Map 30). Bolivia.

Material Examined. Known only from unique type, in poor condition.

Discussion. Zikanyrops dubiosa differs, according to Hopp, from the unique male type of *Zikanyrops sparsa* in wing venation. The forewing accessory cell is somewhat narrower and does not project half-way toward the outer margin, but it is simply a section of the anterior part of the cell. *Zikanyrops dubiosa* appears to have a frenulum base similar to that of a female *Dalcerides*, but it is obliterated by glue. The Río Espíritu Santo is a headwater to the Río Chaparé, but I have not located Yungas del Espíritu Santo.

Zikanyrops sparsa Hopp
Map 30

Zikanyrops sparsa Hopp, 1928a: 287.—Sick, 1939: 1310.

Diagnosis. Ground color creamy white, forewing sprinkled with dark brown scales; known only from original description.

Adult Male. Forewing length 8.5 mm. *Head:* Creamy white. Labial palpi brownish. *Thorax:* Creamy white. Forewings creamy white, delicately sprinkled with dark brown scales, especially between apex and cell; transverse vein of cell and veins M_1 and M_2 with white hairs. Hindwings creamy white. Ventral wings creamy white [?], basal half of forewing costa dark brown. Legs creamy white, one side of foreleg femora and tibiae dark brown. *Abdomen:* Creamy white. [Genitalia unknown.]

Adult Female. Unknown.

Type. Holotype male, originally in Hopp collection, now lost.

Type Locality. Brazil, Minas Gerais, "Passa Quatro," 26-XI-1917, J. F. Zikan.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. November.

Distribution (Map 30). Southern Brazil, in Subtropical Lower Montane Moist Forest Life Zone.

Discussion. I have not seen this species and cannot locate the unique type. The preceding description is taken from the original description. The type was collected at Fazenda dos Campos, 1,500 m, near Passa Quatro. The site was, at that time, *Araucaria* forest, but almost all of the region has now been deforested (W. Zikan, personal communication, 1985).

Subfamily Dalcerinae

Diagnosis. Distinguished from Acraginae by absence of the forewing accessory cell (Figs. 47, 49–56).

Discussion. This subfamily includes *Minonoa*, *Paracraga*, *Ca*, *Minacragides*, *Oroya*, *Dalcera*, *Dalcerina*, and *Minacraga*. Orfila (1961: 252) based his diagnosis of the subfamily, in part, on the presence of apical scale tufts on the male antennae, but only *Dalcera*, *Dalcerina*, and *Minacraga* possess this synapomorphy. *Oroya* differs significantly from the other genera in several characters of wing venation and male genitalia, but because *Oroya* is known only from males of one species it seems best to leave it in Dalcerinae. For further discussion, see Discussion of cladogram.

Minonoa Dyar

Minonoa Dyar, 1905a: 176; 1910c: 120.—Dyar and Strand, 1913b: 30.—Hopp, 1921: 277.—Sick, 1939: 1308.—D'Almeida, 1945: 195.—Fletcher and Nye, 1982: 103. Type species: *Minonoa perbella* Schaus, 1905, by original designation.

Diagnosis. Fuscous with distinctive white, yellow, or orange patterns (Figs. 125–128); forewing R_1 free, R_{2+3} fused, R_{4+5} fused, and hindwing frenulum present (Fig. 53).

Adult Male. Medium size, forewing 11 mm. Ground color: Fuscous and white with maculation. Antennae: apical scale tuft absent. Forewing: accessory cell absent; R_{2+3} and R_{4+5} short-stalked basally; R_{2+3} fused; R_{4+5} fused; retinaculum present. Hindwing: Rs fused with Sc + R_1 in cell; frenulum present. Genitalia: tegumen and sociuncus fused complex; anal tube opening in shelflike subscaphium; socii not distinct, but sociuncus lobes hairy; gnathos a thin plate parallel to ventral surface of sociuncus; vinculum long and narrow; valvae reduced to lateral lobes of valvae–vinculum–juxta complex; juxta not identified interiorly, projection from valvae complex externally; saccus present but very reduced; aedoeagus medium length and stout.

Adult Female. Medium size, forewing

10–14 mm. Genitalia: sterigma broad; ostium bursae broad; ductus bursae broad to bend, narrowing and becoming membranous; corpus bursae elongate ovate; ductus seminalis arising after bend; apophyses posteriores wide and short to thin and long; "accessory glands" ovate in lateral view.

Discussion. My identification of forewing radial veins in *Minonoa* and *Paracraga* is based on the tendency for R_1 to be separate from the others in dalcerids, and the scenario of wing evolution in which the *radius anterior* forms R_1 and the *radius posterior* forms R_{2-5} (Kukalová-Peck, 1983; Lawrence *et al.*, 1991: 15–16). However, the homologies of the veins and the role of cross-veins are uncertain.

KEY TO *MINONOA*

1. Hindwing entirely dark fuscous (Fig. 127) .... *pachitea*
   Hindwing at least half yellow, orange, or white (Figs. 125, 126, 128) 2
2. Forewing simply bicolored, dark fuscous and yellow or white (Figs. 125, 126) .... *elvira*
   Forewing multicolored with complex pattern (Fig. 128) .... *perbella*

Minonoa elvira (Dognin)
Figures 53, 125, 126, 205, 256; Map 31

Acraga elvira Dognin, 1909: 233.—Sick, 1939: 1306.
Acraga? elvira:—Dyar and Strand, 1913b: 29.
Minonoa elvira:—Dyar, 1927: 551.

Diagnosis. Distinguished by the white or yellow markings on both forewings and hindwings (Figs. 125, 126).

Adult Male (Fig. 125). Forewing length 11 mm. *Head:* Vertex and frons and antennae dark fuscous with intermixed white scales. Labial palpi white. *Thorax:* Dorsum dark fuscous with white; venter white. Forewings dark fuscous, except triangle pointing forward with side on inner margin; triangle is yellow with white proximally. Hindwings white-edged with dark fuscous (1–2 mm wide) around margins. Ventral wings: forewing dark fuscous suffused with white in center and inner margin; hindwing as dorsal but dark fuscous margin reduced around anal angle. Legs white. *Abdomen:* Dorsum dark fuscous with white, venter white. Genitalia as in Figure 205.

Adult Female (Fig. 126). Forewing length 14 mm. Body dark fuscous with legs white. Forewings (dorsal and ventral) yellow with broad (2–3 mm) dark fuscous costal margin and narrow brown outer margin. Hindwing (dorsal and ventral) with broad yellow central band from base almost to anal angle; broad dark fuscous marginal bands on either side of yellow. Genitalia as in Figure 256.

Types. Lectotype male, paralectotype male and female, here designated, USNM 29808.

Type Locality. Colombia, Valle del Cauca, Villa Elvira, 1,600 m.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. June to August.

Distribution (Map 31). Colombia.

Material Examined. 3 males and 1 female. COLOMBIA: *Valle del Cauca:* Villa Elvira, 1,600 m, 20-VII-1908, A. H. Fassl (USNM) (lectotype and paralectotype); Villa Elvira, 1,800 m, 24-VIII-1908, Fassl (USNM) (paralectotype female); Alto de Las Cruces, 2,200 m, VI-1909, Fassl (USNM).

Discussion. I cannot accurately locate the localities. They were apparently on the road between Cali and Buenaventura and probably in Tropical Lower Montane and Premontane Wet Forest Life Zones. The bodies of the types are partly denuded of scales, so coloration is uncertain.

Minonoa pachitea Hopp
Figures 127, 255; Map 31; Color Plate, Figure 18

Minonoa pachitea Hopp, 1922: 430.—Sick, 1939: 1308.

Diagnosis. Entirely dark fuscous with a diagonal orange band across forewing (Fig. 127).

Adult Male. Unknown.

Adult Female (Fig. 127). Forewing length 10 mm. *Head:* Dark fuscous. *Thorax:* Dark fuscous. Forewings apical and basal areas dark fuscous with a broad orange band between them, orange projecting into the apical area from the middle of the apical side of the band. Hindwings dark fuscous. Ventral wings as dorsal. Legs whitish. *Abdomen:* Dark fuscous. Genitalia as in Figure 255.

Type. Holotype female [not male as stated in original description], ZSBS.

Type Locality. Peru, Dept. Huánuco, Pachitea.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. Unknown.

Distribution (Map 31). Peru, probably in Tropical Moist Forest (maybe Tropical Dry Forest) Life Zone.

Discussion. Minonoa pachitea is known only from the holotype, which is missing its left hindwing.

Minonoa perbella Schaus
Figures 128, 257; Map 31;
Color Plate, Figure 17

Minonoa perbella Schaus, 1905: 332.—Dyar, 1910c: 120; 1927: 551.—Dyar and Strand, 1913b: 30.—Sick, 1939: 1308.
Dalcera variegata Jones, 1908: 176. NEW SYN.
Dalcera? variegata:—Dyar and Strand, 1913b: 27.—Sick, 1939: 1304.
Minonoa variegata:—Dyar, 1927: 551.

Diagnosis. Distinguished by complex multicolored pattern on forewing (Fig. 128).

Adult Male. Unknown.

Adult Female (Fig. 128). Forewing length 11 mm. *Head:* Vertex and frons and antennae grey. Labial palpi ochreous. *Thorax:* Dorsum golden yellow, tegulae and patagia fuscous; venter golden yellow. Forewings yellow, outer half suffused with fuscous, very dark at termen; wavy antimedian line; brown spot in cell; orange line bordered by dark fuscous on discocellulars followed distally by yellow space; yellow spaces between veins at margin, especially at apex. Hindwings orange-yellow; inner and outer margins broadly dark fuscous. Ventral wings: forewings yellow, outer half dark fuscous with two yellow spots at apex; hindwings yellow, broadly black on outer margin. Legs ochreous, tarsi white, claws dark fuscous. *Abdomen:* Dorsum golden yellow; venter pale ochreous. Genitalia as in Figure 257.

Types. Holotype female, USNM 8906 (*perbella*); holotype female, BMNH (*variegata*).

Type Localities. Brazil, Rio de Janeiro, Petrópolis (*perbella*); Brazil, Paraná, Castro, 950 m, E. D. Jones (*variegata*).

Host. Unknown.

Immature Stages. Unknown.

Flight Period. Unknown.

Distribution (Map 31). Southern Brazil, in Subtropical Wet Forest and Warm Temperate Moist Forest Life Zones.

Discussion. Known only from the two types, both of which are missing parts of forewing pattern.

Paracraga Dyar

Paracraga Dyar, 1905a: 176; 1910c: 121.—Dyar and Strand, 1913b: 30.—Hopp, 1921: 277.—Sick, 1939: 1309.—D'Almeida, 1945: 195.—Fletcher and Nye, 1982: 118. Type species: *Paracraga innocens* Schaus, 1905, by original designation.

Diagnosis. White or tan ground color with brown or metallic silver ovate maculation on forewing (Figs. 117–124); forewing R_1 arising separately from $R_{2+3,}$ R_{2+3} fused, and R_{4+5} fused (e.g., Fig. 51); large spine on aedoeagus (Figs. 204, 207–213).

Adult Male. Medium to large, forewing 8–13 mm. Ground color: white with maculation; brown ovate outline on forewing, usually silvered inside. Antennae: apical scale tuft absent. Forewing: accessory cell absent; R_{2+3} and R_{4+5} short-stalked basally; R_{2+3} fused; R_{4+5} fused; retinaculum absent. Hindwing: Rs not fused with Sc + R_1 in cell; frenulum absent. Genitalia: tegumen and sociuncus fused complex; socii not distinct, a few setae on dorsal surface of sociuncus; gnathos a thin plate parallel to ventral surface of sociuncus; vinculum long and narrow (except in valvae complex); valvae fused into valvae–vinculum–juxta complex; juxta platelike internally, fused into complex externally; saccus short and fairly narrow, apex blunt; aedoeagus long but stout, bulbous at interior end, triangular spine (tip facing toward moth's right) at exterior end.

Adult Female. Medium to large, forewing 12–16 mm. Genitalia: sterigma a wide round depression; ostium bursae narrow; ductus bursae long, narrow to medium width; corpus bursae ovate; ductus seminalis arising about middle of ductus bursa; apophyses posteriores rudimentary; "accessory glands" ovate in lateral view, longer dorsoventrally than in most genera.

Discussion. In contrast to most dalcerids, the species of this genus all possess very similar male genitalia. Species concepts in *Paracraga* are based primarily on wing pattern, because variation in male genitalia between species is very subtle.

KEY TO MALE *PARACRAGA*

1. Forewing ovate completely surrounded by brown border (Figs. 120, 121, 123, 124) 4
Forewing ovate not completely surrounded by brown border (Figs. 117, 119, 122) 2
2(1). Forewing ovate silvered (metallic) inside 3
Forewing ovate not silvered inside (Fig. 117); border of ovate reaching costa (Fig. 117); northern South America .... *innocens*
3(2). Dorsal forewing ground color whitish (Fig. 122); Peru and Brazil .... *halophora*
Dorsal forewing ground color light brown (Fig. 119); Guyana .... *amianta*
4(1). Sides of forewing ovate (lines from costa to inner margin) almost parallel (Fig. 121); Peru and Colombia .... *canalicula*
Sides of forewing ovate not parallel; ovate oval or pear-shaped (Figs. 120, 123, 124) 5
5(4). Forewing ovate silvered (metallic) inside (Fig. 120); Central America .... *argentea*
Forewing ovate not silvered inside (Figs. 123, 124) 6
6(5). Forewing length 9–11 mm (Fig. 123); northern South America .... *necoda*
Forewing length 8 mm (Fig. 124); Guatemala .... *pulverina*

Paracraga innocens Schaus
Figures 51, 117, 118, 204, 207, 258; Map 32

Paracraga innocens Schaus, 1905: 331.—Dyar, 1910c: 121.—Dyar and Strand, 1913b: 31.—Sick, 1939: 1309.

Paracraga oxydata Hopp, 1921: 277.—Sick, 1939: 1310. NEW SYN.

Diagnosis. Similar to *Paracraga argentea*, but forewing ovate is narrower, not metallic inside, and its brown border reaches costal margin (Fig. 117).

Adult Male (Fig. 117). Forewing length 9–11 mm. *Head:* Vertex and frons and antennae white. Labial palpi white with brown outside. *Thorax:* White. Forewings white suffused with rusty brown; rusty patch along costal margin past end of discal cell; thin wavy brown line across cell, around brown spot at fork of R_{2+3} and R_{4+5}, back down wing to anal angle; brown dots on veins at outer margin, especially on R_{4+5}; brown dot behind 1A + 2A near base. Hindwings white with brown marginal shading at anal angle. Ventral wings white with brown shading along forewing costa. Legs white; foreleg coxa, femur, and tibia brown on inside; last tarsi of all legs brown tipped. *Abdomen:* White. Genitalia as in Figures 204 and 207.

Adult Female (Fig. 118). Forewing length 12–14 mm. Colored as in male. Genitalia as in Figure 258.

Types. Holotype male, USNM 8904 (*innocens*); holotype male, SMF (*oxydata*).

Type Localities. French Guiana, Maroni River, Saint-Laurent (*innocens*); Brazil, Estado Amazonas, Tefé (*oxydata*).

Host. Unknown.

Immature Stages. Unknown.

Flight Period. October to July.

Distribution (Map 32). Venezuela, Guyana, Surinam, French Guiana, and northern Brazil (Amazon Basin), in Tropical Moist and Tropical Premontane Wet Forest Life Zones.

Material Examined. 37 males and 7 females. BRAZIL: *Amazonas:* Fonte Boa, VII, X-1906, S. M. Klages (BMNH); Hyutanahan [now Huitanaã], Rio Purus, I–III, V, VI-1922, Klages (CMNH); Rio Tapajós, [no date] (USNM); Santo Antônio de Javari, V-1907, Klages (BMNH); São Paulo de Olivença, [no date], A. H. Fassl (ZSBS); Tefé, 12-XII-1919 (CMNH), [no date] (SMF, holotype of *oxydata*); "Uypiranga," VII-1931, W. Hopp (ZSBS); *Para:* Rio Guamá, 27-1-1894 (BMNH); FRENCH GUIANA: Nouveau Chantier, VII, X-[no year] (BMNH, USNM); Piste de la Montagne des Singes, Km 10, 150 m, 8-I-1985, J. F. Landry (USNM); Saint-Jean, III–V-1904, W. Schaus, [no date] (BMNH, USNM); Saint-Laurent, IX, XI-1904, Schaus (USNM), II-1906, VII, X, XII-1905, III-[no year], (BMNH), [no date] (MNHP); GUYANA: Mackenzie, Demerara River, 21-VI-1927, [W. T. M. Forbes] (CU); SURINAM: Aroewarwa Creek, Maroewym Valley, IV-1905, Klages (BMNH); Berg en Dal, IV-1892, C. W. Ellacombe (BMNH); VENEZUELA: *Aragua:* Rancho Grande, 1,100 m, 26-V-1946, 26-VI-1946 (AMNH).

Discussion. It is possible that the northern Brazilian specimens represent a distinct species (for which the name *Paracraga oxydata* is available, see later), but I have been unable to find consistent characters for their separation. The wings of the unique male holotype of *oxydata* are very worn, and its identity is not certain, but I cannot find any characters to separate it from *innocens.*

I have seen five males from Peru that are probably *P. innocens*; the forewing pattern appears somewhat different than normal *innocens,* but the specimens are all in poor condition: PERU: *Madre de Dios:* Río Tambopata Reserve, 30 air km SW Puerto Maldonado, 290 m, 11–20-XI-1979, J. B. Heppner (4 males in very poor condition, FSCA, USNM); *Puno:* La Union, Río Huacamayo, 2,000 feet [600 m], XI-1904, wet season, G. Ockenden (BMNH).

Paracraga amianta Dyar
Figures 119, 208; Map 33

Paracraga amianta Dyar, 1910a: 137, fig. 42, no. 22; 1910c: 121.—Dyar and Strand, 1913b: 31.—Sick, 1939: 1309.

Diagnosis. Similar to *Paracraga innocens* but larger and forewing brown lines not reaching costa (Fig. 119).

Adult Male (Fig. 119). Forewing length 11.5 mm. *Head:* Buff. *Thorax:* Buff. Forewings light brown; costa at apex and outer margin yellow; ovate silvery, surrounded by thin brown line from just above anal angle, almost to costal margin, around brown shading in cell apex and back down to lower limit of cell; brown dot near 1A + 2A near base; dots on veins on outer margin. Hindwings white with brownish suffusion. Ventral wings buff, brownish along forewing costal margin. Legs buff with brown. *Abdomen:* Genitalia as in Figure 208.

Adult Female. Unknown.

Type. Holotype male, USNM 12641.

Type Locality. Guyana, Hoorie [now Huri] Creek, Hoorie Gold Mine, February 1908, C. W. Beebe.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. February.

Distribution (Map 33). Guyana, in Tropical Moist Forest Life Zone.

Discussion. Paracraga amianta is known only from the holotype.

Paracraga argentea (Schaus)
Figures 120, 209, 260; Map 34

Minacraga argentea Schaus, 1910: 415.

Paracraga argentea:—Dyar and Strand, 1913b: 31.—Dyar, 1925: 45.—Hoffmann, 1933: 295.—Sick, 1939: 1309.—Schröder, 1963: 493—Beutelspacher, 1992: 145.

Paracraga cyclophera Dyar, 1914: 253.—Sick, 1939: 1310. NEW SYN.

Diagnosis. Similiar to *Paracraga innocens,* but the forewing silver area is completely enclosed by brown line and does not reach costal margin (Fig. 120).

Adult Male (Fig. 120). Forewing length 10–12 mm. *Head:* Vertex and frons and antennae white. Labial palpi white with brown. *Thorax:* White. Forewings silvery buff (ranging from white to pale brownish); ovate silvery white, irregular, thinly outlined with brown extending from near middle of costal margin (but not touching margin) to inner margin near anal angle; brown dots on veins at outer margin, especially on R_{4+5}; brown spot just behind middle of 1A + 2A. Hindwings silvery white. Ventral wings silvery white. Legs white with brown on foreleg inner femur and tibia. *Abdomen:* White. Genitalia as in Figure 209.

Adult Female. Forewing length 12–15 mm. Colored as in male. Genitalia as in Figure 260.

Types. Holotype female, USNM 16951

(*argentea*); lectotype male, and paralectotype male, here designated, USNM 16101 (*cyclophera*).

Type Localities. Costa Rica, Juan Viñas (*argentea*); Panama, Cabima (*cyclophera*).

Hosts. Terminalia buceras Wright (Combretaceae) (Dyar, 1925: 45); *Adelia triloba* (Müller Argoviensis) Hemsley (Euphorbiaceae) (Aiello lot 79-8); *Prunus cerasifera* Ehrhart var. *pissardi* Carrière (Rosaceae) (USNM); *Trema micrantha* (Linnaeus) Blume (Ulmaceae) (Aiello lot 83-9, died as pupa, but same species as lot 79-8); *Uncaria tomentosa* (Willdenow) (Rubiaceae) (Aiello lot 84-23).

Immature Stages. Discussed by Dyar (1925: 45–47).

Flight Period. Year-round.

Distribution (Map 34). Mexico, Honduras, Belize, Guatemala, El Salvador, Costa Rica, and Panama, in Tropical Wet, Tropical Moist, Tropical Premontane Wet, Tropical Premontane Moist, Subtropical Wet, and Subtropical Moist Forest Life Zones.

Material Examined. 54 males and 22 females. BELIZE: Cayo, 13-VII-1972, V. O. Becker (VOB); Punta Gorda, VIII-1934, J. J. White (BMNH); Río Grande, IX-1932, White (BMNH); Río Temash, VII-1934, White (BMNH); [San Pedro] Columbia, III-1932 (USNM); COSTA RICA: Fila Esquinas, 35 km S Palmar Norte, 150 m, 7–8-I-1983, D. H. Janzen & W. Hallwachs (USNM); Hacienda La Suerte/Tapezco, 29 km W Tortuguero, 40 m, 13–31-VIII-1979, J. P. Donahue *et al.* (LACM); Juan Viñas, VI-1909, W. Schaus (USNM, holotype of *argentea*); Orosí, 1,200 m, [no date], A. H. Fassl (BMNH); Rincón de Osa, 20 m, 10–14-XI-1972, Becker (VOB); San José, [no date] (ZSBS), 24-I-1932, F. Nevermann (ZSBS), V, VIII-[no year], H. Schmidt (BMNH); San Pedro de Montes de Oca, reared on *Prunus cerasifera* var. *pissardi*, 25-II-1937, emerged 11–12-III-1937, C. H. Ballou (USNM); Sirena, Corcovado Nat. Park, Osa Peninsula, 5-11-I-1981, 19–27-III-1981, 23-III, 1-V-1984, 10–19-VIII-1980, Janzen & Hallwachs (USNM); "am [=on Mount] Turrialba," [no date], Nevermann (ZSBS); 9.4 km W Bribri, Suretka, 200 m, 9–11-VI-1983, Janzen & Hallwachs (USNM); Turrialba, 600 m, 20-V-1972, 25-VIII-1971, 20-X-1972, Becker (VOB); GUATEMALA: Cayuga, IV & V [no year], Schaus & Barnes (USNM); Cayuga, [no further data] (CMNH); Quiriquá, [no date], Schaus & Barnes (BMNH); HONDURAS: La Cumbre, 700 m, 2-II-1922, J. Lienhart (BMNH); Siguatepeque, 10–16-VIII-1978, J. Chemsak & E. G. Linsley (UCB); MEXICO: *Chiapas:* "La Florida," [800 m], VIII-1931 (AMNH); Tapachula, Finca Violeta, 3-X-1954, G. Hartig (ZSBS); *Tabasco:* [no further locality], I-1914, XII-1913, W. Gugelmann (USNM), "ex larva XII-1913," Gugelmann (AMNH), XI–XII-1913 (ZSBS); Teapa, XII-1913, "R. Müller" [probably collected by Gugelmann] (AMNH, USNM); PANAMA: Barro Colorado Island, 17-V-1984 as larvae on *Uncaria tomentosa*, eclosed 5-7-VI-1984, A. Aiello lot 84-23 (USNM); Cabima, 16–31-V-1911, A. Busck (USNM, paralectotype of *cyclophera*); Cabima, 23-V-1911, Busck (USNM, lectotype of *cyclophera*); Fort Kobbe, VII-1958, 18-IX-1958, W. D. Thomas (CMNH); Pipeline Road, 4 miles [6.4 km] NW Gamboa, ex larva collected 10-III-1979 on *Adelia triloba*, emerged 29–31-III-1979, R. Robbins (USNM) (Aiello lot 79-8).

Discussion. I have seen one male (USNM, genitalia 22588) labeled only "Nicaragua, D. Denning," which probably represents a new species. It is patterned as in *Paracraga argentea*, but the dorsal ground color is light brown and the area inside the forewing ovate outline is light brown. The locality data are not only vague, but also probably wrong. The trichopterist Donald G. Denning reported (personal communication, 1985) that he never collected in Nicaragua, and I can find no record (including in USNM Registrar files) of any other D. Denning who may have collected the specimen.

I have seen two worn specimens from Maracay, Venezuela, which appear to be *Paracraga argentea* (male XI-1934, female VII-1934, P. Vogl in ZSBS).

Paracraga canalicula Dognin
Figures 121, 210, 259; Map 32

Paracraga canalicula Dognin, 1910: 42.—Dyar, 1910c: 121.—Dyar and Strand, 1913b: 31.—Sick, 1939: 1310.

Diagnosis. Similar to *Paracraga argentea*, differing in having forewing lines straighter and more parallel (Fig. 121).

Adult Male (Fig. 121). Forewing length 10–11 mm. Colored as in *Paracraga argentea*, but lines on forewing are straighter and more parallel, enclosing a narrower space. Genitalia as in Figure 210.

Adult Female. Forewing length 15 mm.

Colored as in male. Genitalia as in Figure 259.

Type. Holotype male, USNM 29809.

Type Locality. Peru, Dept. Puno, Provincia de Carabaya, Río Inambari, La Oroya, [ca. 900 m].

Host. Unknown.

Immature Stages. Unknown.

Flight Period. October to March, and May.

Distribution (Map 32). Colombia and Peru, in Tropical Wet, Tropical Moist, and Tropical Premontane Wet Forest Life Zones.

Material Examined. 28 males and 1 female. COLOMBIA: *Meta:* Villavicencio, 400 m, [no date], A. H. Fassl (ZSBS); PERU: *Loreto:* [Cruzmuyuna], Middle Río Ucayali, 17-II-1927, H. Bassler F6041 (AMNH); *Puno:* La Oroya, Río Inambari, [no further data] (USNM, holotype); La Oroya, 3,000 feet [900 m], V-1905, dry season, G. R. Ockenden (ZSBS), I-1906, III-1905, X-1904, XI–XII-1905, wet season, Ockenden (BMNH); La Union, Río Huacamayo, 2,000 feet [600 m], XI-1904, wet season, Ockenden (BMNH); Santo Domingo, 6,000 feet [1,800 m], XI-1904, Ockenden (BMNH).

Discussion. One male (La Union, Peru, BMNH) has its forewing ovate broken at CuP.

Paracraga halophora Dyar

Figures 122, 211, 263; Map 35;
Color Plate, Figure 13

Paracraga halophora Dyar, 1928: 10.—Sick, 1939: 1310.

Diagnosis. Similar to *Paracraga argentea*, but larger and forewing silver ovate not completely outlined in brown (Fig. 122).

Adult Male (Fig. 122). Forewing length 11–13 mm. *Head:* White. *Thorax:* White. Forewings white with rusty tint; ovate large and silver, surrounded by very narrow brown line running from anal angle around apex of cell (almost to costa) and back to lower margin of cell; brown dots on veins on outer margin, especially on R_{4+5}; brown dot near 1A + 2A near base. Hindwings white. Ventral wings white. Legs white with brown. *Abdomen:* White. Genitalia as in Figure 211.

Adult Female. Forewing length 16 mm. Colored as in male. Genitalia as in Figure 263.

Type. Holotype male, CU 896.

Type Locality. Peru, Dept. Junín, Colonia del Perené, Pueblo Pardo.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. March to June, November, and December.

Distribution (Map 35). Brazil and southern Peru, in Tropical Moist, Tropical Premontane Wet, and Subtropical Wet Forest Forest Life Zones.

Material Examined. 14 males and 1 female. BRAZIL: *Amazonas:* Santo Antônio de Javari, V-1907, S. M. Klages (BMNH); *Goiás:* Leopoldo de Bulhões, 25-XI, 12-XII-1935, R. Spitz (BMNH); 20 km N São João da Aliança, [ca. 1,000 m], 15-IV-1956, F. S. Truxal (LACM); *São Paulo:* Anhangahi [now Anhangabaú], XI-1926, Spitz (BMNH); PERU: *Junín:* Pueblo Pardo, Colonia del Perené, [1920] (CU, holotype); *Puno:* La Oroya, Río Inambari, 3,000 feet [900 m], V-1905, G. R. Ockenden (ZSBS), III-1905, Ockenden (BMNH); La Union, Río Huacamayo, 2,000 feet [600 feet], XI–XII-1904, Ockenden (BMNH); Río Huacamayo, 3,100 feet [900 feet], VI-1904, Ockenden (BMNH); Yahuarmayo, 1,200 feet [350 m], IV-V-1912 (BMNH).

Discussion. The holotype bears no date but the following is recorded under CU lot 607 sub 104: "Bought of Srta. Salvatierra, Pueblo Pardo, said to have been caught there at light on various dates," by the CU Expedition of 1920.

There is some variation in the length of the saccus relative to the internal juxta and in the shape of the apex of the external juxta complex (rounded to slightly convex in the middle, from ventral view), but this variation does not seem to be concordant (seven male genitalia examined). The Brazil specimens tend to be smaller (forewing under 12 mm) than the Peru specimens (forewing over 12 mm).

Paracraga necoda (Druce)

Figures 123, 212, 264; Map 33;
Color Plate, Figure 8

Dalcera necoda Druce, 1901: 435.
Paracraga necoda:—Dyar and Strand, 1913b: 31.—Sick, 1939: 1310.

Diagnosis. Similar to *Paracraga argentea*, but darker and inner margin of ovate inflected along M stem (Fig. 123).

Adult Male (Fig. 123). Forewing length 9–11 mm. Similar to *Paracraga argentea*, but wing ground color (dorsal and ventral) light brown or tan; forewing ovate with inner line deflected distally along M (bottom of cell). Genitalia as in Figure 212.

Adult Female. Forewing length 16 mm. Similar to male, but larger and almost white. Genitalia as in Figure 264.

Type. Lectotype male, here designated, and 4 male and 1 female paralectotypes, BMNH.

Type Locality. Colombia, Dept. del Magdalena, Don Amo, 2,000 feet [600 m].

Host. Unknown.

Immature Stages. Unknown.

Flight Period. March, June, and July.

Distribution (Map 33). Colombia, Ecuador, and Venezuela, in Tropical Moist and probably Tropical Premontane Wet and Moist Forest Life Zones.

Material Examined. 12 males and 3 females. COLOMBIA: *Magdalena:* Don Amo, 2,000 feet [600 m], VII-[no year], H. H. Smith (BMNH, types); Minca, 2,000 feet [600 m], [no date], Smith (BMNH); *Not located:* "W slopes of Colombia 4400 ft [1300 m]," II-1908 (BMNH) [determination questionable]; ECUADOR: *Esmeraldas:* Río Cayapas, [no date], G. Flemming & R. Miketta (BMNH); VENEZUELA: *Aragua:* El Limon, 450 m, 19–22-VI-1976, F. Fernandez Y. (UCV); *Carabobo:* Las Quiguas, Esteban Valley, XI-1909–III-1910 (BMNH); Río Borburata, 250 m, 17–24-VI-1971, Fernandez & J. Salcedo (USNM); San Esteban, VII-1909, S. M. Klages (BMNH).

Discussion. Minca, Colombia, is transitional between Tropical Dry and Tropical Premontane Wet Forest Life Zones.

Paracraga pulverina Schaus
Figures 124, 213; Map 36

Paracraga pulverina Schaus, 1920: 150.—Hopp, 1921: 282.—Sick, 1939: 1310.

Diagnosis. Differs from *Paracraga argentea* in smaller size and brown (not silver) forewing ovate (Fig. 124).

Adult Male (Fig. 124). Forewing length 8 mm. Similar to *Paracraga argentea*, but without silvering inside brown forewing ovate outline, and smaller. Genitalia as in Figure 213.

Adult Female. Unknown.

Type. Holotype male, USNM 22498.

Type Locality. Guatemala, Cayuga, June, W. Schaus and J. Barnes.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. June.

Distribution (Map 36). Guatemala, probably in Tropical Moist Forest Life Zone.

Discussion. Paracraga pulverina is known only from the unique holotype, which is in poor condition. It might be an aberrant individual of *Paracraga argentea.*

Ca Dyar

Ca Dyar, 1914: 252.—Hopp, 1921: 279.—Sick, 1939: 1310.—Fletcher and Nye, 1982: 27. Type species: *Ca anastigma* Dyar, 1914, by original designation.

Diagnosis. Similar to both *Paracraga* and *Minacragides,* differing in much smaller size, coloration (color similar to *Minacragides* but lacking ovate forewing pattern of *Paracraga*) (Fig. 138), venation (forewing with only two radial veins) (Fig. 52), and male genitalia (Fig. 206).

Adult Male. Small, forewing 6 mm. Ground color: pale yellow with brown suffusion and maculations. Antennae: apical scale tuft absent. Forewing: accessory cell absent; only two radial veins, apparently R_{1-3} and R_{4-5} fused; R_{1-3} and R_{4+5} arising separately from cell; retinaculum absent. Hindwing: Rs fused with Sc + R_1 in cell; CuA_1 stalked with M_3; frenulum absent. Genitalia: tegumen and sociuncus fused into dorsoventrally flattened complex; socii absent; gnathos thin plate parallel to ventral surface of tegumen–sociuncus complex; vinculum long and (except in valvae–juxta complex) narrow; valvae apparently reduced to lateral angular lobes of vinculum–valvae–juxta complex; juxta internally slender tapered rod, externally fused into vinculum–valvae–juxta complex; saccus long and slender, with bulb at apex; aedoeagus external end slender, retracted into saclike interior portion.

Adult Female. Unknown.

Discussion. My identification of the forewing radial veins is based on comparison to *Minacragides*, assuming further fusion of R_{1-3} However, comparison to *Minonoa* and *Paracraga* and the scenario of wing evolution in which the *radius anterior* forms R_1 and the *radius posterior* forms R_{2-5} (Kukalova-Peck, 1983; Lawrence *et al.*, 1991: 15–16) would suggest identification as R_1 and R_{2-5}, but the homologies of the existing veins and role of cross-veins is not clear.

Ca anastigma Dyar
Figures 52, 138, 206; Map 37

Ca anastigma Dyar, 1914: 252–253.—Sick, 1939: 1310.—Forbes, 1942: 395.

Diagnosis. Similar to *Minacragides arnacis*, differing in smaller size, venation (forewing with only two radial veins; Fig. 52), and male genitalia (Fig. 206).

Adult Male (Fig. 138). Forewing length 6 mm. *Head:* White. *Thorax:* Dorsum light yellow; venter white. Forewings light yellow; wavy poorly defined olivaceous shade across inner third of wing and in submarginal area; outer margin with concave light yellow areas between veins; small elongate discal spot; two black dots on margin near apex. Hindwings white. Ventral wings white with brown forewing costal margin. Legs white. *Abdomen:* White. Genitalia as in Figure 206.

Adult Female. Unknown.

Type. Lectotype male and 3 paralectotype males, here designated, USNM 16100.

Type Locality. Panama, Río Trinidad.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. February, March, June, and October to December.

Distribution (Map 37). Panama, in Tropical Moist Forest Life Zone.

Material Examined. 10 males. PANAMA: Río Trinidad, III-1912 (lectotype), 15–31-III-1912 (paralectotype), 20–25-III-1912 (paralectotype), 1–10-VI-1912 (paralectotype), all A. Busck (USNM); Barro Colorado Island, 9-X, 16-XI, 14-XII-[1934], M. Bates (MCZ, USNM), 5–14-II-1936, Wood, Gertsch & Lutz (AMNH).

Minacragides Dyar

Minacragides Dyar, 1910a: 137; 1910c: 120.—Dyar and Strand, 1913b: 30.—Hopp, 1921: 279.—Sick, 1939: 1308.—D'Almeida, 1945: 194.—Fletcher and Nye, 1982: 103. Type species: *Minacragides arnacis* Dyar, 1910, by monotypy.

Diagnosis. Similar to *Ca*, differing in larger size, venation (forewing has three, not two, radial veins) (Fig. 49), and genitalia (Figs. 214–216).

Adult Male. Small, forewing 8–9 mm. Ground color: pale yellow with brown suffusion and maculation. Antennae: apical scale tuft absent. Forewing: accessory cell absent; R_1 and R_{2+3} stalked; R_{2+3} fused; R_{4+5} fused; retinaculum absent. Hindwing: Rs not fused with Sc + R_1 in cell; frenulum absent. Genitalia: tegumen and sociuncus fused complex; socii not distinct, but sociuncus lobes hairy; gnathos a thin plate parallel to ventral surface of sociuncus, setose ventrally; vinculum long and narrow; valvae reduced to paired lobes ventral to aedoeagus, not fused, tips more sclerotized and bluntly hooked; juxta rodlike internally, platelike externally; saccus short and fairly narrow; aedoeagus long and medium thickness.

Adult Female. Small, forewing 10 mm. Genitalia: sterigma medium width; ostium bursae medium width; ductus bursae medium width, very long, recurved at about one-third of length, recurved again at two-thirds, then narrowing; corpus bursae elongate ovate; ductus seminalis arising from ductus bursae where it narrows; apophyses posteriores triangular, small; "accessory glands" ovate in lateral view.

Discussion. My identifications of forewing radial veins are based on comparison to *Minacraga* and assume further fusion of R_{2+3} and R_{4+5}.

KEY TO *MINACRAGIDES*

1. Forewings pale yellow or tan, with light brown maculation; forewings not falcate 2

Forewings brown; forewings falcate (Fig. 136) .... species A
2. Forewings with large ovate area suffused with black scales (Fig. 137) .... species B
Forewings lacking well-defined ovate area (Fig. 135) .... *arnacis*

Minacragides arnacis Dyar
Figures 49, 135, 214; Map 37; Color Plate, Figure 12

Minacragides arnacis Dyar, 1910a: 137, fig. 42, no. 23; 1910c: 120.—Dyar and Strand, 1913b: 30.—Sick, 1939: 1308.

Ca restricta Schaus, 1940: 86. NEW COMB., NEW SYN.

Diagnosis. Similar to *Ca anastigma*, differing in larger size, venation (Fig. 49), genitalia (Fig. 214), and lobes of eighth abdominal tergite (Fig. 214c).

Adult Male (Fig. 135). Forewing length 8–9 mm. *Head:* Vertex and frons white. Antennae yellowish white. Labial palpi yellow. *Thorax:* White. Forewings pale yellow suffused with light brown; outer margin with concave white areas around dark fuscous streaks between veins; discal spot dark brown; tuft of brown-tipped scales below anal angle. Hindwings white, with faint terminal line. Ventral wings white. Legs white with brown. *Abdomen:* White. Eighth tergite with a posterior hooklike lobe protruding over each side of genitalia. Genitalia as in Figure 214.

Adult Female. Unknown.

Types. Holotype male, USNM 12642 (*arnacis*); holotype male, USNM 34742 (*restricta*).

Type Localities. Guyana, Hoorie [now Huri] Creek, Hoorie Gold Mine (*arnacis*); Guyana, Bartica District, Kartabo [now Kartabu] (*restricta*).

Host. Unknown.

Immature Stages. Unknown.

Flight Period. February to August and November to December.

Distribution (Map 37). Colombia, Venezuela, Guyana, Surinam, and Peru, in Tropical Moist, Tropical Premontane Wet, and Tropical Premontane Moist Forest Life Zones.

Material Examined. 28 males. COLOMBIA: *Cundinamarca:* Monterredondo, 1,420 m, 26-V–18-VI-1961, P. B. Schneble (ZSBS); GUYANA: Hoorie Gold Mine [specimen's data label bears only a typewritten "24"], [II-1908], C. W. Beebe (USNM, holotype of *arnacis*); Kartabu, 21-VII-1922 (USNM, holotype of *restricta*); Rockstone, 25-IV–9-V-[1901], W. J. Kaye (BMNH); PERU: *Puno:* La Oroya, Río Inambari, 3,100 feet [900 m], III, XI–XII-1905, wet season, G. R. Ockenden (BMNH); Yahuarmayo, 1,200 feet [350 m], IV-1913 (BMNH); SURINAM: Aroewarwa Creek, Maroewym Valley, IV-1905, S. M. Klages (BMNH); VENEZUELA: *Aragua:* Rancho Grande, 1,100 m, 8–14-VI-1967, R. W. Poole (USNM), 26-VI-1946 (AMNH); *Bolívar:* El Dorado to Santa Elena road, Km 107, 520 m, 16-VIII-1957, F. Fernandez Y. & C. J. Rosales (UCV); *Carabobo:* Río Borburata, 300 m, 19–22-XI-1955, Fernandez & Rosales (UCV).

Minacragides new species A
Figures 136, 215; Map 37

Diagnosis. Differs from *Minacragides arnacis* in brown coloration and falcate forewings (Fig. 136).

Adult Male (Fig. 136). Forewing length 9 mm. *Head:* Vertex and frons brown. Antennae brown. Labial palpi white. *Thorax:* Dorsum brown, venter white (?, denuded). Forewings brown; falcate. Hindwings brown, pale along costal margin. Ventral wings brown, forewing inner margin and hindwing costal margin white. Legs white with brown tufts on foretibia and all last tarsal segments. *Abdomen:* Dorsum brown, venter white. Genitalia as in Figure 215.

Adult Female. Unknown.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. October.

Distribution (Map 37). Southeastern Brazil, in Subtropical Wet Forest Life Zone.

Material Examined. 1 male. BRAZIL: *Rio de Janeiro:* [Itatiaia, 400 m], 24-X-1935, J. F. Zikan (IOC).

Discussion. I refrain from naming this species because only one specimen is available. The lines on the wings, evident in the photograph, are artifacts of spreading the wings.

Minacragides(?) new species B
Figures 50, 137, 216, 262; Map 37

Diagnosis. Differs from *Minacragides arnacis* in forewing pattern (Fig. 137) and venation (Fig. 50).

Adult Male (Fig. 137). Forewing length 8.5 mm. *Head:* Tan. *Thorax:* Tan, with a few brown scales. Forewings light brown or tan; large ovate area running from about Sc to CuP suffused with dark fuscous scales; ovate area is centered on a white patch, which runs along the end of the discal cell from M_1 to CuA_1. Hindwing pale tan. Ventral wings pale tan, costal edge of forewing suffused with brown. Legs tan, with a few brown scales. *Abdomen:* Tan. Genitalia as in Figure 216.

Adult Female. Forewing length 9.5–10 mm. Apparently colored as in male. Genitalia as in Figure 262.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. November.

Distribution (Map 37). Central Brazil, in Tropical Premontane Moist Forest Life Zone.

Material Examined. 1 male and 2 females. BRAZIL: *Distrito Federal:* Planaltina, 1,000 m, 11-XI-1976, 13-XI-1975, 23-XI-1975, V. O. Becker (VOB, USNM).

Discussion. I refrain from naming this species because all the available specimens are badly rubbed. Although this species is very close to *Minacragides* in male genitalia, it may not belong in *Minacragides*, because it differs in venation from the other species in having a forewing accessory cell and anal loop and having the hindwing Rs fused with Sc + R_1 in the discal cell (Fig. 50).

Oroya, new genus

Type Species. Oroya aurora, new species, by present designation.

Diagnosis. Entirely orange; forewing with accessory cell absent, R_1 free, $R_2 + R_3$ stalked (Fig. 47), $R_4 + R_5$ stalked; male genitalia with long processes on uncus (Fig. 220).

Adult Male. Medium size, forewing 9–10 mm. Ground color: orange without markings. Antennae: apical scale tuft absent. Forewing: accessory cell absent; well-developed pterostigma present between R_1 and costa; $R_2 + R_3$ stalked; $R_4 + R_5$ stalked; retinaculum present. Hindwing: base of Rs fused with Sc + R_1; frenulum present. Genitalia: tegumen and sociuncus fused complex with pair of posterior arms from uncus; socii present as oval hairy pads; gnathos reduced to small processes on inner sides of socii, not fused; vinculum slender, short; valvae fused into complex with juxta (and anellus?), maybe represented by squared lateral lobes of complex; juxta fused into complex with valvae; saccus long, slender; aedoeagus long, slender.

Adult Female. Unknown.

Discussion. Known only from males of type species. The generic name is feminine and refers to the type locality of the type species, La Oroya.

Oroya aurora, new species

Figures 47, 150, 220; Map 44;
Color Plate, Figure 11

Diagnosis. Superficially similar to a small *Acraga*, easily distinguished by venation (Fig. 47) and genitalia (especially long posterior processes of uncus; Fig. 220).

Adult Male (Fig. 150). Forewing length 9–10 mm. Entirely orange, dorsal forewings deep orange with no markings. Genitalia as in Figure 220.

Adult Female. Unknown.

Type. Holotype male, BMNH.

Type Locality. Peru, Dept. Puno, Río Inambari, La Oroya, 900 m.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. January, March, May, and October to December.

Distribution (Map 44). Southern Peru and adjacent Bolivia, in Tropical Premontane Wet, Tropical Premontane Moist(?) (Peru), and Subtropical (Lower?) Montane Wet (Bolivia) Forest Life Zones.

Material Examined. 11 males (all paratypes). BOLIVIA: *La Paz:* Yungas de Coroico, 1,900 m, 19-V-1950, W. Forster (ZSBS); PERU: *Cuzco:* Pilcopata, 600 m, 11–14-XII-1979, J. B. Heppner (USNM); *Puno:* La Oroya, Río Inambari, 3,100 feet [900 m], I-1906, III-1905, X-1904, G. R. Ockenden, wet season (BMNH, including holotype, USNM, VOB); Santo Domingo, 6,000 feet [1,800 m], XI-1904, Ockenden (BMNH).

Discussion. The species name is from the Latin word *aurora* and refers to the orange color of a sunrise. W. Hopp recognized the ZSBS specimen as a new species, but never published his description. The Pilcopata male has a forewing length of 7.5 mm.

Dalcera Herrich-Schäffer

Dalcera Herrich-Schäffer, [1854]: wrapper, pl. 37, fig. 180.—Walker, 1855b: 1106.—Möschler, 1878: 672.—Druce, 1887: 213.—Kirby, 1892: 542.—Dyar, 1898: 231, 1910c: 114.—Pagenstecher, 1909: 439.—Dyar and Strand, 1913b: 27.—Sick, 1939: 1303.—D'Almeida, 1945: 194.—Orfila, 1961: 259.—Fletcher and Nye, 1982: 48. Type species: *Dalcera abrasa* Herrich-Schäffer, [1854], by monotypy.

Diagnosis. Very similar to *Dalcerina*, differing in forewing R_1 arising separately from R_{2+3} (rather than arising together on a short stalk) (Fig. 55), the vinculum processes in the male genitalia (Figs. 218, 219), the more rounded forewing, and less maculation on the male forewing (Figs. 129, 131, 132).

Adult Male. Large, forewing 16–21 mm. Ground color: orange with maculation and overshading. Antennae: apical scale tuft present. Forewing: accessory cell absent; R_1 arising independently from cell; R_2 + R_3 stalked; R_4 + R_5 stalked; retinaculum present. Hindwing: Rs not fused with Sc + R_1 in cell; frenulum present. Genitalia: tegumen and sociuncus fused complex; socii paired rounded hairy lobes; gnathos a single strongly sclerotized, ridged, near triangular plate; vinculum elongate; valvae not identified (see later); juxta fused into vinculum (see later); saccus elongate, broad, narrowing toward apex; aedoeagus long and slender; two pairs of setose processes arising from vinculum complex.

Adult Female. Large, forewing 20–26 mm. Genitalia: sterigma broad, with deep, narrow cleft in middle; ostium bursae medium width; ductus bursae long, medium width for about one-third of length, recurved, then narrow for one-third of length to ductus seminalis, then recurved to corpus bursae; corpus bursae elongate ovate; ductus seminalis arising at second bend in ductus bursae; apophyses posteriores wide at base, narrowing to apex, medium length; "accessory glands" ovate in lateral view.

Discussion. The two pairs of setose processes arising from the vinculum complex both appear solidly fused with this complex. The more ventral process (long in *abrasa*, short in *canescens*) might be the bifid end of a juxta fused into vinculum, the more dorsal (rudimentary in *abrasa* [just ventral of setose lump in Figure 218], long in *canescens*) may represent valvae.

KEY TO MALE *DALCERA*

1. No dark terminal stripe on hindwing 2
Dark terminal stripe on hindwing 3
2(1). No scarlet patch in anal area of forewing (Fig. 129) .... *abrasa*
Scarlet patch in anal area of forewing .... *haywardi*
3(1). Dark terminal stripe on hindwing narrow and usually faint, less than 2 mm wide (Fig. 129) .... *abrasa*
Dark terminal stripe on hindwing wider than above 4
4(3). Dark terminal stripe 2–4 mm wide, up to one-quarter width of wing (Fig. 131) .... *canescens*
Dark terminal stripe over 4 mm wide, about half as wide as wing (Fig. 132) .... *semirufa*

Dalcera abrasa Herrich-Schäffer
Figures 7, 18, 19, 21, 55, 129, 130, 218, 261; Map 38

Dalcera abrasa Herrich-Schäffer, [1854]: 7, 59, 79, fig. 180.—Walker, 1855b: 1106.—Möschler, 1878: 673.—Kirby, 1892: 542.—Dyar, 1898: 231; 1910c: 114.—Dyar and Strand, 1913b: 27.—Hopp, 1921: 277, 282.—Koehler, 1924: 25; 1928: 9.—Sick, 1939: 1304, pl. 168a.—Araujo, 1951: 55–57.—Orlando and Ribeiro, 1955: 140–146.—Sarmento, 1958: 20.—Mariconi, 1963: 334–335.—Silva *et al.*, 1968: 295.—Le Pelley, 1968: 59, 205, 456.—Watson and Whalley, 1975: 188, pl. 48c.

Diagnosis. Most males differ from *Dalcera canescens* and *D. semirufa* in having dark terminal stripe on hindwing absent (Fig. 129); if stripe is present, then less than 2 mm wide.

Adult Male (Fig. 129). Forewing length 15–20 mm. *Head:* Vertex straw yellow, hairs tipped with dark brown forming brown spot in center. Antennae dark brown with touches of white along sides of shaft, especially near tip; apical seven segments bear brown hair tuft with white tip. Labial palpi dark brown with varying amounts of white, especially on outer surface. *Thorax:* Dorsum pale yellow at front becoming yellow posterad; brown spot at base of wing behind head; venter pale yellow. Forewings light dirty orange with costal margin yellow (pale along margin, interior bright) with dark fuscous at base; most specimens with fuscous shading along outer margin and/or a small oblique discal mark. Hindwings yellow-orange with white fringe, sometimes with outer margin slightly to moderately darkened. Ventral wings colored like dorsal wings, except colors not so bright. Forelegs orange, coxa, outer femora and tibia and all the tarsi dark brown, the distal edge of the tibia and each tarsomere ringed with white; midlegs orange, tibia and tarsomeres as in forelegs; hindlegs orange, fourth and fifth tarsomeres brown tipped. *Abdomen:* Yellow-orange of hindwings. Genitalia as in Figure 218.

Adult Female (Fig. 130). Forewing length 20–26 mm. Colored as in male, usually with less fuscous shading on outer margin of forewing. Genitalia as in Figure 261.

Type. Lost?.

Type Locality. Colombia.

Host. Coffea arabica Linnaeus (Rubiaceae) (Araujo, 1951; Orlando and Ribeiro, 1955; Le Pelley, 1968); *Echinochloa polystachia* (Kunth) Hitchcock (Gramineae) (INPA); *Eucalyptus robusta* Smith and *Eucalyptus* sp. (Myrtaceae) (UCV); *Spondias purpurea* Linnaeus (Anacardiaceae) (USNM).

Immature Stages. Described by Araujo (1951).

Flight Period. Year-round.

Distribution (Map 38). Colombia, Venezuela, Guyana, Surinam, French Guiana, Brazil, Peru, and Bolivia. Recorded from Tropical Wet, Tropical Moist, Tropical Dry, Tropical Premontane Wet, Tropical Premontane Moist, Tropical Lower Montane Moist, Subtropical Moist, Subtropical Lower Montane Moist, Warm Temperate Moist, and Warm Temperate Dry Forest Life Zones.

Material Examined. Over 350 males and 52 females. Abbreviated data: BOLIVIA: *Cochabamba:* Chaparé, 400 m, XII (ZSBS); *El Beni:* Santa Ana, Río Yacuma, 220 m, V (ZSBS); *La Paz:* Río Zongo, 750 m (NHMV, USNM, ZSBS); *Santa Cruz:* "Prov. del Sara" [now Gutiérrez], 450 m, VIII (BMNH, CMNH); Puerto Suarez, 150 m, XII (CMNH); BRAZIL: *Amapá:* Serra do Navio, III (MNRJ); *Amazonas:* Amataurá, Rio Solimões, II (CU); Amazon between Tefé and Tonantins, XI (USNM); Canal Maturaca, Mission Cauaburi, 70 m, XII (ZSBS); Codajás, IV (BMNH); Fonte Boa, IV, VI–X (BMNH); Hyutanahan [now Huitanaã], Rio Purus, I–IV (CMNH); Ilha de Marchantaria, Rio Solimões, larva 7-XII-1983 on *Echinochloa polystachia*, pupated 9-XII, emerged 4-I-1984, J. Adis (INPA); Lower Amazon and Rio Madeira, II–III (BMNH); Manaus, IX (BMNH); Miracema, Rio Purus, IV (CMNH); Nova Olinda, Rio Purus, IV (CMNH); Parana de Buyassu [now Igarapé Buiuçu], Lower Amazon, I (BMNH); Rio Madeira (BMNH); Rio Negro, "Kl. 12," VII–VIII (IOC); Rio Tapajós (USNM); Santo Antônio de Javari, VI (BMNH); São Paulo de Olivença, I, XI–XII (BMNH, USNM); Tapurucuara, Rio Negro, XI (ZSBS); Tefé, I, X, XII (BMNH, CMNH); "Uypiranga," VI (ZSBS), XI (IOC); *Distrito Federal:* Planaltina, 1,000 m, IV, XI, XII (CPAC, VOB); *Goiás:* Veadeiros [now Alto Paraiso], IV (LACM); 20 km N São João da Aliança, IV–V (LACM); *Maranhão:* Maranhão (BMNH); *Mato Grosso:* Chapada dos Gumarães, IV (MNRJ); "Matto Grosso" (ZSBS); Rio Brilhante, I (VOB); *Mato Grosso do Sul:* Corumbá, IV (VOB); Salobra V, XI (IOC); *Minas Gerais:* Serrinha, Diamantina, X–IV (AMNH); Sete Lagoas, 720 m, IV, V (VOB); *Pará:* Capim, II (MNRJ); Capitão Poço, XI (VOB); Marabá, I (VOB); "Pará" [=Belém] (BMNH); Rio Xingu Camp, 52°22′W, 3°39′S, ca. 60 km S Altamira (USNM); Santarém (BMNH); São Félix do Xingu, Moyen [=middle] Xingu, IX (MNHP); Taperinha (NHMV, USNM); *Rondônia:* Calama, Rio Madeira, VIII–X (BMNH); *Santa Catarina:* "St. Catherines" (USNM); *São Paulo:* Emas, near Piraçununga, III, XII (IOC); Piraçununga, VI (IOC); *Not located:* Canalitae, Rio Magdalena, VII (ZSBS); COLOMBIA: *Cauca:* Popayan (BMNH, female only); *Cundinamarca:* Medina, 500 m (BMNH); *No locality:* (AMNH); FRENCH GUIANA: Maroni (MNHP); Nouveau Chantier, I, II, V, VII, VIII, XI (BMNH, CMNH, ZSBS); Pied Saut, II, XII (CMNH); Saint-Jean, IV, V (BMNH, USNM); Saint-Laurent, II–IV, VII–XII (BMNH, MNHP, USNM); 60 miles [100 km] up Maroni River, VIII (USNM); GUYANA: Bartica, I (BMNH, CMNH); Berbice [now New Amsterdam] (BMNH); Fort Akayma, Rio Demerara (UMO); Kartabu, III, VI, X, XII (AMNH, CMNH, USNM); Kutari Sources, I–II (BMNH); MacKenzie, VI (CU); Moraballi Creek, Essequibo River, XI (BMNH); New

Amsterdam (BMNH); New River, I–III (BMNH); Omai (USNM); Plantain Is., III (USNM); Potaro, I, II, V (BMNH); Potaro River (UMO); Rio Demerara (BMNH); Rockstone, VII, IX (AMNH, USNM); Tumatumari, VI, XII (BMNH, CU); Upper Courantyne River, King Frederick William IV Falls, III (BMNH); Wismar, V, VI (AMNH); PERU: *Amazonas:* Chanchamayo (BMNH); *Cuzco:* Buenos Aires, 53 km W Pilcopata, 2,280 m, XII (USNM); Marcapata (ZSBS); Pilcopata, 600 m, XII (FSCA); *Huánuco:* Tingo María, XII (MPM); *Junín:* La Merced, Chanchamayo (USNM); *Loreto:* Contamana, Río Ucayali, X–XII (BMNH); Lower Río Ucayali, II (AMNH); Río Ucayali (BMNH); San Miguel, VIII (AMNH); Río Napo, VI (CMNH); *Madre de Dios:* Río Tambopata Reserve, 290 m, XI (FSCA); *Puno:* La Union, Río Huacamayo, 600 m, XII (BMNH); La Oroya, Río Inambari, 900 m, I (BMNH); Río Huacamayo, 900 m, VI (BMNH); Santo Domingo, 1,900 m, XII (BMNH); Yahuarmayo, 350 m, II–III (BMNH); *San Martín:* Jepelacio (USNM); Shapaja, Upper Río Huallaga, XI (AMNH); Upper Río Huallaga, XI (CU); SURINAM: Aroewarwa Creek, Maroewym Valley, IV, VII (BMNH); Brokopondo (RNHL); Moengo, Boven, Cottica River, V (CU, USNM); Paramaribo (RNHL); Patamakka River (RNHL); VENEZUELA: *Amazonas:* Mount Marahuaca, N. Slopes, Benitez Camp, V (USNM); San Carlos de Río Negro, VIII, X (UCV); Santa Lucía, Río Negro, II, VIII, XI (UCV, USNM); Cerro de la Neblina basecamp, 0°50'N, 66°9'44"W, 140 m, II–III (USNM); *Aragua:* El Castaño, "en *Eucaliptus* [sic]," VI (UCV); Rancho Grande, 1,100 m, XII (UCV); *Bolívar:* El Bochinche Res. Forestal Imataca, 200 m, XII (UCV); El Dorado to Santa Elena Road, Km 107, 520 m, VIII (UCV); *Carabobo:* Las Quiguas, Esteban Valley (CMNH); San Esteban, VI, XI (BMNH, UCV); Río Borburata, 250 m, I (UCV); *Mérida:* Mérida, IX, no date (BMNH, CMNH, MNHP, NHMV, UMO, USNM, ZMUC, ZSBS); Mérida, 1,630 m (BMNH, CMNH, ZSBS); Mérida, Terre temperee (USNM); Valle, 2,200 m (BMNH); *Monagas:* Uverito, X ("en *Eucaliptus* [sic] *robusta*"), XI (UCV); *Zulia:* San José de Los Altos, Sierra de Perija, 1,150 m, X (UCV); *Not located:* Andes, 1,500–4,000 m (RNHL); "L. Laglaize," XII (USNM); "Venezuela" (BMNH, CMNH, USNM, ZSBS).

Discussion. This is the most common dalcerid in collections and has the widest known distribution. The darkness of the outer margins of both wings and the size of the forewing discal spot are all highly variable. I have seen one Venezuela female (USNM) in which the right side forewing venation is normal (R_1 and R_{2+3} arise separately from cell) but R_1 and R_{2+3} arise together on the cell on the left side.

Herrich-Schäffer (1856: 7) listed his figure 509 as *Dalcera abrasa* but correctly cited figure 509 elsewhere (l.c. 59, 84) as *Scopelodes palpalis* Walker (now a synonym of *Scopelodes unicolor* Westwood; Limacodidae).

Dalcera haywardi Orfila

Map 39

Dalcera haywardi Orfila, 1961: 260–261, fig. 9, pl. I, fig. 7.

Diagnosis. Similar to *Dalcera abrasa,* supposedly differing in having a scarlet spot in the anal area of the dorsal forewing; probably not a valid species.

Adult Male. Wing expanse 34–38 mm (Orfila, 1961). Very similar to *Dalcera abrasa,* but with a scarlet spot in the anal area of the dorsal forewing.

Adult Female. Unknown.

Type. Holotype, male, lost?.

Type Locality. Argentina, Salta, Dept. Oran, Río Aguai, Vespucio.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. October.

Distribution (Map 39). Known only from the type locality in northern Argentina, probably in Warm Temperate Moist Forest Life Zone.

Material Examined. None.

Discussion. This species is known to me only by the description. The curators at MBR (where Orfila's collection is now located), MLP, IML, and INTA were unable to locate any specimens. It is distinguished from the closely related *Dalcera abrasa* only by the scarlet spot in the "anal area" of the forewing and is probably a synonym of *D. abrasa.*

Dalcera canescens Tams

Figures 131, 219; Map 39;
Color Plate, Figure 3

Dalcera canescens Tams, 1926: 35.—Sick, 1939: 1311, pl. 168c.

Dalcera consanguinea Dyar, 1927: 550.—Sick, 1939: 1311. NEW SYN.

Diagnosis. Similar to *Dalcera abrasa,* differing in darker forewing than the darkest *abrasa*, wider hindwing margin (Fig. 131), and male genitalia (Fig. 219).

Adult Male (Fig. 131). Forewing length 18–21 mm. Similar to *Dalcera abrasa* except in coloration of wings. Forewings dirty orange with a fuscous suffusion, especially heavy toward outer margin; costa (except for brown base) and inner margin white. Hindwing yellow-orange with a narrow outer dark fuscous border, less than one-fourth the length of the wing wide. Genitalia as in Figure 219.

Adult Female. Unknown.

Types. Holotype male, BMNH (*canescens*); lectotype male, USNM 40713, here designated (*consanguinea*).

Type Localities. Peru, Puno, Yahuarmayo, 1,200 feet [350 m] (*canescens*); Brazil, Amazonas, Rio Tapajós (*consanguinea*).

Host. Unknown.

Immature Stages. Unknown.

Flight Period. April, July, September, and November to January.

Distribution (Map 39). Surinam, French Guiana, Brazil, and Peru, in Tropical Moist and Tropical Premontane Wet Forest Life Zones.

Material Examined. 18 males. BRAZIL: *Amapá:* Serra do Navio, 7-II-1964, O. H. H. Mielke (MNRJ); *Amazonas:* Miracema, Rio Purus, IV-1917, S. M. Klages (CMNH); Rio Tapajós (USNM, lectotype of *consanguinea*); *Pará:* Marabá, 50 m, 9-1-1977, V. O. Becker (VOB); "Pará" [=Belém], [no date], A. M. Moss (BMNH); *Rondônia:* Porto Velho, Rio Madeira (USNM, paralectotype of *consanguinea*); FRENCH GUIANA: Pied Saut, Oyapock River, XII-1917 (CMNH); PERU: *Huánuco:* Tingo María, 24-XII-1949, H. A. Allard (USNM); *Puno:* La Oroya, Río Inambari, 3,100 feet [900 m], IX-1905, G. R. Ockenden (BMNH); La Union, Río Huacamayo, 2,000 feet [600 m], XI-1904, wet season, Ockenden (BMNH); Yahuarmayo, 1,200 feet [350 m], IV-1912 (BMNH, holotype of *canescens*); SURINAM: Aroewarwa Creek, Maroewym Valley, VII-1905, Klages (BMNH).

Discussion. This species has sometimes been collected at the same sites and dates as *Dalcera abrasa.*

Dalcera semirufa Druce
Figure 132; Map 39;
Color Plate, Figure 1

Dalcera semirufa Druce, 1910: 177.—Dyar and Strand, 1913b: 27.—Sick, 1939: 1304.

Diagnosis. Similar to *Dalcera abrasa* and *D. canescens* except forewings are darker and dark fuscous margin of hindwing is very wide (Fig. 132).

Adult Male (Fig. 132). Forewing length 16–17 mm. Similar to *Dalcera abrasa* except in coloration of wings. Forewings deep reddish brown dorsally. Ventral forewings dark fuscous forward of bottom of cell and CuA_2 and along outer margin, area around inner margin orange yellow. Hindwings (dorsum and venter) orange-yellow with very broad dark fuscous border, one-third to one-half the length of the wing wide. Genitalia as in *D. abrasa.*

Adult Female. Unknown.

Types. Lectotype male, here designated, and paralectotype male, BMNH.

Type Locality. Colombia, Dept. del Chocó, Río "Somana," Río San Juan, Novita, 150 feet [45 m].

Host. Unknown.

Immature Stages. Unknown.

Flight Period. Unknown.

Distribution (Map 39). Western slopes of Andes of Colombia, in Tropical Wet and Tropical Rain Forest Life Zones.

Material Examined. 3 males. COLOMBIA: *Cauca:* Río [San Juan de] Micay, [no date], W. Hopp (ZSBS); *Chocó:* Novita, Río "Somana" [Tamaná], Río San Juan, 45 m, [no date], G. M. Palmer (BMNH, types).

Discussion. The male genitalia of *Dalcera semirufa* are almost identical to those of *Dalcera abrasa. Dalcera semirufa* may be a small, dark subspecies of *D. abrasa,* but because of the great external differences and the absence of data on females and immatures, I prefer to retain it as a valid species. Only a few specimens of *D. abrasa* are known from Colombia, including a female from Popayan, which I am assuming is *D. abrasa* because it has the size (forewing 23 mm) and coloration of *D. abrasa*.

Dalcerina Dyar

Dalcerina Dyar, 1898: 232; 1910c: 115.—Dyar and Strand, 1913b: 28.—D'Almeida, 1945: 194.—Fletcher and Nye, 1982: 48. Type species: *Dalcera tijucana* Schaus, 1892, by original designation.

Zadalcera Dyar, 1910c: 114, 115.—Dyar and Strand, 1913b: 27.—D'Almeida, 1945: 195.—Orfila, 1961: 261.—Fletcher and Nye, 1982: 171. Type species: *Dalmera* [sic] *fumata* Schaus, 1894, by original designation. [synonymized under *Dalcerina* by Hopp, 1921: 277]

Diagnosis. Very similar to *Dalcera*, differing in forewing R_1 arising together with R_{2+3} on a short stalk from the cell (rather than R_1 and R_{2+3} arising separately) (Fig. 56), vinculum processes in the male genitalia (Fig. 217), more triangular forewing (less rounded, especially at anal angle), and submedial shading and curved inner half-band on the male dorsal forewing (Fig. 133).

Adult Male. Medium to large, forewing 14–20 mm. Ground color: orange with maculation. Antennae: apical scale tuft present. Forewing: accessory cell absent; R_1 arising together with R_{2+3} on a short stalk from cell; $R_2 + R_3$ long-stalked; $R_4 + R_5$ short-stalked; retinaculum present. Hindwing: Rs not fused with Sc + R_1 in cell; frenulum present. Genitalia: tegumen and sociuncus fused complex; socii paired hairy lobes; gnathos one strongly sclerotized, ridged, near triangular plate; vinculum elongate; valvae not identified, probably the squarish paired processes dorsal of the aedoeagus in the diaphragma (see below); juxta Y-shaped, with single tapered branch interiorly, externally with paired setose lobes, with small, short lobe between them (it is possible that these paired setose lobes could be valvae); saccus elongate, broad, tapering to apex; aedoeagus long and slender; a semicircular slender, flexible, rod attached at the middle between the outside of the juxta and the inside of the ventral wall of the saccus.

Adult Female. Large, forewing 20–24 mm. Genitalia: sterigma broad, with broad U-shaped cleft in middle; ostium bursae narrow; ductus bursae long, medium width about first $\frac{2}{6}$ then recurved $\frac{1}{6}$ of length to ductus seminalis, then recurved to corpus bursae; corpus bursae ovate; ductus seminalis arising at second bend in ductus bursae; apophyses posteriores narrow, long; "accessory glands" ovate in lateral view.

Discussion. The homology of the semicircular rodlike process already mentioned is unknown, but the structure may be related to the bifid anellus attached to the vinculum of some Epipyropidae (see Heinrich, 1931: fig. 5).

Dalcerina tijucana (Schaus)
Figures 1–3, 56, 133, 134, 217, 267; Map 40; Color Plate, Figure 4

Dalcera tijucana Schaus, 1892: 322.

Dalcerina tijucana:—Dyar, 1898: 232; 1910c: 115.—Dyar and Strand, 1913b: 28.—Hopp, 1921: 277–279.—Sick, 1939: 1305, pl. 168f.—Schoorl, 1990: 253.—Miller, 1993: 179.—Hogue, 1993: 327.

Dalmera [sic] *fumata* Schaus, 1894: 238.

Dalcera fumata:—Dyar, 1898: 231.

Zadalcera fumata:—Dyar, 1910c: 115.—Dyar and Strand, 1913 b: 27.—Sick, 1939: 1304.—Gomes and Reiniger, 1939: 26.—Lima, 1945: 181–184, figs. 76–81.—Gomes, 1940: 60–61, 72, 89, 106, 107, 246.—Duarte, 1947: 189.—Biezanko *et al.*, 1949: 169; 1966: 5.—Orfila, 1961: 262–263, figs. 4, 10–12, pl. 1, figs. 8, 9.—Biezanko, 1961a: 3; 1961b: 4.—Ruffinelli Rey, 1967: 20.—Silva *et al.*, 1968: 296.—Borror and DeLong, 1969: 339, figs. 26–65.—Gonçalves and Gonçalves, 1973: 13.—Biezanko *et al.*, 1974: 124; 1978: 58.—Guimarães, 1977: 39. [synonymized under *tijucana* by Hopp, 1921: 277]

Zadalcera arhathodota Dyar, 1910c: 115.—Dyar and Strand, 1913b: 27.—Sick, 1939: 1304. NEW SYN.

Zadalcera muncia Dyar, 1923: 30.—Sick, 1939: 1304. NEW SYN.

Zadalcera dierrhyeoa Dyar, 1923: 30.—Sick, 1939: 1304. NEW SYN.

Diagnosis. See diagnosis of *Dalcerina*.

Adult Male (Fig. 133). Forewing length 14–20 mm. *Head:* Vertex light orange. Antennae dark brown with touches of white along sides of shaft, especially near tip; apical seven segments bear brown hair tuft with white tip. Labial palpi dirty orange. *Thorax:* Dorsum pale yellow becoming yellow posterad; venter orange. Forewings pale yellow dorsally, faintly reddish along outer and inner margins, lightest along costal margin; elongate oblique dark fuscous discal mark; below discal mark and from near the base of Sc to middle of outer margin a smokey suffusion, often broadening at outer margin to cover M_1–M_3; below this a crescent-shaped mark extends to inner margin. Dorsal hindwing yellow-orange. Ventral wings yellow-orange, with dark fuscous base of costal margin and discal mark on forewing. *Abdomen:* Yellow-orange. Genitalia as in Figure 217.

Adult Female (Fig. 134). Forewing length 20–24 mm. Colored as in male, except forewing markings reduced to discal spot only or absent. Genitalia as in Figure 267.

Types. Holotype male, USNM 12547 (*tijucana*); lectotype male, USNM 12547, and 4 male paralectotypes, here designated (*fumata*); holotype male, USNM 25424 (*muncia*); holotype female, USNM 13056 (*arhathodota*); holotype female, USNM 25304 (*dierrhyeoa*).

Type Localities. Brazil, Estado do Rio de Janeiro, Rio de Janeiro, Tijuca (*tijucana*); Brazil, Estado do Paraná, Castro (*fumata*); Paraguay, Dept. Cordillera, San Bernardino (*muncia* and *dierrhyeoa*); Brazil, "Rio Janeiro" (*arhathodota*).

Hosts. Citrus sinensis (Linnaeus) Osbeck (Rutaceae) (Biezanko *et al.*, 1949: 169); *Eucalyptus saligna* Smith (Myrtaceae) (Silva *et al.*, 1968: 296); *Ouratea* sp. (Ochnaceae) (CPAC 9400, V. O. Becker, personal communication, 1985).

Immature Stages. Described and illustrated by Gomes and Reiniger (1939) and Lima (1945).

Flight Period. Year-round.

Distribution (Map 40). Brazil, eastern Peru, Paraguay and northern Argentina. Recorded from Tropical Wet, Tropical Moist, Tropical Premontane Moist, Subtropical Wet, Subtropical Moist, Subtropical Dry, Subtropical Lower Montane Moist Forest, and Warm Temperate Moist Forest Life Zones.

Material Examined. Over 200 males and 27 females. Abbreviated data: ARGENTINA: *Misiones:* Eldorado, III–VI (ZSBS), XII (BMNH); Loreto, V (ZSBS); Puerto Bemburg, IV (BMNH); BRAZIL: *Bahia:* Itabuna, I (VOB); *Distrito Federal:* Planaltina, 1,000 m, IV–VI, XI–XII (VOB, CPAC); *Goiás:* Leopoldo de Bulhões, XI–XII (BMNH); 20 km N São João da Aliança, IV–V (LACM); 24 km E Formoso, V (LACM); Veadeiros [now Alto Paraiso], IV–V (LACM); *Mato Grosso do Sul:* Campo Grande (ZSBS); *Minas Gerais:* Fazenda dos Campos, 1,500 m (ZSBS), I, II (IOC); "Minas Geraes," XII (BMNH); Passos, XII (IOC); Serrinha, Diamantina (AMNH); Oliveira, XII (VOB); Ouro Preto (BMNH, UMO); Uberaba (ZSBS); *Paraná:* Castro (BMNH, MMU, USNM); Castro, 950 m (BMNH); Foz do Iguaçu, I (VOB); Iguaçu, I, XII (BMNH, UMO); Rolândia, V (ZSBS); *Rio de Janeiro:* Cantagalo (MCZ); Engenheiro Passos, III (IOC); Maricá, I, X (USNM, VOB); Organ Mts. near Tijuca (BMNH); "Rio de Janeiro" (NHMV), IX (ZSBS); *Rio Grande do Sul:* Barracão, XI (CMNH); Elsenau (BMNH); Guaraní, XI–XII (CMNH, CU); Pelotas, IV, XII (CMNH, MCZ); *Santa Catarina:* Lajes, III (LACM); Nova Brémen, Rio Laeiss, II (ZSBS); Nova Teutonia, III (PMY, USNM); "St. Cath." (BMNH); *São Paulo:* Alto da Serra, II–V, XII (BMNH); Araçatuba, 450 m, IV (BMNH); Campos do Jordão, II (IOC); Campos do Jordão, Umuarama, 1,700 m, I, III (IOC); Campos do Jordão, Lagoinha, 1,500 m, II (IOC); Emas, near Piraçununga, III, XII (IOC); Piraçununga, III, XII (IOC); 3.4 km NNW Padua Sales, Mun. de Mogi Guaçu, IV (AMNH); Ipiranga, IV, XII (BMNH, USNM, ZSBS); Paranapanema (USNM); São Paulo, XI (USNM); São Paulo, 750 m, IV (BMNH); São Paulo, 900 m, I (VOB); PARAGUAY: *Central:* Asunción (AMNH); Patiño Cué (BMNH); *Cordillera:* San Bernardino, XII (USNM); *Guairá:* Villarrica, II, V, VII, XII (BMNH, NHMV, USNM, ZSBS); *Itapúa:* Encarnación (USNM); *Paraguarí:* Sapucaí, I, XI, XII (BMNH, USNM); PERU: *Ucayali:* Aguaytía, Huallaga, 400 m, VII (BMNH).

Discussion. This is a widespread and variable species. The smokey suffusion on the forewings, the branching of M_1 from the forewing cell (Hopp, 1921), and the shape of the juxta and vinculum processes in the male genitalia are quite variable (Fig. 217, inset). Despite Hopp's (1921) synonymy of *Zadalcera fumata* under *Dalcerina tijucana*, all references to this species in the agricultural literature have been published as *Z. fumata*.

Females with reduced forewing maculation are very similar to female *Dalcera abrasa*, although the forewing ground color of *Dalcerina tijucana* is sometimes darker; the forking of forewing R will distinguish them. The cleft in the sterigma is usually more broad and shallow in *tijucana* (Fig. 267) than in *abrasa* (Fig. 261).

I have seen one female labeled "Col./ Coll. J. Arp" (ZSBS), which may mean that the specimen was collected in Colombia, but I do not trust the locality.

Minacraga Dyar

Minacraga Dyar, 1905a: 176; 1910c: 120.—Dyar and Strand, 1913b: 30.—Hopp, 1921: 279.—Sick, 1939: 1309.—D'Almeida, 1945: 194.—Fletcher and Nye, 1982: 103. Type species: *Minacraga disconitens* Schaus, 1905, by original designation.

Diagnosis. Wings usually bronze with metallic maculation (Figs. 139–146); forewing R_1 short-stalked with R_{2+3}, R_2 + R_3 stalked, R_4 + R_5 stalked (e.g., Fig. 54); male genitalia with tusk- or bladelike process (Figs. 221–228).

Adult Male. Medium to large, forewing 12–17 mm. Ground color: bronze with maculation. Antennae: apical scale tuft present. Forewing: accessory cell absent; R_1 short-stalked with R_{2+3}; R_2 + R_3 long-stalked; R_4 + R_5 long-stalked; retinaculum present. Hindwing: Rs not fused with Sc + R_1 in cell; frenulum present. Genitalia: tegumen and sociuncus forming complex, not fully fused; socii large hairy pads; gnathos median lobe a strongly sclerotized, ridged, near triangular plate, with paired bifid lateral arms, dorsal branch of arms membranous and saclike, ventral (and sometimes anterior) branch more slender and strongly sclerotized [lateral arms absent in *aenea* and *hyalina*]; vinculum elongate; valvae reduced to setose lobes or processes [except in *aenea* and *hyalina*, where developed as narrow-based pointed setose triangular processes fused to vinculum]; juxta strongly developed as independent, long, slender rod, internally almost as long as saccus, externally protrudes about as far as aedoeagus [weakly developed externally in *aenea* and *hyalina*]; saccus medium length, broad; aedoeagus usually long and slender, often slightly curved; tusk- or bladelike processes arising adjacent to and below valvae.

Adult Female. Large, forewing 19–22 mm. Genitalia: sterigma medium to wide; ostium bursae narrow to wide; ductus bursae long, recurved; corpus bursae ovate; ductus seminalis arising near second bend in ductus bursae; apophyses posteriores rudimentary; "accessory glands" ovate in lateral view.

Discussion. Minacraga aenea and *M. hyalina* differ considerably from the other *Minacraga* species in male genitalia, and *M. hyalina* differs in wing shape and pattern as well. They may eventually require a new genus, but I prefer to leave them as *Minacraga*, because they share most characters of other *Minacraga* male and female genitalia and agree in wing venation.

The tusk- or bladelike processes of the male genitalia are reminiscent of geometrid furca described by Okagaki *et al.* (1956) and are similar in appearance to processes that occur in some Mimallonidae (especially some *Cicinnus* species) and some Limacodidae (such as *Euclea cupostriga* Dyar).

An alternative intrepretation of my "valvae" and "tusklike processes" is that my "valvae" are processes of the vinculum and my "tusklike processes" are the true homologues of valvae. A possible analog of the later case occurs in some eumaeine hairstreaks (Lycaenidae), where there are "lateral processes" of the fused vinculum and tegumen, and the slightly reduced valvae surround the aedeaogus (see Forbes, 1960: fig. 158).

KEY TO MALE *MINACRAGA*

1. Dorsal forewing with brown streak at base of inner margin (Figs. 141–146); gnathos with bifid lateral arms; valvae reduced to setose lobes or processes (Figs. 221–226) 2

Dorsal forewing without brown streak at base of inner margin (Figs. 139, 140); gnathos lacking lateral arms; obvious valvae present (Figs. 227, 228) 7

2(1). Processes of genitalia tusklike, round in cross section; branches of gnathos lateral arms well separated from each other (Figs. 221, 222, 225, 226) 3

Processes of genitalia bladelike, flattened laterally in cross section; branches of gnathos lateral arms not well separated from each other, the dorsal branch arising from ventral surface of ventral arm (Figs. 223, 224) 6

3(2). Tusklike processes gently curved, with no sharp bends in lateral view (Figs. 221, 222, 225) 4

Tusklike processes in lateral view sharply bent dorsally at two-thirds of length, then recurved near tips (Fig. 226); southern Brazil .... *itatiaia*

4(3). Tusklike processes long, reaching to or beyond apex of gnathos median lobe (Fig. 221); South America .... *disconitens*

Tusklike processes short, not reaching to apex of gnathos median lobe (Figs. 222, 225) 5

5(4). The two branches of gnathos lateral arm similar (but not the same) length and thickness (Fig. 225); South America .... *argentata*

Dorsal branch of gnathos lateral arm very short and slender [hard to see unless well stained], compared to very long ventral arm (Fig. 222); Venezuela .... *similis*

6(2). Dorsal forewing pattern well marked, as in *disconitens*; processes narrowing toward tip (Fig. 223); Central America .... *plata*

Dorsal forewing pattern dull and mottled; processes broadened toward tip (Fig. 224); South America .... *indiscata*

7(1). Forewings rounded; wing ground color bronze, opaque (typical of *Minacraga*) (Fig. 139); southern Brazil .... *aenea*

Forewings falcate; wing ground color buff, semitransparent (Fig. 140); northern South America .... *hyalina*

Minacraga disconitens Species-Group

See discussion under *Minacraga*, earlier.

Minacraga disconitens Schaus
Figures 13, 17, 54, 141, 142, 221, 268; Map 41; Color Plate, Figure 5

Minacraga disconitens Schaus, 1905: 331.—Dyar, 1910c: 120.—Dyar and Strand, 1913b: 30.
Minacraga disconitens Dyar [sic]—Sick, 1939: 1309.

Diagnosis. The most common *Minacraga*, differing from other species in long tusklike processes of male genitalia, reaching to or beyond apex of median lobe of gnathos (Fig. 221).

Adult Male (Fig. 141). Forewing length 14–16 mm. *Head:* Vertex and frons pale buff. Antennae pale buff with occasional brown scales on shaft; apical five segments with brown scale tuft. Labial palpi dark brown, buff at tips. *Thorax:* Dorsum light brown, patagia with dense dark brown elongate scales; venter pale buff. Forewings pale metallic buff, except outer margin, which is dull; broad dark brown streak at base of inner margin; dark fuscous dot at end of cell; subterminal wavy light brown line, followed by metallic buff spots between M_2 and CuA_1, followed by a dark brown shade along margin; lobe of light brown scales on inner margin. Hindwings pale buff, outer margin shaded with brown, especially around anal angle. Ventral wings pale buff, brownish along outer margins. Legs pale buff, foreleg with brown on anterior side of coxa and inner sides of femur and tarsus. *Abdomen:* Light brown. Genitalia as in Figure 221.

Adult Female (Fig. 142). Forewing length 19–22 mm. Colored as in male, but size larger and wings more broadly rounded. Genitalia as in Figure 268.

Types. Lectotype male, USNM 8905, and 6 paralectotypes (1 in BMNH), here designated.

Type Locality. French Guiana, 100 miles [160 km] up Maroni River.

Hosts. "Macadamia" (*Macadamia* species, probably *M. integrifolia* Maiden & Betche; Proteaceae) (BMNH).

Immature Stages. Unknown.

Flight Period. February to August and October to December.

Distribution (Map 41). Venezuela, Trinidad, Guyana, Surinam, French Guiana, Brazil, eastern Peru, and Bolivia. It has been recorded from Tropical Moist, Tropical Premontane Wet, Tropical Premontane Moist, Subtropical Moist, and Warm Temperate Moist or Dry Forest Life Zones. The Bolivia localities are transitional between Tropical Premontane Dry Forest and Subtropical Moist Forest Life Zones (Becker, 1982: 265, 267).

Material Examined. 77 males and 20 females. BOLIVIA: *Cochabamba:* Chaparé, 400 m, 10-VIII-1951 (ZSBS); *Santa Cruz:* "Prov. del Sara" [now Gutiérrez], 450 m, VIII-1914 (CMNH); Santa Cruz de la Sierra, 450 m, XII-1914 (CMNH); BRAZIL: *Amapá:* Serra do Navio, 16-II-1964 (MNRJ); *Amazonas:* Manaus, III-1945 (AMNH); Amazon between Tefé and Tonantins, XI-1921 (USNM); *Distrito Federal:* Planaltina, 1,000 m, 10-IV-1979, 2-IV-1980 (CPAC); *Mato Grosso do Sul:* Corumbá, 19–25-IV-1985 (VOB); *Minas Gerais:* Sete Lagoas, 15-IV-1979 (VOB); *Pará:* "Pará" [=Belém], [no date] (BMNH); FRENCH GUIANA: Nouveau Chantier, [no date] (USNM), IV–V-[no year] (BMNH); Pied Saut, Oyapock River, XII-1917 (CMNH); Saint-Jean, III, VII–VIII-1904, [no date] (BMNH, USNM, includes paralectotypes); Saint-Laurent, I, II, IV, V, VII, X–XII-[various years], [no date] (BMNH, MNHP, USNM); 60 miles [100 km] up Maroni River, VIII-1904 (USNM, paralectotype); 100 miles [160 km] up Maroni River, IV-1904 (USNM, lectotype and paralectotypes); GUYANA: Kartabu, 8-III-1922 (AMNH); Takutu Mountains, 6°15'N, 59°5'W, 14-XII-1983 (USNM); Upper Kutari River, 15-XII-1935 (BMNH); PERU: *Loreto:* Cavallo-Cocho [Caballococha], IV–VII-1884 (ZSBS); SURINAM: Aroewarwa Creek, Maroewym Valley, IV-1905 (BMNH); TRINIDAD: Arima Valley, 11-IV-1951 (AMNH); Caparo, XII-1905 (BMNH); Morne Bleu, Textel Installation, 4-II-1979 (MJWC); VENEZUELA: *Aragua:* Rancho Grande, 1,100 m, 4-VI-1974, 16-VI-1976, 17-VI-1952, 21-XI-1975 (UCV), 8–14-VI-1967 (USNM), 28-VI–18-VII-1974 (BMNH); *Carabobo:* Las Quiguas, Esteban Valley, XI-1909–III-1910 (BMNH); *Miranda:* Los Teques, 1,600 m, II-1951 (ZSBS); Nucleo El Laurel, 1,200–1,300 m, ex larva on *Macadamia*, 25-V-1971 (BMNH).

Discussion. Schaus described this species from an unstated number of specimens from "Maroni River." The USNM has six males from the Schaus collection, all collected in 1904: three from 100 miles up Maroni River, one from 60 miles up Maroni River, and two from "St. Jean, Maroni"; I consider them all part of the type series. Another Saint-Jean male in BMNH was labeled "cotype" by Schaus. There is also a female from "St. Laurent, Maroni," from the Schaus collection (USNM), but because it does not fit within the wing expanse given by Schaus, it is not considered a type.

I have seen one male that is probably *M. disconitens*, but it differs genitalically in having short tusklike processes and smoother valval lobes: VENEZUELA: *Tachira:* Río Frio, 600 m, 2–10-IX-1981, F. Fernandez Y. *et al.* (USNM, genitalia 85-51). I have seen two additional females, without associated males, which are probably *disconitens*: BOLIVIA: *Not located:* "Nuflo de Chavez, Esperanza, E. Bolivia," 1926–1929 (BMNH); BRAZIL: *São Paulo:* Araçatuba, 450 m, 3-IV-1913 (BMNH).

Minacraga plata, new species
Figure 223; Map 42

Diagnosis. Differs from other *Minacraga* in narrow bladelike processes of male genitalia (Fig. 223).

Adult Male. Forewing length 15–17 mm. *Head:* Vertex and frons pale buff. Antennae pale buff with dark fuscous scale tuft at tip. Labial palpi brown, very dark on outside sides. *Thorax:* Dorsum light brown; venter buff. Forewings pale buff, light brown on outer margin, with light subterminal line through this brown shading; outer margin edged with pale buff with dark brown spots in fringe; discal spot dark brown; some dark brown scales in inner margin. Hindwings pale buff, outer margin shaded with brown, especially around anal angle. Ventral wings pale buff with brown shading around anal angle. Legs buff with brown on foreleg anterior coxa, inner femur and tarsus. *Abdomen:* Pale buff. Genitalia as in Figure 223.

Adult Female. Unknown.

Type. Holotype male, USNM 103449.

Type Locality. Costa Rica, Turrialba, 600 m.

Host. Alibertia edulis L. Richard (A. Richard) (Rubiaceae) (Aiello lot 80-48).

Immature Stages. Undescribed.

Flight Period. January, July, and October.

Distribution (Map 42). Costa Rica and Panama, in Tropical Moist, Tropical Premontane Wet, and Tropical Premontane Moist Forest Life Zones.

Material Examined. 4 males. COSTA RICA: Turrialba, 600 m, VII-1981, V. O. Becker (USNM, holotype), 10-I-1973, Becker (VOB, paratype); PANAMA: Canal Zone, Fort Kobbe, VII-1958, W. D. Thomas (CMNH, not designated paratype due to denuded wings); Barro Colorado Island, Snyder/Molino Trail, 7-V-1980 as larva, pupated 25-VII-1980, eclosed 22-VIII-1980, A. Aiello lot 80-48 (USNM, paratype).

Discussion. Minacraga plata is similar to *Minacraga disconitens*, but neither the dark brown nor metallic silver on the forewing is as intense. The reared specimen is smaller than the others and is not included in the measurements given. The species name is a noun in apposition from the Spanish word for "silver," honoring the late Robert Silberglied's contributions to knowledge of the Lepidoptera of Panama as well as the silvering of the moths' forewings.

Minacraga similis, new species
Figure 222; Map 42

Diagnosis. Differs from other *Minacraga* in short, curved tusklike processes and configuration of lateral arms of gnathos (Fig. 222).

Adult Male. Forewing length 14 mm. Colored as in *Minacraga disconitens.* Holotype appears to have less brown maculation than *M. disconitens*, but this is due to wear, especially of wing fringe. Genitalia as in Figure 222.

Adult Female. Unknown.

Type. Holotype male, USNM 103450.

Type Locality. Venezuela, Amazonas, Cerro de la Neblina Basecamp.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. February.

Distribution (Map 42). Southern Venezuela, in Tropical Wet Forest Life Zone (probably occurs in adjacent northern Brazil).

Material Examined. Known only from holotype. VENEZUELA: *Amazonas:* Cerro de la Neblina Basecamp, 0°50′N, 66°9′44″W, 140 m, 4–12-II-1984, D. R. Davis & T. McCabe (USNM, genitalia 28015).

Discussion. Male genitalia differ from those of *Minacraga disconitens* in median lobe of gnathos being thicker and more heavily sclerotized; lateral arms of gnathos having dorsal branch very reduced in length and width and ventral branch longer and more slender; and tusklike processes being shorter and more strongly curved inward apically.

Minacraga indiscata Dyar
Figures 143, 224; Map 43

Minacraga indiscata Dyar, 1910c: 120.—Dyar and Strand, 1913b: 30.—Sick, 1939: 1309, pl. 168e.

Diagnosis. Differs from other *Minacraga* in broad bladelike processes of male gentalia (Fig. 224) and dull forewing pattern (Fig. 143).

Adult Male (Fig. 143). Forewing length 15 mm. *Head:* Vertex and frons buff. Antennae buff with dark fuscous scale tuft at tip. Labial palpi brown, dark on outer sides. *Thorax:* Dorsum light brown; venter buff. Forewings dull light brown, darker toward outer margin and anal angle; occasional dark brown scales; subterminal line light, especially when passing through darker areas; discal spot small, brown. Hindwings pale brown, darker toward anal angle. Ventral wings light brown. Legs buff. *Abdomen:* Light brown. Genitalia as in Figure 224.

Adult Female. Unknown.

Types. Lectotype male, USNM 13060, and paralectotype male, here designated.

Type Locality. French Guiana, Maroni River, Saint-Jean.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. July, November, and December.

Distribution (Map 43). French Guiana, northwestern Brazil, and Peru, in Tropical Moist Forest Life Zone.

Material Examined. 6 males. BRAZIL: *Pará:* "Pará" [=Belém], "CIV," [no date], A. M. Moss (BMNH); FRENCH GUIANA: Nouveau Chantier, XII-[no year], Dognin Collection from LeMoult (USNM, paralectotype); Saint-Jean, VII-1904, W. Schaus (USNM, lectotype); PERU: *Madre de Dios:* Río Tambopata Reserve, 30 air km SW Puerto Maldonado, 290 m, 26–30-XI-1979, J. B. Heppner (FSCA, USNM).

Discussion. Minacraga indiscata is colored as in *Minacraga disconitens*, but the forewings are more uniform dull brown, apparently lacking the silver scaling on the disk and the brown patch at base of inner margin. However, the wings of the known specimens of *M. indiscata* are rather rubbed, so these differences must be confirmed on fresh specimens.

Minacraga argentata Hopp
Figures 144, 225; Map 43

Minacraga argentata Hopp, 1922: 429.—Sick, 1939: 1309.

Diagnosis. Differs from other *Minacraga* in configuration of forewing submarginal line (Fig. 144) and short round tusklike processes of male genitalia (Fig. 225).

Adult Male (Fig. 144). Forewing length 13–14 mm. *Head:* Vertex and frons buff. Antennae buff with apical brown scale tuft. Labial palpi buff with brown outside. *Thorax:* Dorsum buff with brown; venter buff. Forewings buff with thin brown submarginal line produced distally between M_2 and CuA_2, brown suffusion between submarginal line and outer margin; outer margin darkened between M_2 and CuA_2; small discal spot; brown streak at base of inner margin, scattered brown scales elsewhere. Hindwings buff, with brownish shading around anal angle. Ventral wings buff. Legs buff. *Abdomen:* Buff. Genitalia as in Figure 225.

Adult Female. Unknown.

Type. Holotype male, ZSBS.

Type Locality. Peru, Dept. Huánuco, Pachitea.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. January, April, May, September, and October.

Distribution (Map 43). Colombia, eastern Brazil, and Peru, in Tropical Wet, Moist, and Premontane Wet Forest Life Zones.

Material Examined. 9 males. BRAZIL: *Amazonas:* Fonte Boa, V, IX-1906, S. M. Klages (BMNH); COLOMBIA: *Guainía:* Ob. [=Upper] Río Negro, 800 m, [no date], A. H. Fassl (BMNH); PERU: *Huánuco:* Pachitea, [no date] (ZSBS, holotype); Tingo Maria, 672 m, 25–31-I-1980, J. B. Heppner (USNM); *Loreto:* [mouth of Río Samiria], Lower Río Marañon, 23-X-1928, H. Bassler F6132 (AMNH); *Puno:* Yahuarmayo, 1,200 feet [365 m], IV-1912 (CMNH, USNM).

Discussion. The single male from Río Negro, Colombia, is larger (forewing 18 mm) and has a longer aedoeagus and saccus (genitalia 85-47). It apparently belongs here, although its wing pattern is rubbed.

I have seen one male from Brazil (*Pará:* Taperinha, 1–10-VII-1927, Zerny, NHMV), which is similar to *Minacraga argentata* but differs in male genitalia in having the external portion of juxta longer and thicker, without a lobe at apex, and the tusklike processes shorter, more sinuate, thicker, and more flattened dorsoventrally. The wings are small (forewing 10 mm) and very worn, so the pattern is uncertain.

Minacraga itatiaia, new species
Figures 145, 146, 226, 265;
Map 44

Diagnosis. Coloration similar to *Minacraga aenea*, but lighter and forewings broader (Fig. 145); similar to *M. argentata* but submarginal line less distinct (wings rubbed in all specimens) and genitalia differ, especially in medium length sinuous tusklike processes, long narrow aedoeagus, and configuration of branches of lateral arms of gnathos (Fig. 226).

Adult Male (Fig. 145). Forewing length 14–15 mm. *Head:* Buff, tips of antennae and outsides of labial palpi brown. *Thorax:* Dorsum buff with brown, venter buff. Forewings buff with submarginal shading as in *Minacraga aenea* (rubbed in available specimens). Hindwings buff with brown shading around anal angle. Ventral wings buff. Legs buff. *Abdomen:* Buff. Genitalia as in Figure 226.

Adult Female (Fig. 146). Forewing length 19 mm. Colored as in male. Genitalia as in Figure 265.

Type. Holotype male, BMNH.

Type Locality. Brazil, Rio de Janeiro, Pico do Itatiaia.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. March and April.

Distribution (Map 44). Southern Brazil, in Subtropical Wet, Subtropical Lower Montane Moist, and Warm Temperate Moist Forest Life Zones.

Material Examined. 5 males and 1 female. BRAZIL: *Minas Gerais:* [Ouro] Preto, [no date] (UMO, paratype); *Paraná:* Castro, 950 m, [no date], E. D. Jones (BMNH, USNM, paratypes); *Rio de Janeiro:* Pico do Itatiaia, 28-III–1-IV-1958, H. B. D. Kettlewell (BMNH, holotype); *Santa Catarina:* "St. Catherina," [no date] (BMNH, paratype male and female).

Discussion. The association of the female specimen is questionable and is based on coloration and assumes that the match of the sexes of *Minacraga aenea* is correct. In some male specimens, the external juxta bears a short bifid process (Fig. 226, inset). The species name is a noun in apposition honoring the type locality, a mountain and surrounding national park.

Minacraga aenea Species-Group

See discussion under *Minacraga*, earlier.

Minacraga aenea Hopp
Figures 139, 227, 266; Map 44

Minacraga aenea Hopp, 1921: 279; 1922: 429.—Sick, 1939: 1309.

Diagnosis. Distinguished from all *Minacraga* except *M. hyalina* by obvious, although rudimentary, valvae and lack of gnathos lateral arms (Fig. 227); distinguished from *M. hyalina* by rounded forewing shape and bronze ground color (Fig. 139).

Adult Male (Fig. 139). Forewing length 14–16 mm. *Head:* Vertex and frons buff. Antennae buff with apical brown scale tuft. Labial palpi buff with brown outside. *Thorax:* Dorsum buff; venter buff. Forewings buff, darker toward outer margin; brown subterminal line, outside of which are lustrous white spots in cells between veins M_1 and 1A + 2A; brown shading in middle of outer margin; discal spot small, brown. Hindwings buff, darker toward anal angle, with brown at anal angle. Ventral wings buff with brown hindwing anal angle. Legs buff with brown. *Abdomen:* Buff. Genitalia as in Figure 227.

Adult Female. Forewing length 21 mm. Colored as in male. Genitalia as in Figure 266.

Type. Holotype male (not female as stated in original description), ZSBS.

Type Locality. Brazil, Santa Catarina, "Joinville?".

Host. Unknown.

Immature Stages. Unknown.

Flight Period. April.

Distribution (Map 44). Southeast Brazil, in Subtropical Wet and Moist Forest Life Zones.

Material Examined. 5 males and 2 females. BRAZIL: *Santa Catarina:* Blumenau, 1-IV-1955 (MCZ); Joinvile, [no date], J. Arp (ZSBS, 1 female), [no date] (USNM); "Joinville?", [no date], E. & A. Boettcher (ZSBS, holotype); "St. Catherina," [no date] (BMNH, 1 female); *São Paulo:* Alto da Serra, Santos, 800 m, 7-10-III-1913, E. D. Jones (BMNH).

Discussion. This species and *Minacraga hyalina* differ from other *Minacraga* in having valvae less reduced and lacking lateral arms of gnathos and may eventually require a new genus. The association of the female is questionable; the genitalia of the only specimens available are damaged by fungus.

Minacraga hyalina, new species
Figures 140, 228; Map 42;
Color Plate, Figure 6

Diagnosis. Differs from all *Minacraga* in falcate forewings, forewing subterminal line, and semitransparent wing coloration (Fig. 140).

Adult Male (Fig. 140). Forewing length 12–15 mm. *Head:* Vertex and frons buff. Antennae buff with apical dark fuscous scale tuft. Labial palpi buff with brown outsides. *Thorax:* Dorsum buff; venter buff. Forewings buff, darker along costal margin, falcate; subterminal line with brown inside, white outside; line inflexed between veins CuA_2 and CuP; discal spot and apex brown. Hindwings buff. Ventral wings buff. Legs buff. *Abdomen:* Buff. Genitalia as in Figure 228.

Adult Female. Unknown.

Type. Holotype male, BMNH.

Type Locality. Peru, Puno, Yahuarmayo, 365 m.

Host. Unknown.

Immature Stages. Unknown.

Flight Period. March and May.

Distribution (Map 42). Surinam, French

Guiana, Peru, and northern Brazil (Amazon Basin), in Tropical Moist Forest Life Zone.

Material Examined. 5 males. BRAZIL: *Amazonas:* Hyutanahan [now Huitanaã], Rio Purus, III-1922, S. M. Klages (CMNH, paratype); FRENCH GUIANA: Saint-Laurent, [no date] (ZSBS, paratype); PERU: *Puno:* Yahuarmayo, 1,200 feet [365 m], "May–June 1912" (BMNH, holotype; USNM, paratype); SURINAM: Aroewarwa Creek, Maroewym Valley, V-1905, Klages (BMNH, paratype).

Discussion. Minacraga hyalina is very close in male genitalia to *Minacraga aenea* but differs externally in more produced apex and coloration of forewing, especially the subterminal line. As already discussed, these two species may eventually require separation from *Minacraga* into a new genus. The species name refers to the hyaline wings, which distinguish this species from other *Minacraga*.

CHECKLIST

Family Dalceridae
Subfamily Acraginae

- *Acraga* Walker, 1855
    - *Pinconia* Moore, 1882
    - *Epipinconia* Dyar, 1898
    - *Anacraga* Dyar, 1905, NEW SYN.
    - *Dalargentina* Orfila, 1961, NEW SYN.
  - *Acraga goes* Species-Group
    - *goes* Schaus, 1910, RESURRECTED COMB.
    - *ingenescens* (Dyar, 1927), NEW COMB.
    - *luteola* (Hopp, 1921), NEW COMB., UNIDENTIFIED
    - new species F
  - *Acraga hamata* Species-Group
    - *hamata* Schaus, 1910
    - *andina*, new species
  - *Acraga flava* Species-Group
    - *flava* (Walker, 1855)
      - *sulphurea* (Burmeister, 1878)
    - *obscura* (Schaus, 1896)
  - *Acraga infusa* Species-Group
    - *ria* (Dyar, 1910), NEW COMB.
    - *neblina*, new species
    - *serrata*, new species
    - *infusa* Schaus, 1905
    - *philetera* (Schaus, 1910), STATUS UNCERTAIN
    - *conda* Dyar, 1910, STATUS UNCERTAIN
  - *Acraga ciliata* Species-Group
    - *ciliata* Walker, 1855
    - *moorei* Dyar, 1898
      - *ochracea* (Moore, 1882, not Walker, 1855)
    - *coa* (Schaus, 1892)
      - *moribunda* Schaus, 1920, NEW SYN.
    - *canaquitam* Dyar, 1925
    - *chicana*, new species
  - *Acraga concolor* Species-Group
    - *concolor* (Walker, 1865), NEW COMB.
    - *citrinopsis* (Dyar, 1927)
    - species C
    - *beebei*, new species
  - *Acraga melinda* Species-Group
    - *melinda* (Druce, 1898)
    - *amazonica*, new species
    - *meridensis* Dognin, 1907
    - *mariala* Dognin, 1923
    - *perbrunnea* Dyar, 1927
  - *Acraga citrina* Species-Group
    - *citrina* (Schaus, 1896), RESURRECTED COMB.
      - *albescens* (Hopp, 1928), NEW SYN., NEW COMB.
    - *hoppiana*, new species
  - *Acraga ferruginea* Species-Group
    - *ferruginea* Hopp, 1922
    - *brunnea*, new species
  - *Acraga ampela* Species-Group
    - *ampela* (Druce, 1890), NEW COMB.
      - *cosmia* Dognin, 1911, NEW SYN.
    - *puno*, new species
    - *boliviana* Hopp, 1921, NEW STATUS
    - *angulifera* Schaus, 1905
    - *isothea* Dognin, 1914
    - *leberna* (Druce, 1890)
      - *arcifera* Dyar, 1910, NEW SYN.
    - *umbrifera* (Schaus, 1905)
  - *Acraga ochracea* Species-Group
    - *ochracea* (Walker, 1855)
    - *victoria*, new species
    - *sexquicentenaria* (Orfila, 1961), NEW COMB.
    - *parana*, new species
- *Dalcerides* Neumoegen and Dyar, 1893
    - *Acragopsis* Dyar, 1905, NEW SYN.
  - *Dalcerides flavetta* Species-Group
    - *flavetta* (Schaus, 1905), NEW COMB.
    - *rebella* (Schaus, 1911), NEW COMB.
    - *chirma* (Schaus, 1920), NEW COMB.
    - new species
    - *radians* (Hopp, 1921), NEW COMB.
    - *dulciola* (Dyar, 1914), NEW COMB.
    - *mesoa* (Druce, 1887), RESURRECTED COMB.
      - *gugelmanni* (Dyar, 1916), NEW COMB., NEW SYN.
    - *nana* (Dognin, 1920), NEW COMB.
    - *sofia* (Dyar, 1910), NEW COMB.
      - *sororcula* (Dyar, 1927), NEW COMB., NEW SYN.
      - *phasma* (Dyar, 1927), NEW COMB., NEW SYN.
  - *Dalcerides ingenita* Species-Group
    - *ingenita* (Hy. Edwards, 1882)
    - *bicolor* Schaus, 1910
    - *alba* (Druce, 1887), NEW COMB.
      - *caretta* (Dyar, 1910), NEW COMB., NEW SYN.
- *Zikanyrops* Hopp, 1928

  - *dubiosa* Hopp, 1928
  - *sparsa* Hopp, 1928, UNIDENTIFIED

Subfamily Dalcerinae

- *Minonoa* Dyar, 1905
  - *elvira* (Dognin, 1909)
  - *pachitea* Hopp, 1922
  - *perbella* Schaus, 1905
    - *variegata* (Jones, 1908), NEW SYN.
- *Paracraga* Dyar, 1905
  - *innocens* Schaus, 1905
    - *oxydata* Hopp, 1921, NEW SYN.
  - *amianta* Dyar, 1910
  - *argentea* (Schaus, 1910)
    - *cyclophera* Dyar, 1914, NEW SYN.
  - *canalicula* Dognin, 1910
  - *halophora* Dyar, 1928
  - *necoda* (Druce, 1901)
  - *pulverina* Schaus, 1920
- *Ca* Dyar, 1914
  - *anastigma* Dyar, 1914
- *Minacragides* Dyar, 1910
  - *arnacis* Dyar, 1910
    - *restricta* (Schaus, 1940), NEW COMB., NEW SYN.
  - new species A
  - new species B, PLACEMENT UNCERTAIN
- *Oroya*, new genus
  - *aurora*, new species
- *Dalcera* Herrich-Schäffer, [1854]
  - *abrasa* Herrich-Schäffer, [1854]
  - *haywardi* Orfila, 1961, UNIDENTIFIED
  - *canescens* Tams, 1926
    - *consanguinea* Dyar, 1927, NEW SYN.
  - *semirufa* Druce, 1910
- *Dalcerina* Dyar, 1898
  - *Zadalcera* Dyar, 1910
    - *tijucana* (Schaus, 1892)
    - *fumata* (Schaus, 1894)
    - *arhathodota* (Dyar, 1910), NEW SYN.
    - *muncia* (Dyar, 1923), NEW SYN.
    - *dierrhyeoa* (Dyar, 1923), NEW SYN.
- *Minacraga* Dyar, 1905
  - *Minacraga disconitens* Species-Group
    - *disconitens* Schaus, 1905
    - *plata*, new species
    - *similis*, new species
    - *indiscata* Dyar, 1910
    - *argentata* Hopp, 1922
    - *itatiaia*, new species
  - *Minacraga aenea* Species-Group
    - *aenea* Hopp, 1921
    - *hyalina*, new species

ACKNOWLEDGMENTS

This revision was undertaken as a doctoral dissertation at Harvard University, with financial support from Harvard University, the Smithsonian Institution, the National Science Foundation (Dissertation Improvement Grant BSR 8413586), and my parents.

All the genital drawings were prepared by L. L. Meszoly. E. R. Hodges, V. Malikul, N. Payzant, and J. G. Stipetic provided additional assistance with artwork. V. Krantz of the Smithsonian Photographic Laboratory and S. Braden, H. Wolf, and W. Brown of the Smithsonian Scanning Electron Microscope Laboratory provided assistance with photographs. B. D'Abrera photographed the color plate. The drawings were partly supported by a special fund to the Museum of Comparative Zoology established by John de Cuevas. The maps were prepared on the Smithsonian Office of Information Resource Management computer system, with the assistance of M. L. Kable and J. A. Louton of the Smithsonian Department of Entomology.

M. F. Mickevich provided assistance with phylogentic analysis. Computer time for phylogenetic analysis was provided by the University of Maryland at College Park Computer Center and the Maryland Center for Systematic Entomology. C. Häuser, R. Stanger, and G. C. Steyskal provided translations. J. Betancourt, L. D. Gomez, and A. L. Weitzman provided botanical advice. I thank A. Aiello, V. O. Becker, C. V. Covell, M. E. Epstein, O. S. Flint, P. Genty, W. Hallwachs, D. H. Janzen, A. L. Lourenção, N. McFarland, R. Monteiro, R. K. Robbins, P. J. Spangler and W. Steiner for their field efforts to collect dalcerids on my behalf and J. A. Coddington, J. Kukalova-Peck, T. M. Kuklenski, G. Lamas, S. H. Love, G. C. Mayer, P. M. Miller, E. G. Munroe, S. Passoa, A. Sibatani, F. W. Stehr, S. J. Weller, and the curators of the collections consulted for varied assistance. E. E. Grissell, P. M. Marsh, and N. E. Woodley of the U.S. Department of Agriculture Systematic Entomology Laboratory and G. Delvare of CIRAD identified parasites. D. R. Davis provided guidance and space at the Smithsonian. The manuscript was read in whole or part (especially the phylogenetic analysis section) by V. O. Becker, J. M. Carpenter, J. A. Coddington,

D. R. Davis, M. E. Epstein, R. W. Hodges, C. L. Hogue, J. D. Holloway, H. W. Levi, P. M. Mabee, R. J. McGinley, M. F. Mickevich, M. G. Pogue, P. F. Stevens, A. L. Weitzman, S. H. Weitzman, E. O. Wilson, and N. E. Woodley. A. G. Wine assisted with the manuscript.

I am especially indebted to V. O. Becker, who provided specimens and information throughout the project and hosted my fieldwork in Brazil, and my parents, who have given both moral and financial support and over the years have tolerated a wide range of animal taxa in their freezer.

Publication costs of this study were covered in part by the Wetmore Colles Fund.

LITERATURE CITED

ALBERTI, B. 1954. Uber die stammesgeschichtliche Gliederung der Zygaenidae nebst Revision einiger Gruppen (Insecta, Lepidoptera). Mitteilungen aus dem Zoologischen Museum in Berlin, **30:** 115–482.

D'ALMEIDA, R. F. 1945. Alguns tipos de generos da Ordem Lepidoptera 6.ⁿ nota: Heterocera, Fam. Dalceridae Dyar. Papéis Avulsos do Departmento de Zoologia, São Paulo, **5:** 193–195.

ARAUJO, R. L. 1951. Dados bionomicos de uma lagarta do cafeeiro: *Dalcera abrasa* Herr.-Sch. 1854 (Lep., Dalceridae). O Biológico, **17:** 55–57.

ARNETT, R. H., JR. 1985. American Insects. New York: Van Nostrand Reinhold Co. xiii + 850 pp.

ARORA, G. S. 1976. A taxonomic revision of the Indian species of the family Cossidae. Records of the Zoological Survey of India, **69:** 1–160.

BALLOU, C. H. 1945. Notas sobre insectos dañinos-observados en Venezuela 1938–1943. Editorial Caracas: "Crisol." 151 pp.

BARNES, W., AND J. MCDUNNOUGH. 1917. Check List of the Boreal Lepidoptera. Decatur, Illinois: Herald Press. viii + 392 pp.

BECKER, V. O. 1982. Stenomine moths of the neotropical genus *Timocratica* (Oecophoridae). Bulletin of the British Museum (Natural History), Entomology, **45:** 211–306.

BERTELS, A., AND O. BAUCKE. 1966. Segunda relação das pragas das plantas cultivadas no Rio Grande do Sul. Pesquisa Agropecuaria Brasileira, **1:** 17–46.

BEUTELSPACHER B., C. R. 1988. Lepidópteros de Chamela, Jalisco, México V. Familias Dalceridae, Psychidae, Megalopygidae, Thyrididae, Epiplemidae, Apatelodidae, Lasiocampidae, Lymantriidae y Agaristidae. Anales del Instituto de Biologia, Universidad Nacional Autónoma de México, Serie Zoología, **58:** 327–340 ("1987").

———. 1992. Catálogo de la colección Roberto Müller (Lepidoptera: Heterocera) del Museo de Historia Natural de la Ciudad de México. Cuadernos del Instituto de Biología, Universidad Nacional Autónoma de México, **15:** 1–465.

BEVEN, S., E. F. CONNOR, AND K. BEVEN. 1984. Avian biogeography in the Amazon basin and the biological model of diversification. Journal of Biogeography, **11:** 383–399.

BIEZANKO, C. M. 1961a. Castniidae, Zygaenidae, Dalceridae, Eucleidae, Megalopygidae, Cossidae et Hepialidae da Zona Sueste do Rio Grande do Sul. Arquivos de Entomologia, Série A (Ministério da Agricultura, Instituto Agronomico do Sul, Escola de Agronomia "Eliseu Maciel," Pelotas, Rio Grande do Sul, Brasil), **14:** 1–12.

———. 1961b. Castniidae, Zygaenidae, Dalceridae, Eucleidae, Megalopygidae, Cossidae et Hepialidae da Zona Missioneira do Rio Grande do Sul. Arquivos de Entomologia, Série B, **14:** 1–8 + 4 pp. inserted bibliography.

BIEZANKO, C. M., R. E. BERTHOLDI, AND O. BAUCKE. 1949. Relação dos principais insetos prejudiciais observados nos arredores de Pelotas nas plantas cultivadas e selvagens. Agros (Pelotas, Brazil), **2:** 156–213.

BIEZANKO, C. M., A. RUFFINELLI, AND C. S. CARBONELL. 1966. Lepidoptera del Uruguay. Notas complementarias. III. Universidad de la Republica, Facultad de Agronomia, Boletin, **91:** 1–53.

BIEZANKO, C. M., A. RUFFINELLI, AND D. LINK. 1974. Plantas y otras sustancias alimenticias de las orugas de los Lepidopteros Uruguayos. Revista Centro Ciencias Rurais (Santa Maria, Brazil), **4:** 104–147.

———. 1978. Catalogo de Lepidopteros do Uruguai. Revista Centro Ciencias Rurais, **8**(Suppl.): 1–84.

BIRKET-SMITH, S. J. R. 1965. A revision of the west African eilemic moths, based on the male genitalia. Papers from the Faculty of Science, Series C (Zoology), Haile Sellassie I University (Addis Ababa, Ethiopia), **1:** 1–161.

———. 1974. Morphology of the male genitalia of Lepidoptera. Entomologica Scandinavica, **5:** 1–22, 161–188.

BLANCHARD, A., AND E. C. KNUDSON. 1985. *Psychonoctua masoni* (Schaus), new combination (Lepidoptera: Cossidae: Zeuzerinae), redescription and first records from Texas and USA. Proceedings of the Entomlogical Society of Washington, **87:** 426–431.

BODE, W., AND C. M. NAUMANN. 1988. Little-known accessory glands in female *Zygaena* moths (Lepidoptera, Zygaenidae). Zoological Journal of the Linnean Society, **92:** 27–42.

BODINE, D. 1896. The taxonomic value of the antennae of the Lepidoptera. Transactions of the American Entomological Society, **23:** 1–56, pls. I–V.

BORROR, D. J., AND D. M. DELONG. 1969. Introdução ao estudo dos insetos. São Paulo, Brazil. Editora Edgard Bluecher Ltda. 653 pp. [Brazilian edition, translated and rewritten by D. D. Correa *et al.*]

BORROR, D. J., D. M. DELONG, AND C. A. TRIPLEHORN. 1981. An introduction to the study of insects, 5th ed. Philadelphia: Saunders College Publ. x + 827 pp.

BOURGOGNE, J. 1951. Ordre des Lepidopteres, pp. 174–448. *In* P. P. Grassé (ed.), Traité de Zoologie, Vol. 10. Paris: Masson.

BRADLEY, J. D. 1966. A comparative study of the coconut flat moth (*Agonoxena argaula* Meyr.) and its allies, including a new species (Lepidoptera, Agonoxenidae). Bulletin of Entomological Research, **56:** 453–472.

BRAUN, A. F. 1924. The frenulum and its retinaculum in the Lepidoptera. Annals of the Entomological Society of America, **17:** 234–256, pl. XXIII.

BRISTOW, C. R. 1979. *Opisphanes quiteria angostura* a new sub-species of Brassolinae (Lepidoptera; Rhopalocera) from western Ecuador, with notes on collectors and localities. Journal of Natural History, **13:** 377–384.

BROCK, J. P. 1971. A contribution towards an understanding of the morphology and phylogeny of the Ditrysian Lepidoptera. Journal of Natural History, **5:** 29–102.

———. 1989. Reply to Scott's criticism. Journal of Research on the Lepidoptera, **26:** 240–247 ("1988").

———. 1990. Origins and phylogeny of butterflies, pp. 209–233. *In* O. Kudrna (ed.), Butterflies of Europe, Vol. 2. Introduction to Lepidopterology. Wiesbaden: AULA-Verlag. 557 pp.

BROWN, F. M. 1941. A gazetteer of entomological stations in Ecuador. Annals of the Entomological Society of America, **34:** 809–851.

BROWN, K. S., JR. 1979. Ecologia geografica e evolução nas florestas neotropicais: apendices. São Paulo, Brazil: Universidade Estadual de Campinas. 120 pp.

BROWN, R. L., AND P. R. MILLER. 1983. Studies of Lepidoptera hindwings with emphasis on ultrastructure of scales in *Cydia caryana* (Fitch) (Tortricidae). Entomography, **2:** 261–295.

BRYK, F. 1953. Lepidoptera aus dem Amazonasgebiete und aus Peru gesammelt von Dr. Douglas Melin und Dr. Abraham Roman. Arkiv für Zoologi (n.s.), **5:** 1–268 ("1952").

BUREAU OF ENTOMOLOGY. 1907. The principal injurious insects of 1906, pp. 508–517. *In* Yearbook of the United States Department of Agriculture for 1906. Washington, D.C.: Government Printing Office.

BURMEISTER, H. 1878. Description physique de la République Argentine d'après des observations personnelles et étrangères. Tome Cinquième. Lépidoptères. Première Partie. Buenos Aires: Paul-Emile Coni. [i–ii] + 1–[526] pp.

———. 1879. Atlas de la description physique de la République Argentine. Contenant des vues pittoresques et des figures d'histoire naturelle. Cinquième Section, Seconde Partie. Lépidoptères. Buenos Aires, Paul-Emile Coni. [i–ii] + 1–64 pp., pls. I–XXIV.

BURNS, J. M. 1984. Evolutionary differentiation: differentiating gold-banded skippers—*Autochton cellus* and more (Lepidoptera: Hesperiidae: Pyrginae). Smithsonian Contributions to Zoology, **405:** 1–38.

BUSKIRK, R. E. 1985. Zoogeographic patterns and tectonic history of Jamaica and the northern Caribbean. Journal of Biogeography, **12:** 445–461.

CALLAHAN, P. S. 1975. Insect antennae with special reference to the mechanism of scent detection and the evolution of the sensilla. International Journal of Insect Morphology and Embryology, **4:** 381–430.

CAMPOS R., F. 1921. Estudios sobre la Fauna Entomologica del Ecuador. 1° Lepidopteros. Revista del Colegio Nacional Vicente Rocafuerte (Guayaquil, Ecuador), **4:** 16–62.

———. 1931. Catalogo preliminar de los Lepidopteros del Ecuador. Segunda parte. Heteroceros. Revista del Colegio Nacional Vicente Rocafuerte, **13:** 1–162.

CARPENTER, F. M. 1992. Superclass Hexapoda. Treatise on Invertebrate Paleontology. Part R. Arthropoda 4. Volumes 3 and 4. Boulder, Colorado and Lawrence, Kansas: Geological Society of America and University of Kansas. xxi + 655 pp.

CHAPMAN, T. A. 1894. Some notes on the Micro-Lepidoptera whose larvae are external feeders, and chiefly on the early stages of *Eriocephala calthella* (Zygaenidae, Limacodidae, Eriocephalidae). Transactions of the Entomological Society of London for 1894, pp. 335–350, pls. VI–VII.

———. 1898. Some remarks on *Heterogyna penella*. Transactions of the Entomological Society of London for 1898, pp. 141–150.

CLARKE, J. F. G. 1941. The preparation of slides of the genitalia of Lepidoptera. Bulletin of the Brooklyn Entomological Society, **36:** 149–161.

———. 1962. Neotropical Microlepidoptera. I. The genus *Homoeoprepes* Walsingham (Lepidoptera: Blastodacnidae). Proceedings of the United States National Museum, **113:** 373–382.

CLENCH, H. K. 1956. Contribution to the study of the neotropical Megalopygidae (Lepidoptera). 1. The genera of the "*Trosia*" group. Neotropica, **2**(7): 9–14.

COCK, M. J. W., H. C. J. GODFRAY, AND J. D. HOLLOWAY (eds.). 1987. Slug and nettle caterpillars: the biology, taxonomy and control of the Limacodidae or economic importance on palms in South-east Asia. Wallingford, Oxon: CAB International. x + 270 pp.

COHN, T. J. 1965. The arid-land katydids of the North American genus *Neobarrettia* (Orthoptera: Tettigoniidae): their systematics and a reconstruction of their history. University of Michigan Museum of Zoology Miscellaneous Publications, **126:** 1–179.

COLLIER, W. A. 1936. Lasiocampidae. Lepidopterorum Catalogus, **7**(73): 1–484.

COMMON, I. F. B. 1969. A wing-locking or stridulatory device in Lepidoptera. Journal of the Australian Entomological Society, **8:** 121–125.

———. 1970. Lepidoptera, pp. 765–866. *In* C.S.I.R.O., The insects of Australia. Melbourne: Melbourne Univ. Press. xiii + 1,029 pp.

———. 1975. Evolution and classification of the Lepidoptera. Annual Review of Entomology, **20:** 183–203.

———. 1990. Moths of Australia. Melbourne: Melbourne Univ. Press. vi + 535 pp.

CAMERON, I. F. B., AND E. D. EDWARDS. 1981. The life history and early stages of *Synemon magnifica* Strand (Lepidoptera: Castniidae). Journal of the Australian Entomological Society, **20:** 295–302.

COMSTOCK, J. A. 1959. *Dalcerides ingenita* (Hy. Edw.). Bulletin of the Southern California Academy of Sciences, **58:** 53.

COMSTOCK, J. H. 1925. An Introduction to Entomology, 2nd complete ed. Ithaca, New York: Comstock Publishing Co. xix + 1,044 pp.

DANIEL, F., AND W. DIERL. 1966. Zur Biologie und Anatomie von *Heterogynis penella* (Hbn.) (Lep.). Zoologischer Anzeiger, **176:** 447–464.

DAVIS, D. R. 1983. Zygaenoidea, pp. 65–67. *In* R. W. Hodges *et al.* (eds.), Check List of the Lepidoptera of America North of Mexico. London: E. W. Classey Ltd. xxiv + 284 pp.

DAY, M. C. 1985. Heterogynidae Rambur, 1866 (Insecta, Lepidoptera) and Heterogyninae Nagy, 1969 (Insecta, Hymenoptera): proposals to remove the homonymy. Bulletin of Zoological Nomenclature, **42:** 385–386.

DELVARE, G. 1993. Les Chalcididae d'importance économique dans les palmeraires d'Amérique tropicale (Hymenoptera). Bulletin de la Société entomologique de France, **97:** 349–372.

DELVARE, G., AND P. GENTY. 1992. Intérêt des plantes attractives pour la faune auxiliaire dans les palmeraies d'Amérique tropicale. Oléagineux, **47:** 551–559.

DIERL, W. 1970. Compsoctenidae: ein neues Taxon von Familienstatus (Lepidoptera). Veröffentlichungen der Zoologischen Staatssammlung München, **14:** 1–41.

DOGNIN, P. 1907. Hétérocères nouveaux de l'Amérique du Sud. Annales de la Société Entomologique de Belgique, **51:** 10–23.

———. 1909. Hétérocères nouveaux de l'Amérique du Sud. Annales de la Société Entomologique de Belgique, **53:** 213–233.

———. 1910. [*Paracraga canalicula*, sp. nov.]. Hétérocères Nouveaux de l'Amérique du Sud, **1:** 42.

———. 1911. [*Acraga cosmia*, sp. nov.] Hétérocères Nouveaux de l'Amèrique du Sud, **3:** 63–64.

———. 1914. [*Acraga isothea*, sp. nov.] Hétérocères Nouveaux de l'Amérique du Sud, **8:** 100–101.

———. 1920. [*Anacraga nana* sp. nov.] Hétérocères Nouveaux de l'Amérique du Sud, **18:** 13.

———. 1923a. [?*Dalcera nigerella* sp. nov.] Hétérocères Nouveaux de l'Amérique du Sud, **22:** 24.

———. 1923b. [*Acraga mariala* sp. nov.] Hétérocères Nouveaux de l'Amérique du Sud, **24:** 17.

DONAHUE, J. P. 1980. Resurrection of the genus *Morpheis* (Cossidae), with description of a new species in the *cognatus* group from southern Arizona. Journal of the Lepidopterists Society, **34:** 173–181.

DOWNEY, J. C., AND A. C. ALLYN. 1975. Wing-scale morphology and nomenclature. Bulletin of the Allyn Museum, **31:** 1–32.

———. 1981. Chorionic sculpturing in eggs of Lycaenidae. Part 1. Bulletin of the Allyn Museum, **61:** 1–29.

DRAUDT, M. 1928. Lasiocampidae. pp. 565–628. *In* A. Seitz (ed.), Macrolepidoptera of the World, Vol. 6. Stuttgart: Alfred Kernen.

DRUCE, H. 1887. Biologia Centrali-Americana. Insecta. Lepidoptera–Heterocera, Vol. I, p. 213.

———. 1898. Biologia Centrali-Americana. Insecta. Lepidoptera–Heterocera, Vol. II, p. 441 (also Vol. III, pl. 87, figs. 23–24).

———. 1890. Descriptions of new species of Lepidoptera Heterocera from Central and South America. Proceedings of the Zoological Society of London for 1890, pp. 493–520.

———. 1895. Descriptions of some new species of Heterocera from tropical America. Annals and Magazine of Natural History, (6) **16:** 36–39.

———. 1901. Descriptions of some new species of Lepidoptera from East Africa and tropical America. Annals and Magazine of Natural History, (7) **7:** 432–444.

———. 1910. Descriptions of some new species of Heterocera from East and West Africa and tropical South America. Annals and Magazine of Natural History, (8) **6:** 168–183.

DUARTE, F. E. 1947. Insetos holometabólicos. Agronomia, **6:** 178–211.

DYAR, H. G. 1895a. Notes on *Carama* and other Megalopygidae. Canadian Entomologist, **27:** 14–15.

———. 1895b. Notes on some southern Lepidoptera. Canadian Entomologist, **27:** 242–247.

———. 1898. Notes on certain South American Cochlidiidae and allied families. Journal of the New York Entomological Society, **6:** 231–239.

———. 1903. A list of North America Lepidoptera and key to the literature of this order of insects. Bulletin of the United States National Museum, **52:** xix + 723 pp. ("1902").

———. 1905a. New genera of South American moths. Proceedings of the United States National Museum, **29:** 173–178.

———. 1905b. A list of American cochlidian moths, with descriptions of new genera and species. Proceedings of the United States National Museum, **29:** 359–396.

———. 1910a. New species of Lepidoptera from British Guiana. Zoologica (New York), **1:** 125–138 ("1909").

———. 1910b. Descriptions of some new species and genera of Lepidoptera from Mexico. Proceedings of the United States National Museum, **38:** 229–273.

———. 1910c. Notes on the family Dalceridae [Lepidoptera: Dalceridae]. Proceedings of the Entomological Society of Washington, **12:** 113–121.

———. 1910d. Notes on Megalopygidae. [Lepidoptera: Megalopygidae]. Proceedings of the Entomological Society of Washington, **12:** 161–176.

———. 1914. Report on the Lepidoptera of the Smithsonian Biological Survey of the Panama Canal Zone. Proceedings of the United States National Museum, **47:** 139–350.

———. 1916. Descriptions of new Lepidoptera from Mexico. Proceedings of the United States National Museum, **51**(2139): 1–37.

———. 1923. New American Lepidoptera. Insecutor Inscitiae Menstruus, **11:** 12–30.

———. 1925a. Some new American moths (Lepidoptera). Insector Inscitiae Menstruus, **13:** 1–19.

———. 1925b. A note on the larvae of the Dalceridae (Lepidoptera). Insector Inscitiae Menstruus, **13:** 44–47.

———. 1927. New species of American Lepidoptera of the families Limacodidae and Dalceridae. Journal of the Washington Academy of Sciences, **17:** 544–551.

———. 1928. Descriptions of four South American moths. Proceedings of the Entomological Society of Washington, **30:** 9–10.

DYAR, H. G., AND E. STRAND. 1913a. Fam. Megalopygidae. Lepidopterorum Catalogus, **5**(16): 7–26.

———. 1913b. Fam. Dalceridae. Lepidopterorum Catalogus, **5**(16): 27–32.

EDWARDS, H. 1882. New species of Heterocera. Papilio, **2:** 9–15.

EPSTEIN, M. E., AND S. E. MILLER. 1990. Systematics of the West Indian moth genus *Heuretes* Grote and Robinson (Lepidoptera: Limacodidae). Proceedings of the Entomological Society of Washington, **92:** 705–715.

EYER, J. R. 1924. The comparative morphology of the male genitalia of the primitive Lepidoptera. Annals of the Entomological Society of America, 17: 275–328, pls. XXV–XXXVIII.

FARRIS, J. S. 1980. The information content of the phylogenetic system. Systematic Zoology, **28:** 483–519.

———. 1983. The logical basis of phylogenetic analysis, pp. 7–36. *In* N. I. Platnick and V. A. Funk (eds.), Advances in Cladistics, Vol. 2. New York: Columbia University Press.

———. 1988. Hennig86, version 1.5. Computer program distributed by author, Port Jefferson Station, New York.

FARRIS, J. S., A. G. KLUGE, AND M. J. ECKARDT. 1970. A numerical approach to phylogenetic systematics. Systematic Zoology, **19:** 172–189.

FARRIS, J. S., AND M. F. MICKEVICH. 1985. PHYSYS computer program installed at University of Maryland, College Park.

FIGUEROA POTES, A. 1977. Insectos y acarinos de Colombia. Palmira, Colombia: Facultad de Ciencias Agropecuarias, Universidad Nacional. ix + 686 pp.

FLETCHER, D. S. 1954. A revision of the genus *Eubaphe* (Lepidoptera: Geometridae). Zoologica, **39:** 153–166.

———. 1979. *In* I. W. B. Nye (ed.), The Generic Names of Moths of the World, Vol. 3. London: British Museum (Natural History). xx + 243 pp.

FLETCHER, D. S., AND I. W. B. NYE. 1982. *In* I. W. B. Nye (ed.), The Generic Names of Moths of the World, Vol. 4. London: British Museum (Natural History). xiv + 192 pp.

FORBES, W. T. M. 1914. The North American families of Lepidoptera. Psyche, **21:** 53–65.

———. 1923. The Lepidoptera of New York and neighboring states [part I]. Cornell Univiversity Agricultural Experiment Station Memoir, **68:** 1–729. [Reprinted 1969 by Entomological Reprint Specialists.]

———. 1942. The Lepidoptera of Barro Colorado Island, Panama. No. 2. Bulletin of the Museum of Comparative Zoology, **90:** 265–406.

———. 1960. Lepidoptera of New York and neighboring states. Part IV. Cornell University Agricultural Experiment Station Memoir, **371:** 1–188.

FRACKER, S. B. 1915. The classification of lepidopterous larvae. Illinois Biological Monographs, **2**(1): 1–169.

GAEDE, M. 1926. Heterogynidae, pp. 39–40. *In* A. Seitz (ed.), The Macrolepidoptera of the World, Vol. 14. Stuttgart: Alfred Kernen.

GENTY, P., R. DESMIER DE CHENON, AND J. P. MORIN. 1978. Les ravaguers du palmier à huile en Amérique Latine. Oléagineux, **33:** 325–419.

GHIRADELLA, H. 1984. Structure of iridescent lepidopteran scales: variations on several themes. Annals of the Entomological Society of America, **77:** 637–645.

———. 1985. Structure and development of iridescent lepidopteran scales: the Papilionidae as a showcase family. Annals of the Entomological Society of America, **78:** 252–264.

GOMES, J. G. 1940. Chave de campo para determinação das principas pragas dos citrus. Revista da Sociedadae Brasileira de Agronomia, **3:** 58–108, 246.

GOMES, J. G., AND C. H. REINIGER. 1939. Nota previa sobre uma nova praga da laranjeira. Revista da Sociedadae Brasileira de Agronomia, **2:** 26.

GOMEZ BUSTILLO, M. R. 1978. Revision de las mas altas categorias sistematicas de los Lepidopteros y su aplicacion a la peninsula Iberica. SHILAP Revista de Lepidopterologia, **6:** 245–261.

GONÇALVES, C. R., AND A. J. L. GONÇALVES. 1973. Novas observações sobre insetos hospedeiros de moscas da família Tachinidae (Diptera). Agronomia, **31:** 9–15.

GROTE, A. R. 1882. New check list of North American moths. New York: [author]. 73 pp.

GUIMARÃES, J. H. 1977. Host–parasite and parasite–host catalogue of South American Tachinidae (Diptera). Arquivos de Zoologia, **28**(3): 1–131.

HALFFTER, G. 1976. Distribucion de los insectos en la zona de transicion Mexicana. Relaciones con la entomofauna de Norteamerica. Folia Entomologia Mexicana, **35:** 1–64.

HAMBLETON, E. J., AND W. T. M. FORBES. 1935. Uma lista de Lepidoptera (Heterocera) do Estado de Minas Geraes. Archivos do Instituto Biologico, São Paulo, Brazil, **6**(Suppl. 2): 213–256.

HAMPSON, G. F. 1898. Catalogue of the Lepidoptera Phalaenae in the British Museum, Vol. I. London: British Museum. xxi + 559 pp.

———. 1918. Some small families of the Lepidoptera which are not included in the key to the families in the catalogue of Lepidoptera Phalaenae, a list of the families and subfamilies of the Lepidoptera with their types and a key to the families. Novitates Zoologicae, **25:** 366–394.

HANDLIRSCH, A. 1925. Geschichte, Literatur, Technik, Paläontologie, Phylogenie, Systematik. *In* C. Schröder (ed.), Handbuch der Entomologie, Vol. III. Jena: Gustav Fischer. viii + 1,202 pp.

HEINRICH, C. 1931. Notes on and descriptions of some American moths. Proceedings of the United States National Museum, **79**(13): 1–16, 7 pls.

HENNIG, W. 1966. Phylogenetic Systematics. Urbana: University of Illinois Press. 263 pp.

HEPPNER, J. B. 1977. The status of the Glyphipterigidae and a reassessment of relationships in Yponomeutid families and Ditrysian superfamilies. Journal of the Lepidopterists Society, **31:** 124–134.

——— (ed.). 1984. Atlas of Neotropical Lepidoptera. Checklist: part 1. The Hague: Dr. W. Junk. xxvii + 112 pp.

HEPPNER, J. B., AND G. LAMAS. 1982. Acronyms for world museum collections of insects, with an emphasis on neotropical Lepidoptera. Bulletin of the Entomological Society of America, **28:** 305–315.

HEPPNER, J. B., AND H. Y. WANG. 1987. A rare moth, *Ratarda tertia* Strand (Lepidoptera: Ratardidae), from Palin, Taiwan. Journal of the Taiwan Museum, **40:** 91–94.

HERING, E. M. 1925. Die Familie der Ratardidae (Lep.). Mitteilungen aus dem Zoologischen Museum in Berlin, **12:** 151–158.

———. 1933. Megalopygidae, pp. 197–199. *In* A. Seitz (ed.), The Macrolepidoptera of the World, Suppl. to Vol. 2. Stuttgart: Alfred Kernan.

———. 1937. Revision der Chrysopolomidae (Lep.). Annals of the Transvaal Museum, **17:** 233–257, pl. IX.

———. 1954. Die Gattung *Crothaema* Btl. (Lep. Cochlidiidae). Annales du Musée Royal du Congo Belge, Tervuren, Série in 4to, Zoologie, **1:** 381–386.

———. 1955. Synopsis der afrikanischen Gattungen der Cochlidiidae (Lepidoptera). Transactions of the Royal Entomological Society of London, **107:** 209–225.

———. 1961. Die erste Chrysopolomide von Madagascar [Lep.]. Bulletin de la Société Entomologique de France, **65:** 302–306 ("1960").

HERRICH-SCHÄFFER, G. A. W. "1850–1858." Sammlung neuer oder wenig bekannter aussereuropäischer Schmetterlinge. Regensburg: G. J. Manz. 84 pp., 551 figs. on unnumbered pls. [Fletcher, 1979 dates p. 7 and fig. 509 as 1856, pp. 79–84 as 1858, and fig. 180 as 1854.]

HESSEL, J. H. 1969. The comparative morphology of the dorsal vessel and accessory structures of the Lepidoptera and its phylogenetic implications. Annals of the Entomolgical Society of America, **62:** 353–370.

HOFFMANN, C. C. 1932. Roberto Mueller y su importancia en el conocimiento de los lepidopteros de México. Anales del Instituto de Biología, Universidad Nacional de México, **3:** 133–148.

———. 1933. La fauna de lepidopteros del Distrito del Soconusco, (Chiapas). Anales del Instituto de Biología, Universidad Nacional de México, **4:** 207–307.

HOFFMANN, F. H. 1936. Sta. Catharina und seine Lepidopterenfauna. Entomologische Zeitschrift, **50:** 301–304.

HOGUE, C. L. 1993. Latin American insects and entomology. Berkeley: University of California Press. xiv + 536 pp.

HOLDRIDGE, L. R. 1978. Ecología basada en zonas de vida. San José, Costa Rica: Instituto Interamericano de Cooperacion para la Agricultura. xv + 216 pp.

HOLDRIDGE, L. R., W. C. GRENKE, W. H. HATHEWAY, T. LAING, AND J. A. TOSI, JR. 1971. Forest environments in Tropical Life Zones: a pilot study. Oxford: Pergamon Press. xxxi + 747 pp, 3 maps.

HOLLAND, W. J. 1903. The moth book. New York: Doubleday, Page and Co. [Reprint 1968, Dover, New York.]

HOLLOWAY, J. D. 1983. Insect surveys—an approach to environmental monitoring. Atti XII del Congresso Nazionale Italiana d'Entomologia (Rome, 1980), pp. 239–261.

———. 1986. The moths of Borneo: Key to families; families, Cossidae, Metarbelidae, Ratardidae, Dudgeoneidae, Epipyropidae and Limacodidae. Malayan Nature Journal, **40:** 1–166.

———. 1987. The moths of Borneo: Superfamily Bombycoidea: Families Lasiocampidae, Eupterotidae, Bombycidae, Brahmaeidae, Saturniidae, Sphingidae. Kuala Lumpur, Malaysia: Southdene Sdn. Bhd. 199 pp., 20 pls.

HOLLOWAY, J. D., J. D. BRADLEY, AND D. J. CARTER. 1987. CIE guides to insects of importance to man. 1. Lepidoptera. Wallingford, Oxon: CAB International. 262 pp.

HOPP, W. 1921. Notizen über Dalceridae (Lep.) nebst Beschreibung neuer Arten. Archiv für Naturgeschichte, (A) **87**(2): 276–282.

———. 1922. Neue Dalceridae und Megalopygidae. (Lep.). Deutsche Entomologische Zeitschrift 1922, pp. 429–434.

———. 1923. Eine Heterogynide in Südafrika. (Lep.). Deutsche Entomologische Zeitschrift 1923, pp. 244–245.

———. 1924. Eine neue Dalceride (Lep. Heteroc.). Deutsche Entomologische Zeitschrift 1924, pp. 553–554.

———. 1926. Megalopygiden-Studien II. Deutsche Entomologische Zeitschrift 1926, pp. 193–198.

———. 1927. Die Megalopygiden-Unterfamilie der Trosiinae. (Lep. Megalopyg.). Mitteilungen aus dem Zoologischen Museum in Berlin, **13:** 209–336.

———. 1928a. Beitrag zur Kenntnis der Dalceriden. Iris, **42:** 283–287.

———. 1928b. Megalopygidae, pp. 445–446. *In* A. Seitz (ed.), The Macrolepidoptera of the World, Vol. 14. Stuttgart: Alfred Kernen.

———. 1929. Nachtrag zu den Trosiinae (Lep. Megalopyg.). Mitteilungen aus dem Zoologischen Museum in Berlin, **15:** 39–51.

———. 1935. Megalopygidae, pp. 1071–1101. *In* A. Seitz (ed.), The Macrolepidoptera of the World, Vol. 6. Stuttgart: Alfred Kernan.

HORAK, M. 1984. Assessment of taxonomically significant structures in Tortricinae (Lep., Tortricidae). Mitteilungen der Schweizerischen Entomologischen Gesellschaft, **57:** 3–64.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1985. International Code of Zoological Nomenclature. Third edition. London and Berkeley: International Trust of Zoological Nomenclature and University of California Press. xx + 338 pp.

———. 1987. Opinion 1445. Heterogynidae Rambur, 1866 (Insecta, Lepidoptera) and Heterogynidae Nagy, 1969 (Insecta, Hymenoptera): a ruling to remove the homonymy. Bulletin of Zoological Nomeclature, **44:** 150–151.

JANSE, A. J. T. 1925a. A revision of the South African Metarbelinae. South African Journal of Natural History, **5:** 61–100, pls. IV–VIII.

———. 1925b. Key to the families, subfamilies and tribes of the order Lepidoptera, with special reference to the South African species. South African Journal of Science, **22:** 318–345, pls. IX–XI.

———. 1964. The moths of South Africa. VII. Limacodidae. Pretoria: Transvaal Museum. 136 pp., 44 pls.

JANZEN, D. H. 1984. Two ways to be a tropical big moth: Santa Rosa saturniids and sphingids. Oxford Surveys in Evolutionary Biology, **1:** 85–140.

JONES, E. D. 1908. Descriptions of new species of Lepidoptera–Heterocera from south-east Brazil. Transactions of the Entomological Society of London for 1908, pp. 143–176.

JONES, E. D., AND F. MOORE. 1882. Metamorphoses of Lepidoptera from Santo Paulo, Brazil, in the Free Public Museum, Liverpool [by E. D. Jones]. With nomenclature and descriptions of new forms [by F. Moore]. And an introductory note [by T. J. Moore]. Proceedings of the Literary and Philosophical Society of Liverpool, **36:** 325–377. [Reprinted 1883, as Free Public Library, Museum, and Gallery of Art, of the City of Liverpool, Museum Report, No. 2.]

JORDAN, K. 1916. On the species of *Somabrachys* in the Tring Museum. Novitates Zoologicae, **23:** 350–358, pls. VII–VIII.

———. 1928. On some Lepidoptera of special interest, with remarks on morphology and nomenclature. Novitates Zoologicae, **34:** 132–146.

KANAZAWA, I. 1987. The male genital morphology of *Metathrinca tsugensis* (Kearfott), with special remarks on the formation of the "valvella" (Lepidoptera: Xyloryctidae). Bulletin of the Osaka Museum of Natural History, **41:** 7–15.

KAYE, W. J., AND N. LAMONT. 1927. A catalogue of the Trinidad Lepidoptera Heterocera (moths). Memoirs of the Department of Agriculture, Trinidad and Tobago, **3:** viii + 144 + xv pp.

KIRBY, W. F. 1892. A synoptic catalogue of Lepidoptera Heterocera. (Moths.) Vol. I. Sphinges and Bombyces. London: Gurney and Jackson. xiii + 951 pp.

KIRKPATRICK, T. W. 1954. Notes on minor insect pests of cacao in Trinidad. Part 2. Lepidoptera (butterflies and moths). A report on cacao research, 1953, Imperial College of Tropical Agriculture, St. Augustine, Trinidad, pp. 67–72.

KLOTS, A. B. 1970. Lepidoptera, pp. 115–130. *In* S. L. Tuxen (ed.), Taxonomist's Glossary of Genitalia in Insects, 2nd ed. Copenhagen: Ejnar Munksgaard. 359 pp.

KLUGE, A. G., AND J. S. FARRIS. 1969. Quantitative phyletics and the evolution of anurans. Systematic Zoology, **18:** 1–32.

KOEHLER, P. 1924. Fauna Argentina. Lepidopterae collectione Alberto Breyer. II. Teil. Heterocera. Systematischer Katalog und Studien, Berichtigungen, Neubeschreibungen. Zeitschrift für de Wissenschaftliche Insekten Biologie, Suppl. to Vol. 19, 28 pp., 8 pls.

———. 1928. Catalogo de Lepidopteros Argentinos. Buenos Aires: Publicaciones Breyer. 12 pp.

KRAMPL, F., AND J. DLABOLA. 1983. A new genus and species of epipyropid moth from Iran ectoparasitic on a new *Mesophantia* species, with a revision of the host genus (Lepidoptera, Epipyropidae; Homoptera, Flatidae). Acta Entomologica Bohemoslovaca, **30:** 451–472.

KRISTENSEN, N. P. 1984. The male genitalia of *Aga-*

thiphaga (Lepidoptera: Agathiphagidae) and the lepidopteran ground plan. Entomologica Scandinavica, **15:** 151–178.

KRUGER, G. 1934. IV° Contributo alla conoscenza della fauna Cirenaica. Heterocera. Bollettino della Societa Entomologia Italiana, **66:** 191–200.

KUIJTEN, P. J. 1974. On the occurrence of a hitherto unknown wing-thorax coupling mechanism in Lepidoptera. Netherlands Journal of Zoology, **24:** 317–322.

KUKALOVÁ-PECK, J. 1983. Origin of the insect wing and wing articulation from the arthropodan leg. Canadian Journal of Zoology, **61:** 1618–1669.

KUZNETSOV, N. Y. 1910. [Russian translation of Insects, D. Sharp, Cambridge Natural History, Vols. V and VI.] Sankt-Peterburg, xiii + 1,059 pp. [Lepidoptera, pp. 809–940, revised by Kuznetsov. Dalceridae are not mentioned in the 1899 English original.]

———. 1967. Fauna of Russia and adjacent countries. Lepidoptera. Vol. I. Introduction. Translated from Russian for the U.S. Department of Agriculture and National Science Foundation by Israel Prog. Sci. Transl., Jerusalem. iv + 305 pp. TT-66-51112. [Originally published 1915 and 1929.]

KUZNETSOV, V. I., AND A. A. STEKOL'NIKOV. 1981. [Functional morphology of the male genitalia and the phylogenetic relationships of some primative superfamilies of the infraorder Papilionomorpha (Lepidoptera: Sesioidea, Cossoidea, Zygaenoidea) of the Asiatic part of the U.S.S.R.] Trudy Zoologischeskogo Instituta, Akademiya Nauk SSSR, **92:** 38–73. [in Russian.]

———. 1986. Morphology of the male genitalia of *Zenophassus schamyl* Chr. (Lepidoptera, Hepialidae) and the evolution of the phallic musculature in Hepialomorpha. Trudy Zoologischeskogo Instituta, Akademiya Nauk SSSR, **145:** 3–10. [In Russian, with English summary.]

LAMAS M., G. 1976. A gazetteer of Peruvian entomological stations (based on Lepidoptera). Revista Peruana de Entomologia, **19:** 17–25.

LAWRENCE, J. F., E. S. NIELSEN, AND I. M. MACKERRAS. 1991. Skeletal anatomy and key to orders, pp. 3–32. *In* CSIRO, the Insects of Australia, 2nd ed. Melbourne: Melbourne Univ. Press. xvi + 1,137 pp. in 2 vols.

LE PELLEY, R. H. 1968. Pests of Coffee. London: Longmans. xii + 590 pp.

LIMA, A. M. DA COSTA. 1936. Terceiro catálogo dos insectos que vivem nas plantas do Brasil. Rio de Janeiro: Ministerio da Agricultura. 460 + iv pp.

———. 1945. Insetos do Brasil, Vol. 5. Rio de Janeiro: Imprensa Nacional. 379 pp.

LINSLEY, E. G., T. EISNER, AND A. B. KLOTS. 1961. Mimetic assemblages of sibling species of lycid beetles. Evolution, **15:** 15–29.

LIPSCOMB, D. L. 1990. Two methods for calculating cladogram characters: transformation series analysis and the iterative FIG/FOG method. Systematic Zoology, **39:** 277–288.

LOURENÇÃO, A. L., L. O. DE CARVALHO, AND D. H. DE CAMPOS LASCA. 1989. *Anacraga citrinopsis* Dyar (Lepidoptera: Dalceridae) em momoneira no Estado de São Paulo. Bragantia, **48:** 109–112.

MADDISON, W. P., M. J. DONOGHUE, AND D. R. MADDISON. 1984. Outgroup analysis and parsimony. Systematic Zoology, **33:** 83–103.

MARICONI, F. A. M. 1963. Inseticidas e seu emprêgo no combate ás pragas. São Paulo: Biblioteca Agronomica Ceres. xv + 607 pp.

MARICONI, F. A. M., AND J. SOUBIHE SOBRINHO. 1961. Contribuição para o conhecimento de alguns insetos que depredam a goiabeira (*Psidium guajava* L.). Publicação Científica, Instituto de Genética, Escola Superior de Agricultura "Luiz de Queiroz," Universidade de São Paulo **2:** 35–67.

MAYR, E., AND R. J. O'HARA. 1986. The biogeographic evidence supporting the Pleistocene forest refuge hypothesis. Evolution, **40:** 55–67.

MCDUNNOUGH, J. 1939. Check list of the Lepidoptera of Canada and the United States of America. Part II. Microlepidoptera. Memoirs of the Southern California Academy of Sciences, **2:** 1–171.

MCFARLAND, N. 1993. [Untitled photograph of *Dalcerides ingenita*]. Tropical Lepidoptera, **4:** 2.

MEHTA, D. R. 1933. Comparative morphology of the male genitalia in Lepidoptera. Records of the Indian Museum, **35:** 197–266.

MICKEVICH, M. F. 1981. Quantitative phylogenetic biogeography, pp. 209–222. *In* V. A. Funk and D. R. Brooks (eds.), Advances in Cladistics: Proceedings of the First Meeting of the Willi Hennig Society. Bronx: New York Botanical Garden.

———. 1982. Transformation series analysis. Systematic Zoology, **31:** 461–478.

MICKEVICH, M. F., AND D. LIPSCOMB. 1991. Parsimony and the choice between different transformations for the same character set. Cladistics, **7:** 111–139.

MICKEVICH, M. F., AND S. J. WELLER. 1990. Evolutionary character analysis: tracing character change on a cladogram. Cladistics, **6:** 137–170.

MIELKE, O. H. H. 1971. As espécies de Hesperiidae descritas por J.F. Zikán (Lepidoptera). Revista Brasileira de Biologia, **31:** 249–262.

MILLER, S. E. 1993. Unique secondary "accessory glands" in the female genitalia of Dalceridae (Lepidoptera). Annals of the Entomological Society of America, **86:** 179–181.

MILLER, S. E., AND J. D. HOLLOWAY. 1991. Priorities for conservation research in Papua New Guinea: non-marine invertebrates, pp. 44–58. *In* M. Pearl, B. Beehler, A. Allison, and M. Taylor (eds.), Conservation and Environment in Papua New Guinea: Establishing Research Priorities. Washington, D.C.: Embassy of Papua New Guinea; and New York: Wildlife Conservation International.

MINET, J. 1982. Les Pyraloidea et leurs principales divisions systématiques [Lep. Ditrysia]. Bulletin de la Société Entomologique de France, **86:** 262–280 ("1981").

———. 1983. Etude morphologique et phylogénétique des organes tympaniques des Pyraloidea. 1—Généralités et homologies. (Lep. Glossata). Annales de la Société Entomologique de France (n.s.), **19:** 175–207.

———. 1986. Ébauche d'une classification moderne de l'ordre des Lépidoptères. Alexanor, **14:** 291–313.

———. 1987. Les Ratardidae proposés comme groupe—frère des Callidulidae [Lep. Ditrysia]. Bulletin de la Société Entomologique de France, **92:** 39–44.

———. 1991. Tentative reconstruction of the Ditrysian phylogeny (Lepidoptera: Glossata). Entomologica Scandinavica, **22:** 69–95.

MÖSCHLER, H. B. 1878. Beiträge zur Schmetterlings-Fauna von Surinam. II. Verhandlungen Zoologisch-botanische Gessellschaft in Wien, **27:** 629–700.

MOSHER, E. 1916. A classification of the Lepidoptera based on characters of the pupa. Bulletin of the Illinois State Laboratory of Natural History, **12:** 17–159, pls. XIX–XXVII.

MOSS, A. M. 1920. Sphingidae of Para, Brazil. Novitates Zoologicae, **27:** 333–424, pls. I–XI.

MUNROE, E. G. 1970. Revision of the subfamily Midilinae (Lepidoptera: Pyralidae). Memoirs of the Entomological Society of Canada, **74:** 1–94.

———. 1982. Lepidoptera, pp. 612–651. *In* S. P. Parker (ed.), Synopsis and Classification of Living Organisms, Vol. 2. New York: McGraw-Hill Book Co.

NAUMANN, C. M. 1977. Stammesgeschichte und tiergeographische Beziehungen der Zygaenini (Insecta, Lepidoptera, Zygaenidae). Mitteilungen der Münchner Entomologischen Gesellschaft, **67:** 1–25.

———. 1988. The internal female genitalia of some Zygaenidae (Insecta, Lepidoptera): their morphology and remarks on their phylogenetic significance. Systematic Entomology, **13:** 85–99.

NAUMANN, C. M., R. FEIST, G. RICHTER, AND U. WEBER. 1984. Verbreitungsatlas der Gattung *Zygaena* Fabricius, 1775 (Lepidoptera, Zygaenidae). Braunschweig, West Germany: Verlag J. Cramer. 45 pp. + 97 maps.

NEUMOEGEN, B., AND H. G. DYAR. 1893a. Descriptions of certain new forms of Lepidoptera. Canadian Entomologist, **25:** 121–126.

———. 1893b. A preliminary revision of the bombyces of America north of Mexico. Journal of the New York Entomological Society, **1:** 97–118, 153–180.

———. 1894. A preliminary revision of the bombyces of America north of Mexico. Journal of the New York Entomological Society, **2:** 1–30, 57–76, 109–132, 147–174.

NIELSEN, E. S. 1978. On the systematic position of the genus *Eriocottis* Zeller, 1847, with remarks on the phylogeny of primitive Tineoidea (Lepidoptera). Entomologica Scandinavica, **9:** 279–296.

———. 1989. Phylogeny of major lepidopteran groups, pp. 281–294. *In* B. Fernholm, K. Bremer, and H. Jörnvall (eds.), The Hierarchy of Life: Molecules and Morphology in Phylogenetic Analysis. Amsterdam and New York: Elsevier Science Publishers.

NIELSEN, E. S., AND I. F. B. COMMON. 1991. Lepidoptera, pp. 817–915. *In* CSIRO, the Insects of Australia, 2nd ed. Melbourne: Melbourne Univ. Press. xvi + 1,137 pp. in 2 vols.

NUTTING, W. L., AND A. B. GURNEY. 1961. A new earwig in the genus *Vostox* (Dermaptera: Labiidae) from the southwestern United States and Mexico. Psyche, **68:** 45–52.

ODENDAAL, F. J., P. R. EHRLICH, AND F. C. THOMAS. 1985. Structure and function of the antennae of *Euphydryas editha* (Lepidoptera: Nymphalidae). Journal of Morphology, **184:** 3–22.

OGATA, M., Y. OKADA, H. OKAGAKI, AND A. SIBATANI. 1957. Male genitalia of Lepidoptera: morphology and nomenclature III. Appendages pertaining to the tenth somite. Annals of the Entomological Society of America, **50:** 237–244.

OITICICA FILHO, J. 1946. Sobre a morfologia do penis em Lepidoptera. Boletim do Museu Nacional, Rio Janeiro, Brazil, Zoologia (n.s.), **50:** 1–79.

OKAGAKI, H., A. SIBATANI, M. OGATA, AND Y. OKADA. 1956. Male genitalia of Lepidoptera: morphology and nomenclature. II. Morphological significance of sacculus and furca. Annals of the Entomological Society of America, **48:** 438–442. ("1955").

ORFILA, R. N. 1961. Las Dalceridae (Lep. Zygaenoidea) Argentinas. Revista de Investigaciones Agricolas, Instituto de Patologia Vegetal, Instituto Nacional de Tecnologia Agropecuaria, Argentina, **15:** 249–264.

ORLANDO, A., AND B. L. RIBEIRO. 1955. Ensaios preliminares de controle a "lagarta gelatinosa" dos cafezais, por meio de polvilhamentos. O Biológico, **21:** 140–146.

OWADA, M. 1993. The systematic position of *Shisa excellens* (Lepidoptera, Ratardidae). Japanese Journal of Entomology, **61:** 251–260.

PAGENSTECHER, A. 1909. Die geographische Verbreitung der Schmetterlinge. Jena: Gustav Fischer. ix + 451 pp.

PAPP, C. S., AND L. A. SWAN. 1984. A Guide to Biting and Stinging Insects and Other Arthropods. Sacramento, California: Entomography Publications. 212 pp.

PAULIAN, R. 1961. La zoogeographie de Madagascar de des Iles Voisines. Faune de Madagascar, **13:** 1–484.

PETERSEN, W. 1900. Beiträge zur Morphologie der Lepidopteren. Zapiski Imperatorskoi Akademii

Nauk (Mémoires de l'Académie Impériale des Sciences de St.-Pétersbourg), VIIIe serie, **9**(6): 1–144, 4 pls.

PHILPOTT, A. 1926. The maxillae in the Lepidoptera. Transactions of the New Zealand Institute, **57:** 721–746.

PIERRE, J. 1986. Morphologie comparée de l'appareil génital femelle des Acraeinae (Lepidoptera, Nymphalidae). Annales de la Société Entomologique de France (n.s.), **22:** 53–65.

PITTIER, H., AND P. BIOLLEY. 1897. Invertebrados de Costa Rica. III. Lepidópteros Heteróceros. San José, Costa Rica: Serie Escuela Costarricense, Instituto Fisico Geografico Nacional: Tipografia Nacional. 66 pp.

PLATNICK, N. I. 1976. Concepts of dispersal in historical biogeography. Systematic Zoology, **25:** 294–295.

POGUE, M. G., AND M. F. MICKEVICH. 1990. Character definitions and character state delineation: the bête noire of phylogenetic inference. Cladistics, **6:** 319–361.

PRANCE, G. T. 1982. A review of the phytogeographic evidences for Pleistocene climatic change in the neotropics. Annals of the Missouri Botanical Garden, **69:** 594–624.

RAZOWSKI, J. 1976. Lepidoptera of Poland. 1—General part. Translated from Polish for the U.S. Department of Agriculture and National Science Foundation by National Center for Scientific, Technical and Economic Information, Warsaw. 157 pp. TT-74-54066. [Originally Monographie Fauny Polski, **2:** 1–125, 1973.]

———. 1981. Musculature of the male genitalia in Cossidae (Lepidoptera). Folia Biologica, **29:** 253–258.

REMINGTON, C. L. 1954. Order Lepidoptera, pp. 226–305. *In* C. T. Brues *et al.*, Classification of Insects. Bulletin of the Museum of Comparative Zoology, **108:** 1–917.

RICHARDS, A. G., JR. 1941. The male genitalia of *Epipomponia multipunctata* (Druce) (Lepidoptera, Epipyropidae). Allan Hancock Pacific Expeditions, **5:** 271–275.

———. 1981. The frenulum of moths. Entomological News, **92:** 111–114.

ROBINSON, G. S. 1976. The preparation of slides of Lepidoptera genitalia with special reference to the Microlepidoptera. Entomologists Gazette, **27:** 127–132.

———. 1988. A phylogeny for the Tineoidea (Lepidoptera). Entomologica Scandinavica, **19:** 117–129.

ROEPKE, W. 1957. The cossids of the Malay Region (Lepidoptera: Heterocera). Verhandlingen der Koninklijke Nederlandse Akademie van Wetenschappen, afdelingen Natuurkunde, **52:** 1–60.

RUFFINELLI REY, A. 1967. Insectos y otros invertebrados de interes forestal. Silvicultura (Universidad de Trabajo, Maldonado, Uruguay), **25:** 5–78.

SALO, J. 1987. Pleistocene forest refuges in the Amazon: evaluation of the biostratigraphical, lithostratigraphical and geomorphological data. Annales Zoologici Fennici, **24:** 203–211.

SANTIS, L. DE. 1987. Himenópteros parasitóides e hiperparasitóides de *Anacraga* sp. (Lepidoptera, Dalceridae) en Brasil. Revista Brasileira de Entomologia, **31:** 97–99.

SARMENTO, A. A. 1958. Lagartas prejudiciais as nossas plantas cultivadas. Boletim de Agricultura, Belo Horizonte, Brazil, 7(11–12): 13–26.

SCHAUS, W. 1892. Descriptions of new species of Lepidoptera Heterocera from Brazil, Mexico, and Peru. Proceedings of the Zoological Society of London for 1892, pp. 318–341.

———. 1894. On new species of Heterocera from tropical America. Proceedings of the Zoological Society of London for 1894, pp. 225–243.

———. 1896a. New species of Heterocera. Journal of the New York Entomolgical Society, **4:** 51–60.

———. 1896b. On Walker's American types of Lepidoptera in the Oxford University Museum. Proceedings of the Zoological Society of London for 1896, pp. 634–650.

———. 1905. Descriptions of new South American moths. Proceedings of the United States National Museum, **29:** 179–345.

———. 1910. New species of Heterocera from Costa Rica.—II. Annals and Magazine of Natural History, (8) **6:** 402–422.

———. 1911. New species of Heterocera from Costa Rica.—VIII. Annals and Magazine of Natural History, (8) **7:** 612–634.

———. 1915. Notes on Costa Rican Heterocera described in the 'Annals and Magazine of Natural History.' Annals and Magazine of Natural History, (8) **15:** 501–502.

———. 1920. New species of Lepidoptera in the United States National Museum. Proceedings of the United States National Museum, **57:** 107–152.

———. 1940. New species of British Guiana Heterocera. Zoologica (New York), **25:** 83–88.

SCHOORL, J. W., JR. 1990. A phylogenetic study on Cossidae (Lepidoptera: Ditrysia) based on external adult morphology. Zoologische Verhandelingen, **263:** 1–295.

SCHRÖDER, H. 1963. Ergebnisse der Forschungsreise A. Zilch 1951 nach El Salvador. 29. Nachtfalter aus El Salvador, II. Senckenbergiana Biologica, **44:** 485–495.

SCOBLE, M. J. 1986. The structure and affinities of the Hedyloidea: a new concept of the butterflies. Bulletin of the British Museum (Natural History), Entomology, **53:** 251–286.

———. 1992. The Lepidoptera: form, function and diversity. Oxford: Oxford University Press. xi + 404 pp.

SCOTT, J. A. 1985. The phylogeny of butterflies

(Papilionoidea and Hesperioidea). Journal of Research on the Lepidoptera, **23:** 241–281 ("1984").

———. 1986. On the monophyly of the Macrolepidoptera, including a reassessment of their relationship to Cossoidea and Castnioidea, and a reassessment of Mimallonidae to Pyraloidea. Journal of Research on the Lepidoptera, **25:** 30–38.

SEITZ, A. 1912. Heterogynidae, pp. 349–350. *In* A. Seitz (ed.), The Macrolepidoptera of the World, Vol. 2. Stuttgart: Alfred Kernen.

SELANDER, R. B., AND P. VAURIE. 1962. A gazetteer to accompany the "Insecta" volumes of the "Biologia Centrali-Americana." American Museum Novitates, **2099:** 1–70.

SHAPIRO, A. M. 1979. The assumption of adaptivity in genital morphology. Journal of Research on the Lepidoptera, **17:** 68–72 ("1978").

SHARPLIN, J. 1964. Wing base structure in Lepidoptera. III. Taxonomic characters. Canadian Entomologist, **96:** 943–949.

SHEPARD, H. H. 1930. The pleural and sternal sclerites of the Lepidopterous thorax. Annals of the Entomological Society of America, **23:** 237–260.

SIBATANI, A. 1972. Male genitalia of Lepidoptera: morphology and nomenclature IV. Notes on Tuxen's "Taxonomist's Glossary of Genitalia in Insects": second enlarged edition. Journal of the Lepidopterists Society, **26:** 117–122.

SICK, H. 1939. Dalceridae, pp. 1303–1312. *In* A. Seitz (ed.), The Macrolepidoptera of the World, Vol. 6. Stuttgart: Alfred Kernen. [Dalceridae on pl. "168 (=186)," none on pl. 185, as incorrectly cited in part of text.]

SILVA, A. G. D'ARAUJO E, *et al.* 1968. Quarto catálogo dos insetos que vivem nas plantas do Brasil, seus parasitos e predadores. Parte II—1.° Tomo. Insetos, hospedeiros e inimigos naturais. Rio de Janeiro: Laboratorio Central de Patologia Vegetal, Ministério da Agricultura. xxiv + 622 pp.

SMITH, J. B. 1903. Check List of the Lepidoptera of Boreal America. Philadelphia: American Entomological Society. v + 136 pp.

STEHR, F. W., AND N. MCFARLAND. 1985. Crochets on abdominal segments 2 and 7 of dalcerid caterpillars: "missing link" or anomaly? Bulletin of the Entomological Society of America, **31:** 35–36.

———. 1987. Dalceridae, pp. 460-462. *In* F. W. Stehr (ed.), Immature Insects, Vol. I. Dubuque, Iowa: Kendall/Hunt Publ. Co. xiv + 754 pp.

STEKOL'NIKOV, A. A., AND V. I. KUZNETSOV. 1986. Origin and general trends of the evolution of the skeleton and musculature of the male genitalia in Lepidoptera. Entomologicheskoye Obozreniye, **65:** 59–73. [In Russian; English translation published in Entomological Review, **65:** 130–145, 1986.]

STEVENS, P. F. 1980. Evolutionary polarity of character states. Annual Review of Ecology and Systematics, **11:** 333–358.

STRAND, E. 1923. Fam. Heterogynididae [sic]. Lepidopterorum Catalogus, **5**(28): 11–14.

TAMS, W. H. T. 1926. A new species of the genus *Dalcera* (Lep. Het. Dalceridae) from Peru. Entomologist, **59:** 35.

———. 1935. Heterocera (exclusive of the Geometridae and the Microlepidoptera). Insects of Samoa, **3**(4): 169–290.

TARMANN, G. 1984. Generische Revision der amerikanischen Zygaenidae mit Beschreibung neuer Gattungen und Arten (Insecta: Lepidoptera). Entomofauna Supplement 2, 176 + 153 pp. in 2 vols.

TOSI, J. A., JR. 1983. Provisional Life Zone Map of Brazil at 1:5,000,000 Scale. San Juan, Puerto Rico: Inst. Trop. Forestry, U.S. Dept. Agr. 25 pp., map.

TREMEWAN, W. G. 1973. A catalogue of the genus-group names of the Zygaenidae (Lepidoptera). Bulletin of the British Museum (Natural History), Entomology, **28:** 111–151.

———. 1988. A Bibliography of the Zygaeninae (Lepidoptera: Zygaenidae). Colchester, England: Harley Books. 188 pp.

UDEA, K. 1978. The male genital structure of some Hepialid moths with a historical review of their terminology. Tyô to Ga, **29:** 191–206. [In Japanese.]

URBAHN, E. 1913. Abdominale Duftorgane bei weiblichen Schmetterlingen. Jenaische Zeitschrift für Naturwissenschaft, **50:** 277–358.

VANZOLINI, P. E., AND N. PAPAVERO. 1968. Indice dos topônimos contidos na carta do Brasil 1:1 000 000 do IBGE. São Paulo: Fundação de Amparo a Pesquiesa do Estado de São Paulo. 201 pp.

VIETTE, P. 1965. Les Zygaenidae de Madagascar (Lep.). Bulletin Mensuel de la Société Linnéenne de Lyon, **34:** 121–125.

———. 1980. Insectes Lepidopteres Limacodidae. Faune de Madagascar, **53:** 1–162.

WALKER, F. 1855a. List of the Specimens of Lepidopterous Insects in the Collection of the British Museum. Part IV.—Lepidoptera Heterocera. London: British Museum, pp. 777–976.

———. 1855b. List of the Specimens of Lepidopterous Insects in the Collection of the British Museum. Part V.—Lepidoptera Heterocera. London: British Museum, pp. 977–1257.

———. 1865. List of the Specimens of Lepidopterous Insects in the Collection of the British Museum. Part XXXII. Supplement.—Part 2. London: British Museum, pp. 323–706.

WATSON, A., AND P. E. S. WHALLEY. 1975. The Dictionary of Butterflies and Moths in Color. New York: McGraw-Hill Book Co. xiv + 296 pp.

WEITZMAN, S. H., AND S. V. FINK. 1985. Xenurobryconin phylogeny and putative pheromone pumps in Glandulocaudine fishes (Teleostei: Characidae). Smithsonian Contributions to Zoology, **421:** 1–121.

WHITEHEAD, D. R. 1972. Classification, phylogeny, and zoogeography of *Schizogenius* Putzeys (Coleoptera: Carabidae: Scaritini). Quaestiones Entomologicae, **8:** 131–348.

WHITMORE, T. C., AND G. T. PRANCE (eds.). 1987. Biogeography and Quaternary History in Tropical America. Oxford Monographs on Biogeography No. **3:** x + 214 pp. Oxford: Oxford Univ. Press.

WILEY, E. O. 1981. Phylogenetics: The Theory and Practice of Phylogenetic Systematics. New York: John Wiley and Sons. xv + 439 pp.

WIRTH, W. W., AND S. NAVAI. 1978. Terminology of some antennal sensory organs of *Culicoides* biting midges (Diptera: Ceratopogonidae). Journal of Medical Entomology, **15:** 43–49.

ZERNY, H., AND M. BEIER. 1936. Lepidoptera=Schmetterlinge. *In* W. Kükenthal and T. Krumbach (eds.), Handbuch der Zoologie: Insecta 2. Berlin: Walter de Gruyter and Co.

ZILLI, A., AND T. RACHELI. 1989. Revisional notes on Spanish *Heterogynis* Rambur, 1837 (Lepidoptera: Heterogynidae). Entomologist's Gazette, **40:** 125–152.

ZIMMERMAN, E. C. 1978. Microlepidoptera. Insects of Hawaii 9. Honolulu: Univ. Hawaii Press. 1,903 pp. in 2 vols.

APPENDIX: SYNOPSIS OF ZYGAENOIDEA

This synopsis supplements the characterizations of Common (1970: 828–833), Munroe (1982: 631–633), and Holloway *et al.* (1987), concentrating on pertinent literature and outlining major systematic problems.

Chrysopolomidae. Medium to large, with broad, rounded wings and a bombycoid appearance. Ten genera and 25 species, restricted to Africa and Madagascar. Revised by Hering (1937, 1961).

Cyclotornidae. Small, with elongate wings. One genus, *Cyclotorna* Meyrick, with five described species, all Australian. Young larvae are external parasites of Homoptera, later becoming social parasites in ant nests. Discussed by Common (1970: 830) but needs revision.

Dalceridae. Small to medium, with heavy hairy bodies and broadly rounded wings. Eleven genera and 84 species, restricted to the Neotropical Region, except one species that occurs as far north as Arizona.

Epipyropidae. Small to medium, broad-winged moths, similar in appearance to Psychidae. Thirteen genera with 33 species in the Americas, Africa, Australia, and Asia. Reviewed by Krampl and Dlabola (1983), currently being revised by D. R. Davis (USNM). Larvae are ectoparasitic on Homoptera. The "retinaculum" described in *Epimesophantia* Krampl and Dlabola (1983: 452) is not a retinaculum but the wing-locking mechanism (e.g., Common, 1969).

Heterogynidae. Small, the males broad-winged and females wingless. Five species (depending on author) of *Heterogynis* Rambur in southern Europe and the Mediterranean region (Seitz, 1912; Strand, 1923; Zilli and Racheli, 1989). The African genus *Janseola* Hopp includes two species (Gaede, 1926; Hopp, 1923). The anomalous biology and anatomy of *Heterogynis penella* (Hübner) is treated by Chapman (1898) and Daniel and Dierl (1966). Heterogynidae Nagy, 1969 (Insecta: Hymenoptera) is a junior homonym; the International Commission on Zoological Nomenclature resolved this problem by emending its spelling to Heterogynaidae under the plenary powers (Day, 1985; IZCN, 1987).

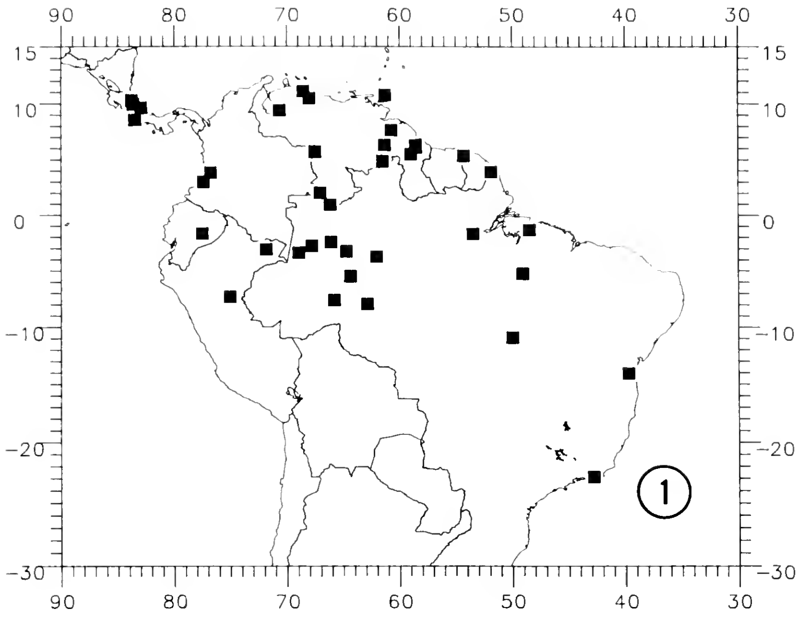
Limacodidae (=Cochlidiidae, Heterogeneidae, Apodidae, Eucleidae). Small to medium-sized moths. Over 200 genera with over 800 species, worldwide, especially in continental tropical regions; very few on oceanic islands and in Holarctic Region. The only modern treatments are for South Africa (Janse, 1964), Madagascar (Viette, 1980), and Borneo (Holloway, 1986). Most species, as well as genera, still need revision. Hering (1954, 1955) separated the subfamily Crothaeminae within Limacodidae, based on hindwing venation, but Janse (1964) did not recognize the subfamily. Larvae are slug-shaped, some with stinging hairs, and can be important as defoliators of trees.

Megalopygidae. Small to large moths. Twenty-three genera with 230 species, mostly neotropical, 11 nearctic. Currently divided into three subfamilies: Aidinae, Megalopyginae, and Trosiinae. The Trosiinae were revised by Hopp (1927), the whole family was reviewed by Hopp (1935), and Clench (1956) revised Hopp's concept of *Trosia* Hübner, but all species and genera need revision. A unique combination of character states makes the relationships of Aidinae (comprised of *Aidos* Hübner [*Xenarchus* Herrich-Schäffer is a synonym] and *Brachycodilla* Dyar) unclear (Dyar, 1895b: figs. 21, 22; 1910d: 161; Hopp, 1935: 1098; Forbes, 1942: 396; Holloway, 1986: 52; M. E. Epstein, personal communication, 1986). Relationship of Megalopygidae to Somabrachyidae is uncertain. Larvae possess stinging hairs and can be agricultural pests.

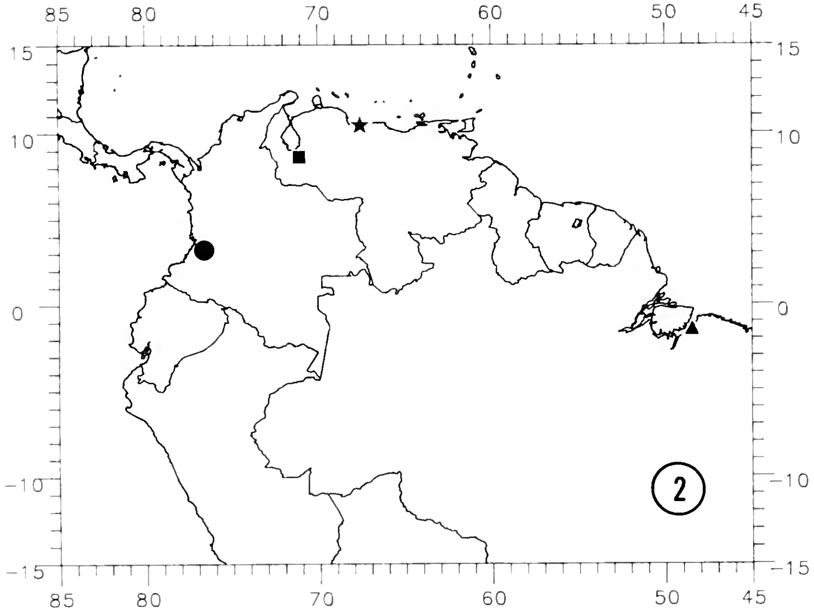
Somabrachyidae (Often Incorrectly Spelled Somabrachidae). One genus, *Somabrachys* Kirby, ranging from Morocco through North Africa to Syria, and South Africa (H. Geertsema, personal communication, 1985). Although earlier authors split *Somabrachys* into more than 20 species, Jordan (1916) and Hopp (1926; 1929: 50) divided it into only three variable species. Hering (1933: 198) described a subspecies, *S. infuscata robusta*, from Algeria, and Kruger (1934: 191) added a supposedly new species, *S. federzonii*, from Libya. *Somabrachys* has been variously included in Megalopygidae (e.g., Minet, 1986) or treated as a separate family; its relationships and biogeography need critical evaluation. *Psycharium* belongs here also (see later).

Zygaenidae (Including Pyromorphidae). Small to large moths with over 300 species placed in five to seven subfamilies, which are especially diverse in tropical Asia and may not be monophyletic. Alberti (1954) reviewed the classification and morphology of the family. Naumann *et al.* (1984) reviewed the large Palearctic genus *Zygaena* (see also Tremewan, 1988). Only the subfamily Procridinae occurs in the New World, the genera of which were revised by Tarmann (1984).

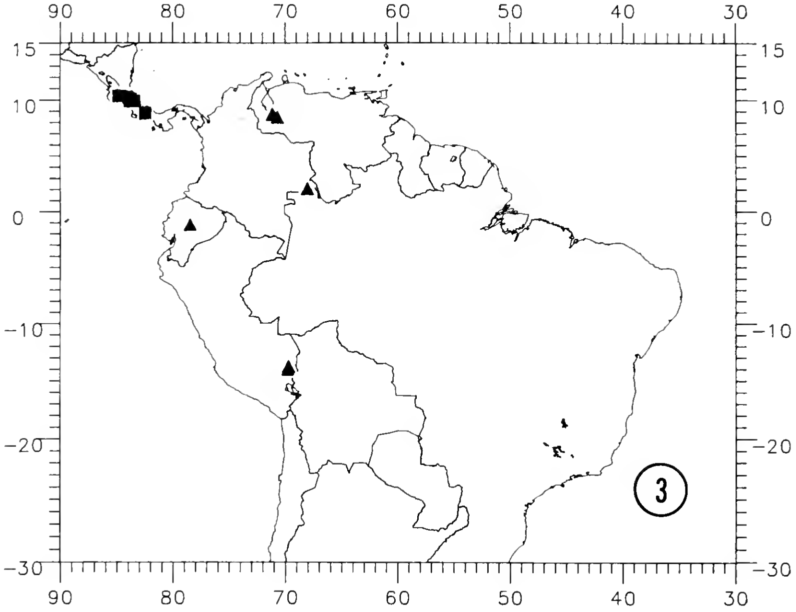
Genera of Doubtful Placement. The placement of these (and other) monotypic African genera has been disputed and emphasizes the problems in family level classification of the Zygaenoidea: *Boisduvalodes* Viette (replacement name for *Perrotia* Oberthur, 1922, not 1916), from Madagascar, originally placed in Megalopygidae, transferred to Zygaenidae by Jordan (1928: 132), to Limacodidae by Paulian (1961: 191) and Viette (1965: 121; 1980: 150) on advice of E. M. Hering, and to Somabrachyidae by Tremewan (1973: 136) on advice of W. H. T. Tams. *Psycharium* Herrich-Schäffer, from South Africa, was placed in Megalopygidae by Hopp (1928b: 445) and Zygaenidae by Jordan (1928: 136) and transferred to Somabrachyidae by Tremewan (1973: 139) on advice of Tams. Unfortunately, Tams and Hering never published the reasons for their placements of these genera.



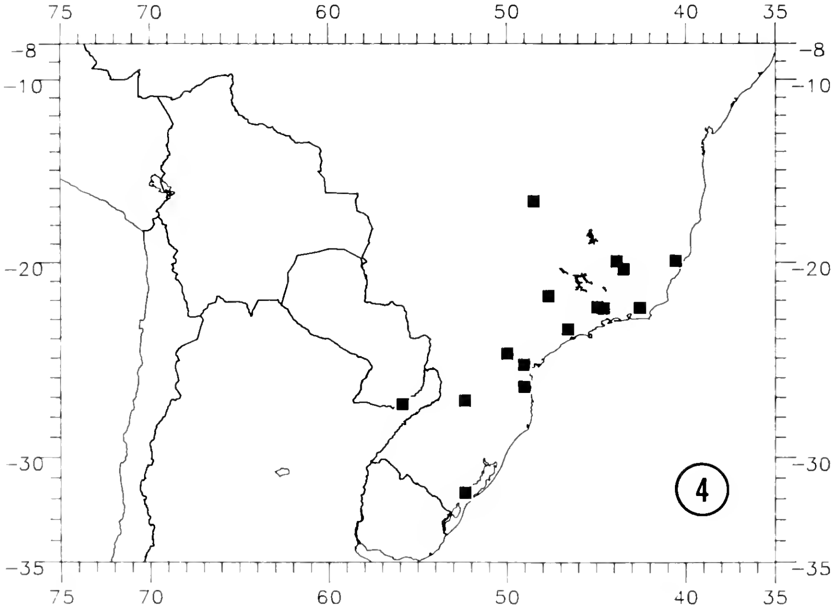
Map 1. Distribution of *Acraga goes.*



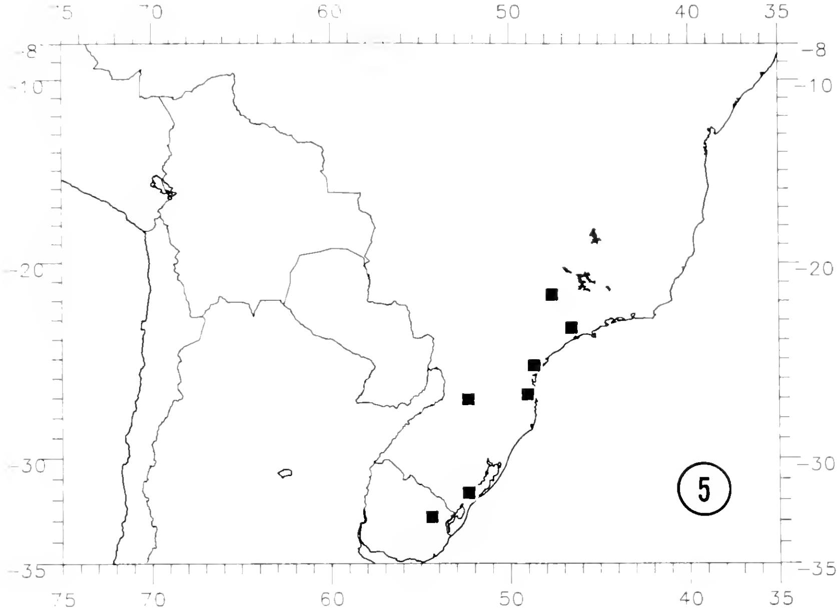
Map 2. Distribution of *Acraga ingenescens* (square), *A. luteola* (triangle), *A. beebei* (star), and *Acraga* new species F (circle).



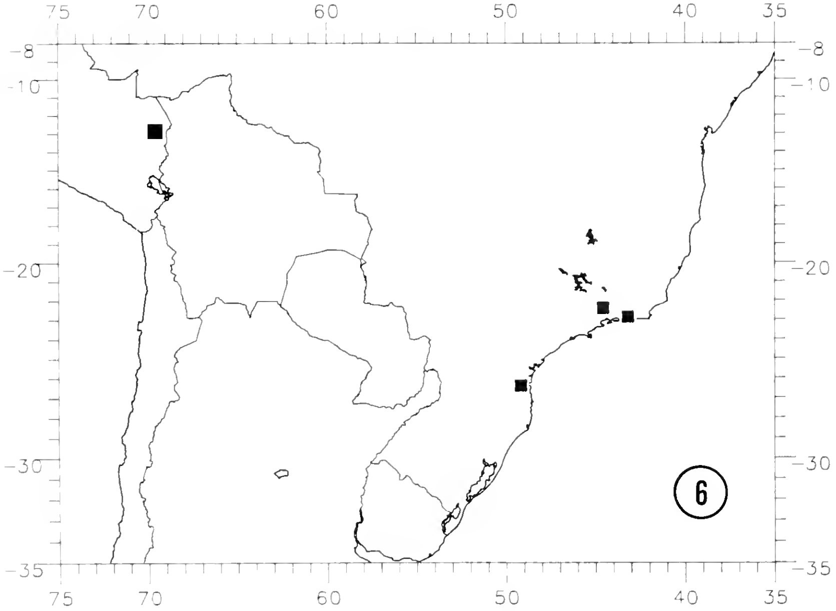
Map 3. Distribution of *Acraga hamata* (squares) and *A. andina* (triangles).



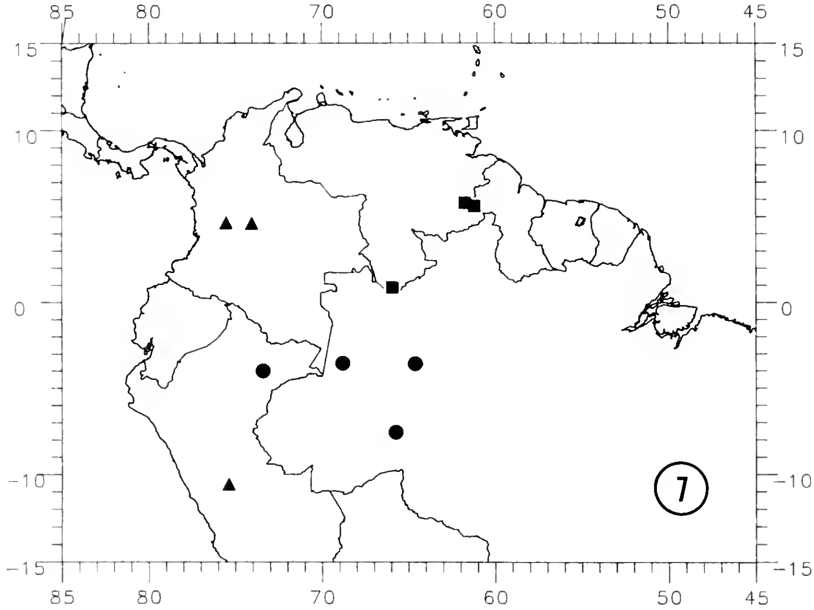
Map 4. Distribution of *Acraga flava*.



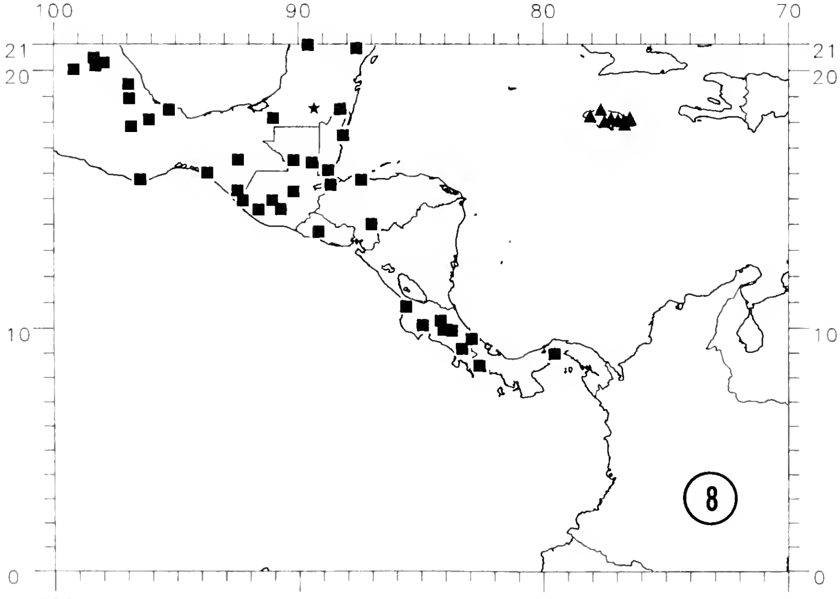
Map 5. Distribution of *Acraga obscura*.



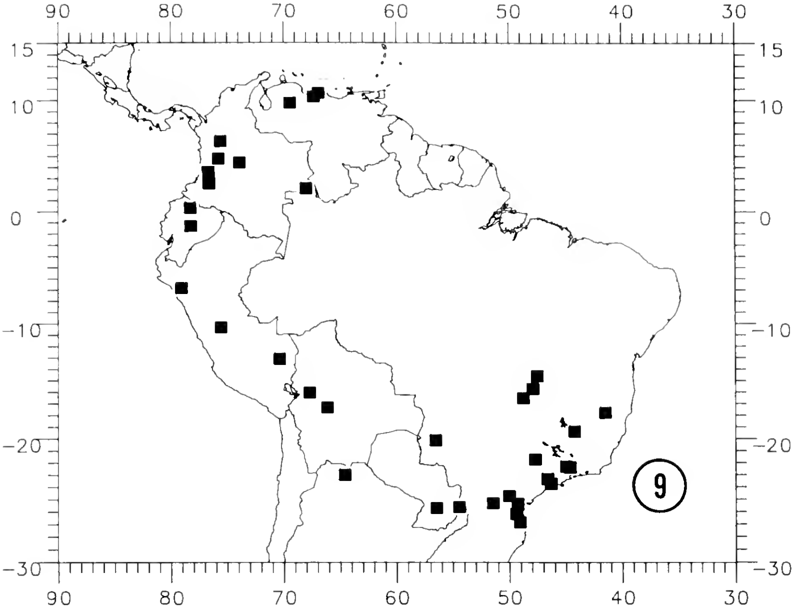
Map 6. Distribution of *Acraga ria*.



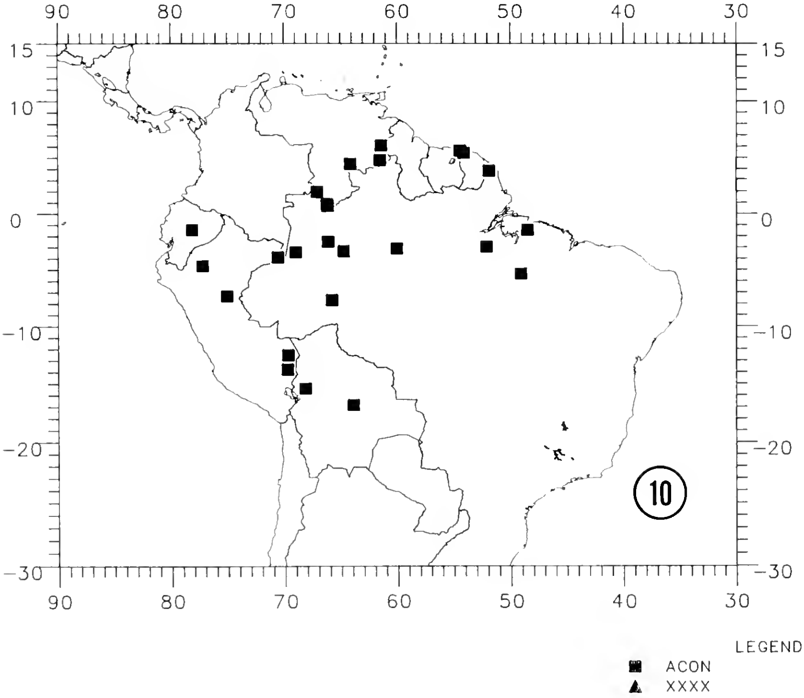
Map 7. Distribution of *Acraga neblina* (squares), *A. perbrunnea* (triangles), and *A. serrata* (circles).



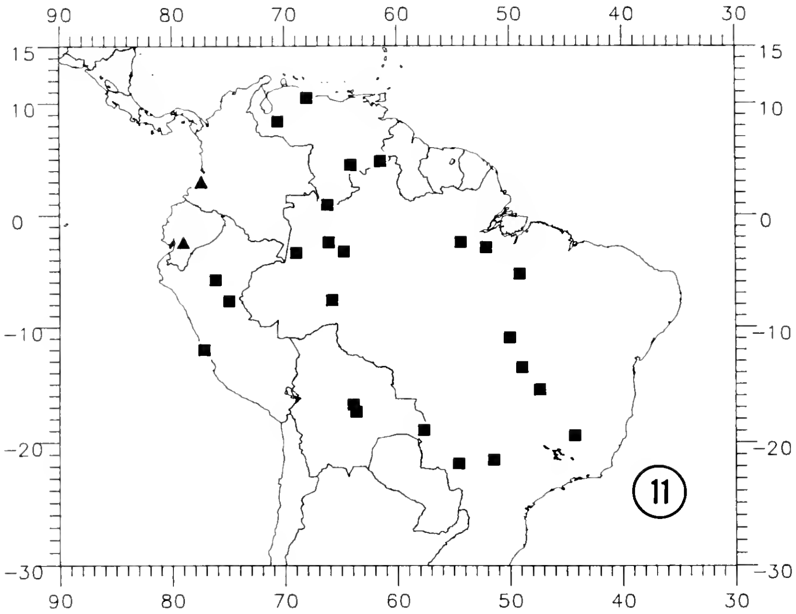
Map 8. Distribution of *Acraga coa* (squares), *A. ciliata* (triangles), and *A. chicana* (star).



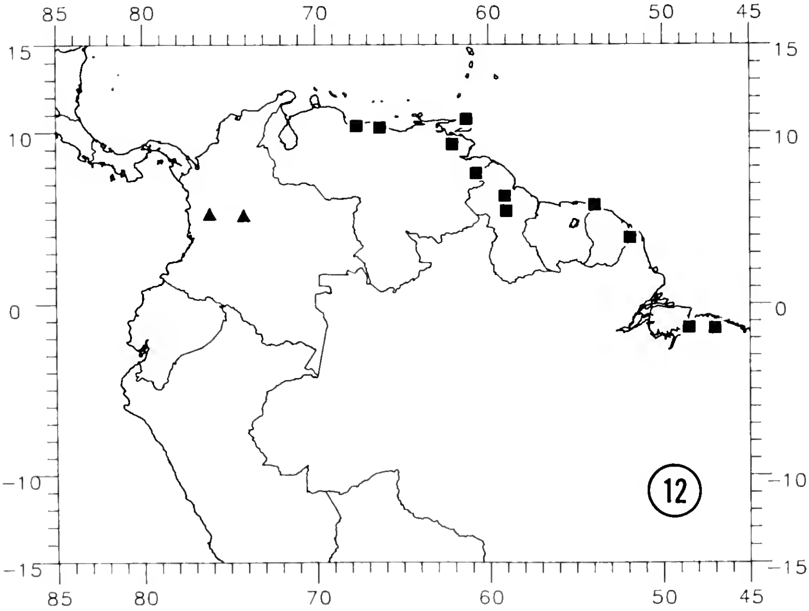
Map 9. Distribution of *Acraga moorei*.



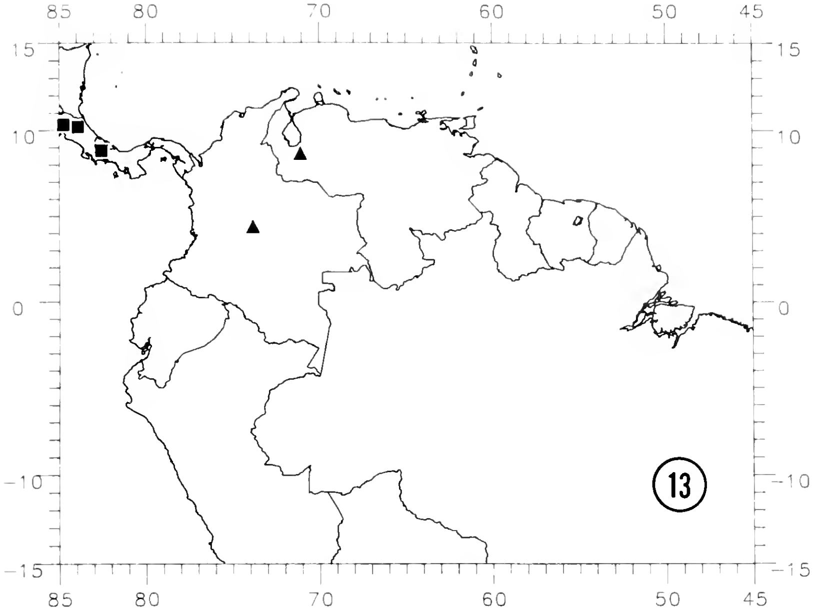
Map 10. Distribution of *Acraga concolor*.



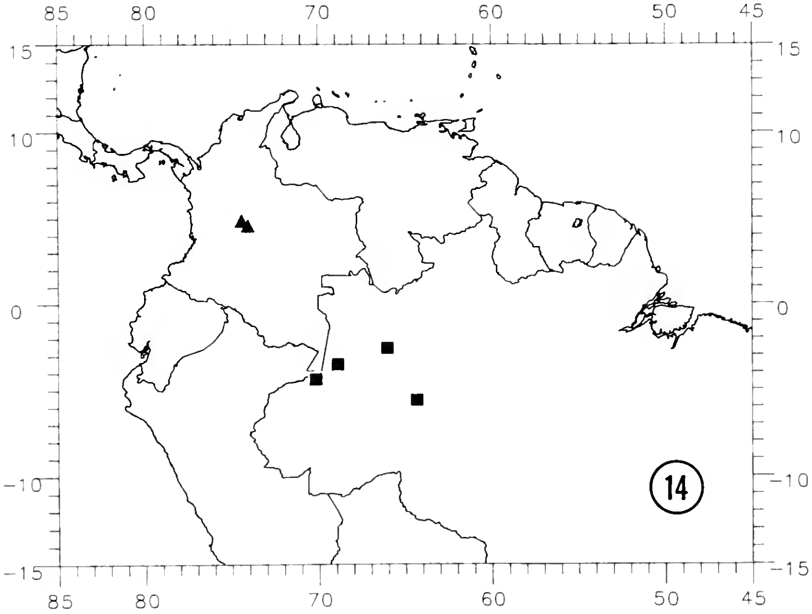
Map 11. Distribution of *Acraga citrinopsis* (squares) and *A. hoppiana* (triangles).



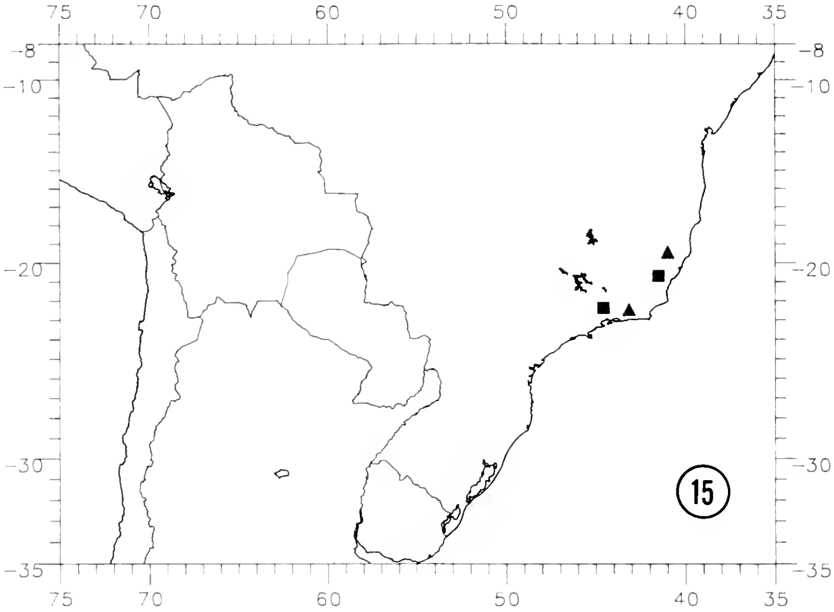
Map 12. Distribution of *Acraga citrina* (squares) and *Acraga* species C (triangles).



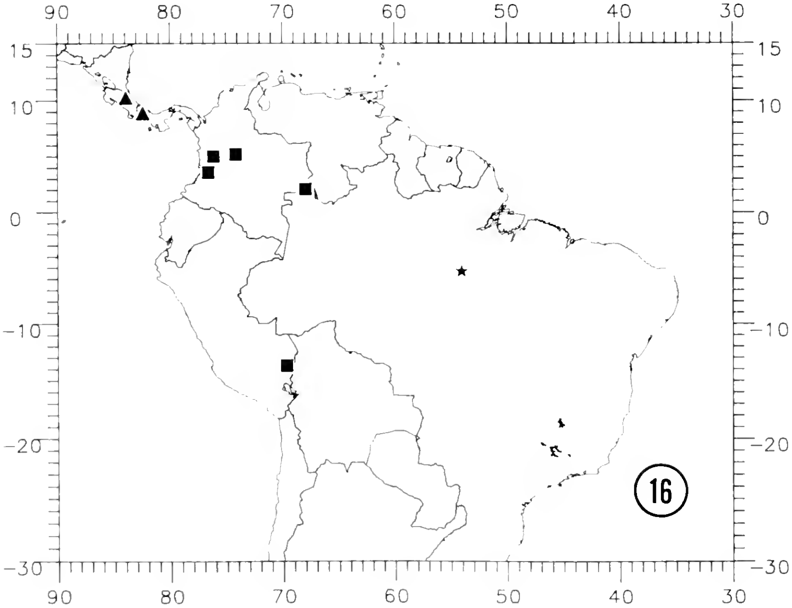
Map 13. Distribution of *Acraga melinda* (squares) and *A. meridensis* (triangles).



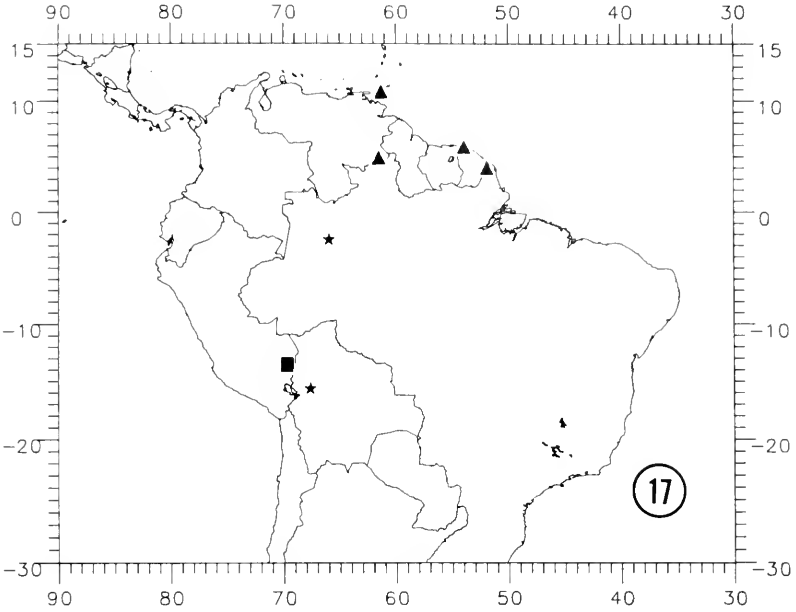
Map 14. Distribution of *Acraga amazonica* (squares) and *A. mariala* (triangles).



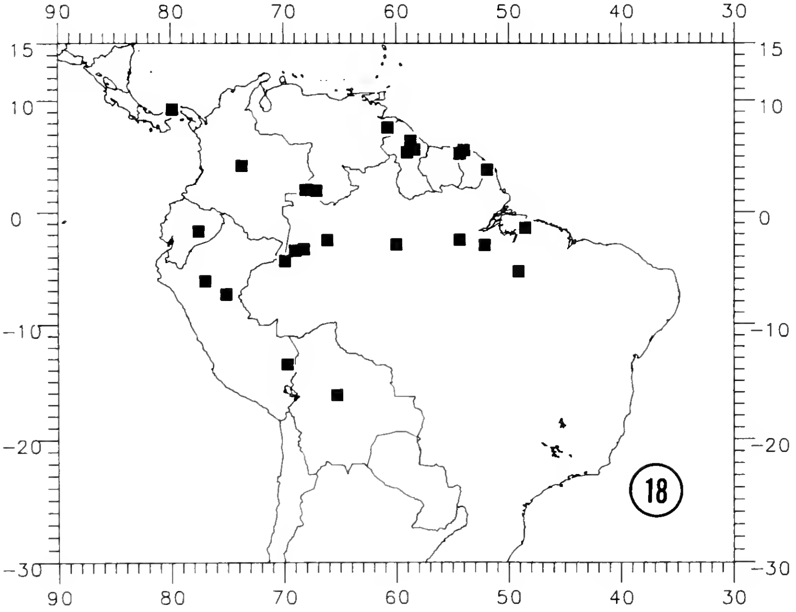
Map 15. Distribution of *Acraga ferruginea* (squares) and *A. brunnea* (triangles).



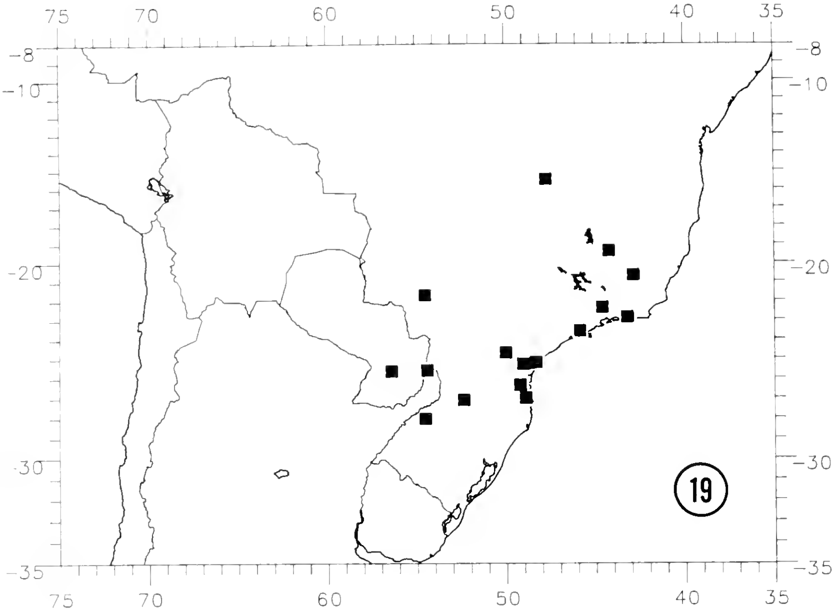
Map 16. Distribution of *Acraga ampela* (squares), *A. isothea* (triangles), and *A. umbrifera* (star).



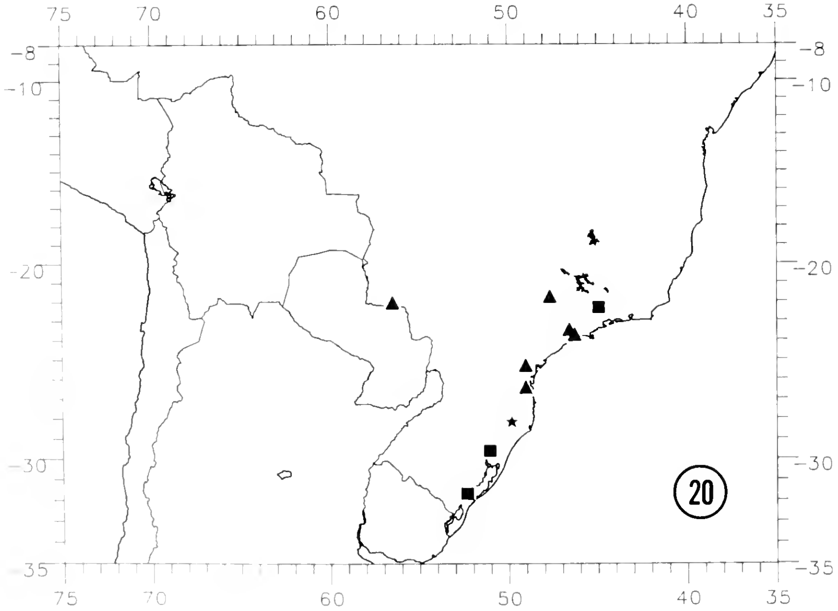
Map 17. Distribution of *Acraga puno* (square), *A. angulifera* (triangles), and *A. boliviana* (stars).



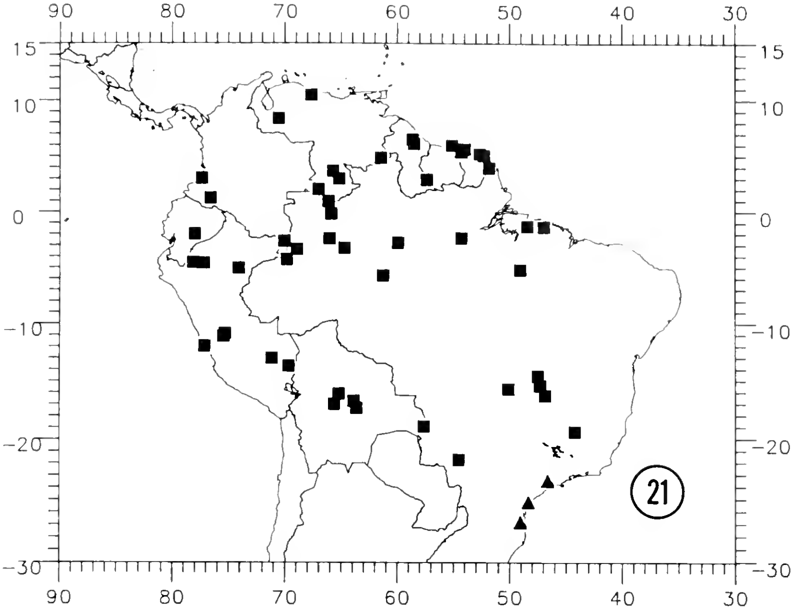
Map 18. Distribution of *Acraga leberna*.



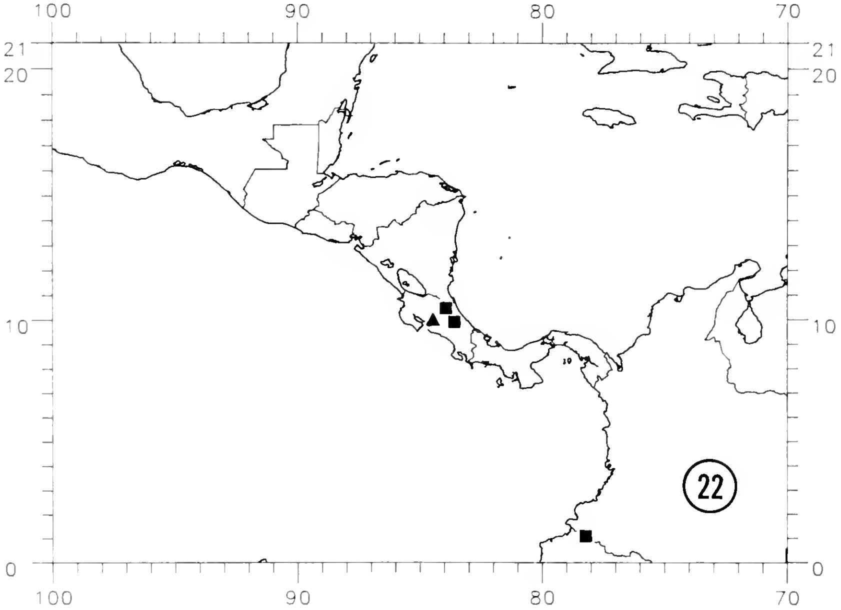
Map 19. Distribution of *Acraga ochracea*.



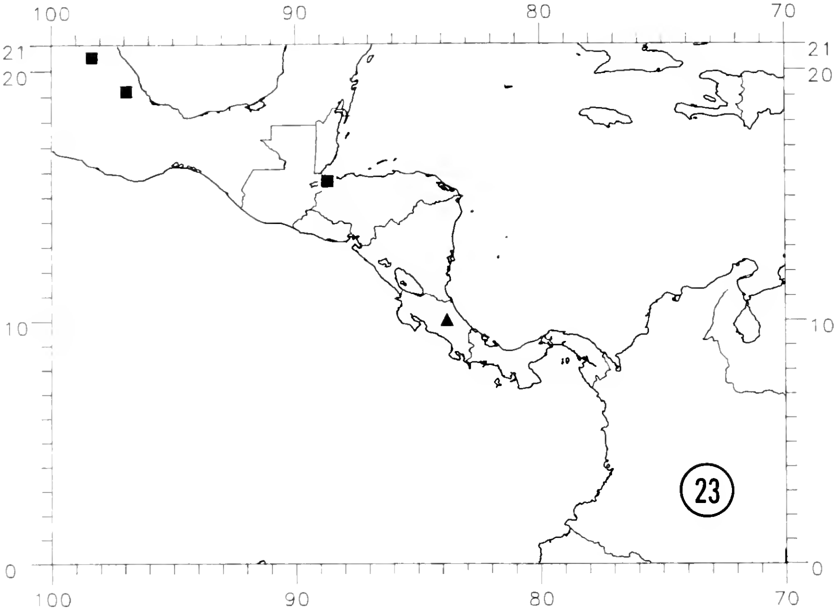
Map 20. Distribution of *Acraga sexquicentenaria* (squares), *A. parana* (triangles), and *A. victoria* (star).



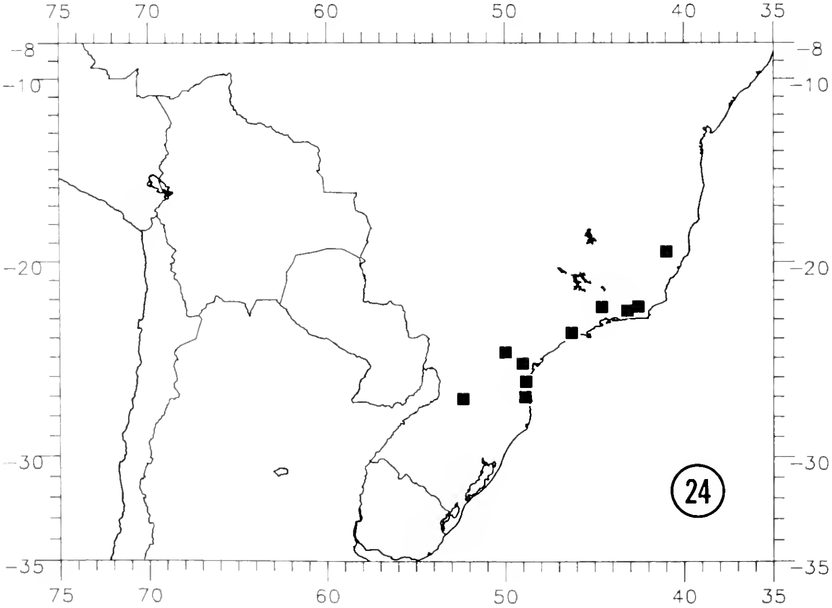
Map 21. Distribution of *Dalcerides flavetta* (squares) and *D. nana* (triangles).



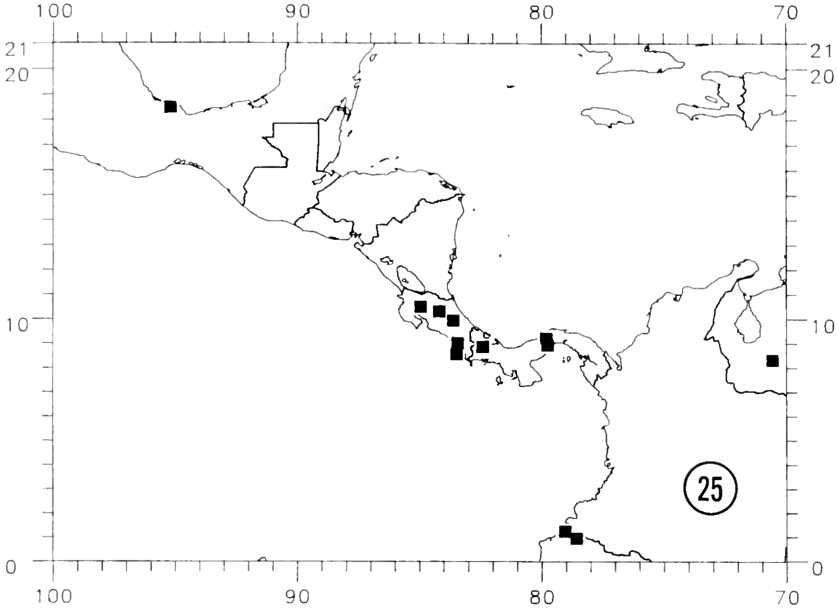
Map 22. Distribution of *Dalcerides rebella* (squares) and *D. bicolor* (triangle).



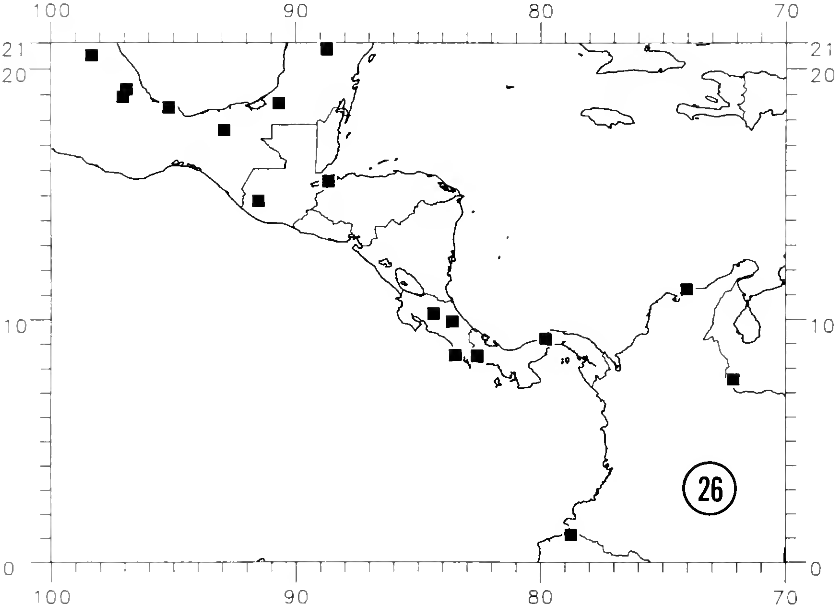
Map 23. Distribution of *Dalcerides chirma* (squares) and *D. new species* (triangle).



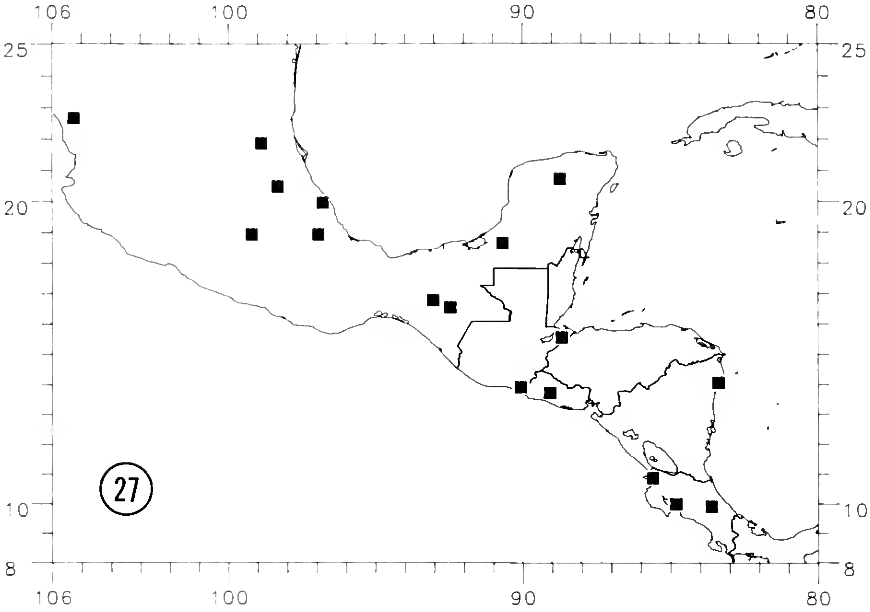
Map 24. Distribution of *Dalcerides radians*.



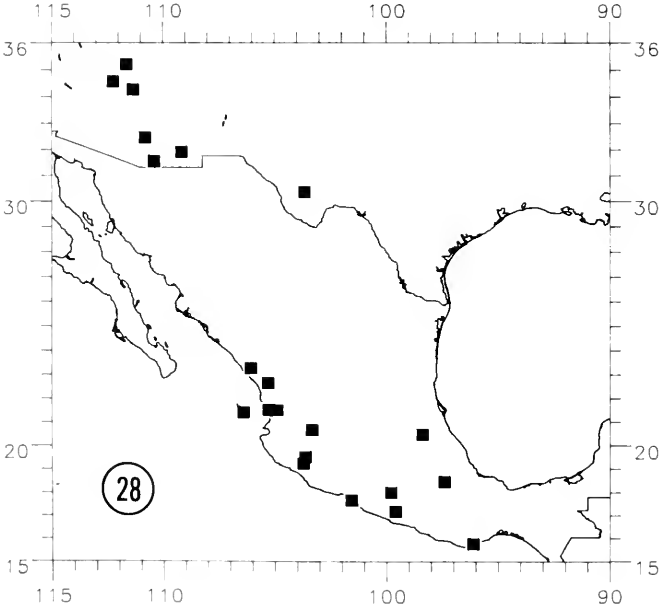
Map 25. Distribution of *Dalcerides dulciola*.



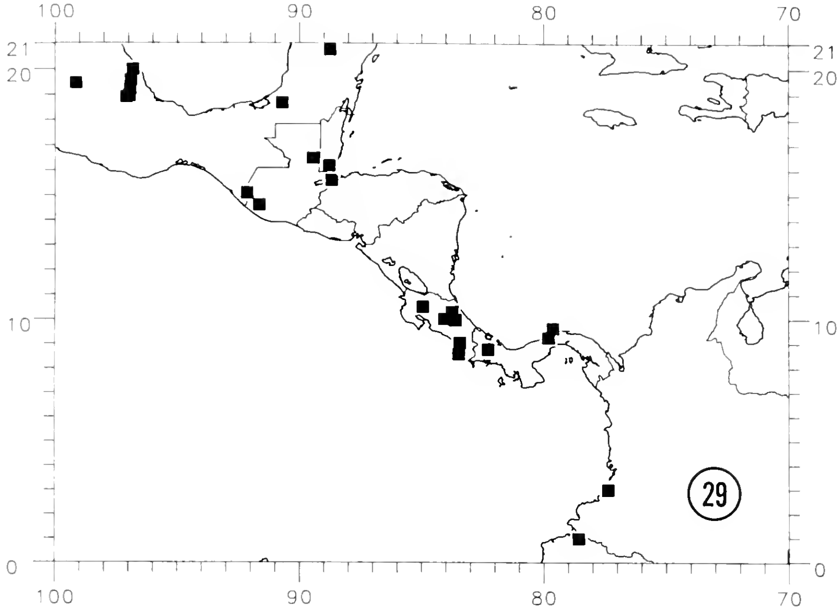
Map 26. Distribution of *Dalcerides mesoa*.



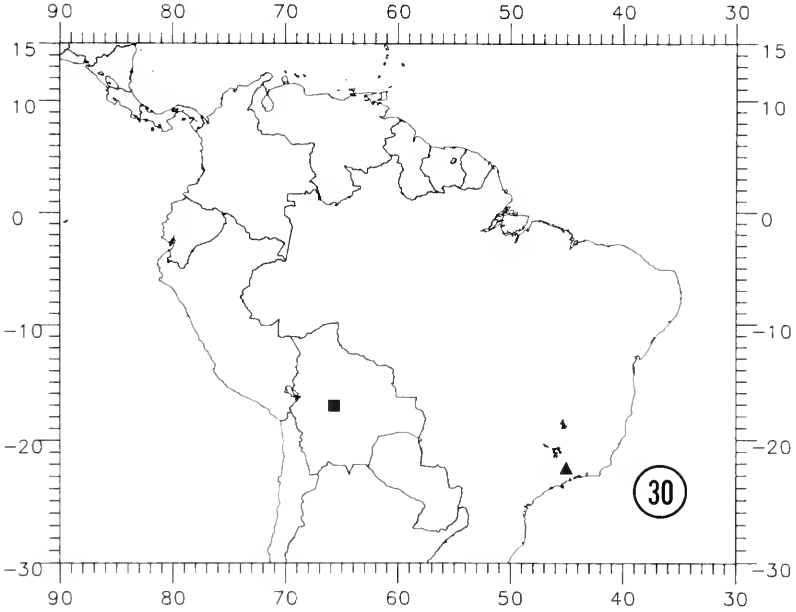
Map 27. Distribution of *Dalcerides sofia*.



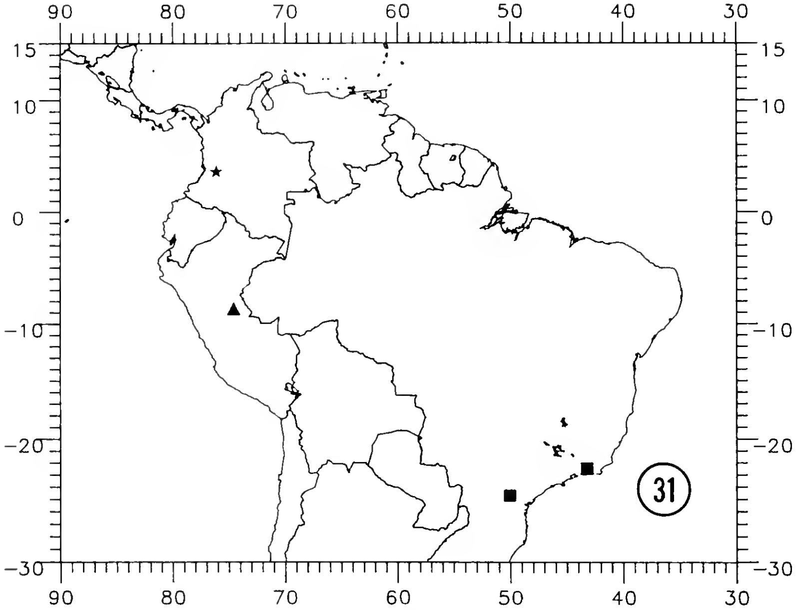
Map 28. Distribution of *Dalcerides ingenita*.



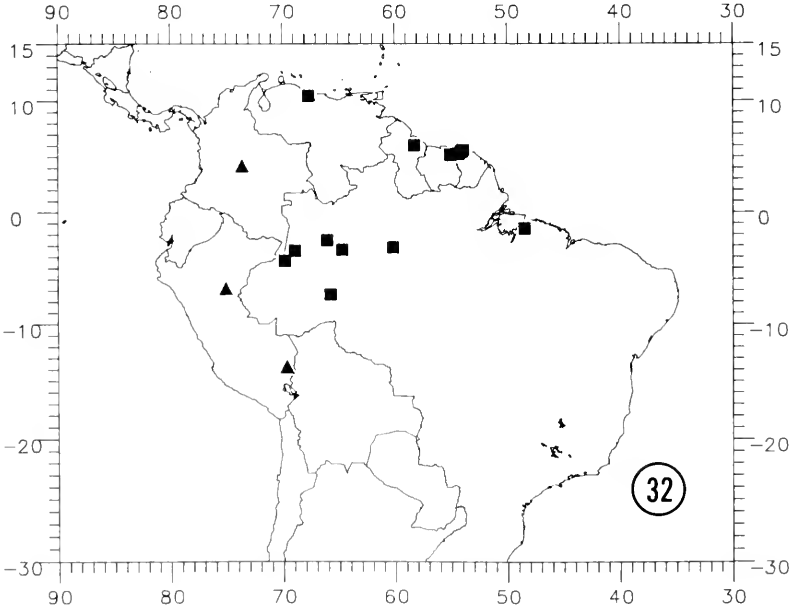
Map 29. Distribution of *Dalcerides alba*.



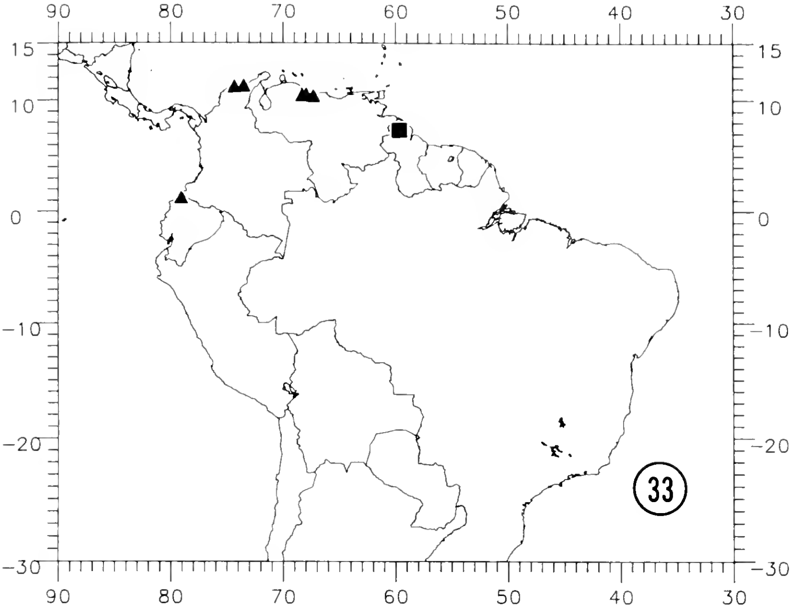
Map 30. Distribution of *Zikanyrops dubiosa* (square) and *Z. sparsa* (triangle).



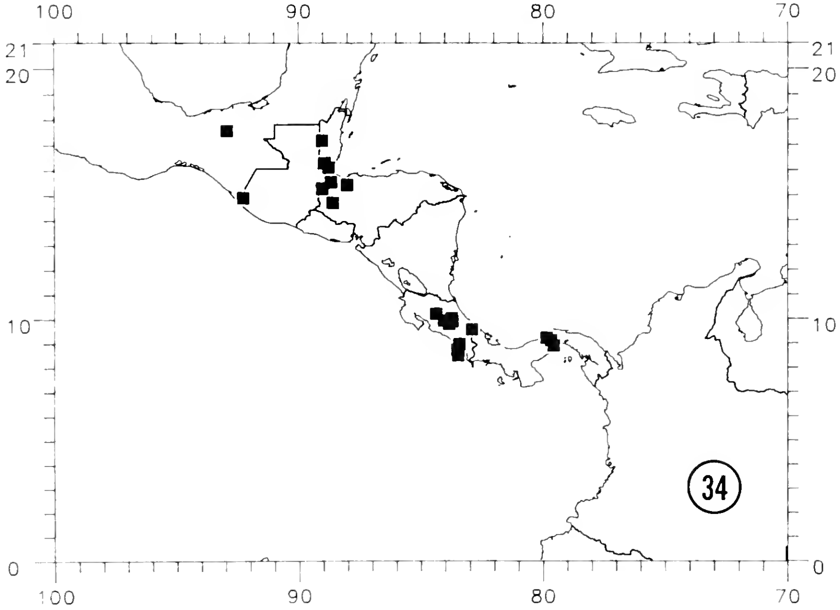
Map 31. Distribution of *Minonoa perbella* (squares), *M. pachitea* (triangle), and *M. elvira* (star).



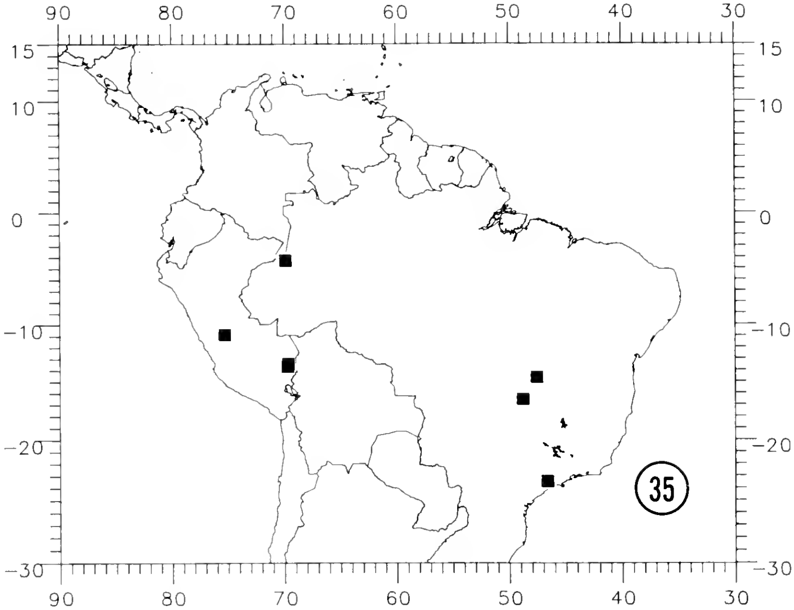
Map 32. Distribution of *Paracraga innocens* (squares) and *P. canalicula* (triangles).



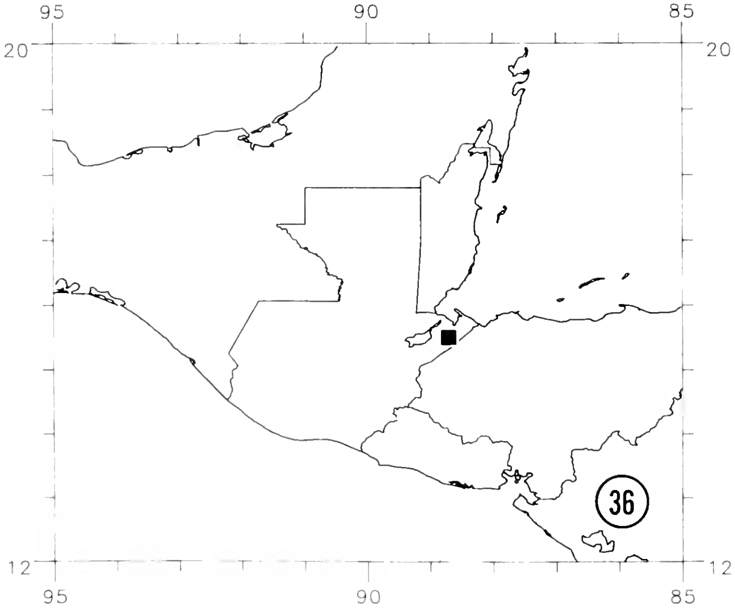
Map 33. Distribution of *Paracraga necoda* (triangles), and *P. amianta* (square).



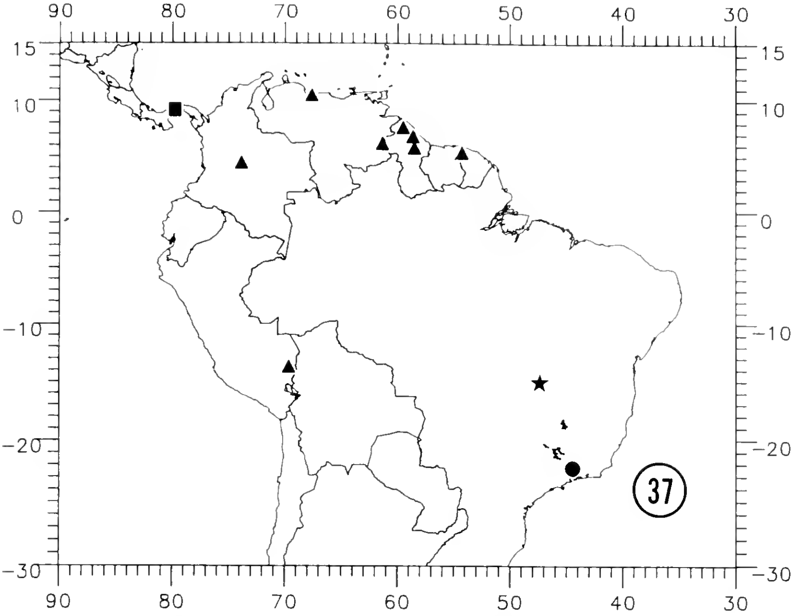
Map 34. Distribution of *Paracraga argentea*.



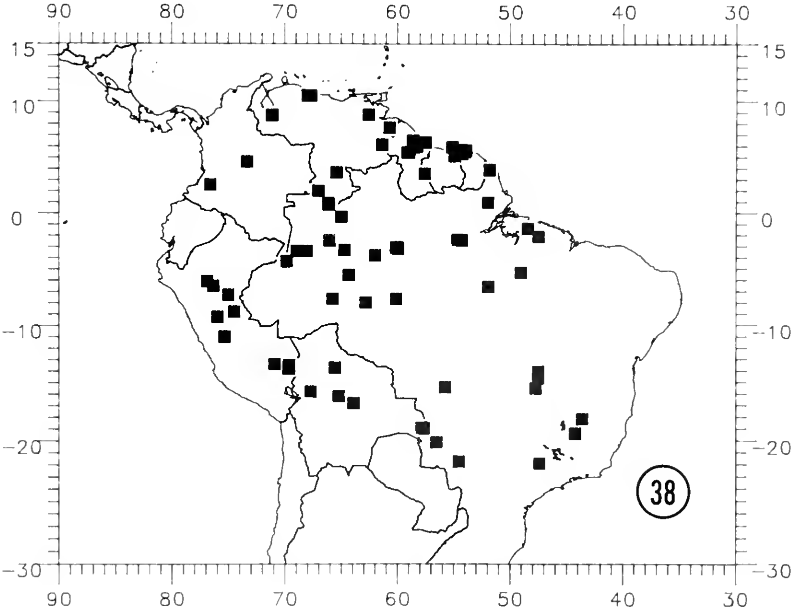
Map 35. Distribution of *Paracraga halophora.*



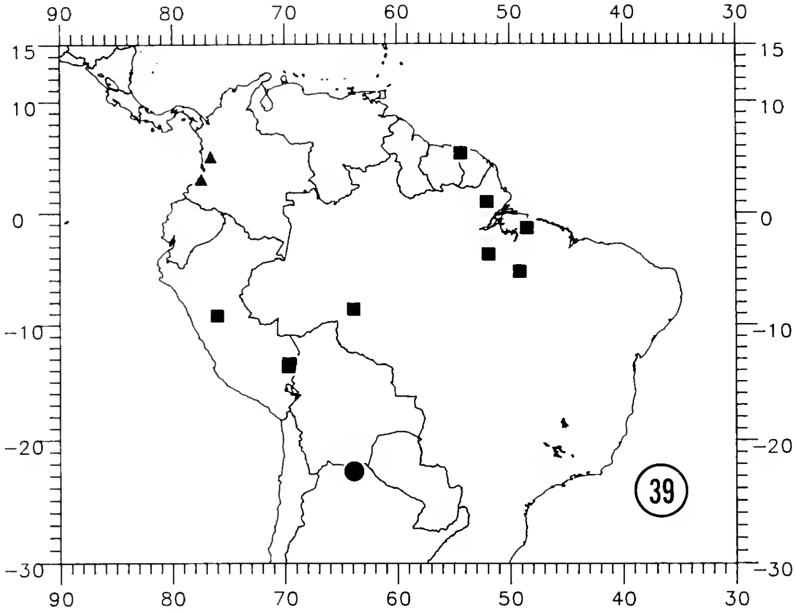
Map 36. Distribution of *Paracraga pulverina.*



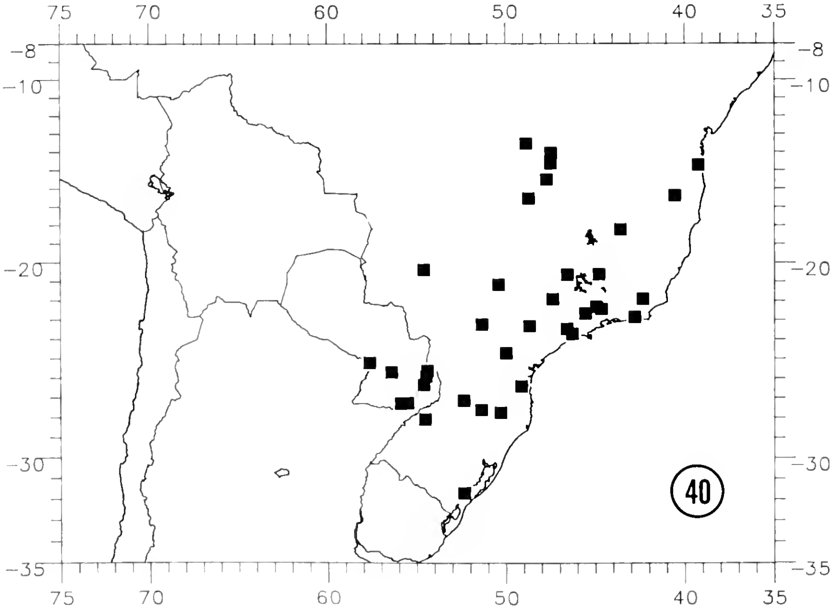
Map 37. Distribution of *Ca anastigma* (square), *Minacragides arnacis* (triangles), *Minacragides* new species A (circle), and *Minacragides* new species B (star).



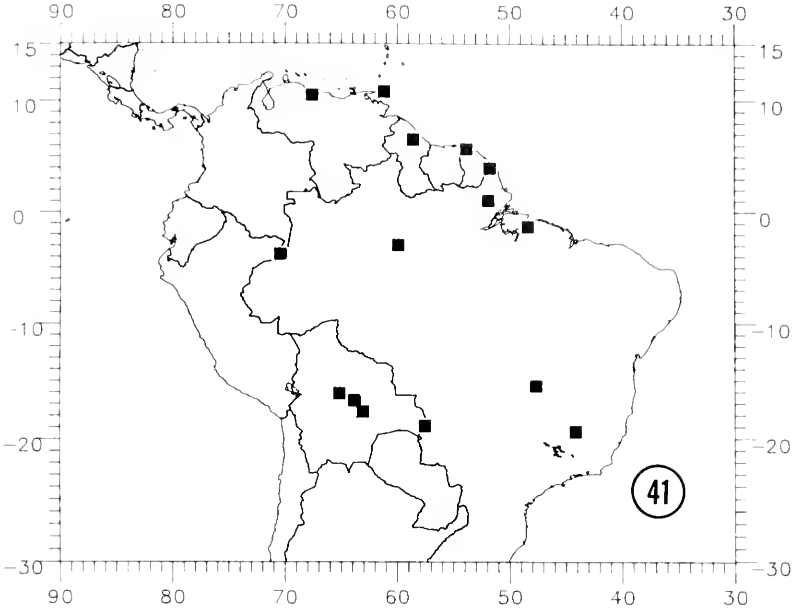
Map 38. Distribution of *Dalcera abrasa*.



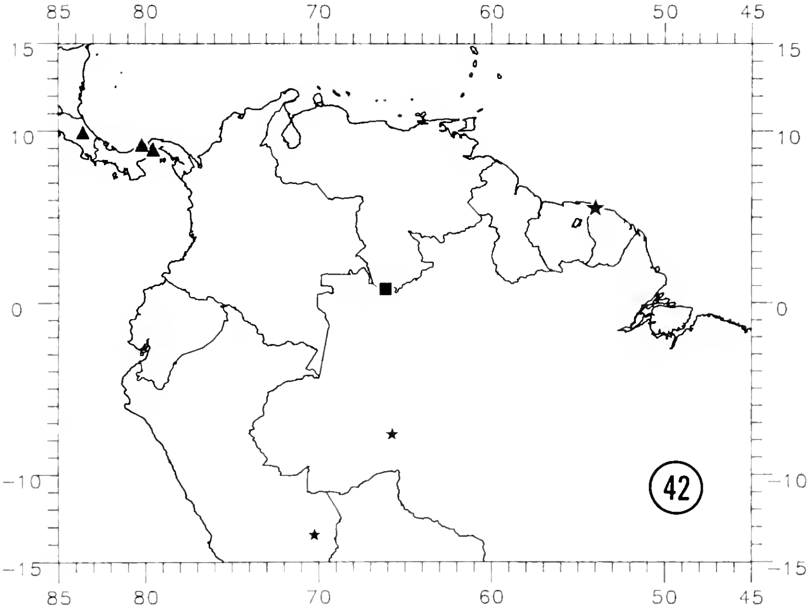
Map 39. Distribution of *Dalcera canescens* (squares), *D. semirufa* (triangles), and *D. haywardi* (circle).



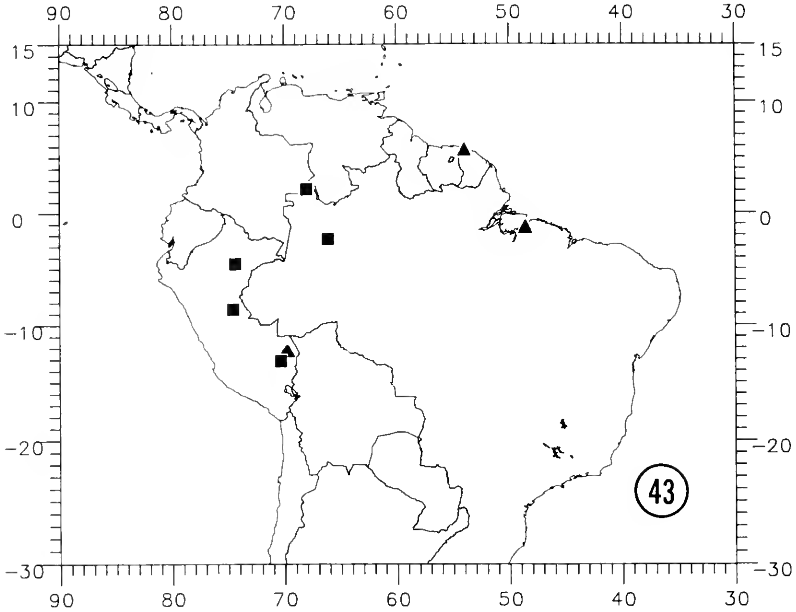
Map 40. Distribution of *Dalcerina tijucana*.



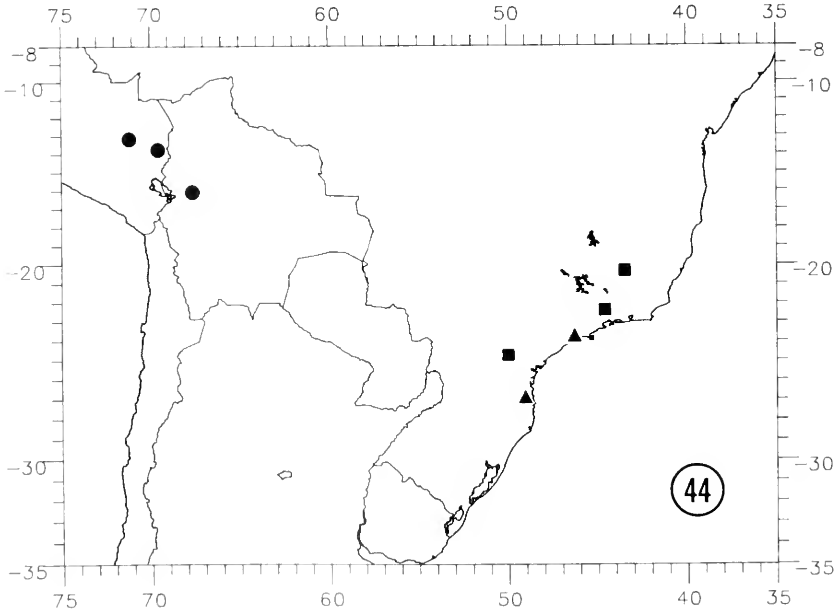
Map 41. Distribution of *Minacraga disconitens*.



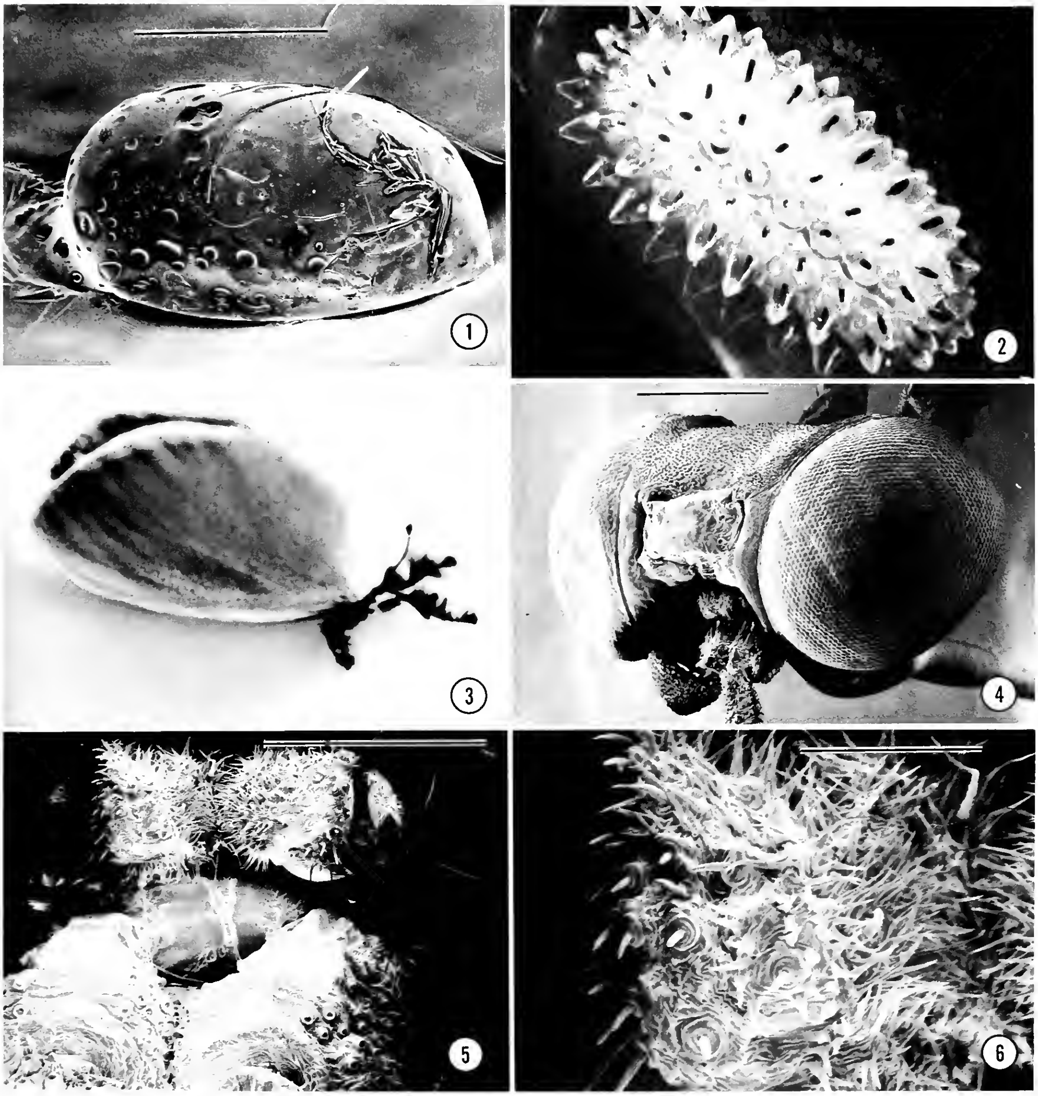
Map 42. Distribution of *Minacraga similis* (square), *M. plata* (triangles), and *M. hyalina* (stars).



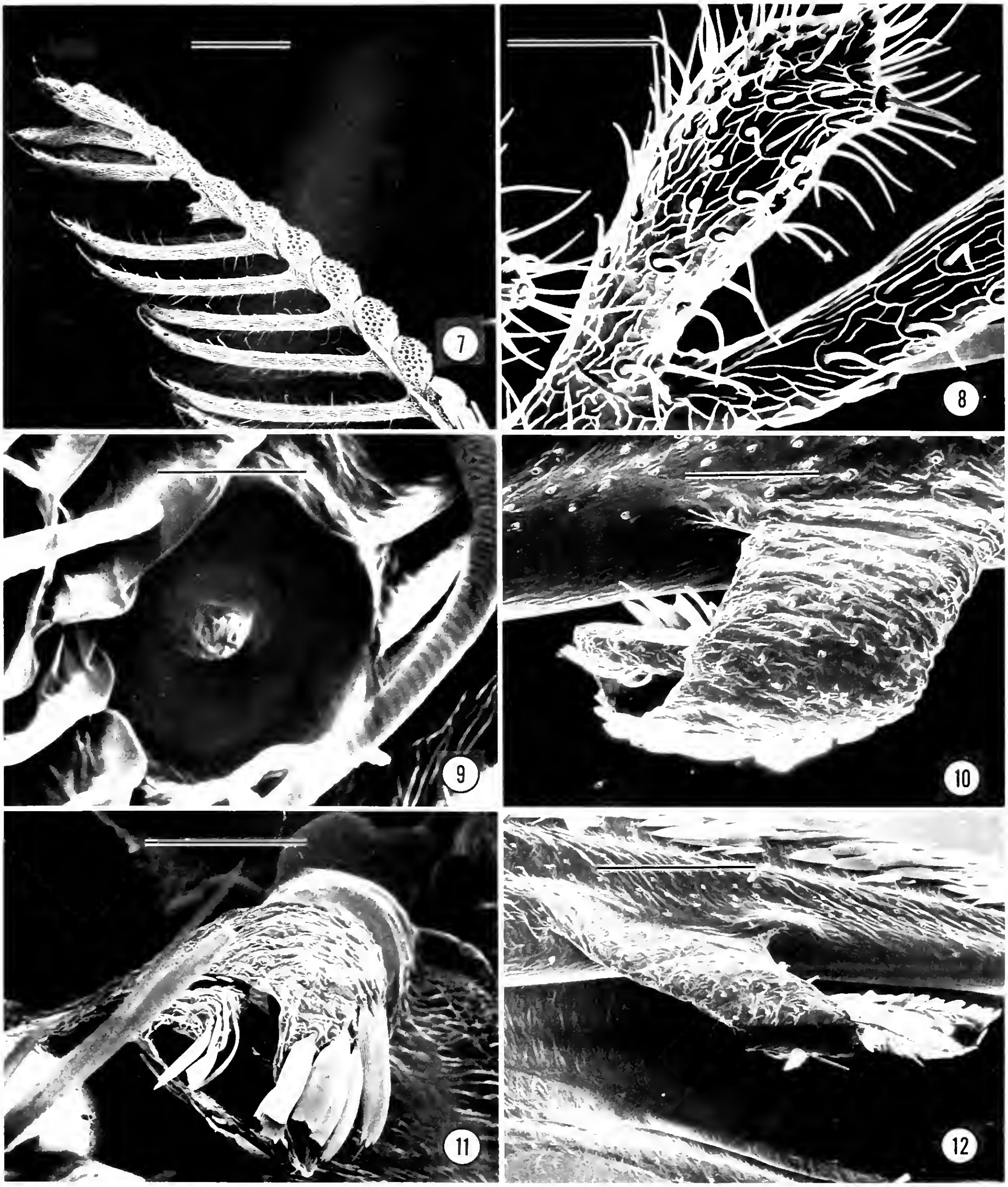
Map 43. Distribution of *Minacraga argentata* (squares) and *M. indiscata* (triangles).



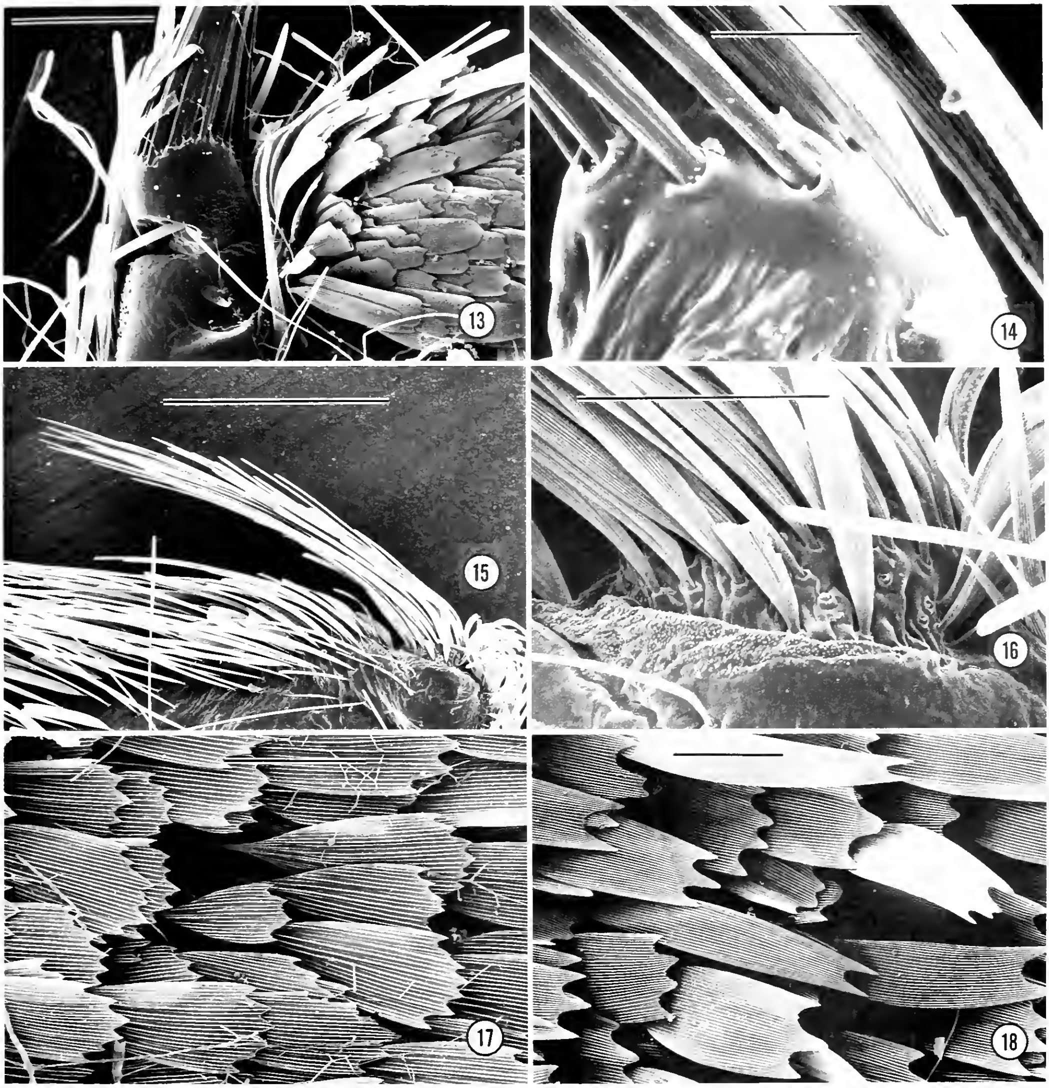
Map 44. Distribution of *Minacraga itatiaia* (squares), *M. aenea* (triangles), and *Oroya aurora* (circles).



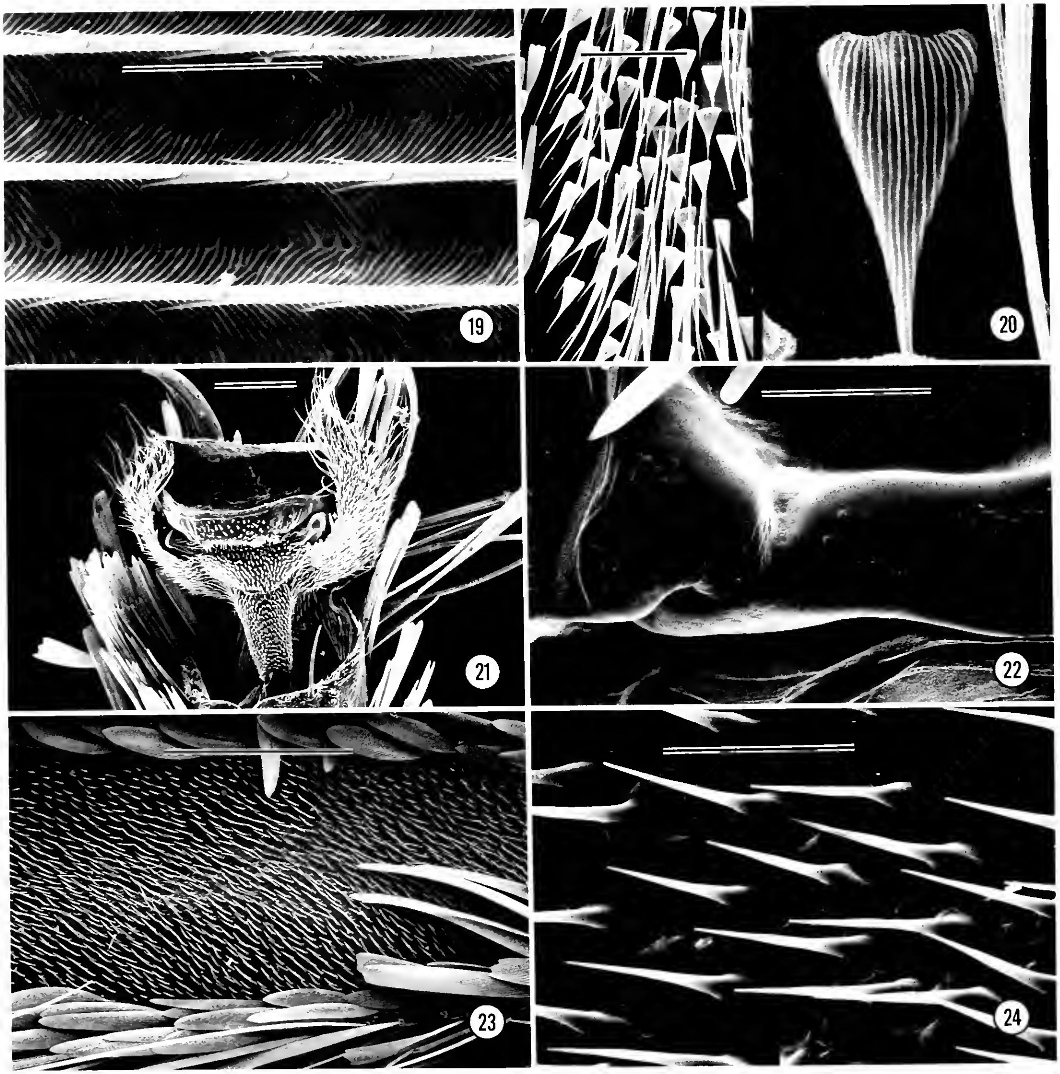
Figures 1–6. Figure 1. Egg of *Dalcerina tijucana*, laid by female reared from eggs laid by female from Maricá, Rio de Janiero, Brazil; egg was carbon- and gold-coated when freshly laid; scale = 0.5 mm. Figure 2. Late-instar larva of *Dalcerina tijucana*, reared from eggs from Maricá, Brazil. Figure 3. Live *Dalcera tijucana* female, reared from eggs from Maricá, Brazil, showing typical resting posture. Figure 4. Head of *Acraga moorei* male; scale = 0.5 mm. Figure 5. Enlargement of mouthparts of *Acraga moorei* male; scale = 200 µm. Figure 6. Enlargement of vestigial maxillary palpi of *Acraga moorei* male; scale = 50 µm.



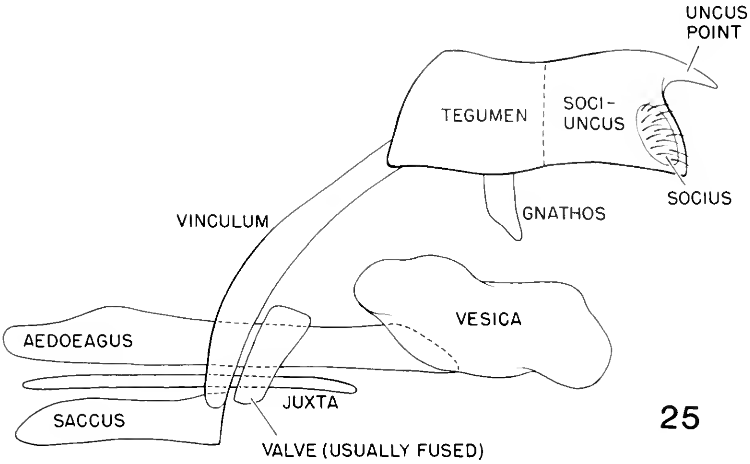
Figures 7–12. Figure 7. Antenna of *Dalcera abrasa* male, with scales removed; scale = 200 μm. Figure 8. Antenna of *Dalcerides ingenita* male, with scales removed; scale = 43 μm. Figure 9. Sensillum coeloconicum on antenna of *Dalcerides ingenita* male; scale = 4 μm. Figure 10. Retinaculum of *Dalcerides ingenita* male, ventral view; scale = 100 μm. Figure 11. Retinaculum of *Dalcerides ingenita* male, lateral view; scale = 100 μm. Figure 12. Retinaculum of *Acraga citrina* male, ventral view; scale = 200 μm.



Figures 13–18. Figure 13. Frenulum base of *Minacraga disconitens* male; scale = 200 μm. Figure 14. Frenulum base of *Dalcerides ingenita* male; scale = 20 μm. Figure 15. Frenulum *Dalcerides ingenita* female; scale = 0.5 mm. Figure 16. Frenulum base of *Dalcerides ingenita* female; scale = 100 μm. Figure 17. Scales of *Minacraga disconitens* male, dorsal hindwing anal area; scale = 100 μm. Figure 18. Scales of *Dalcera abrasa* male, dorsal forewing near discal spot; scale = 100 μm.

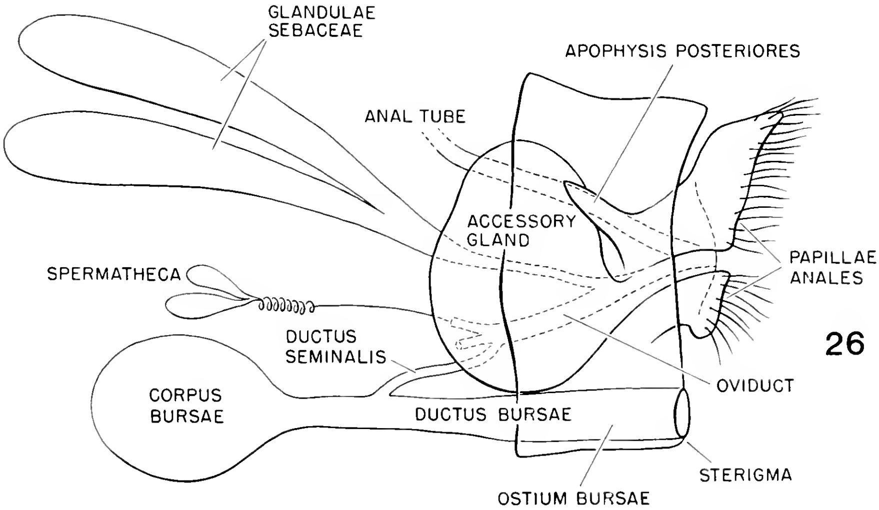


Figures 19–24. Figure 19. Enlargement of Figure 18, showing "microrib-satin" scale structure; scale = 4 μm. Figure 20. Mixed lamellar and piliform scales of *Acraga citrina* male, ventral forewing between M_2 and M_3; scale for left side = 200 μm; right side is enlarged eight times. Figure 21. Foretarsus of *Dalcera abrasa* male; scale = 100 μm. Figure 22. Campaniform sensilla on base of cubital stem on dorsal hindwing of *Acraga citrina* male; scale = 100 μm. Figure 23. Microtrichia on ventral inner margin near base of *Dalcerides ingenita* male forewing; scale = 200 μm. Figure 24. Enlargement of Figure 23; scale = 20 μm.



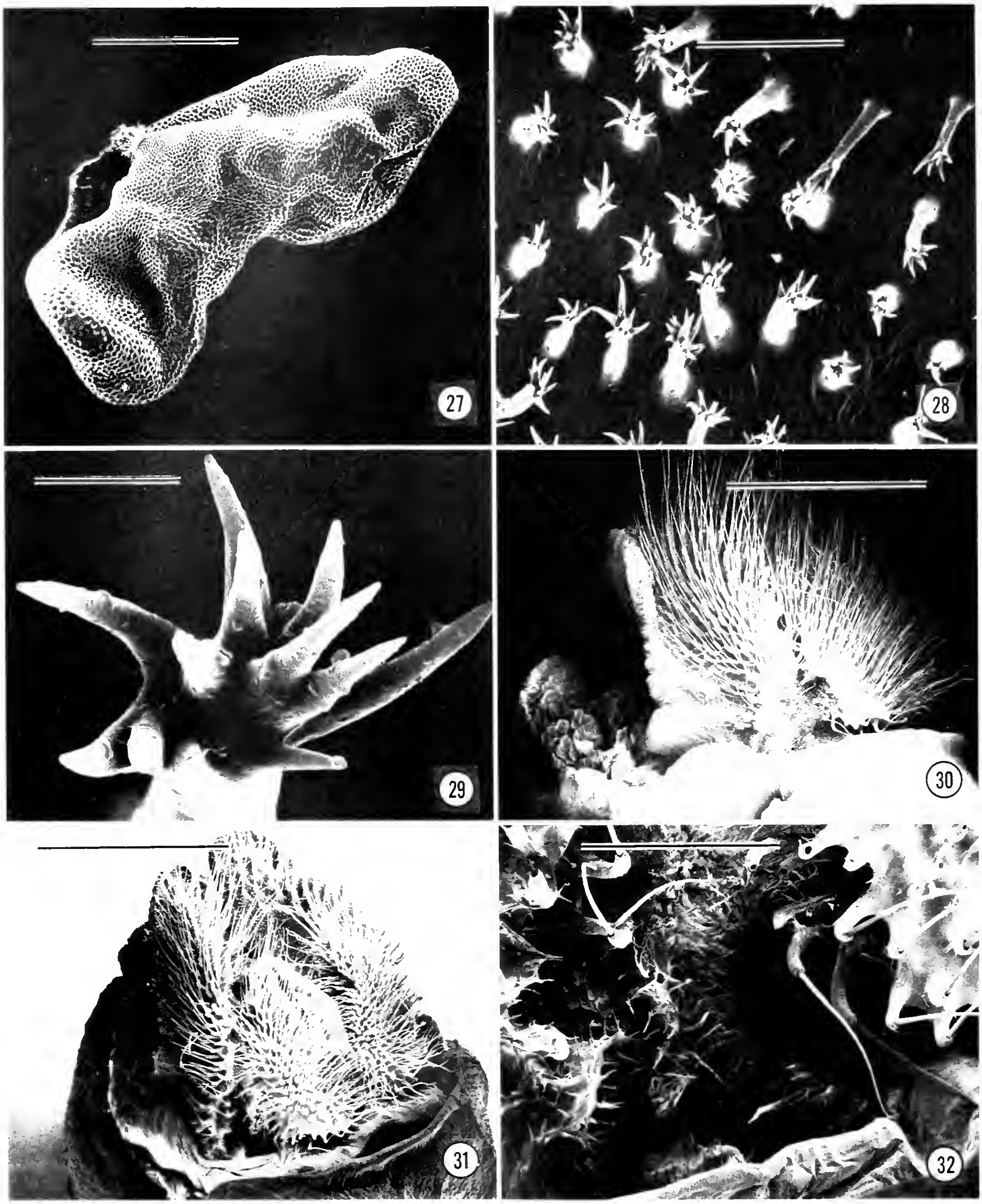
25

Figure 25. Diagrammatic male genitalia, lateral view, illustrating major morphological features.



26

Figure 26. Diagrammatic female genitalia, lateral view, illustrating major morphological features.



Figures 27–32. Figure 27. "Accessory gland" from *Acraga coa* female; scale = 1 mm. Figure 28. Inside surface of "accessory gland" from *Acraga coa* female; scale = 60 μm. Figure 29. Enlargement of Figure 28; scale = 8 μm. Figure 30. Apex of abdomen of *Acraga coa* female, lateral view; scale = 1 mm. Figure 31. Apex of abdomen of *Acraga coa* female, oblique view; scale = 1 mm. Figure 32. Enlargement of cleft between lobes of papillae anales from Figure 31; scale = 200 μm.

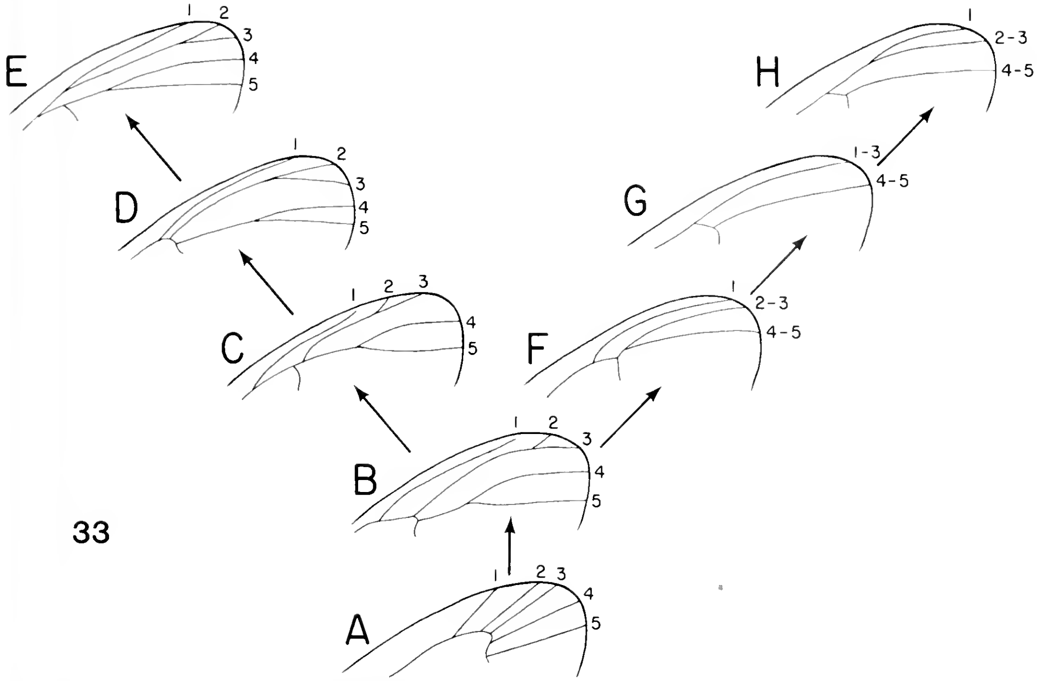


Figure 33. Hypothesized transformation series for forewing radial vein system. See *Ca* and *Minacragides* generic treatments for discussion of assignments of homologies in states G and H.

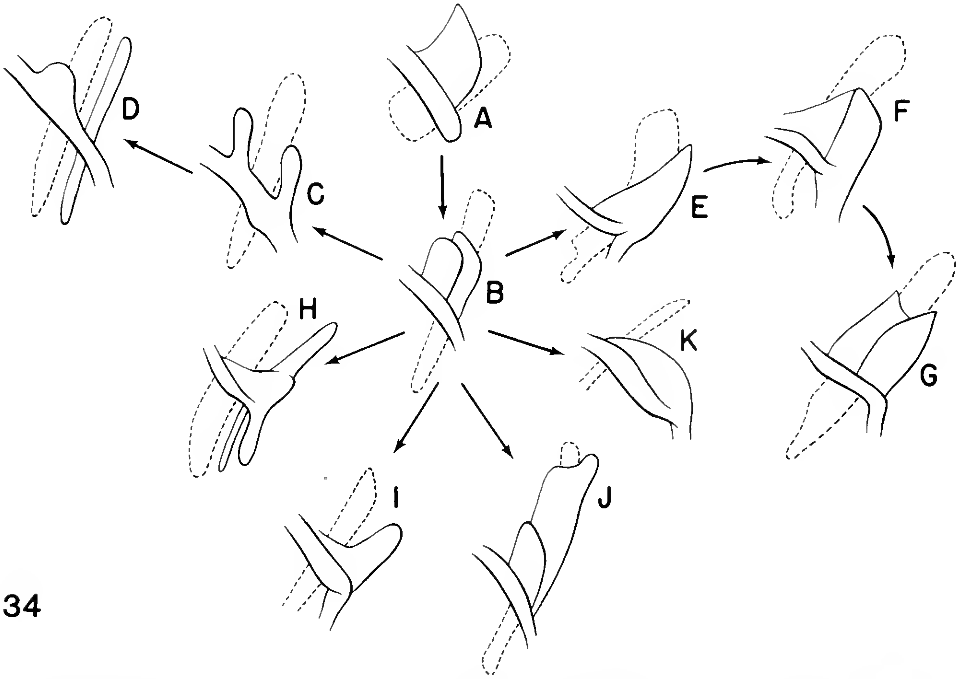
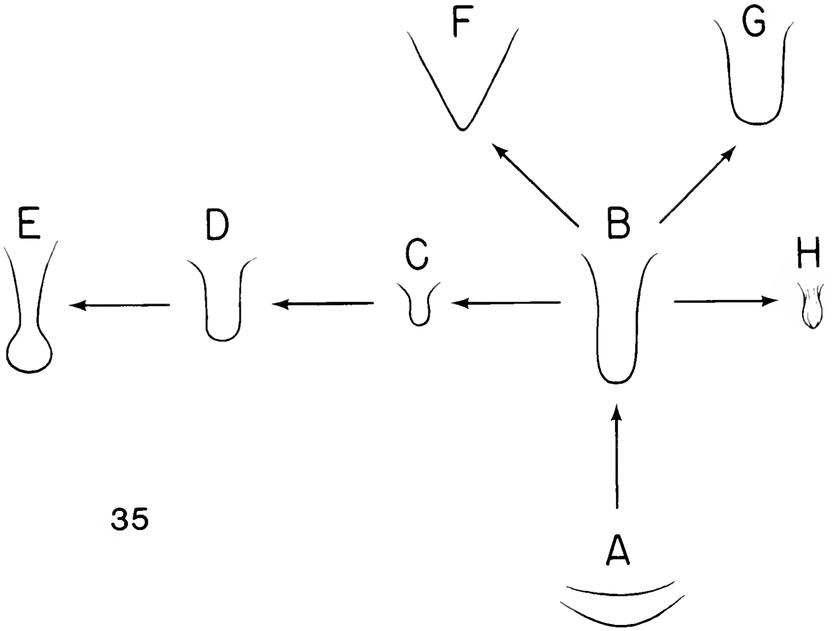
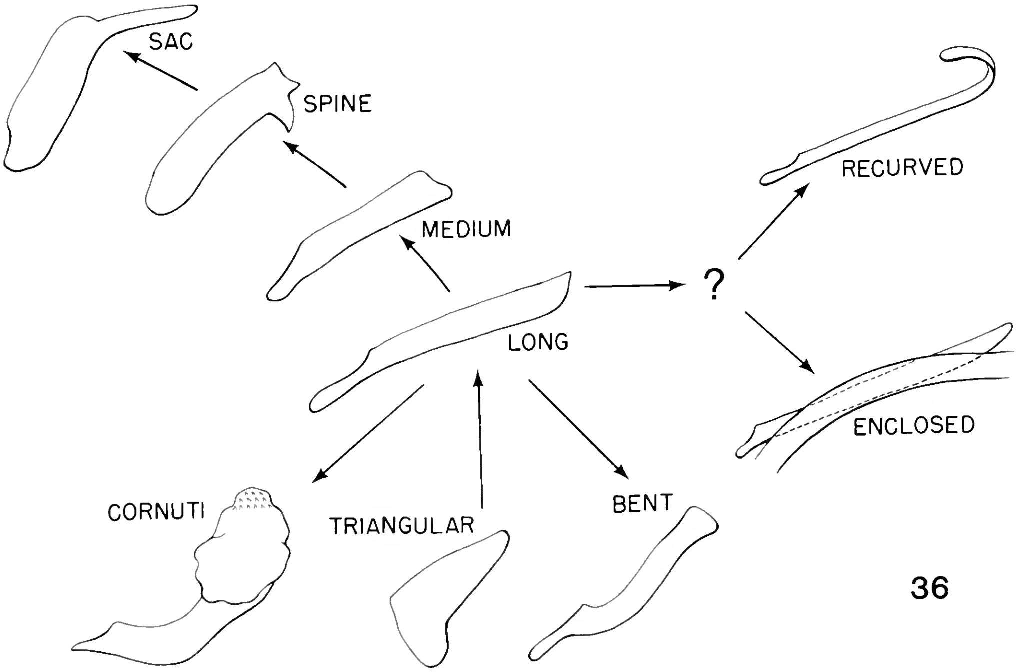


Figure 34. Hypothesized transformation series for juxta-valval region, illustrated in lateral view with dotted aedoeagus outline for perspective.



35

Figure 35. Hypothesized transformation series for saccus shape, illustrated as outline from ventral view.



36

Figure 36. Hypothesized transformation series for aedoeagus shape, illustrated as lateral outlines, with exterior ends toward upper right.

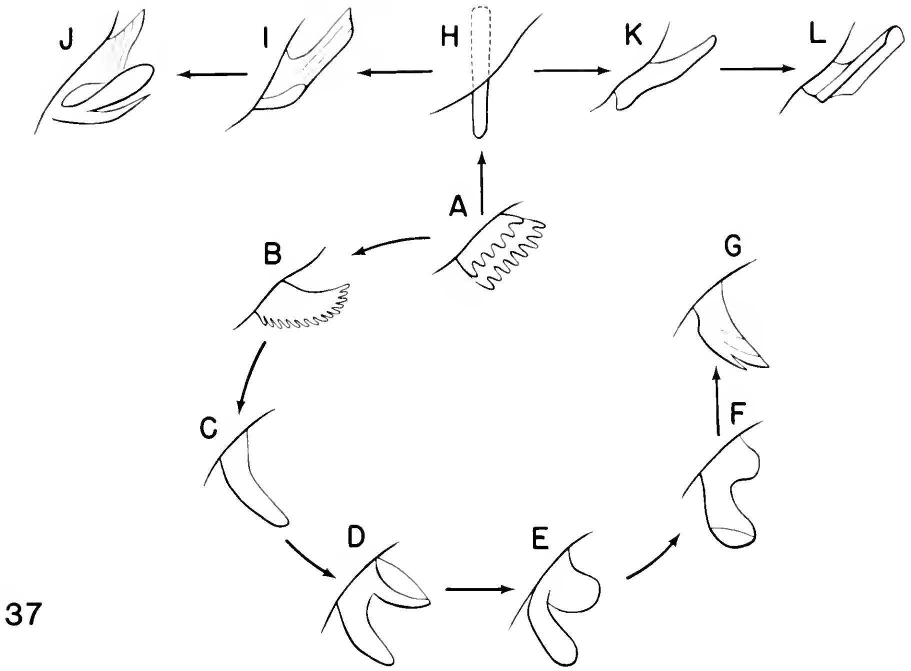


Figure 37. Hypothesized transformation series for gnathos shape, illustrated as lateral views with ventral edge of tegumen–sociuncus complex on upper left.

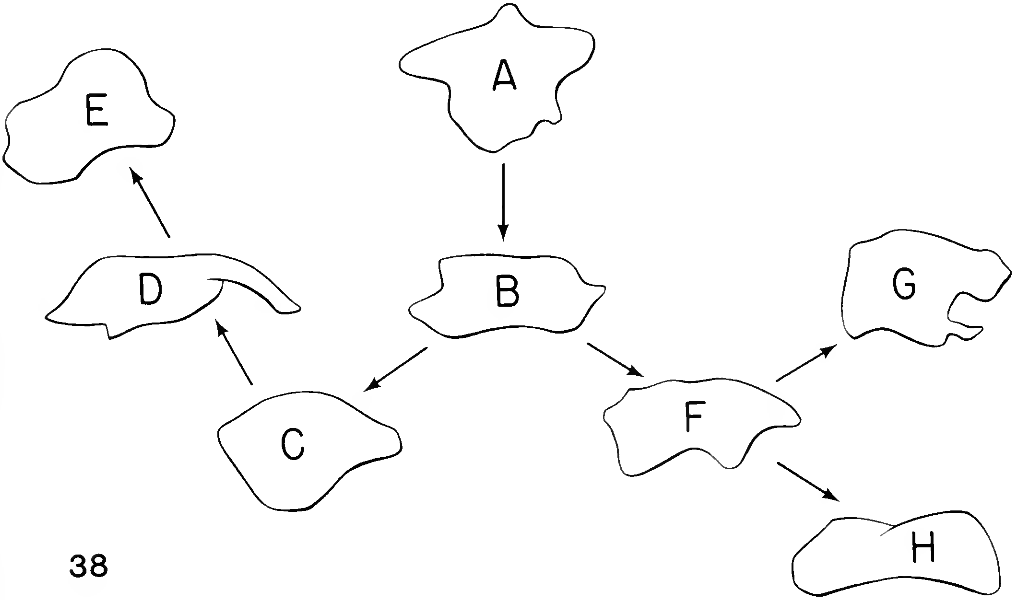
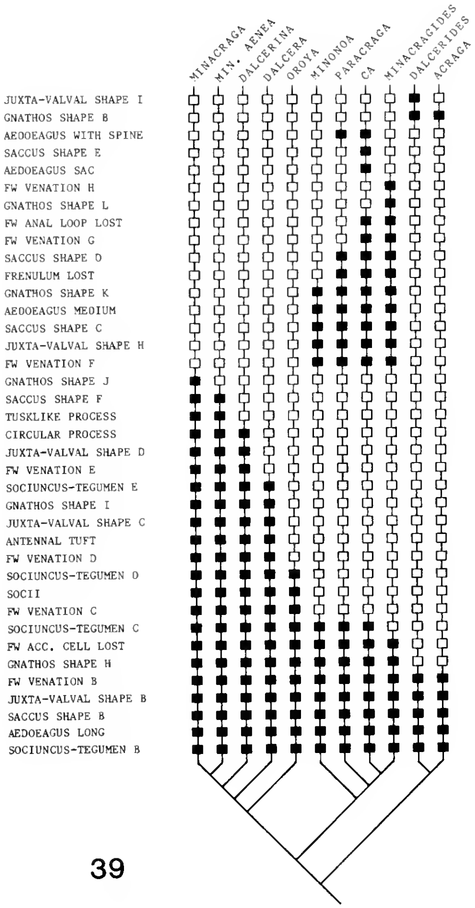
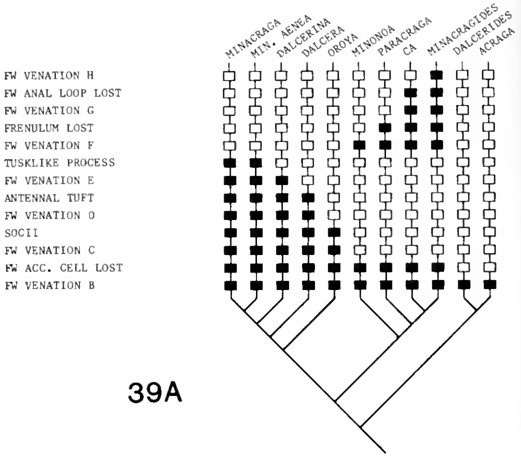


Figure 38. Hypothesized transformation series for sociuncus–tegumen complex, illustrated as lateral outline, with posterior end at right.



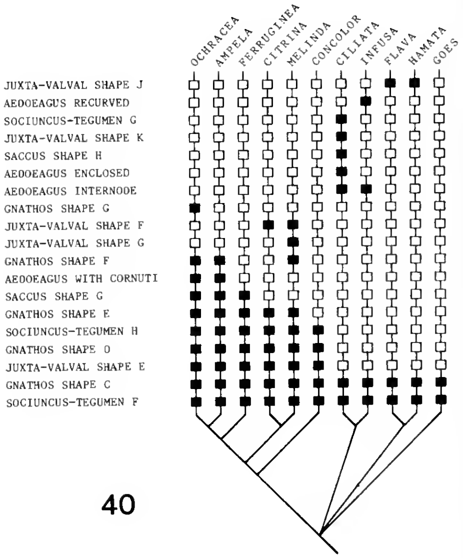
39

Figure 39. Cladogram of genera of Dalceridae (except *Zikanyrops*). Closed squares are derived states; open squares are primitive states. Outgroup (Epipyropidae) is primitive for all states.



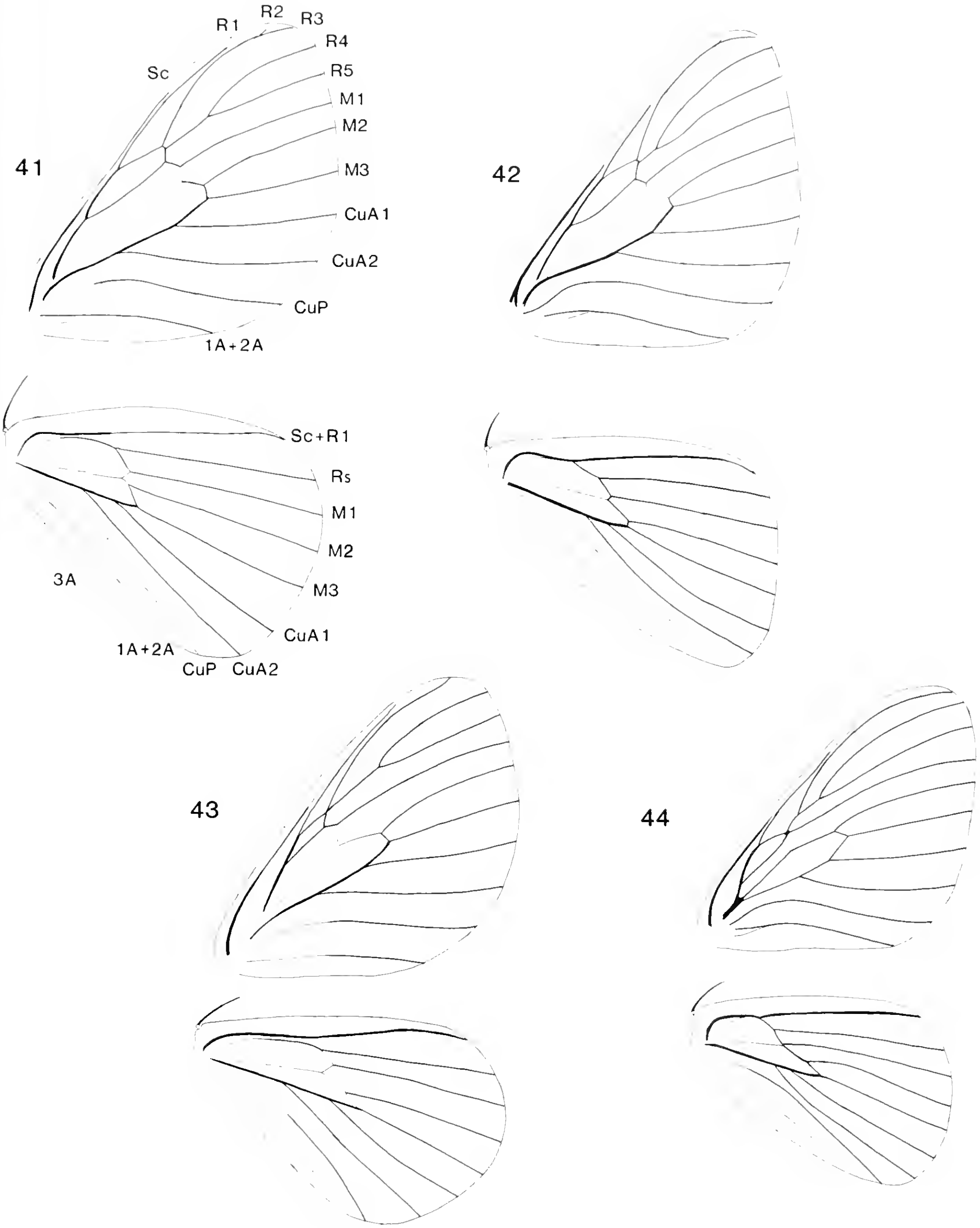
39A

Figure 39A. Cladogram of genera of Dalceridae, generated with data set for Figure 39, but simplified by removal of multistate genital characters. See text for further explanation. Tusklike processes were not in data set, but are included here for clarity.



40

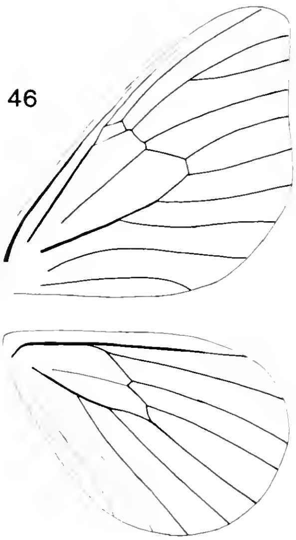
Figure 40. Cladogram of species groups of *Acraga*. Closed squares are derived states; open squares are primitive states.



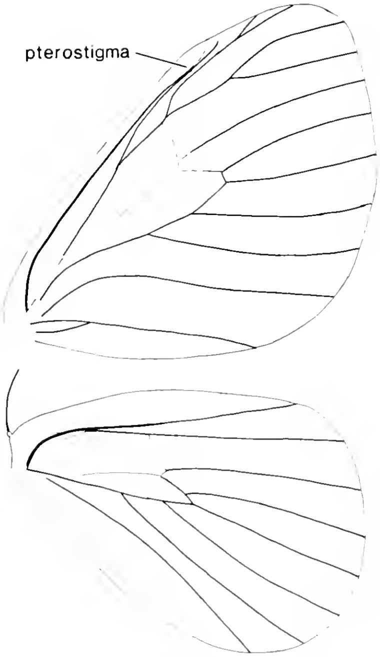
Figures 41–44. Wing venation. Figure 41. *Acraga ciliata*, male (USNM 22541). Figure 42. *Acraga citrina*, male (USNM 22552). Figure 43. *Dalcerides ingenita*, male (USNM 22551). Figure 44. *Dalcerides flavetta*, male (USNM 22542).

45

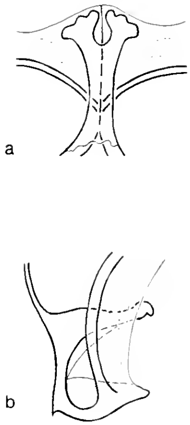
46



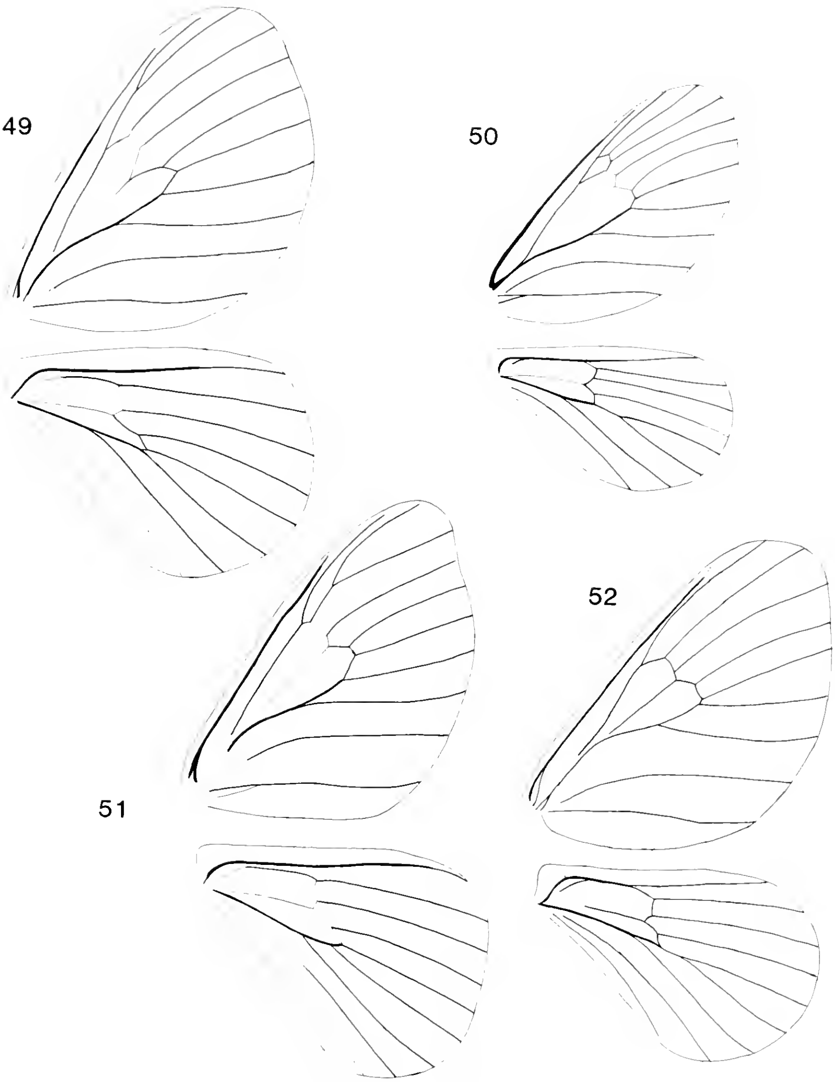
47



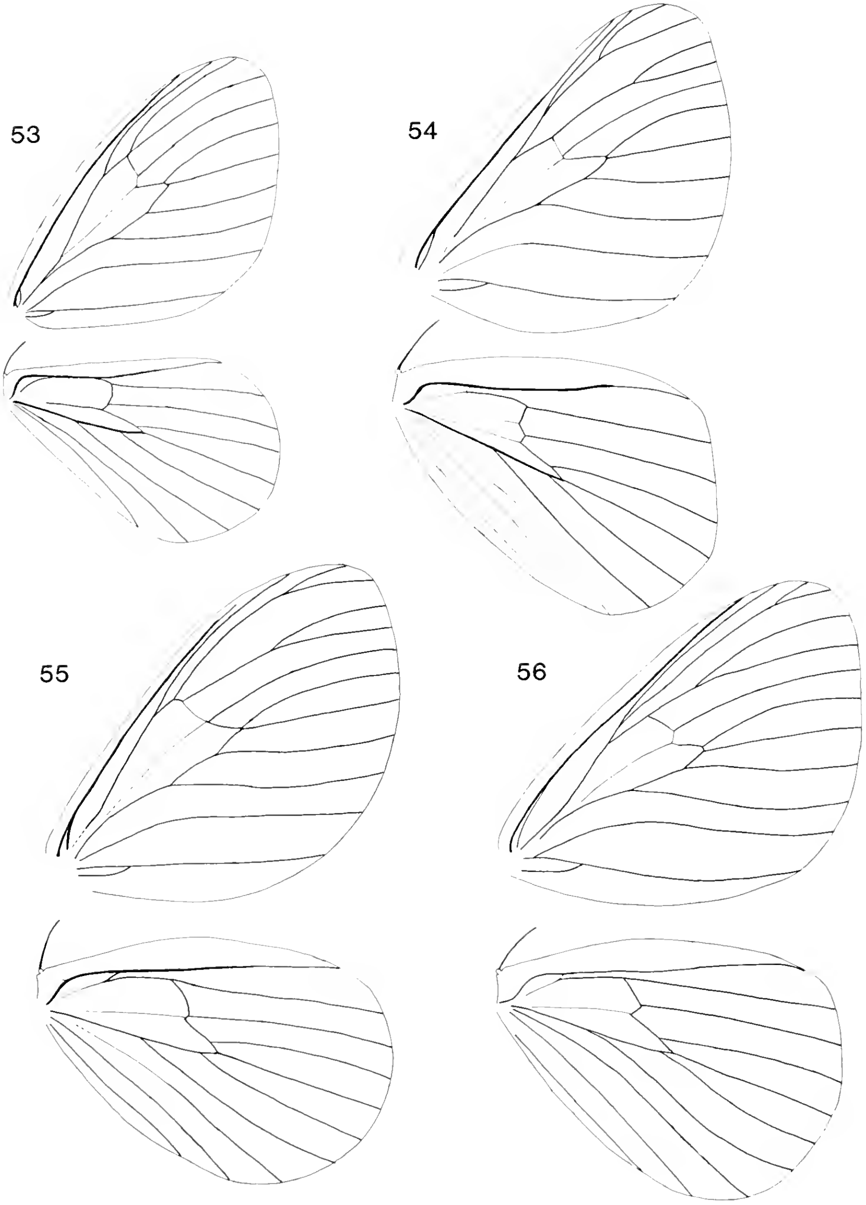
48



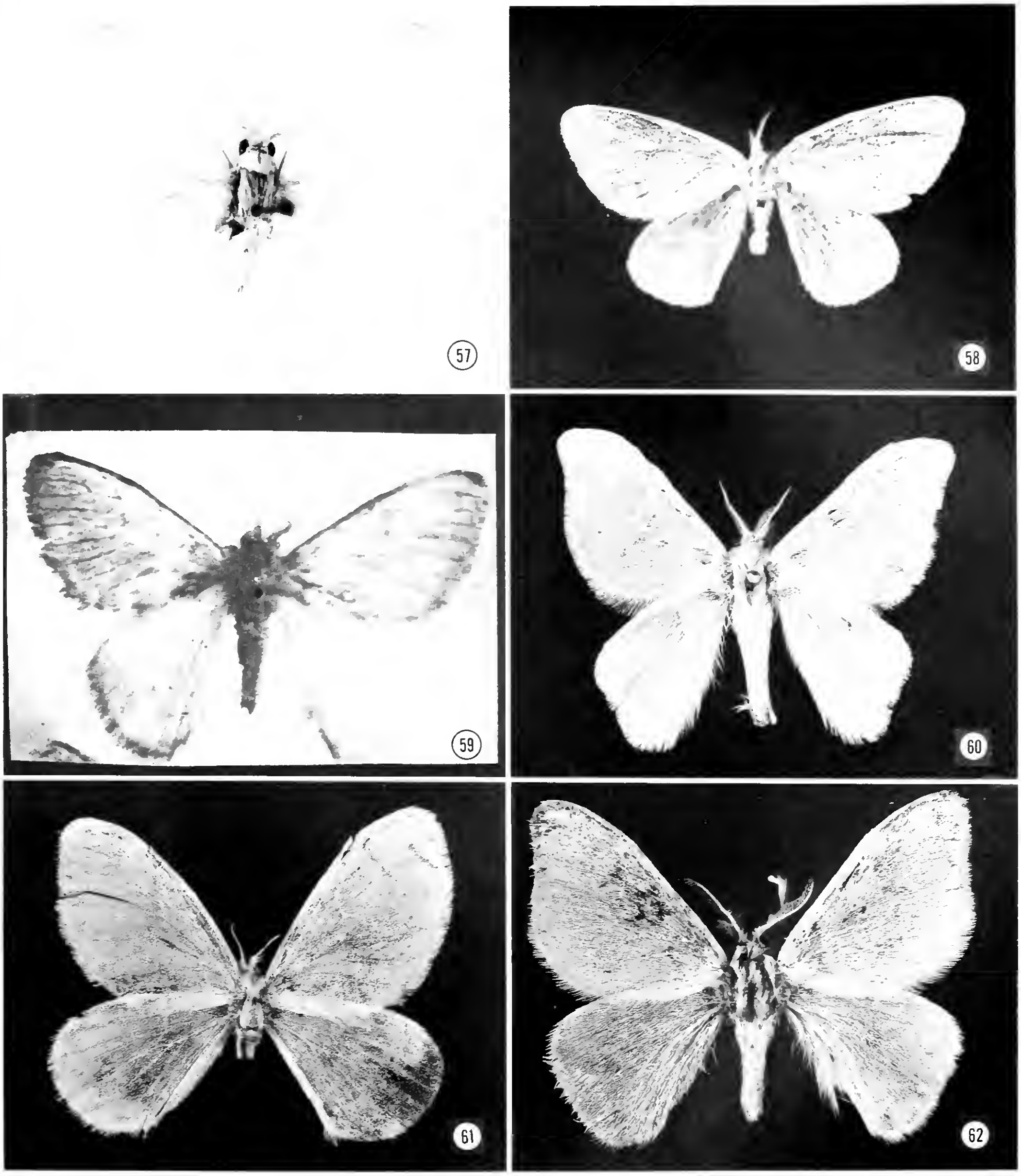
Figures 45–48. Figure 45. *Acraga ferruginea* wing venation, female (IOC 85-52). Figure 46. *Zikanyrops dubiosa* wing venation, female (drawn from holotype, without slide mounting; R_{2+3} might branch at the tip). Figure 47. *Oroya aurora* wing venation, male (BMNH 85-11). Figure 48. *Dalcerides ingenita,* male metathoracic furca, dorsal (top) and lateral (bottom) views (USNM 22556).



Figures 49–52. Wing venation. Figure 49. *Minacragides arnacis*, male (USNM 22602). Figure 50. *Minacragides* (?) new species B, female (USNM 28101). Figure 51. *Paracraga innocens*, male (USNM 22553). Figure 52. *Ca anastigma*, male (USNM 22592).

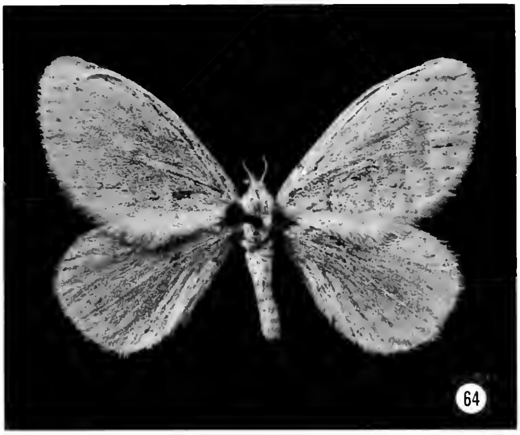


Figures 53–56. Wing venation. Figure 53. *Minonoa elvira*, male (USNM 22554). Figure 54. *Minacraga disconitens*, male (USNM 22548). Figure 55. *Dalcera abrasa*, male (USNM 22546). Figure 56. *Dalcerina tijucana*, male (USNM 22550).



Figures 57–62. Wing patterns. Figure 57. *Acraga goes*, male lectotype, Costa Rica (USNM). Figure 58. *Acraga ingenescens*, female holotype, Venezuela (USNM)—wings very worn. Figure 59. *Acraga luteola*, male holotype, Brazil—copied from old photograph in Hopp Collection (ZSBS). Figure 60. *Acraga hamata*, male lectotype, Costa Rica (USNM). Figure 61. *Acraga hamata*, female, Costa Rica (BMNH). Figure 62. *Acraga andina*, male paratype, Peru (BMNH).


63


64

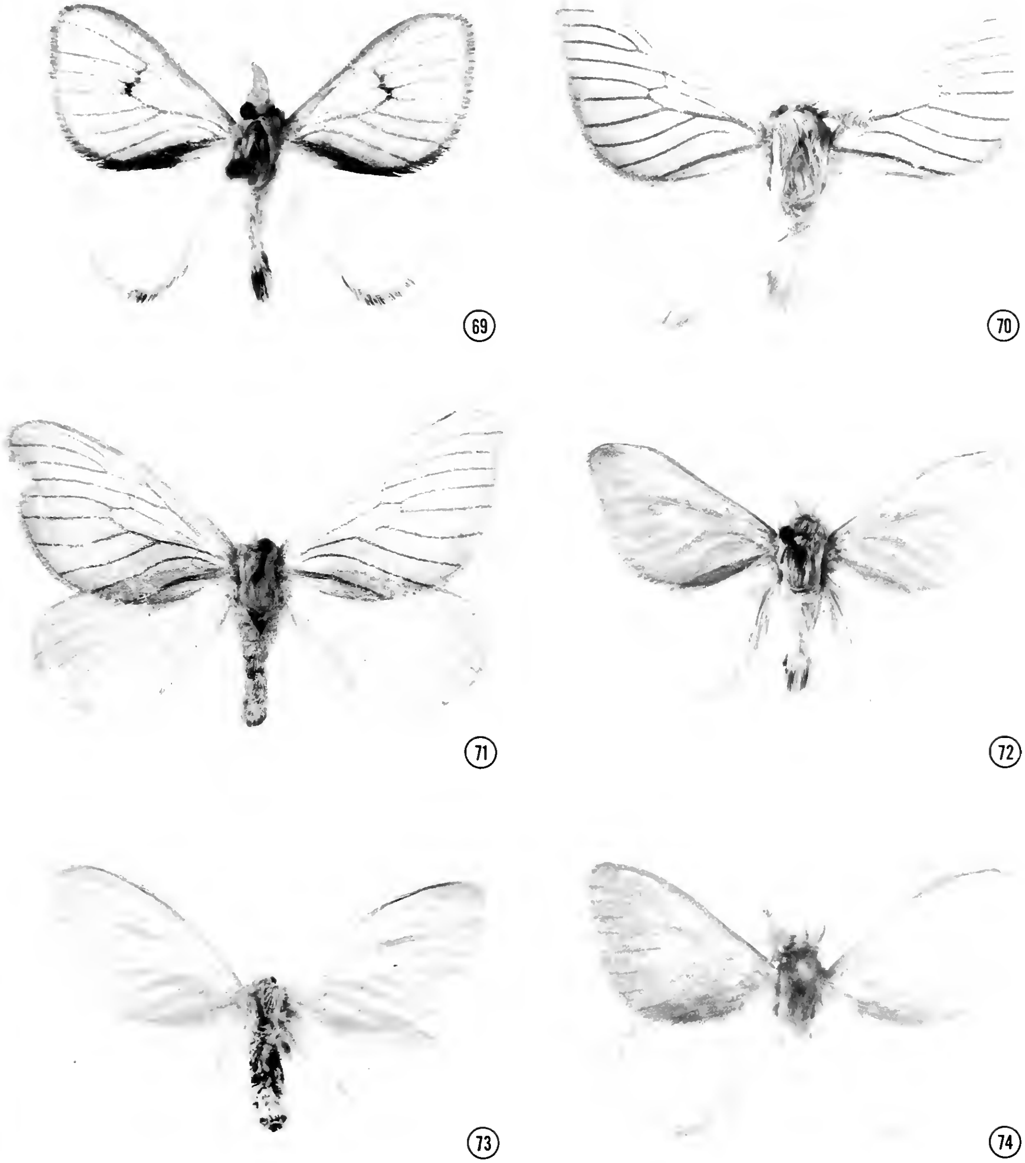

65


66

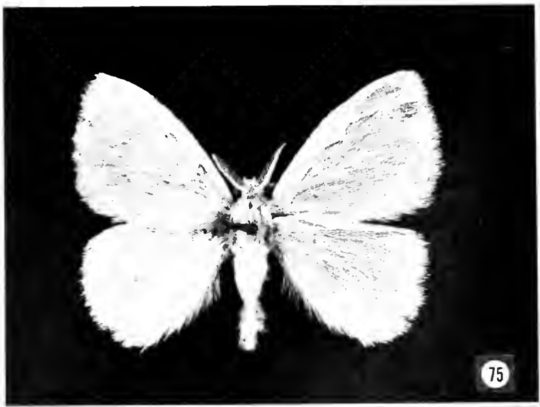

67

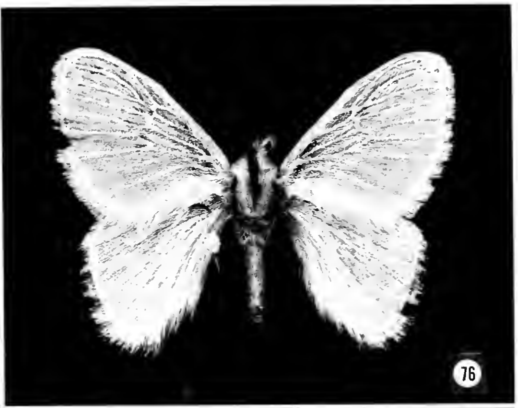

68

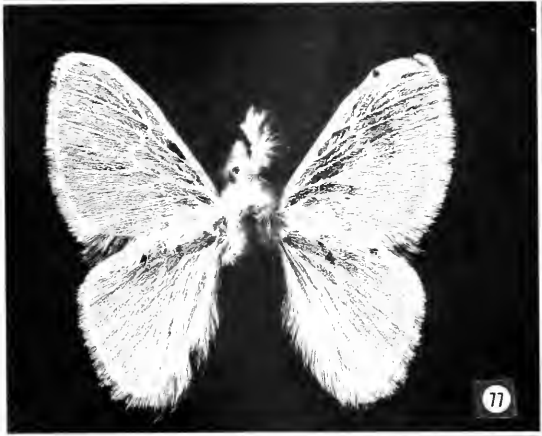
Figures 63–68. Wing patterns. Figure 63. *Acraga flava*, male, Brazil (USNM). Figure 64. *Acraga flava*, female, Brazil (USNM). Figure 65. *Acraga obscura*, male, Brazil (VOB). Figure 66. *Acraga neblina*, male holotype, Venezuela (USNM). Figure 67. *Acraga infusa*, male holotype, French Guiana (USNM). Figure 68. *Acraga philetera*, male syntype, Costa Rica (USNM).

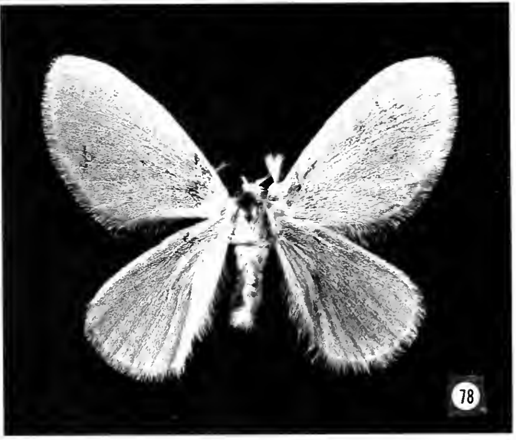


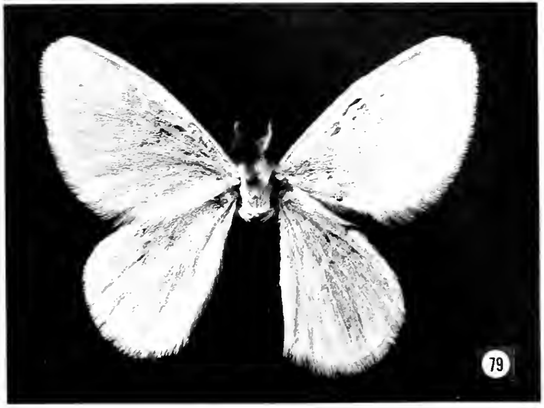
Figures 69–74. Wing patterns. Figure 69. *Acraga ciliata*, male, Jamaica (USNM). Figure 70. *Acraga moorei*, male, Venezuela (USNM). Figure 71. *Acraga moorei*, female, Bolivia (USNM). Figure 72. *Acraga coa*, male (lectotype of *A. moribunda*), Guatemala (USNM). Figure 73. *Acraga coa*, female paralectotype, Mexico (USNM). Figure 74. *Acraga chicana*, male holotype, Mexico (AMNH)—white areas on forewings are due to scale loss.


75


76

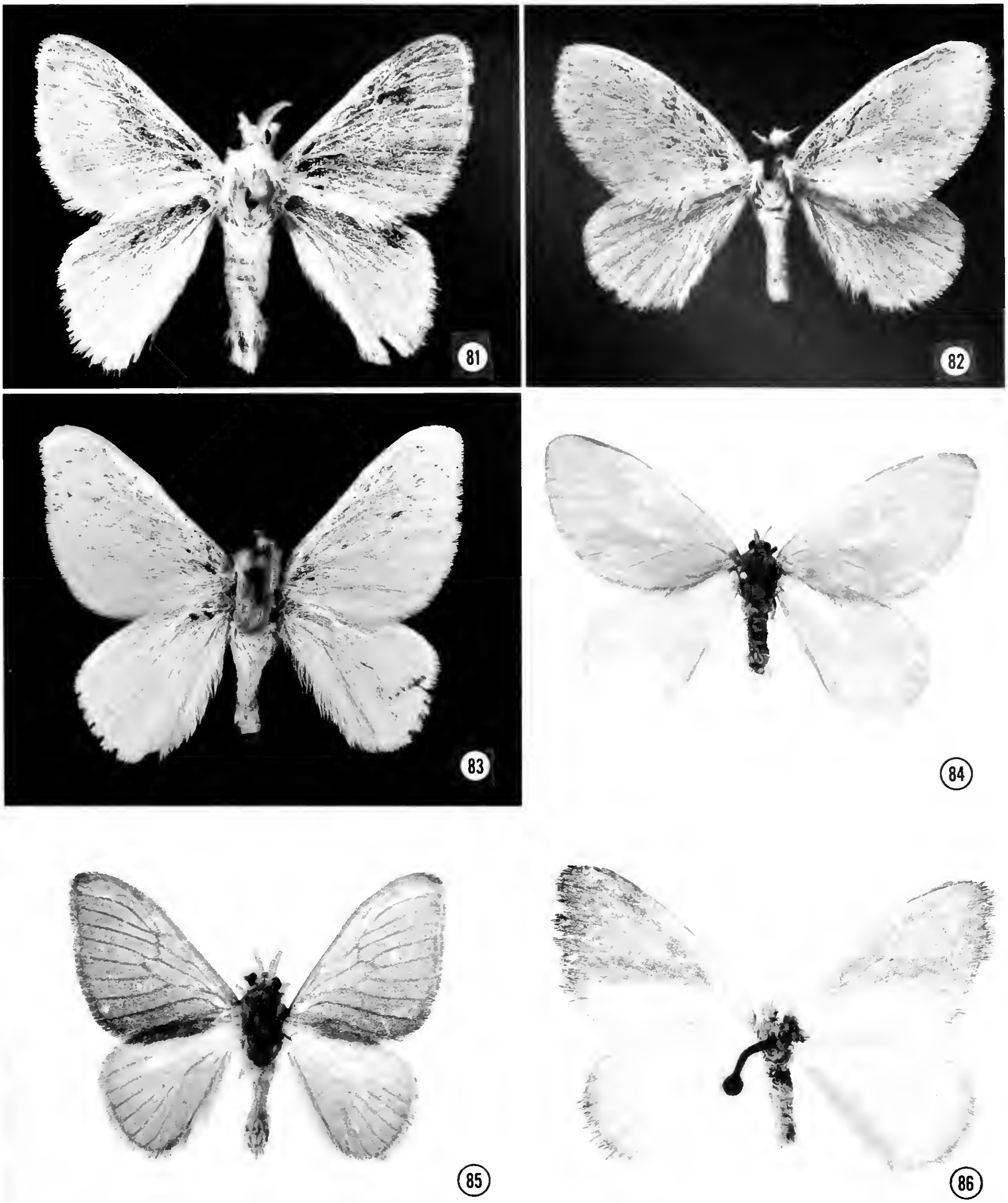

77


78

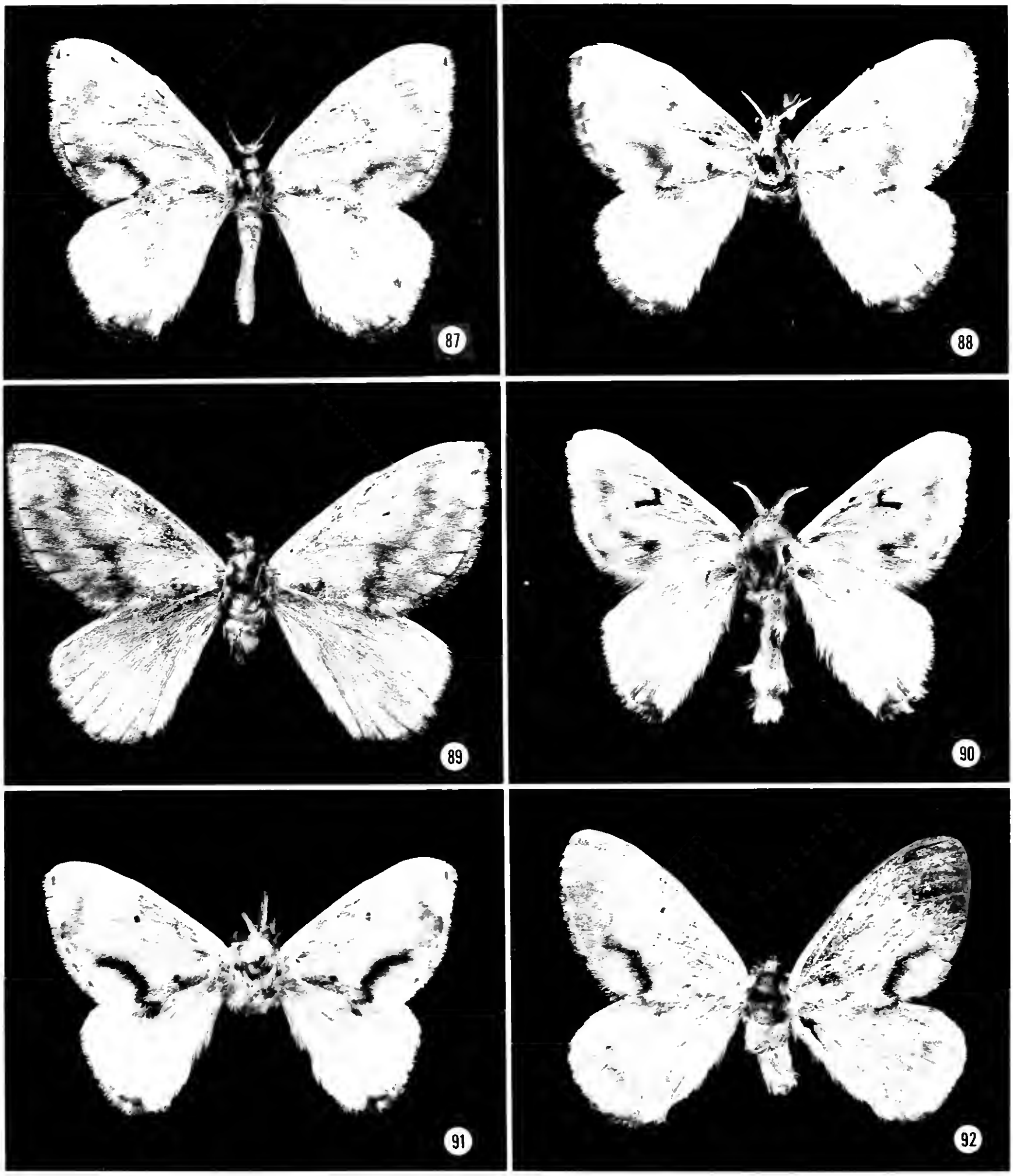

79


80

Figures 75–80. Wing patterns. Figure 75. *Acraga ria*, male, Brazil (BMNH). Figure 76. *Acraga concolor*, male, Brazil (BMNH). Figure 77. *Acraga citrinopsis*, male, Brazil (LACM). Figure 78. *Acraga citrinopsis*, female, Brazil (USNM). Figure 79. *Acraga beebei*, male holotype, Venezuela (USNM). Figure 80. *Acraga perbrunnea*, male, Colombia (USNM).



Figures 81–86. Wing patterns. Figure 81. *Acraga citrina*, male holotype, Trinidad (USNM). Figure 82. *Acraga citrina*, female, Brazil (USNM). Figure 83. *Acraga melinda*, male, Panama (AMNH). Figure 84. *Acraga melinda*, female holotype, Panama (ZMHB). Figure 85. *Acraga meridensis*, male, Colombia (USNM). Figure 86. *Zikanyrops dubiosa*, female holotype, Bolivia (ZMHB).



Figures 87–92. Wing patterns. Figure 87. *Acraga ampela*, male, Colombia (USNM). Figure 88. *Acraga puno*, male paratype, Peru (USNM). Figure 89. *Acraga boliviana*, male, Brazil (BMNH). Figure 90. *Acraga angulifera*, male, French Guiana (USNM). Figure 91. *Acraga leberna*, male (lectotype of *A. arcifera*), French Guiana (USNM). Figure 92. *Acraga leberna*, female, Guyana (USNM).

93

94

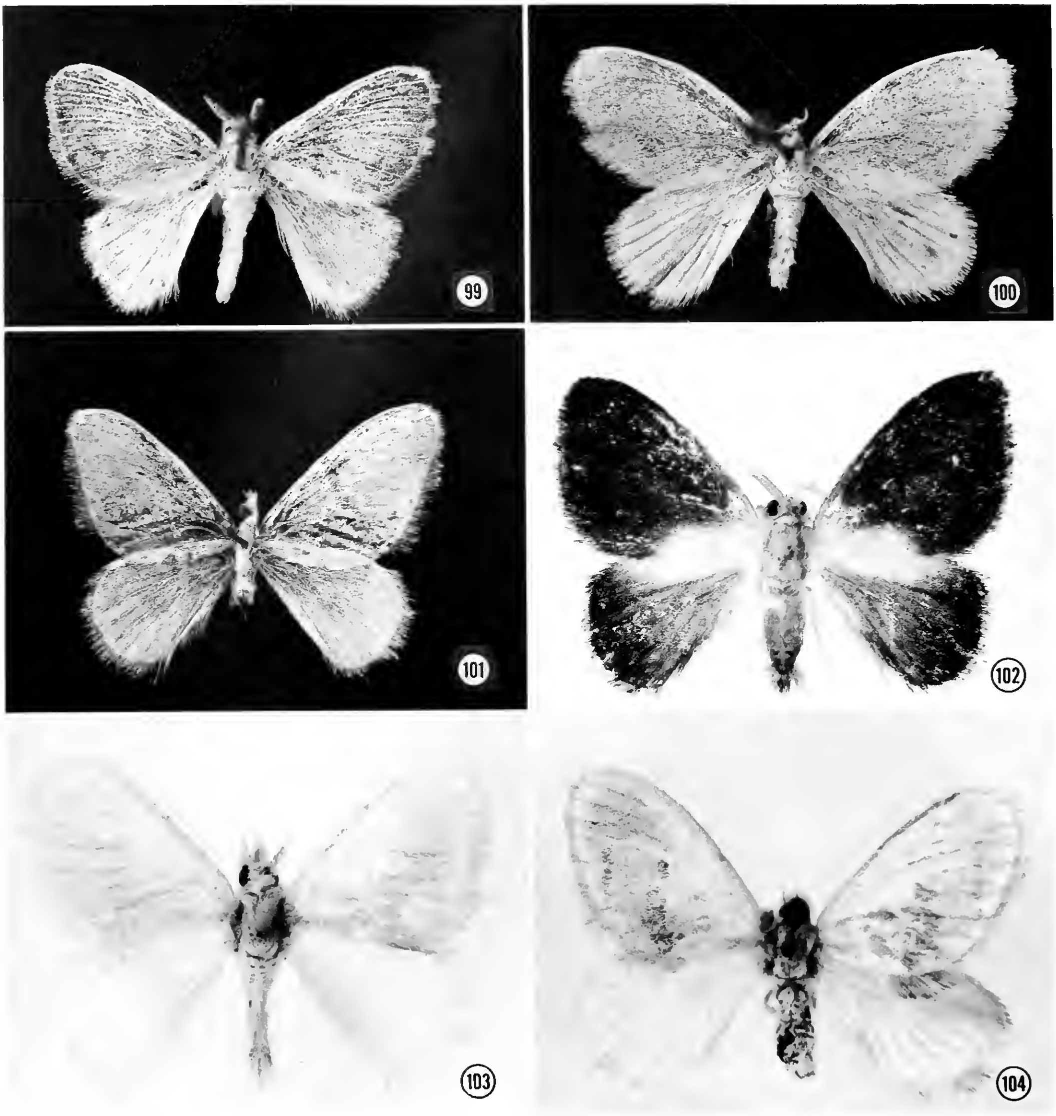
95

96

97

98

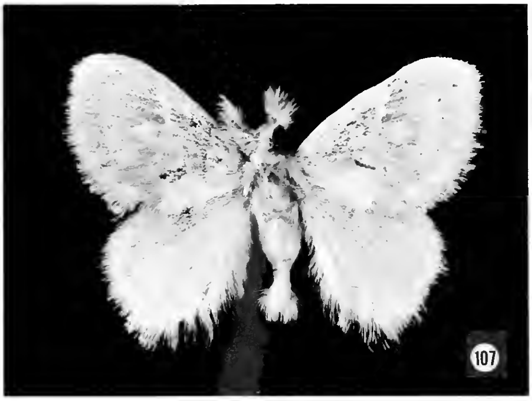
Figures 93–98. Wing patterns. Figure 93. *Acraga ochracea*, male, Brazil (USNM). Figure 94. *Acraga ochracea*, female, Brazil (IOC). Figure 95. *Acraga sexquicentenaria*, male, Brazil (CMNH). Figure 96. *Acraga sexquicentenaria*, female, Brazil (MCZ). Figure 97. *Acraga victoria*, male holotype, Brazil (MNRJ). Figure 98. *Acraga parana*, male paratype, Brazil (BMNH).



Figures 99–104. Wing patterns. Figure 99. *Dalcerides flavetta*, male, Bolivia (USNM). Figure 100. *Dalcerides flavetta*, female, Bolivia (USNM). Figure 101. *Dalcerides* new species, male, Costa Rica (BMNH). Figure 102. *Dalcerides dulciola*, male, Costa Rica (USNM). Figure 103. *Dalcerides radians*, male holotype, Brazil (ZMHB). Figure 104. *Dalcerides radians*, female, Brazil (VOB).


105


106


107


108


109


110

Figures 105–110. Wing patterns. Figure 105. *Dalcerides mesoa*, male, Costa Rica (USNM). Figure 106. *Dalcerides mesoa*, female, Costa Rica (USNM). Figure 107. *Dalcerides sofia*, male, Costa Rica (USNM). Figure 108. *Dalcerides sofia*, female holotype, Mexico (USNM). Figure 109. *Dalcerides nana*, male, Brazil (CU). Figure 110. *Dalcerides bicolor*, female holotype, Costa Rica (USNM).

(111)

(112)

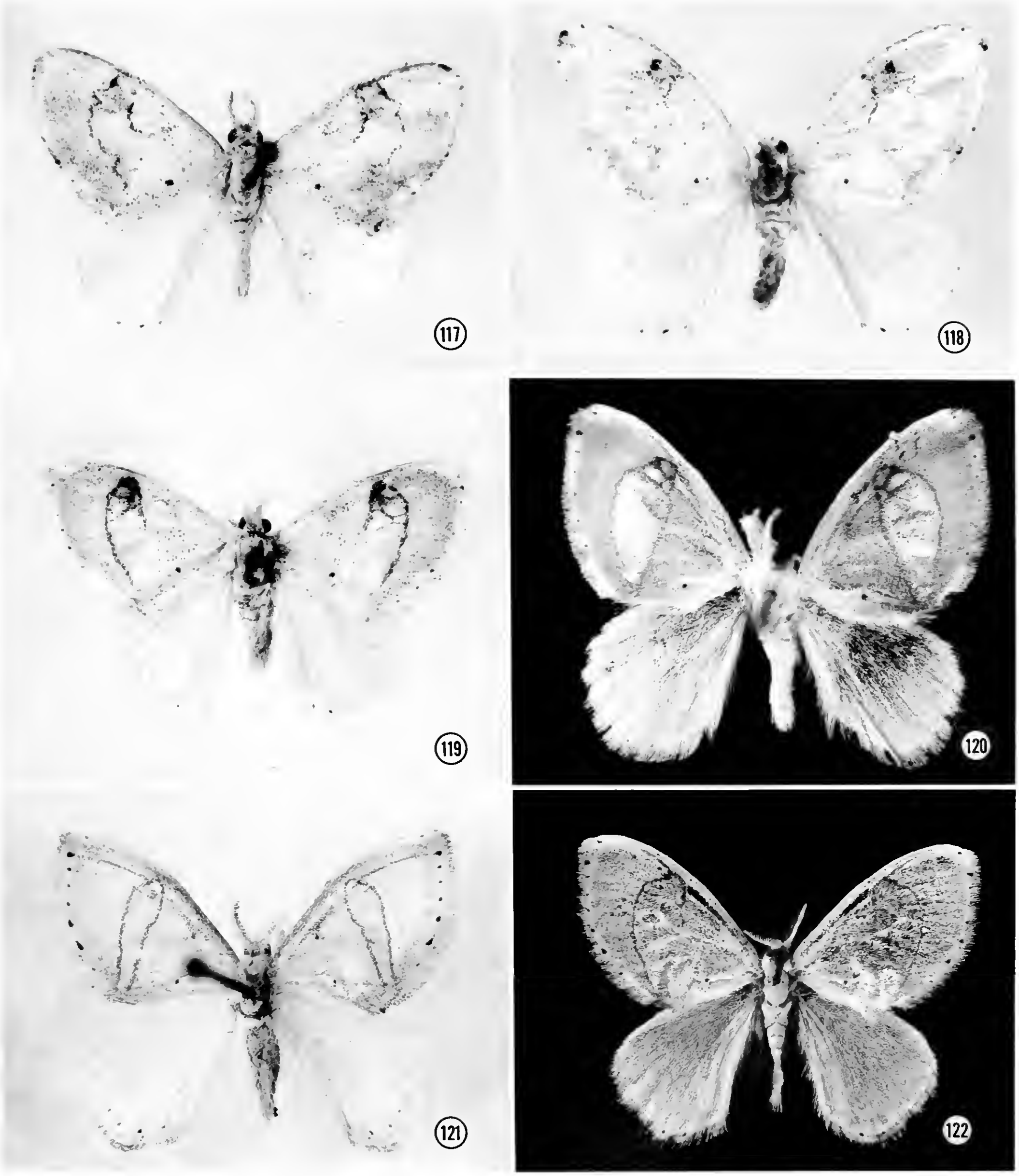
(113)

(114)

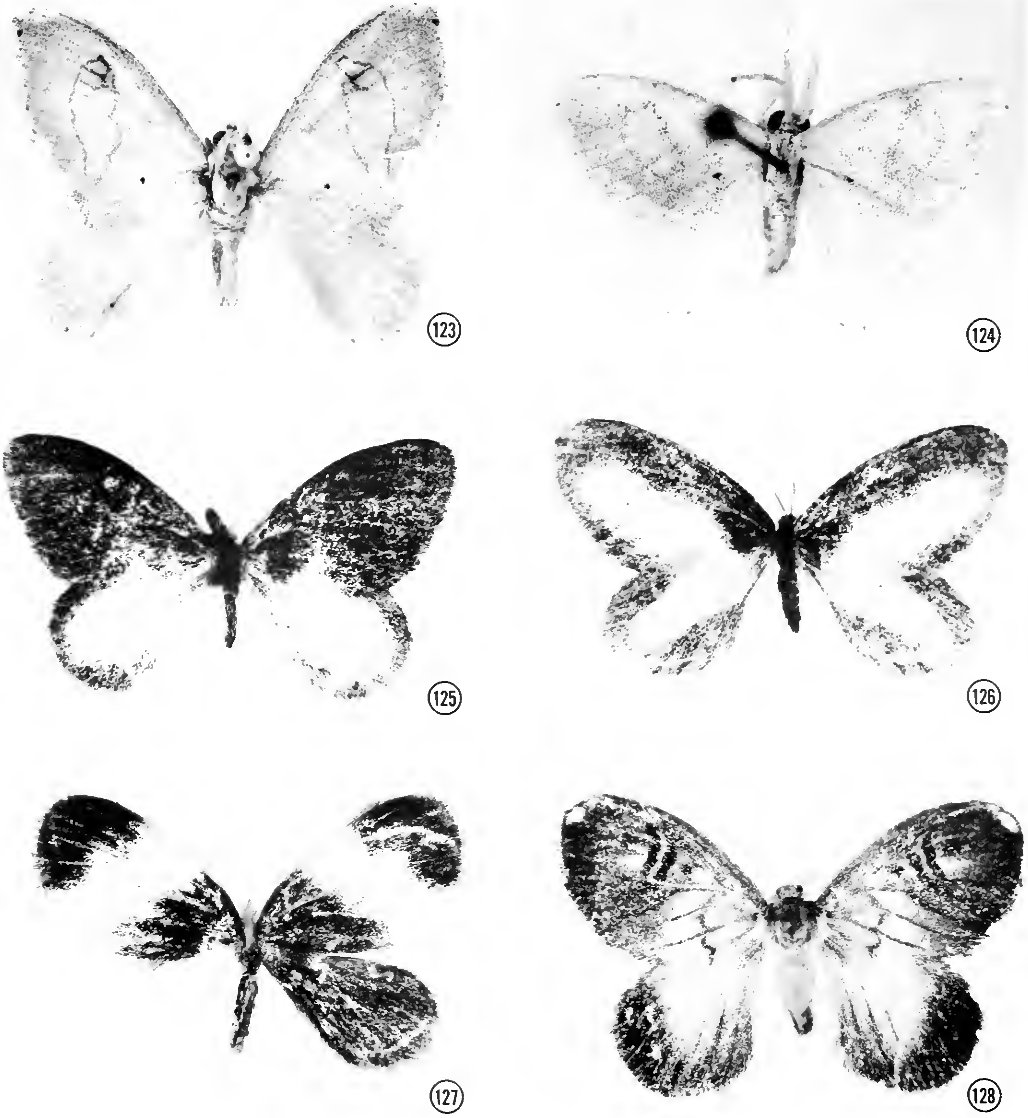
(115)

(116)

Figures 111–116. Wing patterns. Figure 111. *Dalcerides ingenita*, male, Arizona (USNM). Figure 112. *Dalcerides ingenita*, female, Arizona (USNM). Figure 113. *Dalcerides alba*, male, Guatemala (USNM). Figure 114. *Dalcerides alba*, female (paralectotype of *D. caretta*), Mexico (USNM). Figure 115. *Acraga isothea*, male lectotype, Panama (USNM). Figure 116. *Acraga umbrifera*, male holotype, French Guiana (USNM).



Figures 117–122. Wing patterns. Figure 117. *Paracraga innocens*, male holotype, French Guiana (USNM). Figure 118. *Paracraga innocens*, female, French Guiana (USNM). Figure 119. *Paracraga amianta*, male holotype, Guyana (USNM). Figure 120. *Paracraga argentea*, male, Mexico (AMNH). Figure 121. *Paracraga canalicula*, male, Peru (USNM). Figure 122. *Paracraga halophora*, male, Peru (USNM).



Figures 123–128. Wing patterns. Figure 123. *Paracraga necoda,* male paralectotype, Colombia (USNM). Figure 124. *Paracraga pulverina,* male holotype, Guatemala (USNM). Figure 125. *Minonoa elvira,* male lectotype, Colombia (USNM). Figure 126. *Minonoa elvira,* female paralectotype, Colombia (USNM). Figure 127. *Minonoa pachitea,* female holotype, Peru (ZSBS). Figure 128. *Minonoa perbella,* female (holotype of *M. variegata*), Brazil (BMNH).

(129)

(130)

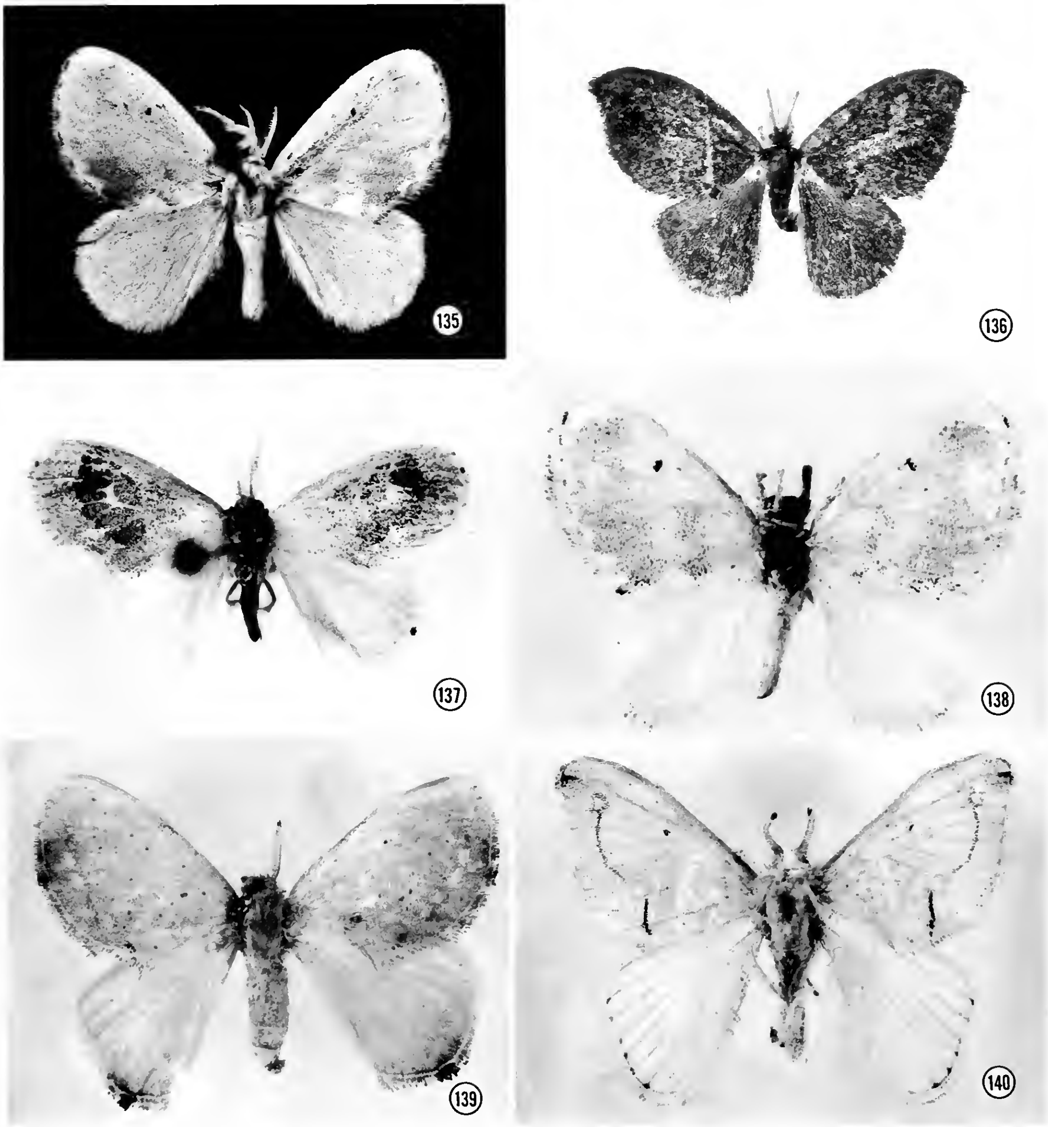
(131)

(132)

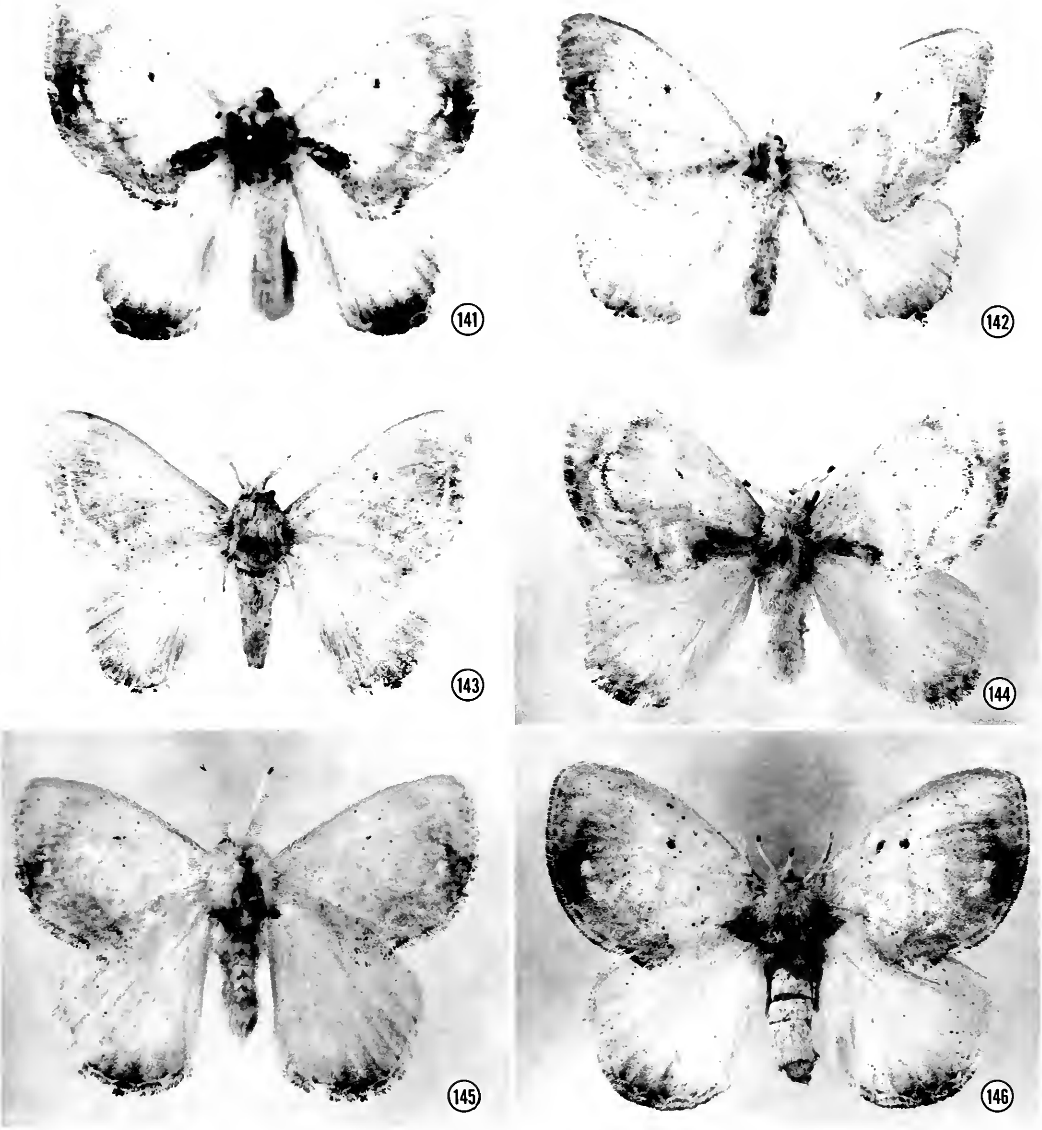
(133)

(134)

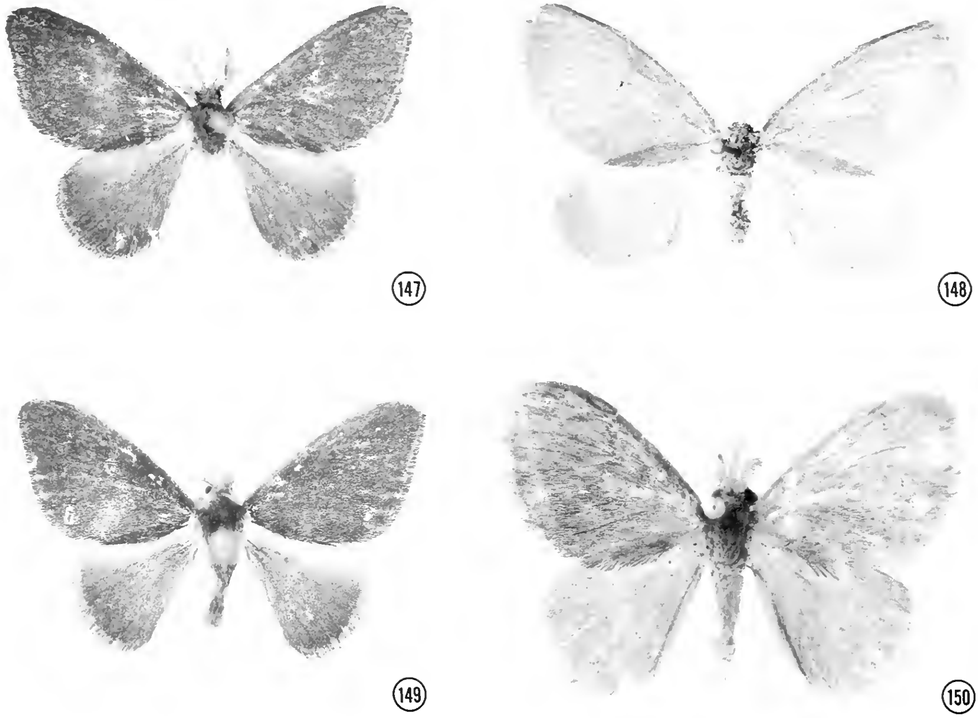
Figures 129–134. Wing patterns. Figure 129. *Dalcera abrasa*, male, Brazil (LACM). Figure 130. *Dalcera abrasa*, female, Brazil (VOB). Figure 131. *Dalcera canescens*, male (lectotype of *D. consanguinea*), Brazil (USNM). Figure 132. *Dalcera semirufa*, male paralectotype, Colombia (BMNH). Figure 133. *Dalcerina tijucana*, male (lectotype of *D. fumata*), Brazil (USNM). Figure 134. *Dalcerina tijucana*, female (holotype of *D. dierrhyeoa*), Paraguay (USNM).



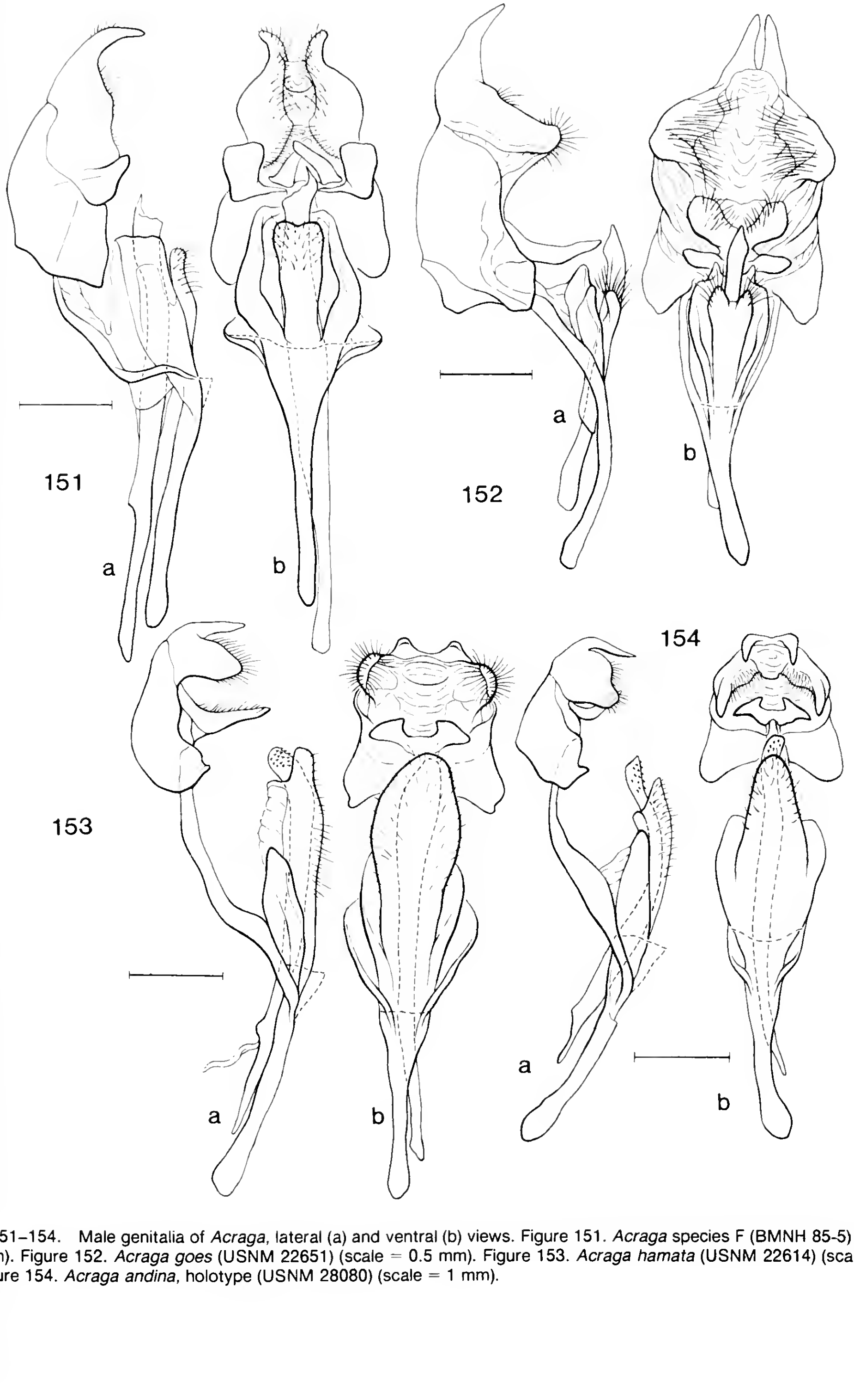
Figures 135–140. Wing patterns. Figure 135. *Minacragides arnacis*, male, Colombia (USNM). Figure 136. *Minacragides* new species A, male, Brazil (IOC)—lines on wings are due to loss of scales. Figure 137. *Minacragides* (?) new species B, male, Brazil (VOB). Figure 138. *Ca anastigma*, male paralectotype, Panama (USNM). Figure 139. *Minacraga aenea*, male holotype, Brazil (ZSBS). Figure 140. *Minacraga hyalina*, male holotype, Peru (BMNH).



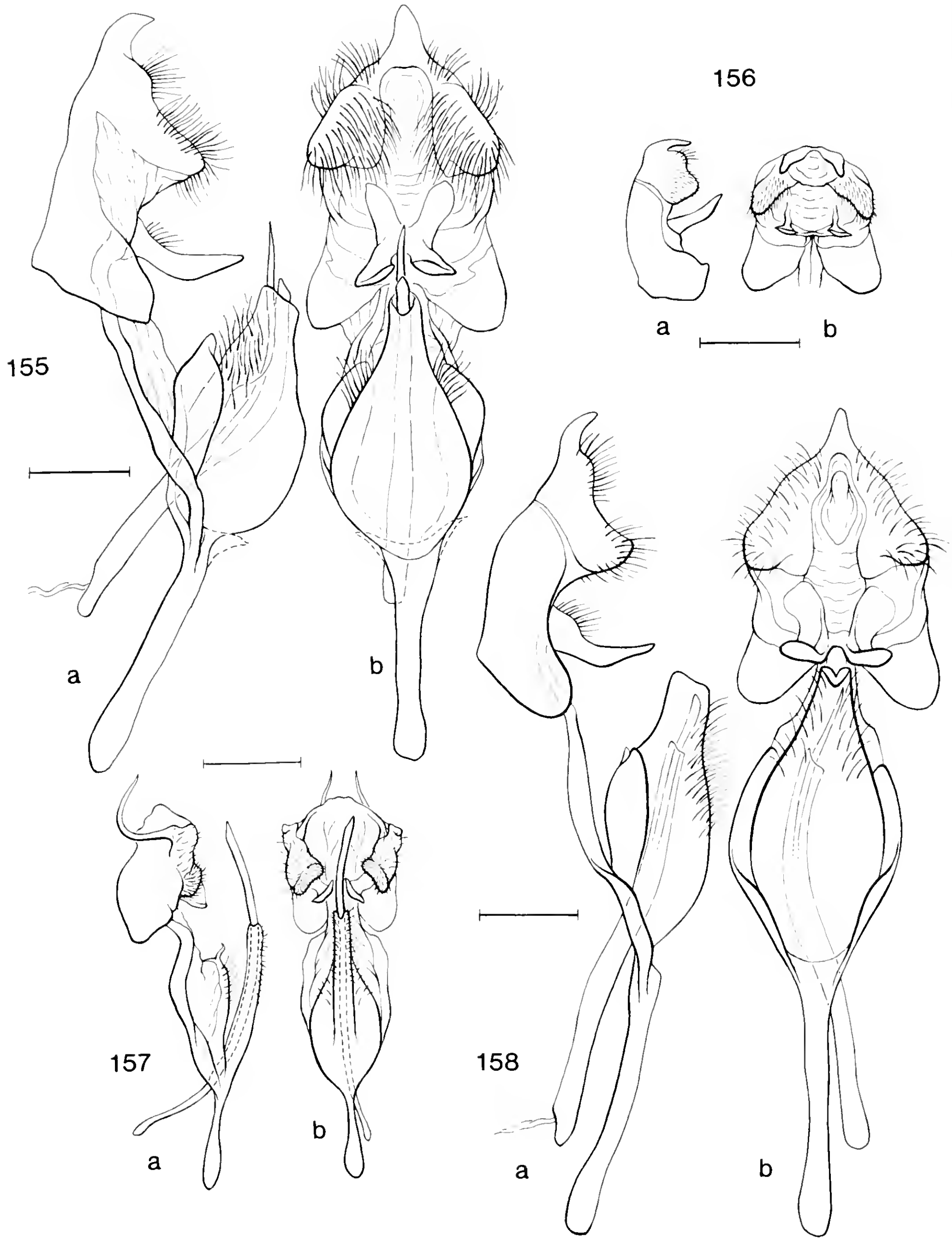
Figures 141–146. Wing patterns. Figure 141. *Minacraga disconitens*, male lectotype, French Guiana (USNM). Figure 142. *Minacraga disconitens*, female, French Guiana (USNM). Figure 143. *Minacraga indiscata*, male paralectotype, French Guiana (USNM). Figure 144. *Minacraga argentata*, male holotype, Brazil (ZSBS). Figure 145. *Minacraga itatiaia*, male, Brazil (BMNH). Figure 146. *Minacraga itatiaia*, female, Brazil (BMNH).



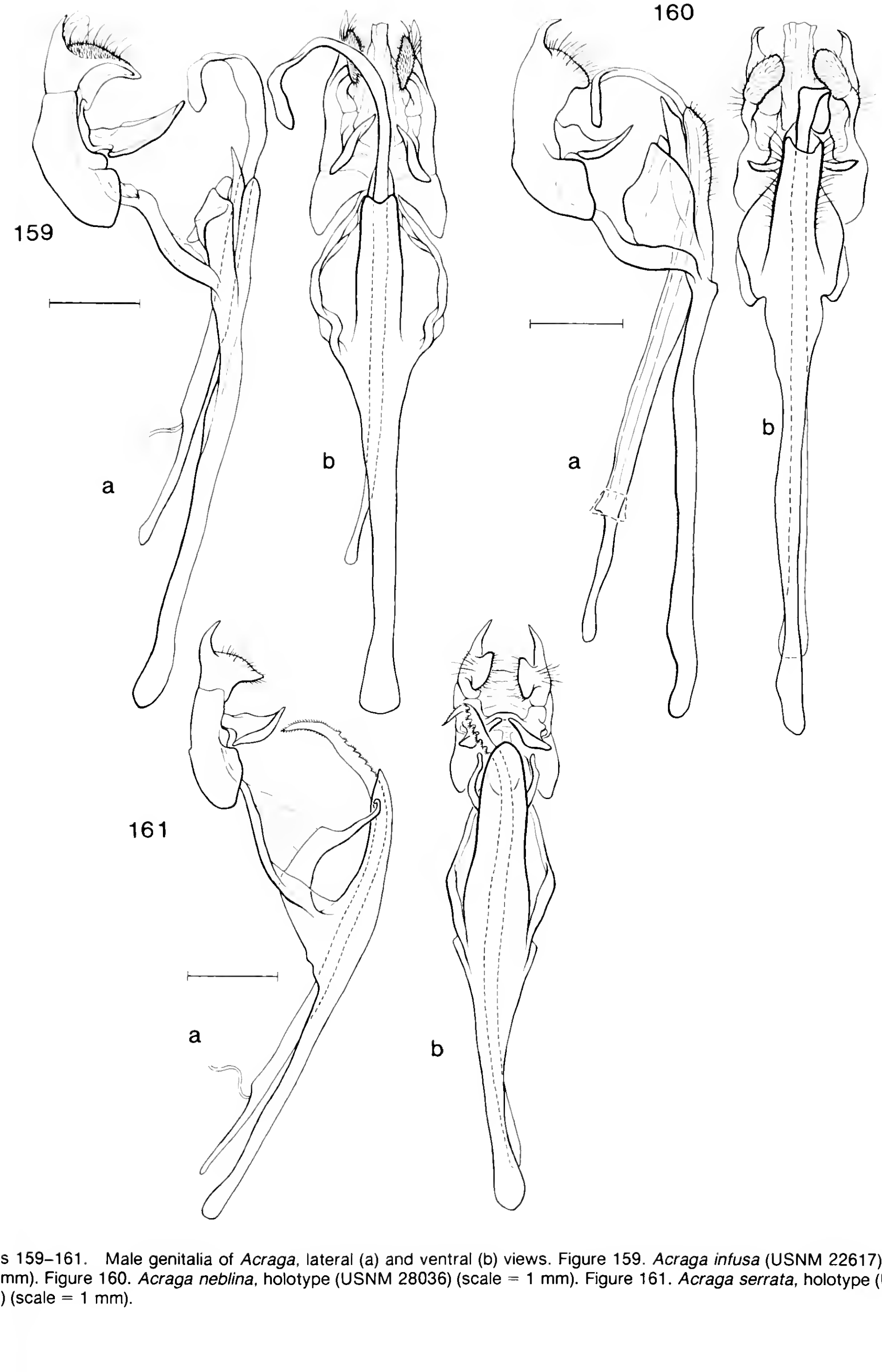
Figures 147–150. Wing patterns. Figure 147. *Acraga ferruginea*, male, Brazil (IOC). Figure 148. *Acraga ferruginea*, female, Brazil (IOC). Figure 149. *Acraga brunnea*, male holotype, Brazil (MNRJ). Figure 150. *Oroya aurora*, male paratype, Peru (BMNH).



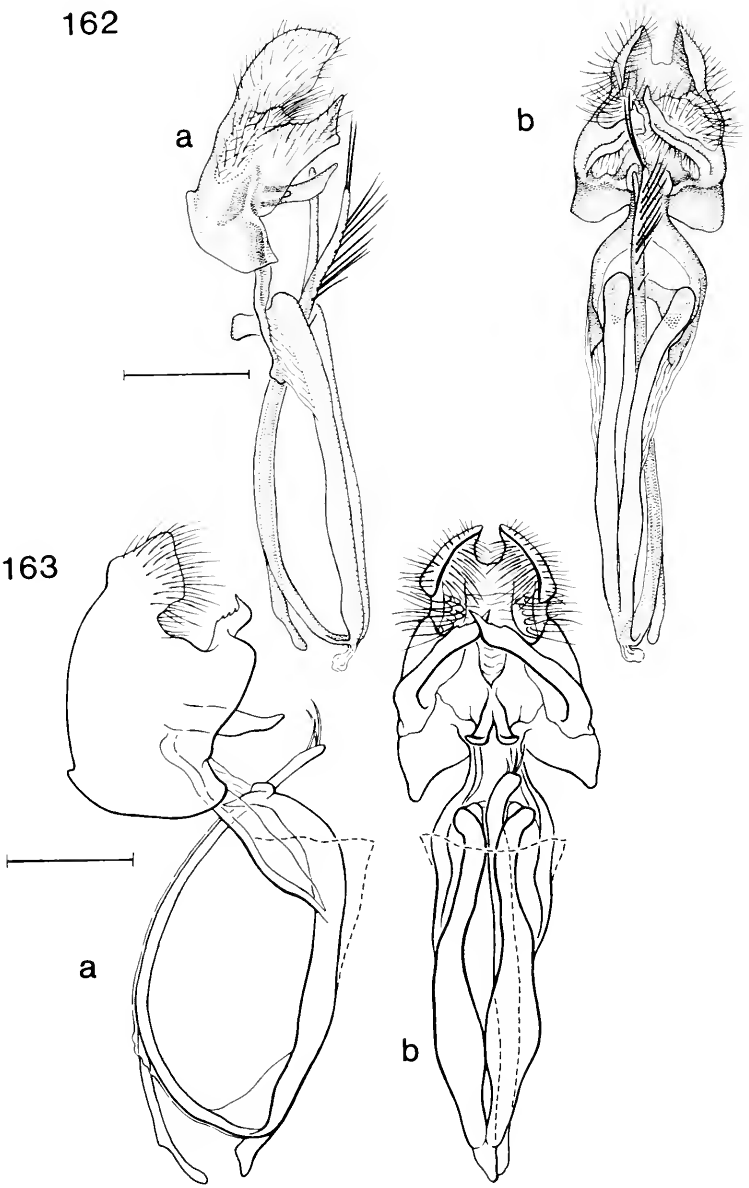
Figures 151–154. Male genitalia of *Acraga*, lateral (a) and ventral (b) views. Figure 151. *Acraga* species F (BMNH 85-5) (scale = 0.5 mm). Figure 152. *Acraga goes* (USNM 22651) (scale = 0.5 mm). Figure 153. *Acraga hamata* (USNM 22614) (scale = 1 mm). Figure 154. *Acraga andina*, holotype (USNM 28080) (scale = 1 mm).



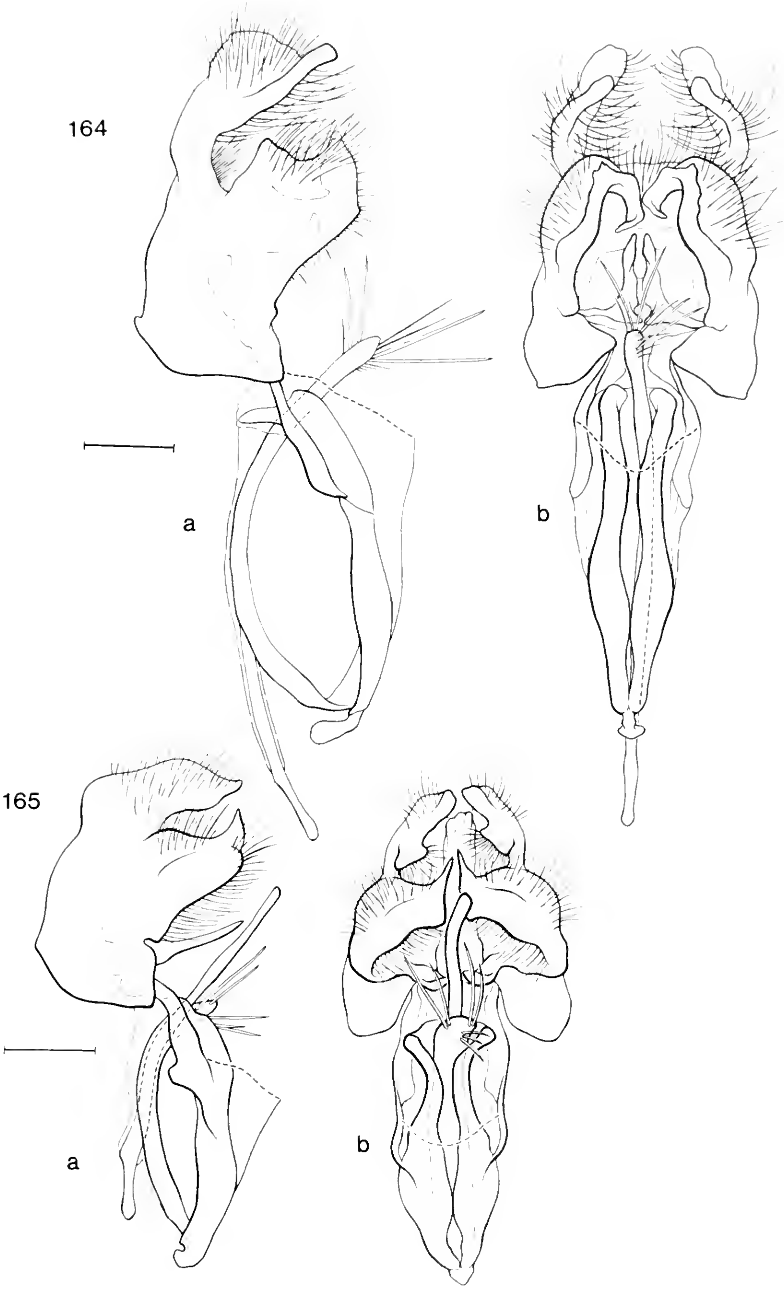
Figures 155–158. Male genitalia of *Acraga*, lateral (a) and ventral (b) views. Figure 155. *Acraga flava* (USNM 22509) (scale = 0.5 mm). Figure 156. *Acraga andina*, Venezuelan variant (UCV 86-23), tegumen–sociuncus complex only (scale = 1 mm). Figure 157. *Acraga ria*, holotype (USNM 22605) (scale = 1 mm). Figure 158. *Acraga obscura*, holotype (USNM 22673) (scale = 0.5 mm).



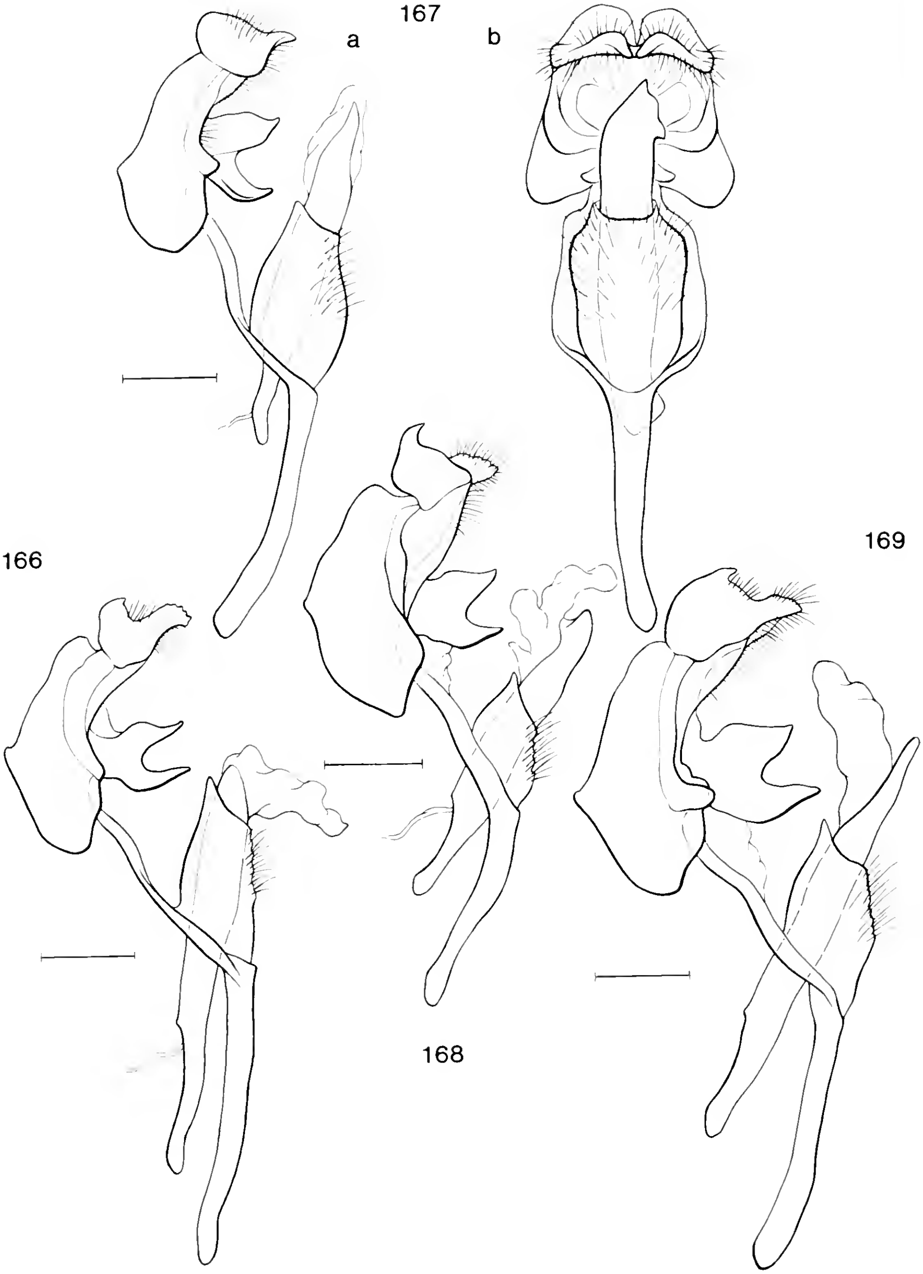
Figures 159–161. Male genitalia of *Acraga*, lateral (a) and ventral (b) views. Figure 159. *Acraga infusa* (USNM 22617) (scale = 0.5 mm). Figure 160. *Acraga neblina*, holotype (USNM 28036) (scale = 1 mm). Figure 161. *Acraga serrata*, holotype (USNM 28073) (scale = 1 mm).



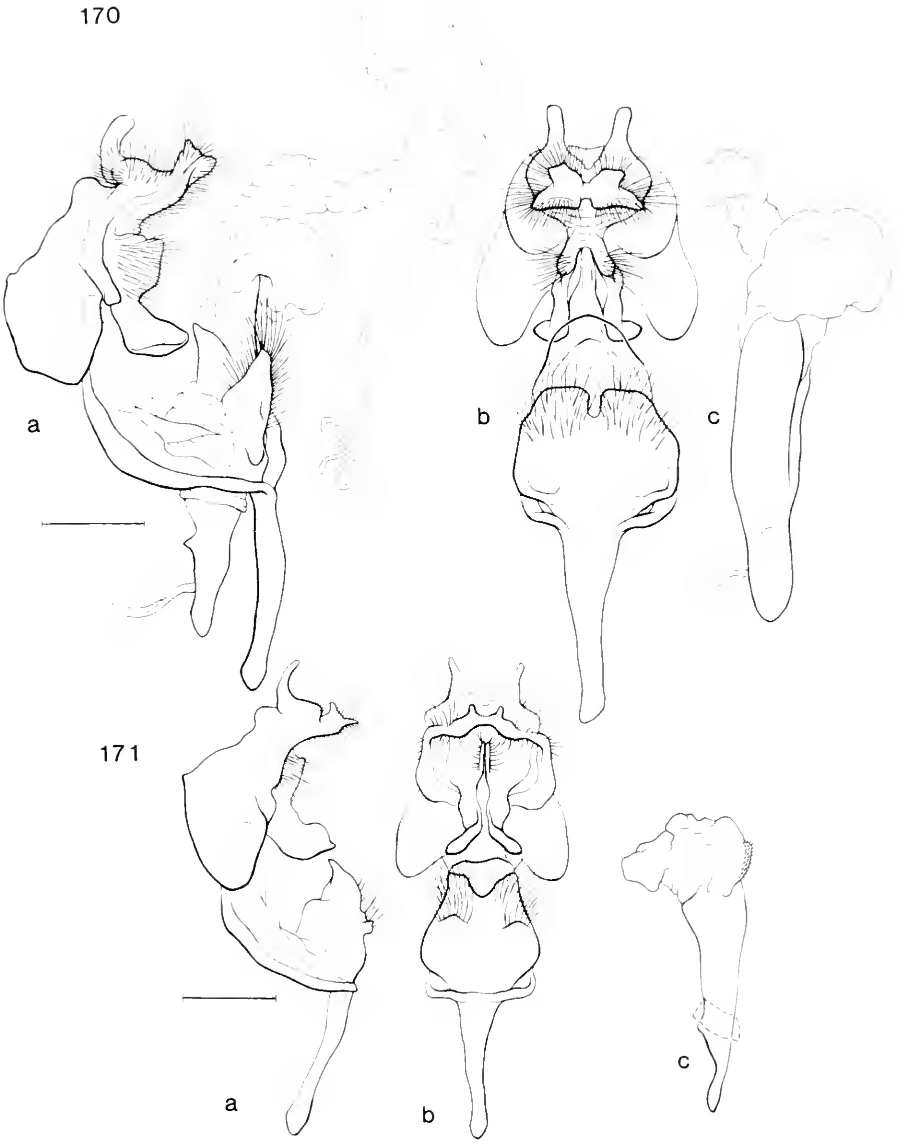
Figures 162, 163. Male genitalia of *Acraga*, lateral (a) and ventral (b) views (scale = 1 mm). Figure 162. *Acraga ciliata* (USNM 22485). Figure 163. *Acraga moorei* (USNM 22615).



Figures 164, 165. Male genitalia of *Acraga*, lateral (a) and ventral (b) views (scale = 1 mm). Figure 164. *Acraga coa* (USNM 22666). Figure 165. *Acraga chicana*, holotype (AMNH 86-18).

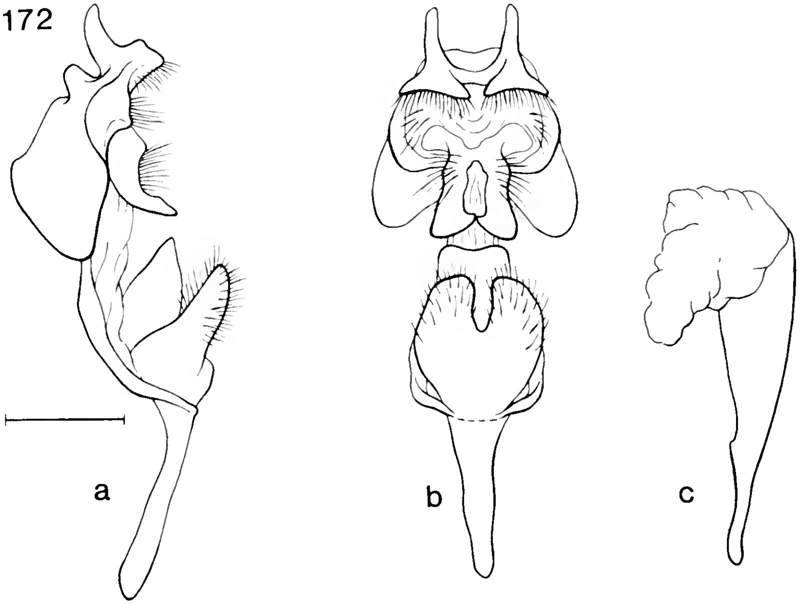


Figures 166–169. Male genitalia of *Acraga* (scale = 0.5 mm). Figure 166. *Acraga* species C (BMNH 85-7), lateral. Figure 167. *Acraga concolor* (BMNH 86-36), lateral (a) and ventral (b). Figure 168. *Acraga beebei*, holotype (USNM 22646), lateral. Figure 169. *Acraga citrinopsis* (BMNH 86-28), lateral.

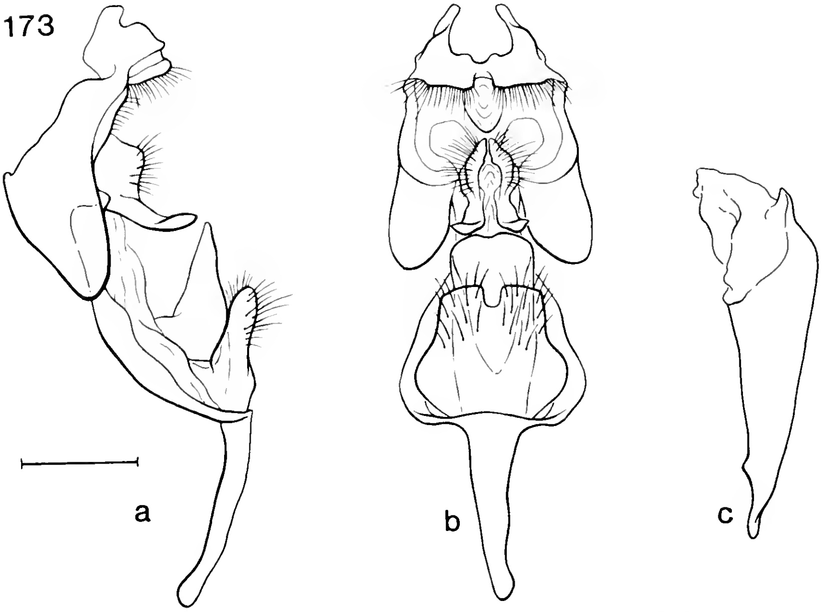


Figures 170, 171. Male genitalia of *Acraga*, lateral (a) and ventral (b) views, with separate ventral aedoeagus with vesica extended (c) (scale = 1 mm). Figure 170. *Acraga melinda* (USNM 22613). Figure 171. *Acraga amazonica*, holotype (BMNH 86-21).

172

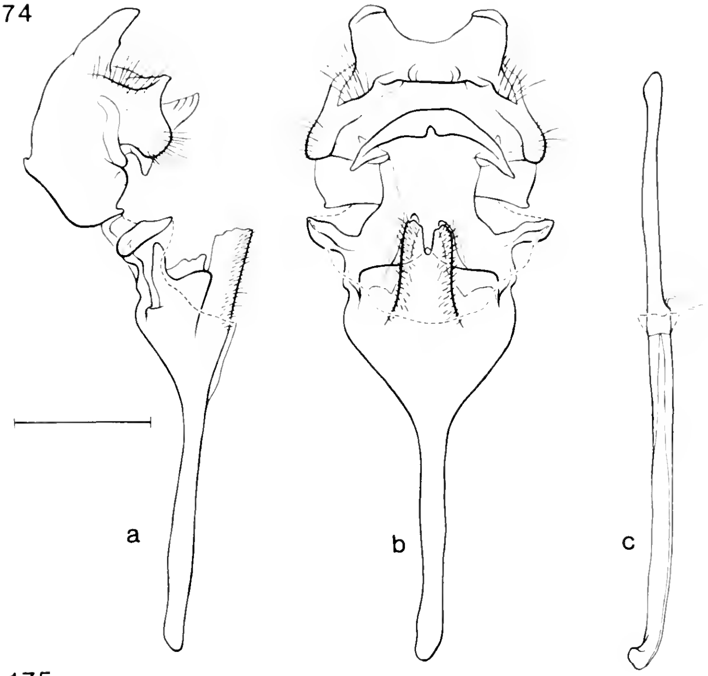


173

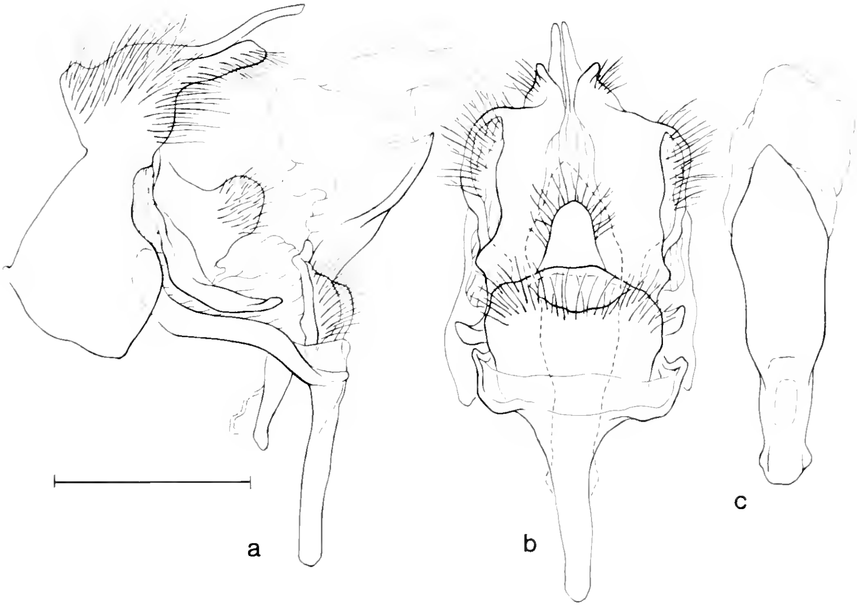


Figures 172, 173. Male genitalia of *Acraga*, lateral (a) and ventral (b) views with separate aedoeagus (c) (scale = 1 mm). Figure 172. *Acraga meridensis*, lateral and ventral (USNM 28074), aedoeagus with vesica extended (USNM 28079, lectotype). Figure 173. *Acraga mariala* (AMNH 86-14).

174

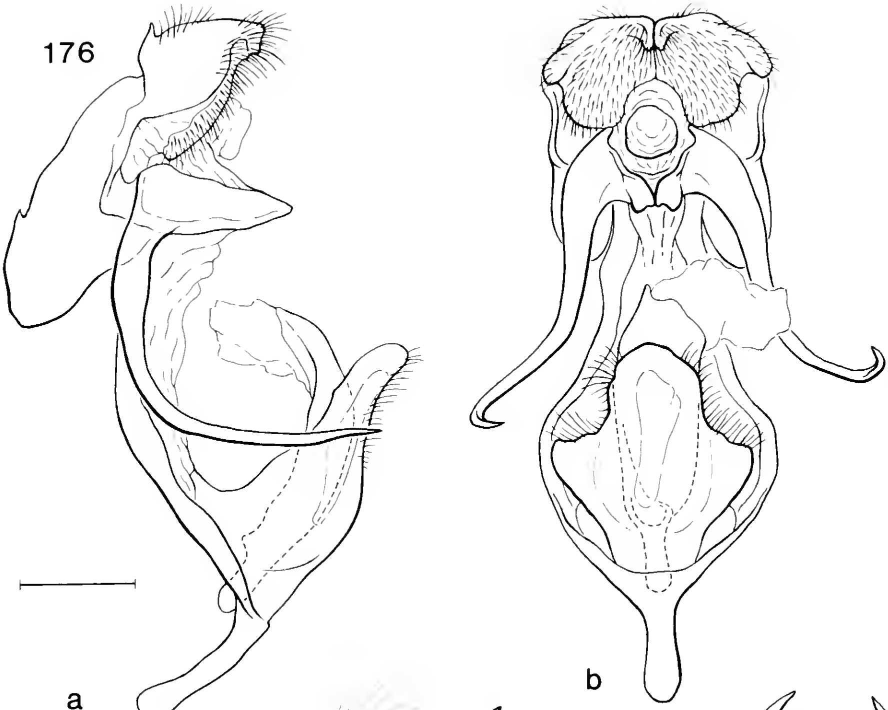


175

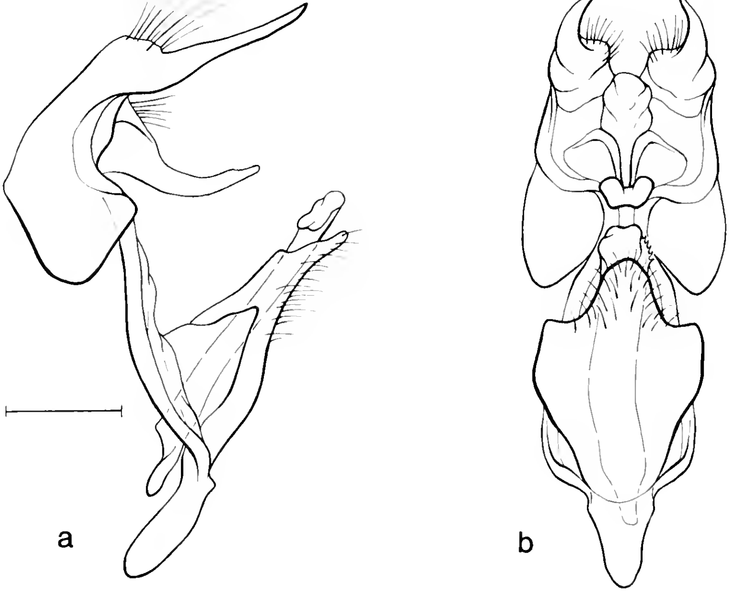


Figures 174, 175. Male genitalia of *Acraga*, lateral (a) and ventral (b) views with separate aedoeagus (c) (scale = 1 mm). Figure 174. *Acraga perbrunnea* (USNM 22515). Figure 175. *Acraga citrina* (USNM 22513).

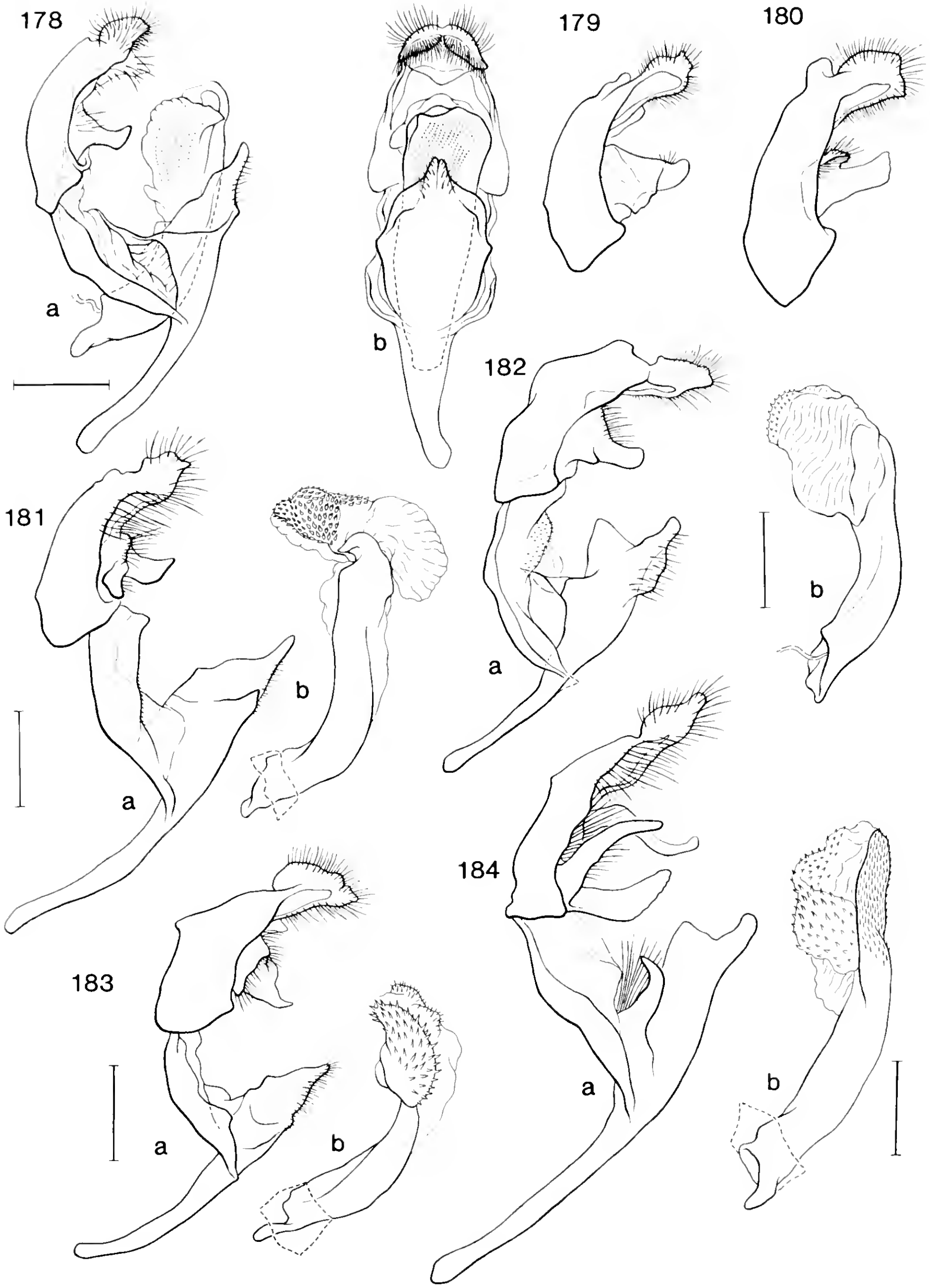
176



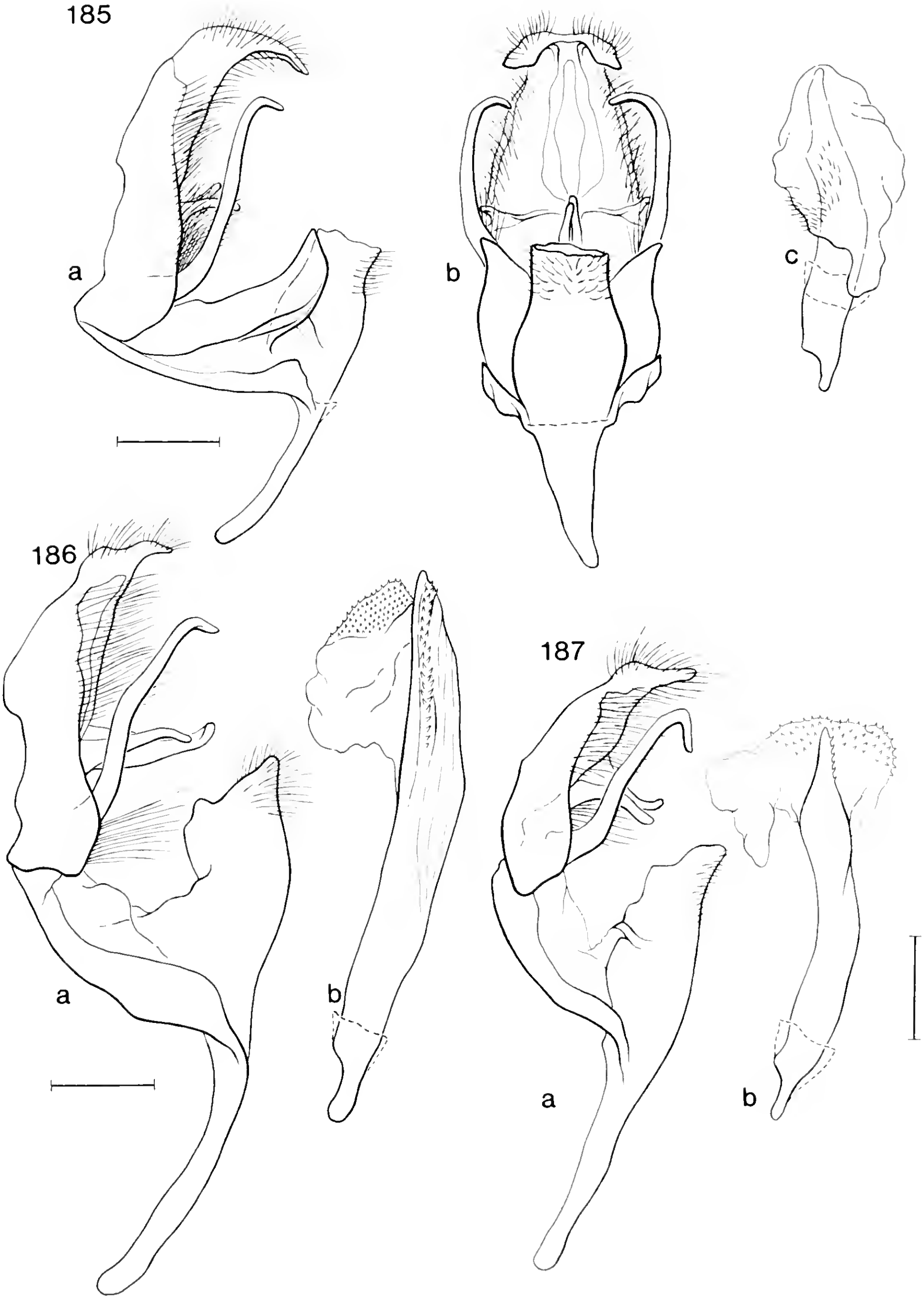
177



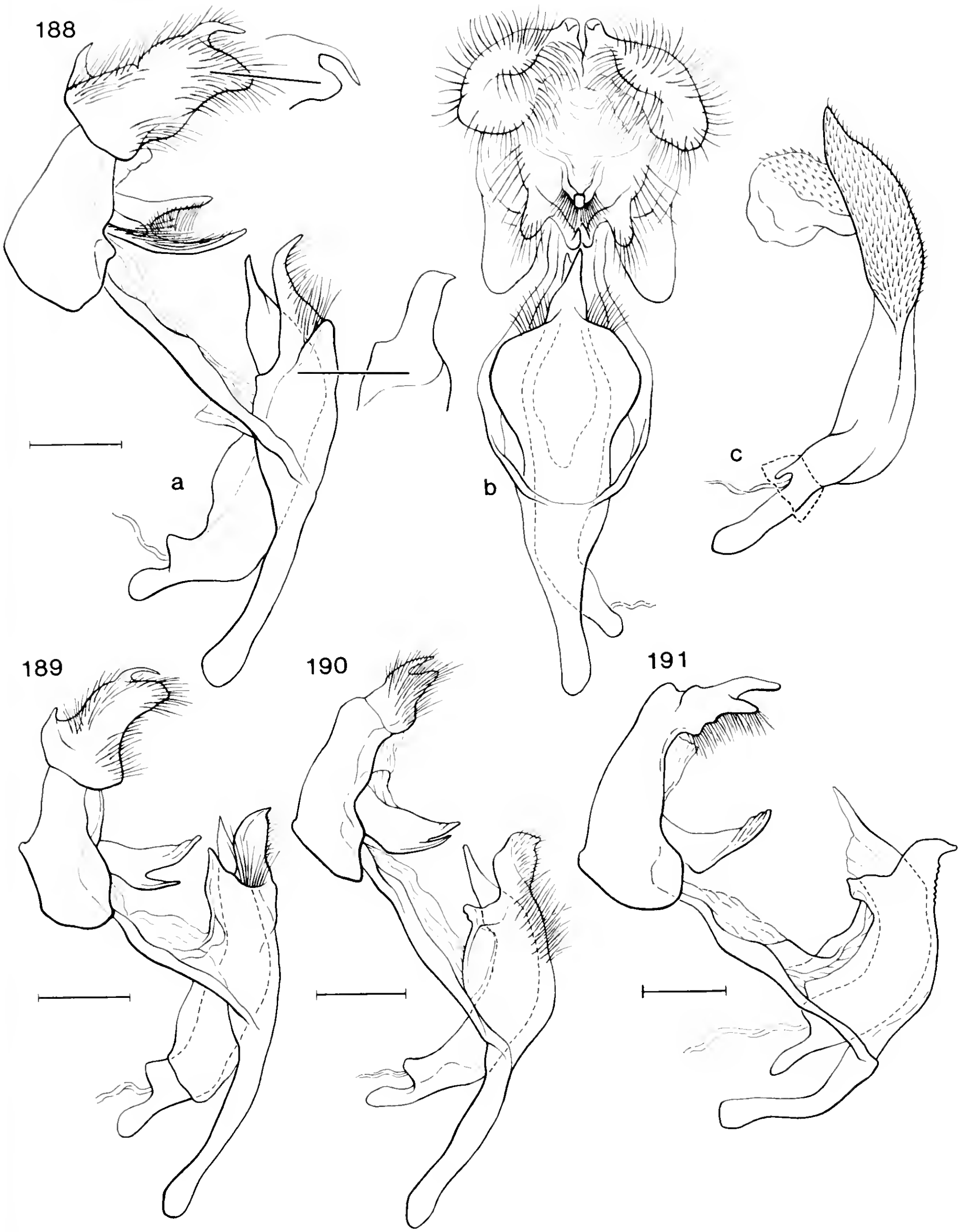
Figures 176, 177. Male genitalia of *Acraga*, lateral (a) and ventral (b) views. Figure 176. *Acraga ferruginea* (IOC 85-53) (scale = 0.5 mm). Figure 177. *Acraga brunnea*, holotype (MNRJ 85-56) (scale = 1 mm).



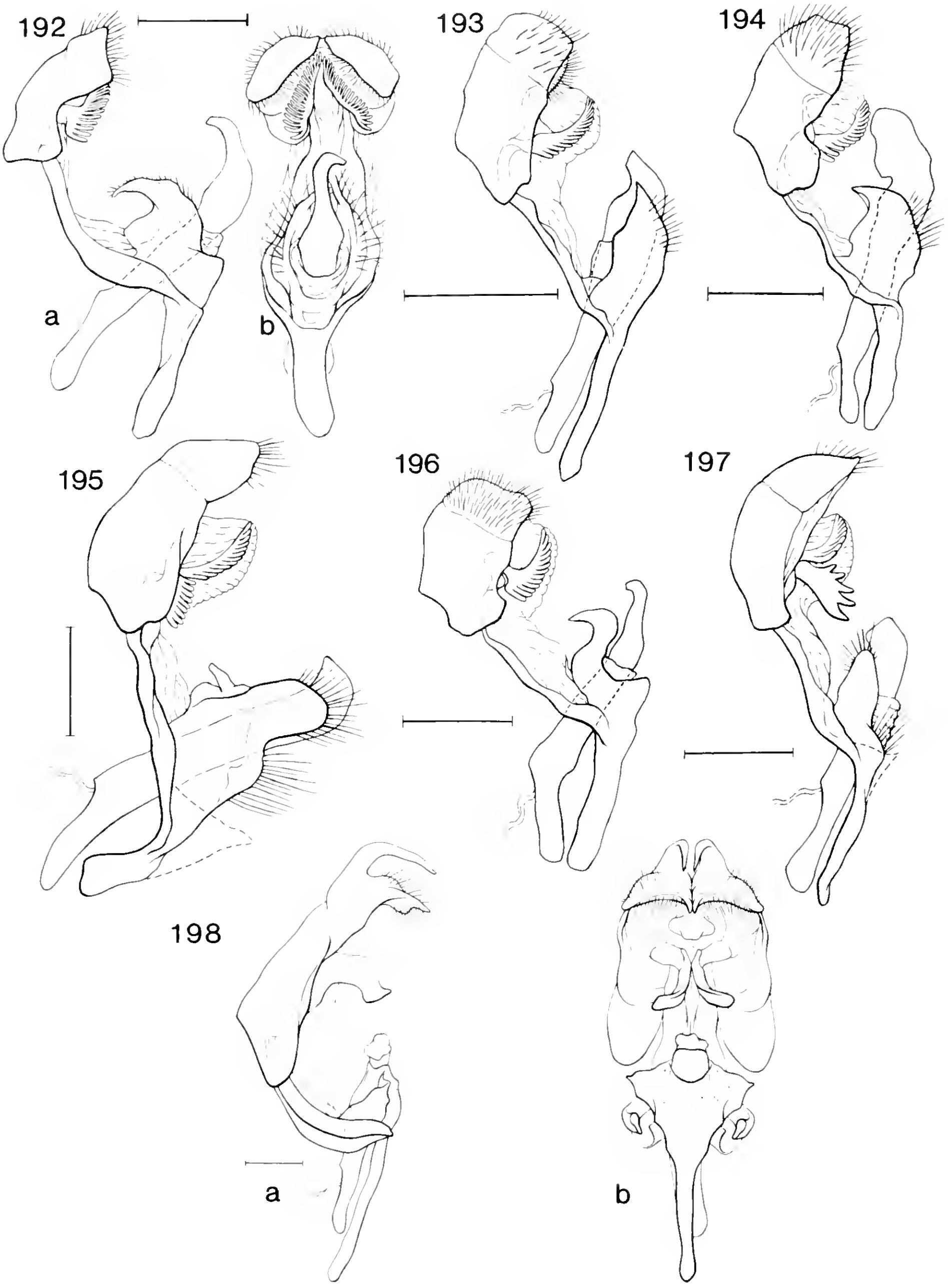
Figures 178–184. Male genitalia of *Acraga* (scale = 1 mm). Figure 178. *Acraga ampela* (USNM 28017), lateral (a) and ventral (b). Figure 179. *Acraga ampela*, holotype (BMNH 85-31), tegumen–sociuncus complex, lateral. Figure 180. *Acraga ampela*, variant (USNM 28097), tegumen–sociuncus complex, lateral. Figure 181. *Acraga boliviana* (BMNH 85-24), lateral (a), with separate aedoeagus (reversed) with vesica extended (b). Figure 182. *Acraga isothea*, paralectotype (USNM 22570), lateral (a), with separate aedoeagus with vesica extended (b). Figure 183. *Acraga angulifera* (USNM 28091), lateral (a), with separate aedoeagus with vesica extended (b). Figure 184. *Acraga puno*, holotype (BMNH 85-50), lateral (a), with separate aedoeagus (b).



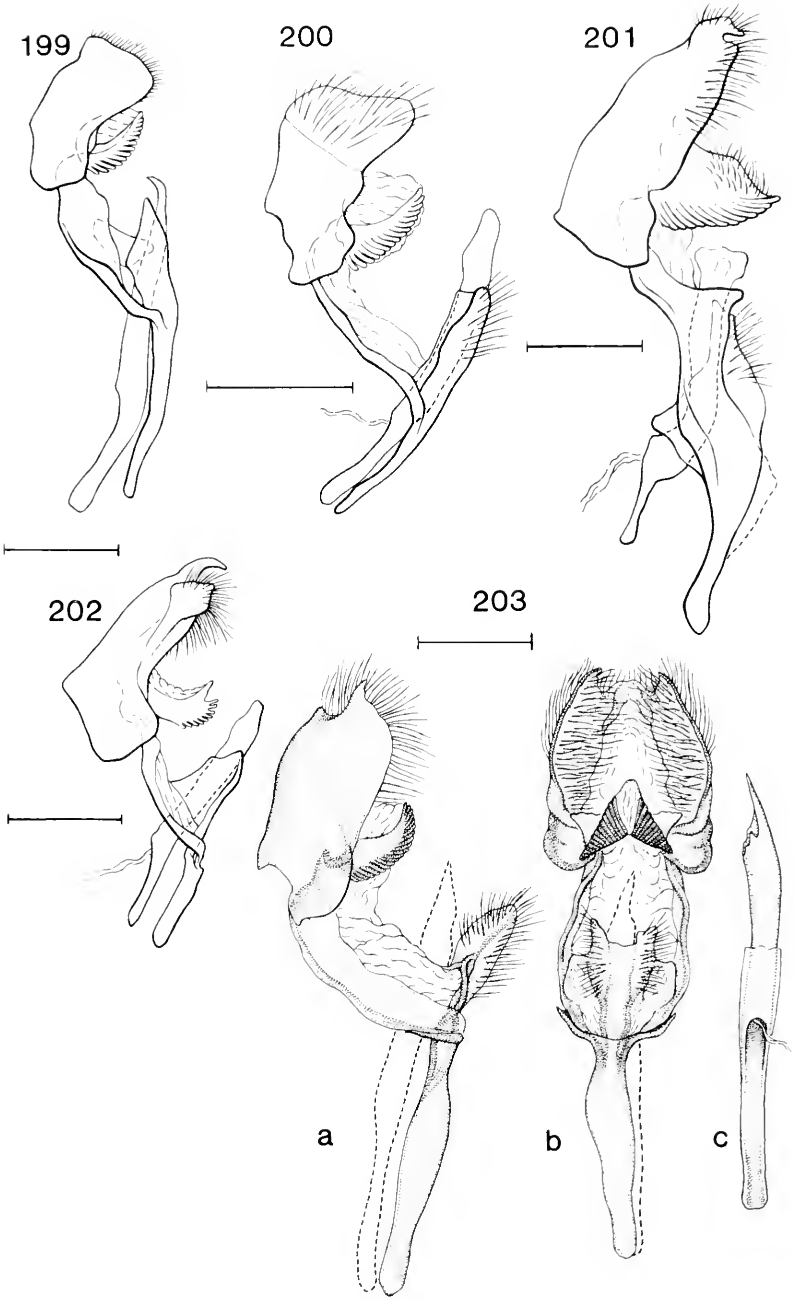
Figures 185–187. Male genitalia of *Acraga* (scale = 1 mm). Figure 185. *Acraga umbrifera* (USNM 22595), lateral (a) and ventral (b), with separate aedoeagus with vesica extended (c). Figure 186. *Acraga leberna*, lectotype (USNM 22597), lateral (a), with separate aedoeagus with vesica extended (b). Figure 187. *Acraga* species near *leberna* (USNM 28112), lateral (a), with separate aedoeagus (aedoeagus reconstructed) (b).



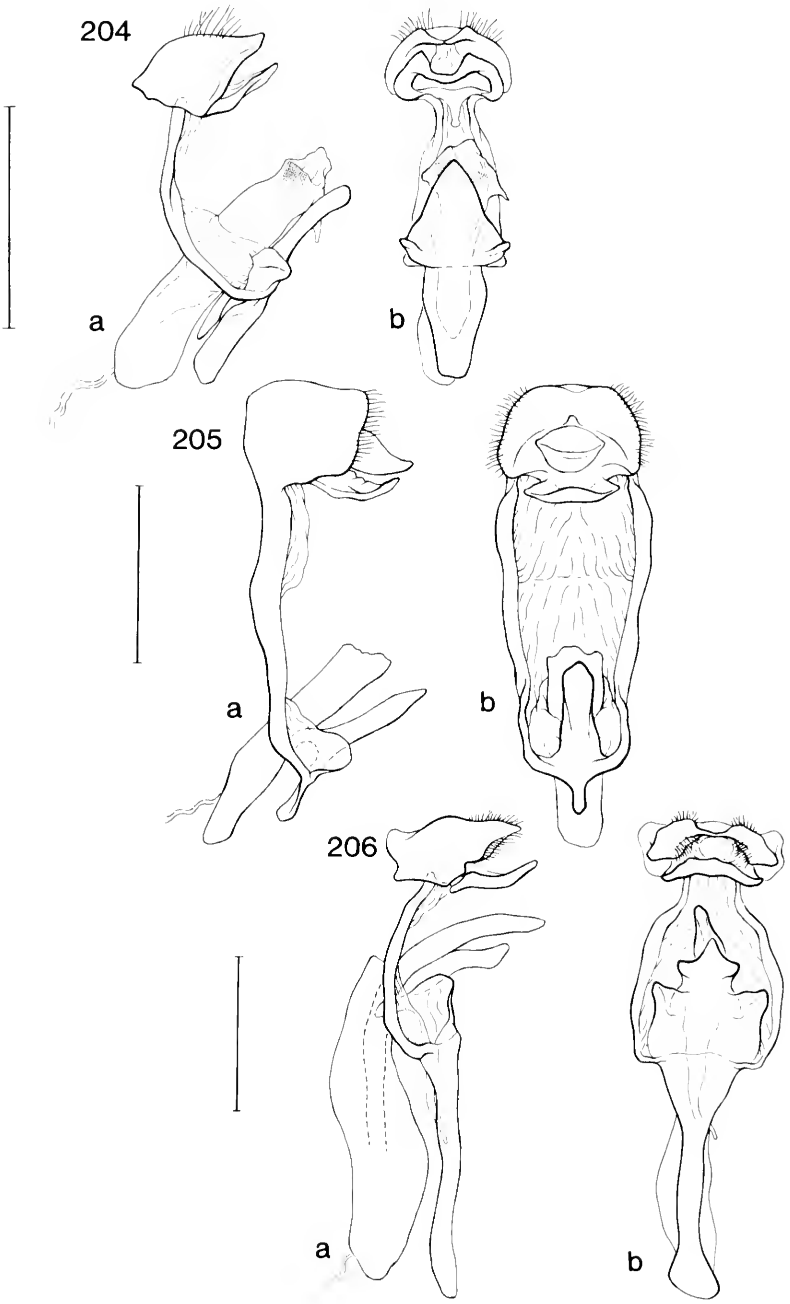
Figures 188–191. Male genitalia of *Acraga*. Figure 188. *Acraga ochracea* (VOB 85-55), lateral (a) and ventral (b), with separate aedoeagus with vesica extended (USNM 28002) (c), and insets of valvae complex tips and sociuncus points (ZMUC 85-41) (scale = 0.5 mm; inset reduced slightly in scale relative to main drawing). Figure 189. *Acraga victoria*, paratype (USNM 28038), lateral (scale = 0.5 mm). Figure 190. *Acraga sexquicentenaria* (USNM 28004), lateral (scale = 0.5 mm). Figure 191. *Acraga parana*, paratype (USNM 28118), lateral (scale = 1 mm).



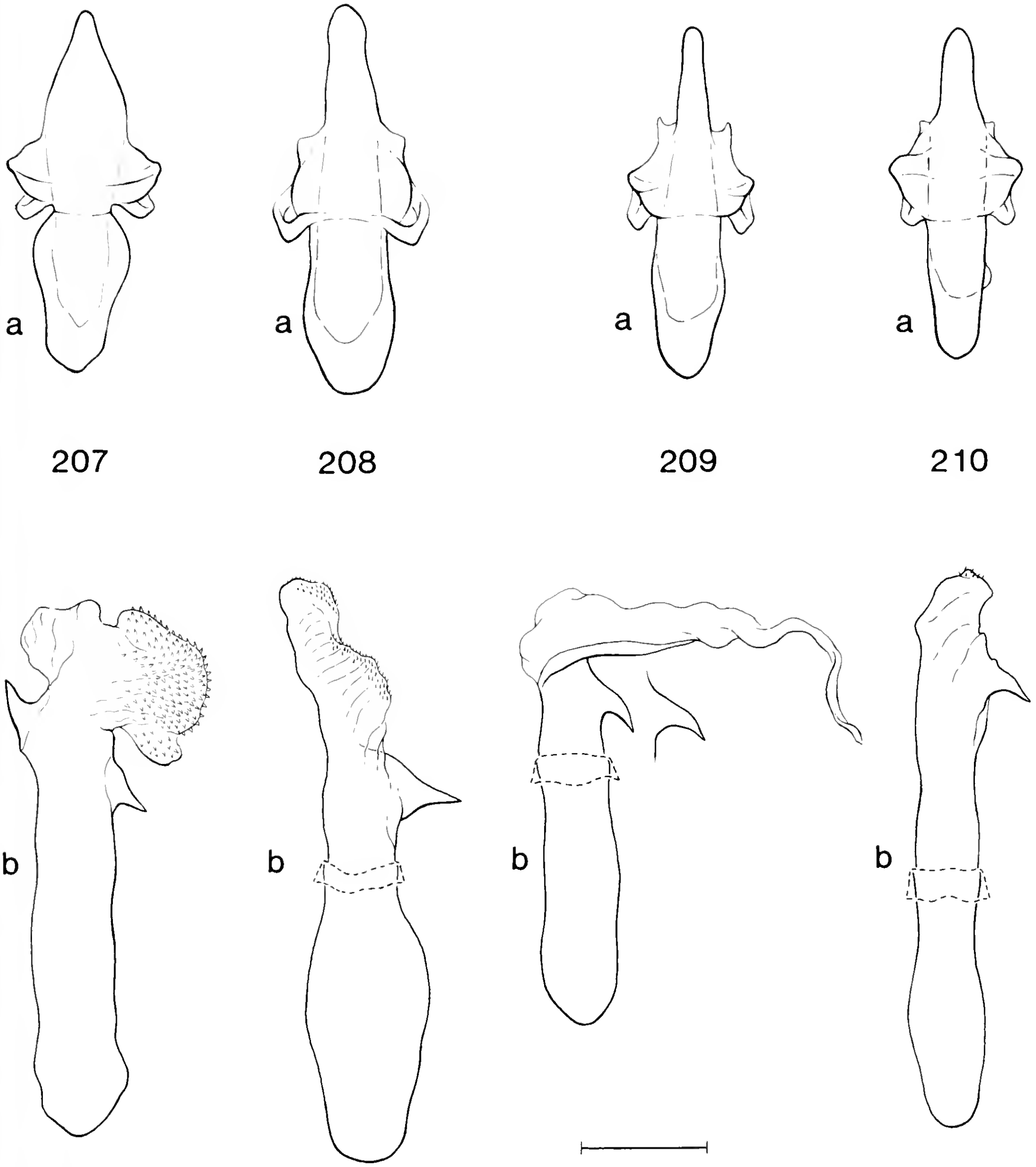
Figures 192–198. Male genitlia. Figure 192. *Dalcerides flavetta* (USNM 22600), lateral (a) and ventral (b) (scale = 1 mm). Figure 193. *Dalcerides rebella* (USNM 22606 (holotype), with aedoeagus position from UCB 84-53), lateral (scale = 0.5 mm). Figure 194. *Dalcerides chirma*, paralectotype (USNM 22607), lateral (scale = 0.5 mm). Figure 195. *Dalcerides* new species (BMNH 85-6), lateral (scale = 0.5 mm). Figure 196. *Dalcerides radians* (USNM 22610), lateral (scale = 0.5 mm). Figure 197. *Dalcerides dulciola* (USNM 22663), lateral (scale = 0.5 mm). Figure 198. *Acraga hoppiana*, holotype (ZSBS 86-37), lateral (a) and ventral (b) (scale = 0.5 mm).



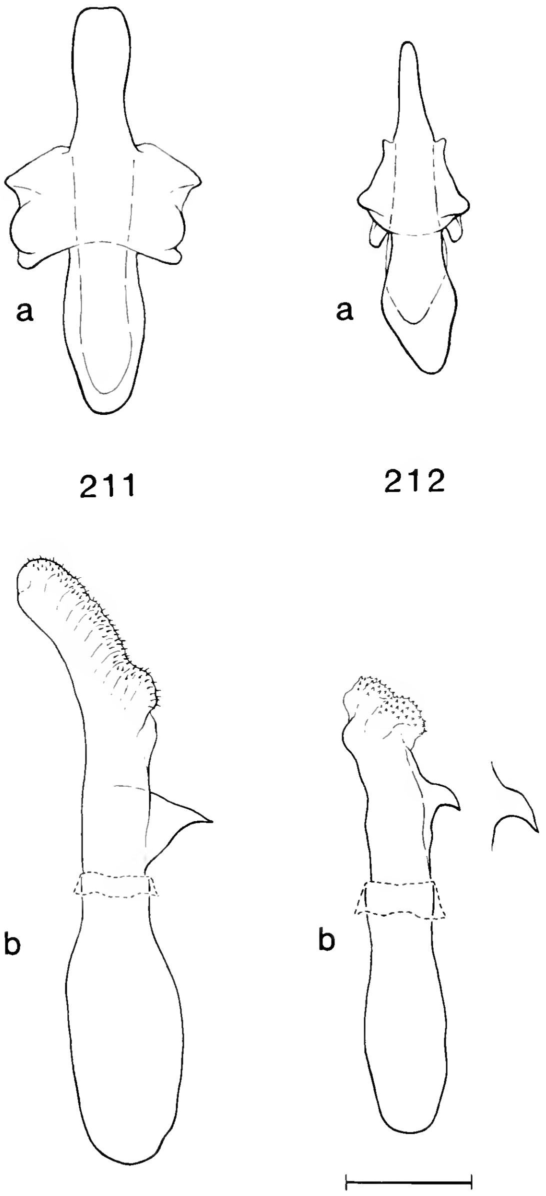
Figures 199–203. Male genitalia of *Dalcerides*. Figure 199. *Dalcerides mesoa* (USNM 22665), lateral (scale = 1 mm). Figure 200. *Dalcerides sofia* (USNM 22507), lateral (scale = 0.5 mm). Figure 201. *Dalcerides alba* (USNM 22529), lateral (scale = 0.5 mm). Figure 202. *Dalcerides nana* (USNM 22609), lateral (scale = 0.5 mm). Figure 203. *Dalcerides ingenita* (USNM 22503), lateral (a) and ventral (b), with separate aedoeagus (c) (scale = 1 mm).



Figures 204–206. Male genitalia, lateral (a) and ventral (b) views. Figure 204. *Paracraga innocens*, holotype (USNM 22591) (scale = 1 mm). Figure 205. *Minonoa elvira* (USNM 22500) (scale = 0.5 mm). Figure 206. *Ca anastigma* (USNM 22593) (scale = 0.5 mm).

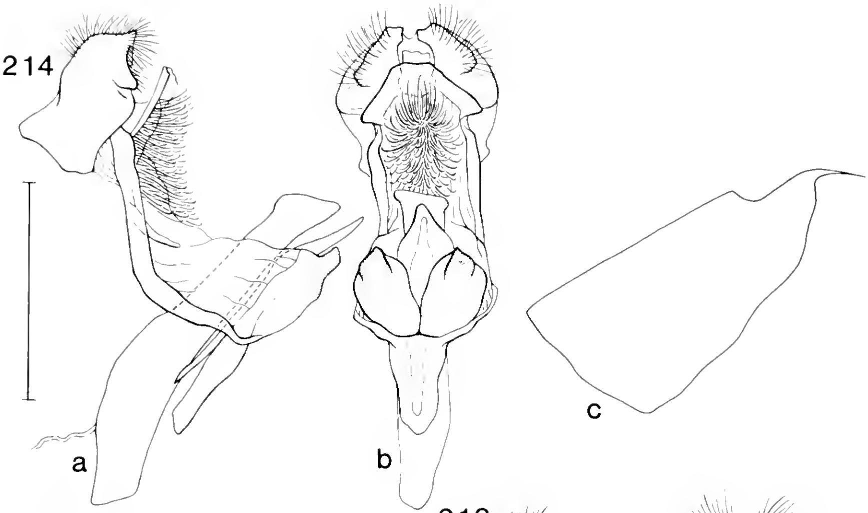


Figures 207–210. Male genitalia of *Paracraga*, ventral oblique view of juxta complex and saccus (a), with separate aedoeagus with vesica extended (b) (scale = 0.5 mm). Figure 207. *Paracraga innocens*, holotype (USNM 22591). Figure 208. *Paracraga amianta*, holotype (USNM 22585). Figure 209. *Paracraga argentea* (USNM 22590). Figure 210. *Paracraga canalicula*, holotype (USNM 22586), aedoeagus with vesica only partially extended.

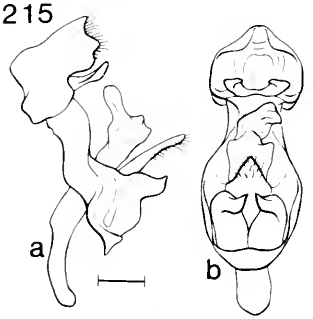


Figures 211–213. Male genitalia of *Paracraga*, ventral oblique view of juxta complex and saccus (a), with separate aedoeagus with vesica extended (b) (scale = 0.5 mm). Figure 211. *Paracraga halophora*, holotype (CU 84-32). Figure 212. *Paracraga necoda*, paralectotype (USNM 22680). Figure 213. *Paracraga pulverina*, holotype (USNM 22589).

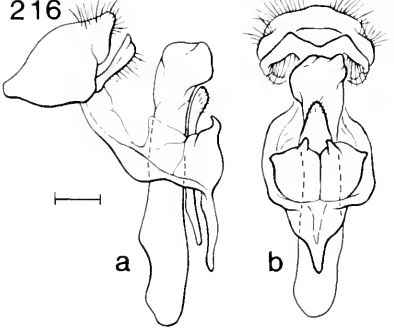
214



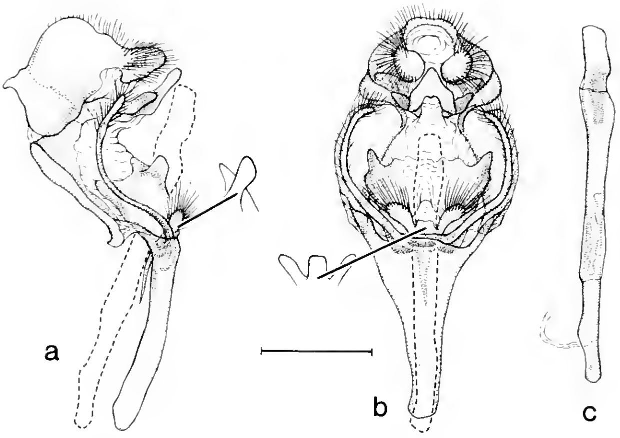
215



216

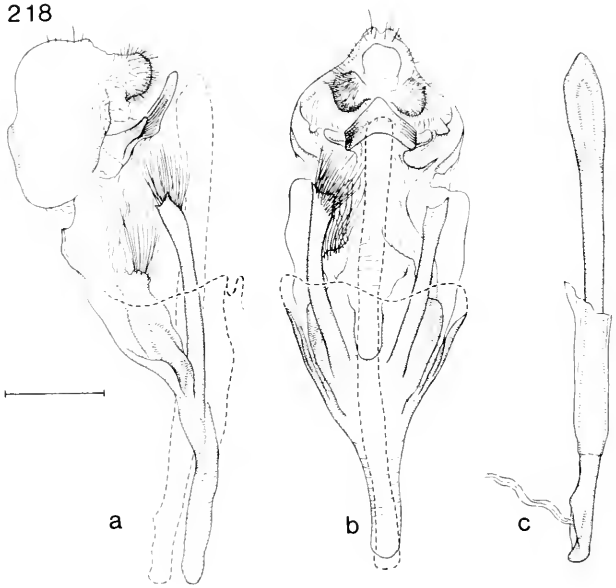


217

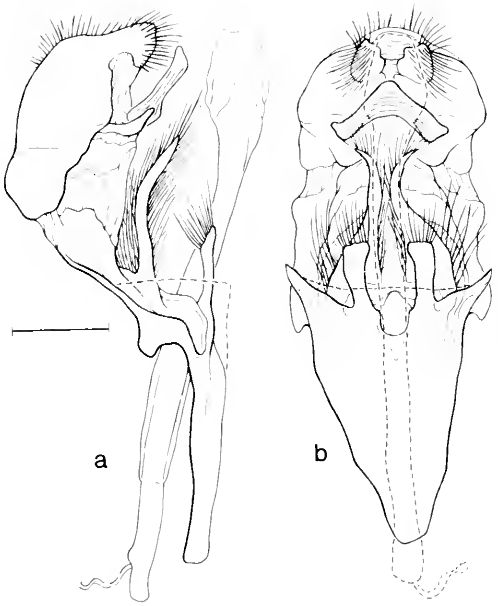


Figures 214–217. Male genitalia, lateral (a) and ventral (b) views. Figure 214. *Minacragides arnacis*, holotype (USNM 22598), with lateral inset of eigth abdominal tergite (c) (scale = 1 mm). Figure 215. *Minacragides* new species A (IOC 85-54) (scale = 0.1 mm). Figure 216. *Minacragides* (?) new species B (VOB 84-57) (scale = 0.1 mm). Figure 217. *Dalcerina tijucana* (USNM 22539, paralectotype of *fumata*), with separate aedoeagus (c), and insets of variation in juxta (USNM 22566, holotype of *tijucana*) (scale = 1 mm).

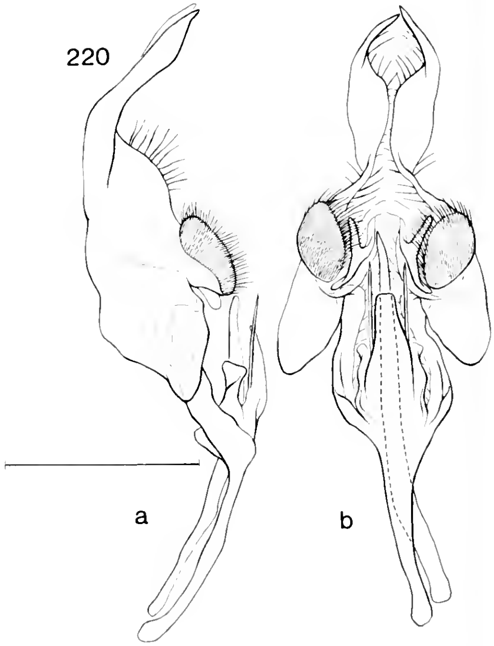
218



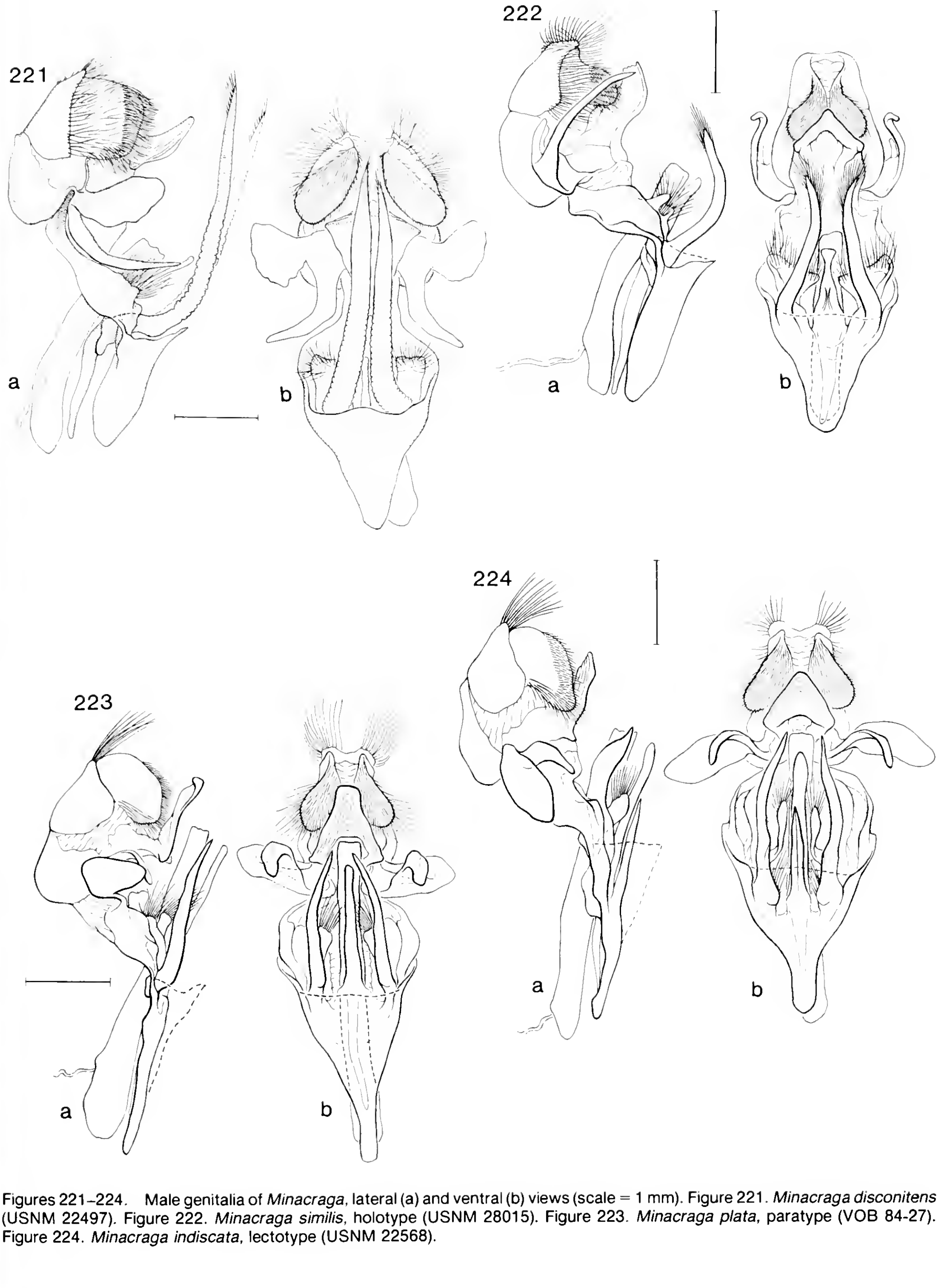
219



220

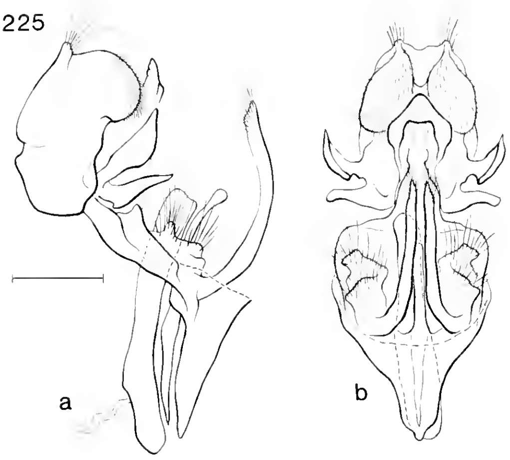


Figures 218–220. Male genitalia, lateral (a) and ventral (b) views (scale = 1 mm). Figure 218. *Dalcera abrasa* (USNM 22488), with separate aedoeagus (c). Figure 219. *Dalcera canescens* (USNM 28089). Figure 220. *Oroya aurora*, paratype (USNM 28108).

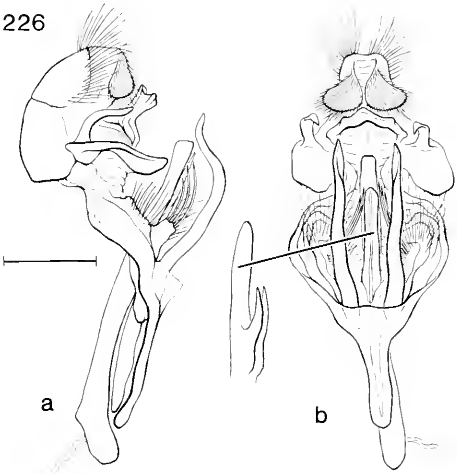


Figures 221–224. Male genitalia of *Minacraga*, lateral (a) and ventral (b) views (scale = 1 mm). Figure 221. *Minacraga disconitens* (USNM 22497). Figure 222. *Minacraga similis*, holotype (USNM 28015). Figure 223. *Minacraga plata*, paratype (VOB 84-27). Figure 224. *Minacraga indiscata*, lectotype (USNM 22568).

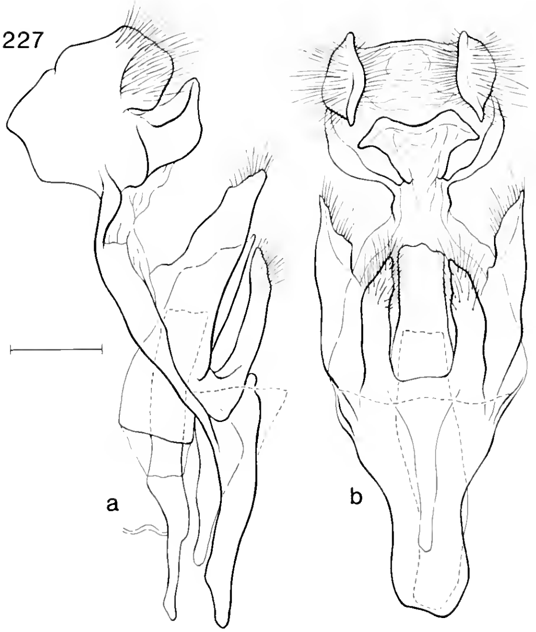
225



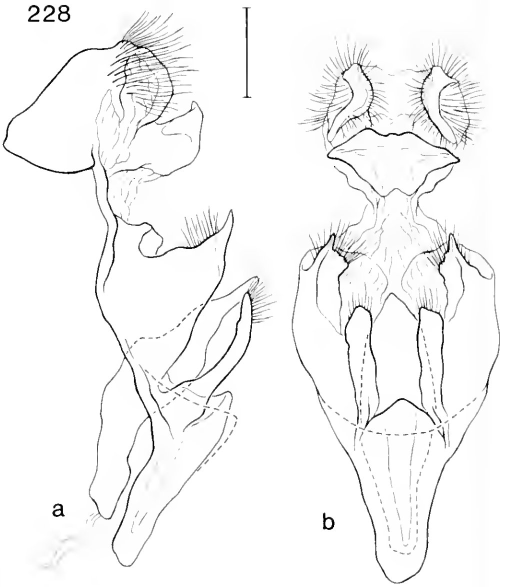
226



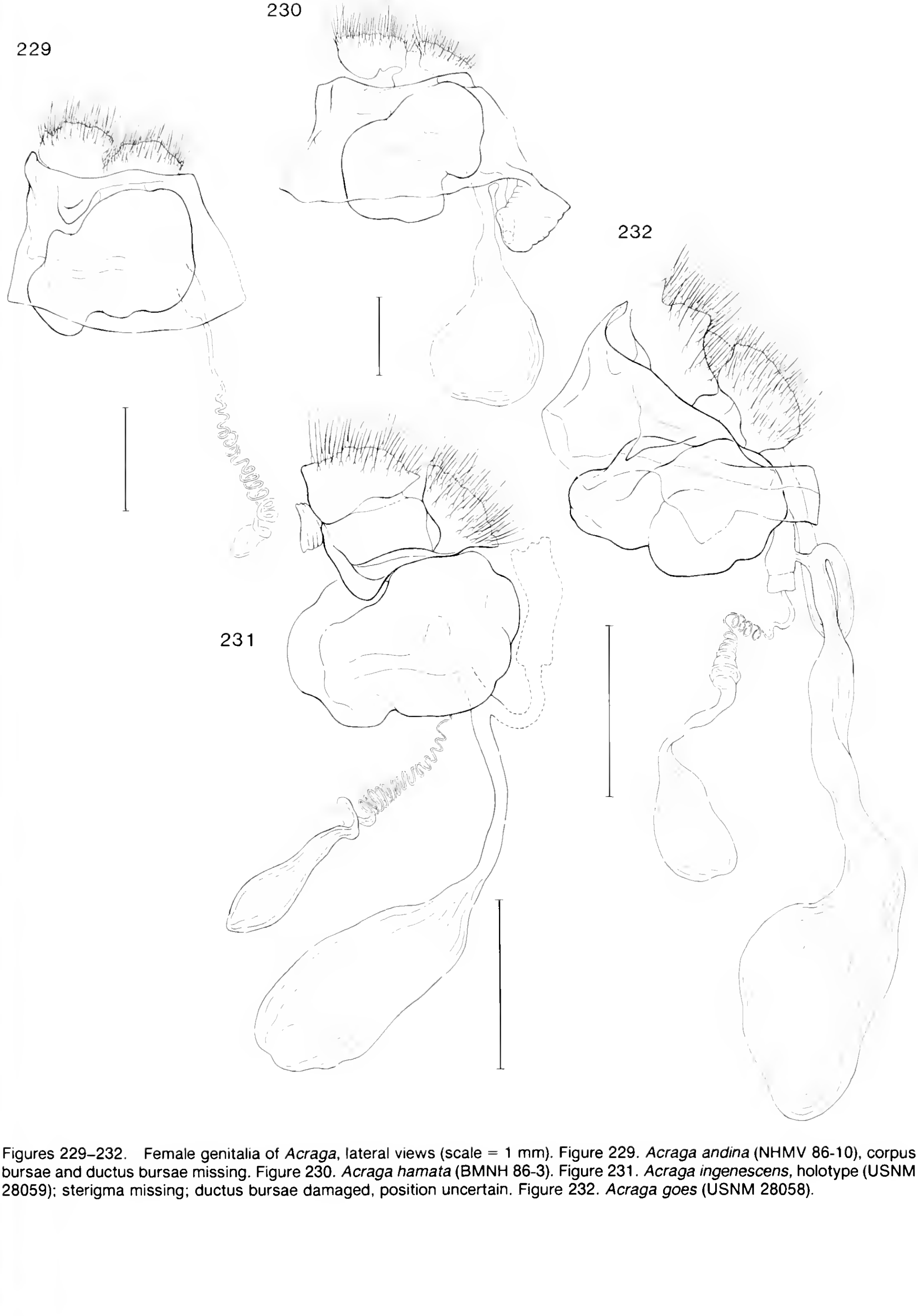
227



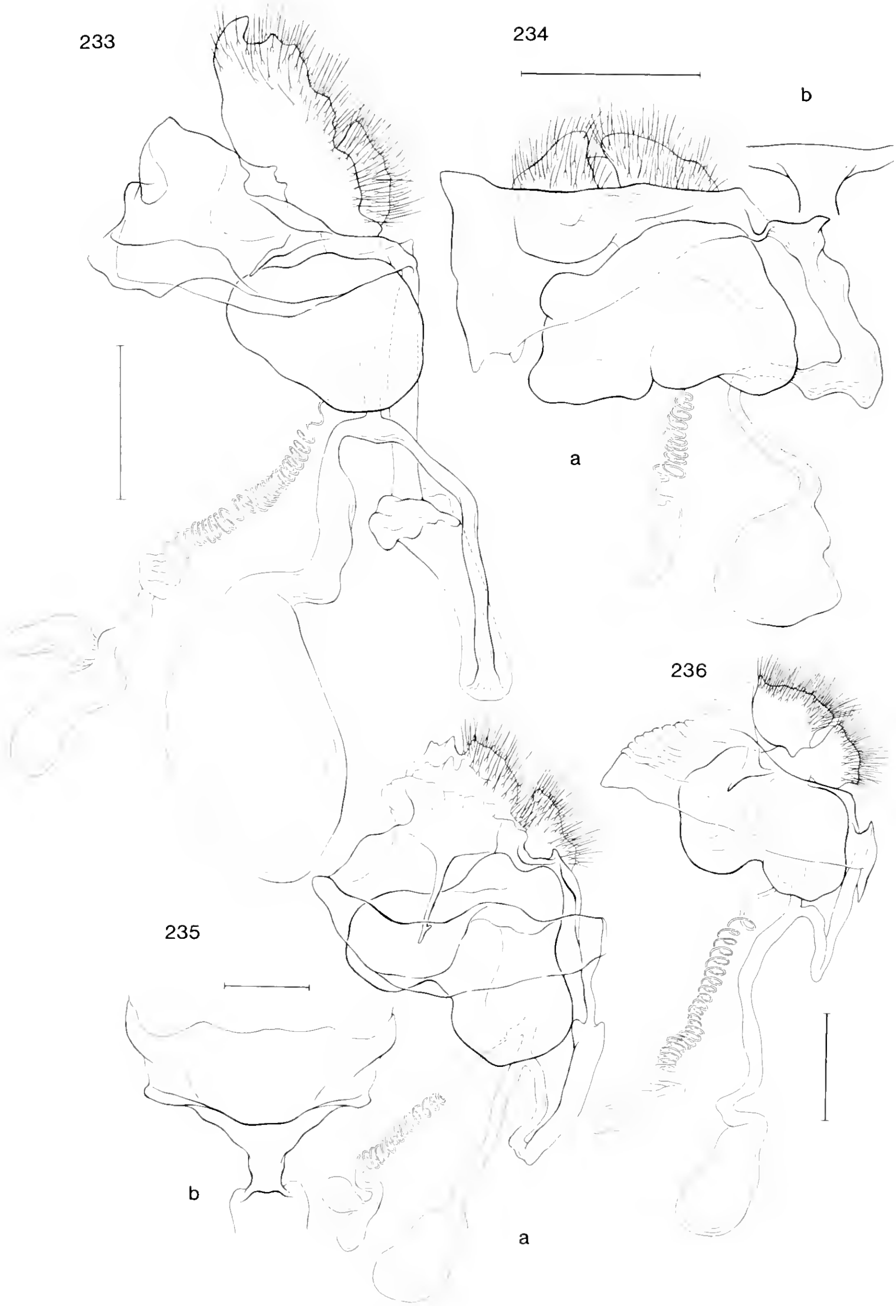
228



Figures 225–228. Male genitalia of *Minacraga*, lateral (a) and ventral (b) views. Figure 225. *Minacraga argentata* (USNM 28097) (scale = 1 mm). Figure 226. *Minacraga itatiaia* (BMNH 85-48, paratype), with inset lateral oblique view of variation in external juxta (BMNH 86-29, paratype) (scale = 1 mm). Figure 227. *Minacraga aenea* (USNM 22564) (scale = 0.5 mm). Figure 228. *Minacraga hyalina*, paratype (CMNH 84-18) (scale = 0.5 mm).

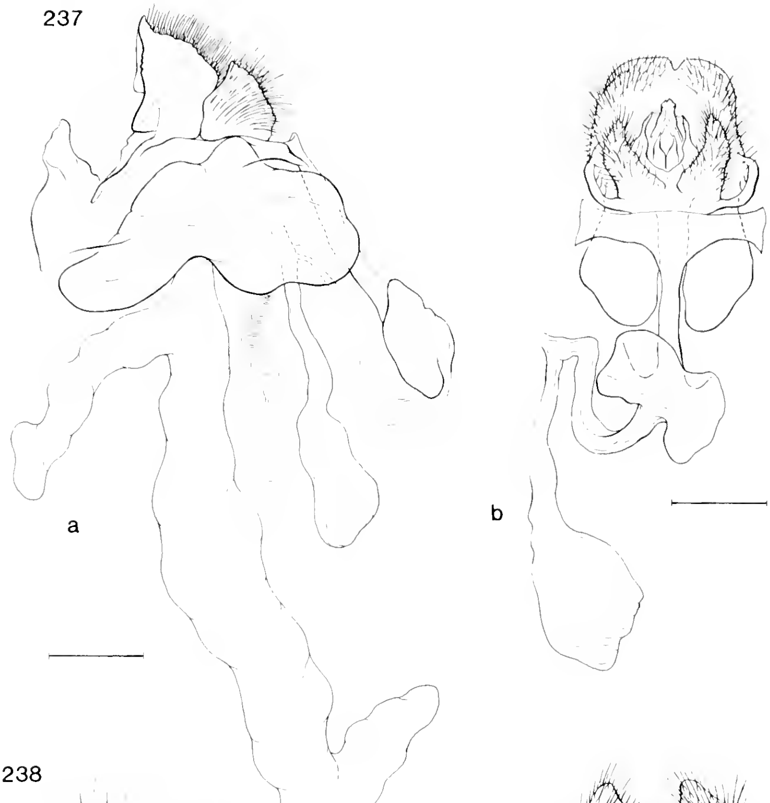


Figures 229–232. Female genitalia of *Acraga*, lateral views (scale = 1 mm). Figure 229. *Acraga andina* (NHMV 86-10), corpus bursae and ductus bursae missing. Figure 230. *Acraga hamata* (BMNH 86-3). Figure 231. *Acraga ingenescens*, holotype (USNM 28059); sterigma missing; ductus bursae damaged, position uncertain. Figure 232. *Acraga goes* (USNM 28058).

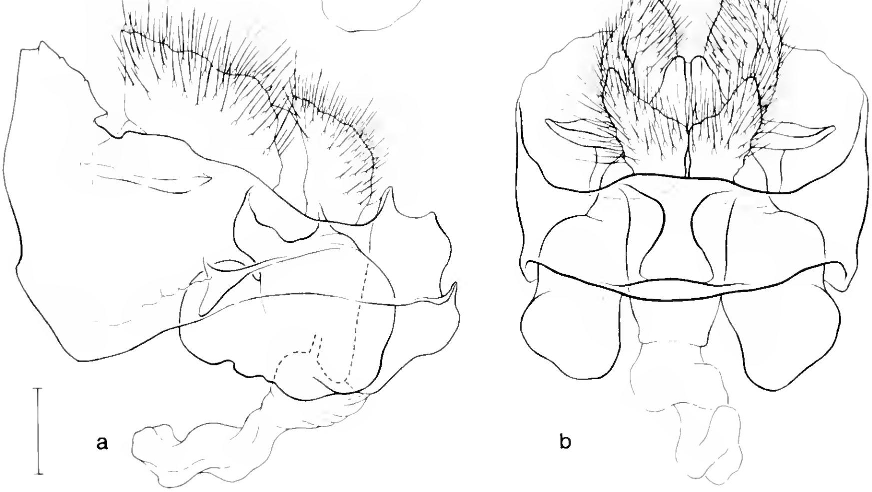


Figures 233–236. Female genitalia of *Acraga*, lateral views (scale = 1 mm). Figure 233. *Acraga ciliata*, holotype (BMNH 86-26). Figure 234. *Acraga flava* (USNM 28043), with inset of ventral view of sterigma (b). Figure 235. *Acraga moorei* (USNM 28053), with inset of ventral view of sterigma (b); composite drawing, "accessory gland" illustrated from left side. Figure 236. *Acraga* species near *A. infusa* (USNM 28065).

237



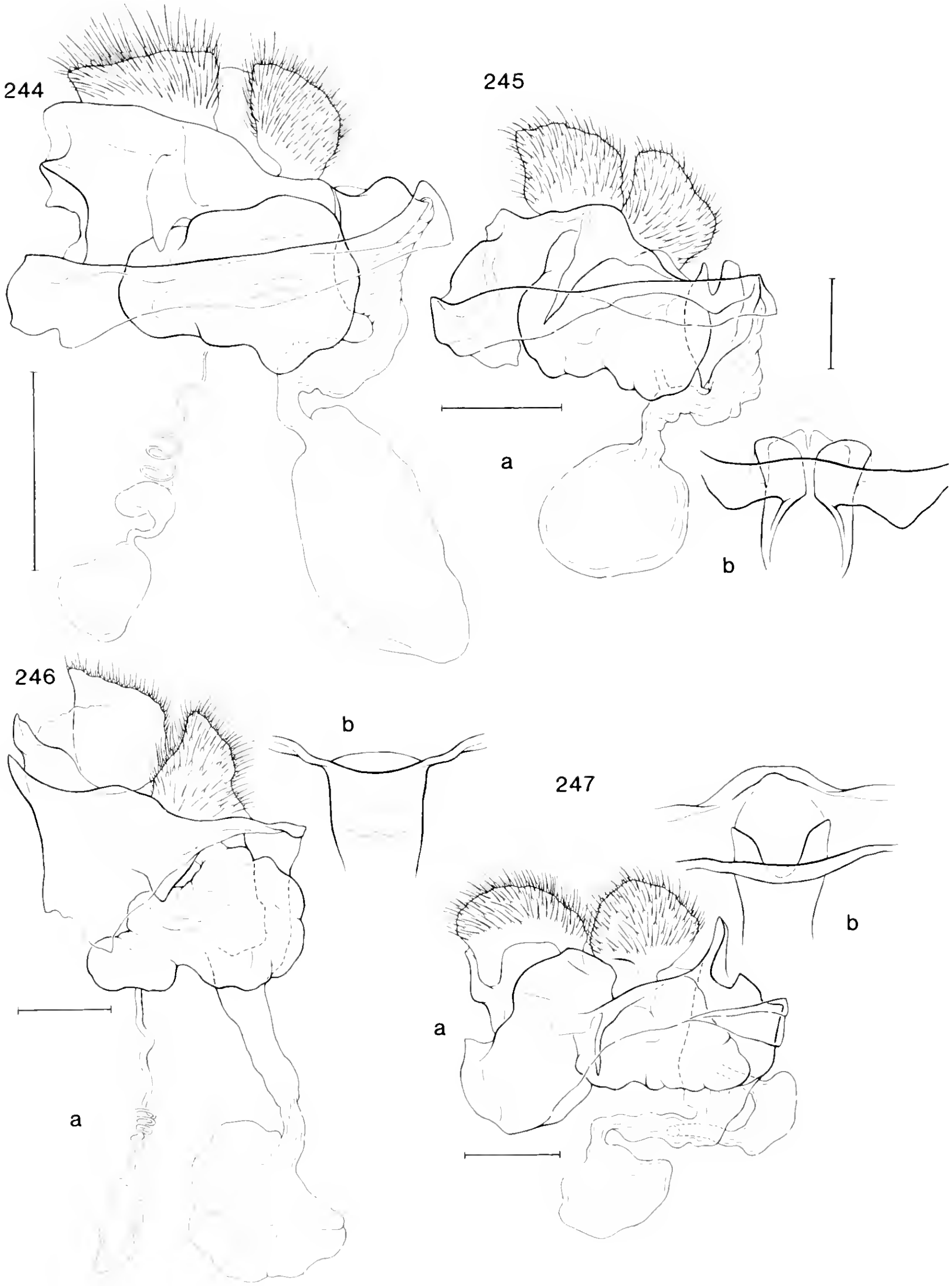
238



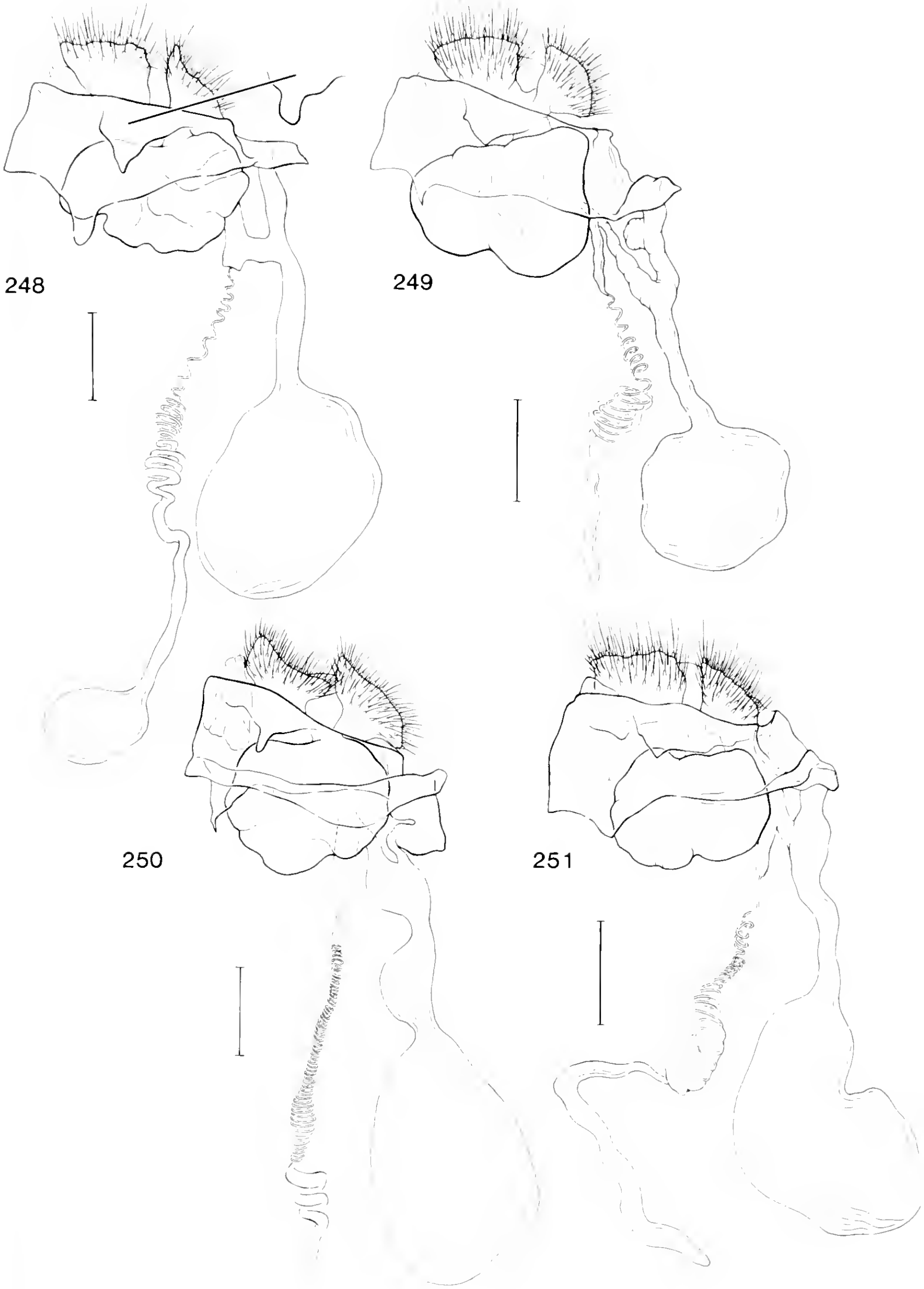
Figures 237, 238. Female genitalia of *Acraga*, lateral (a) and ventral (b) views. Figure 237. *Acraga coa*, lateral with glandulae sebaceae (USNM 28045), ventral (USNM 22528) (scale = 1 mm). Figure 238. *Acraga ferruginea*, lateral (IOC 86-5), ventral (IOC 86-5) (scale = 0.5 mm).

Figures 239, 240. Female genitalia of *Acraga*, lateral views (scale = 1 mm). Figure 239. *Acraga mariala*, holotype (USNM 28064). Figure 240. *Acraga meridensis* (USNM 28062).

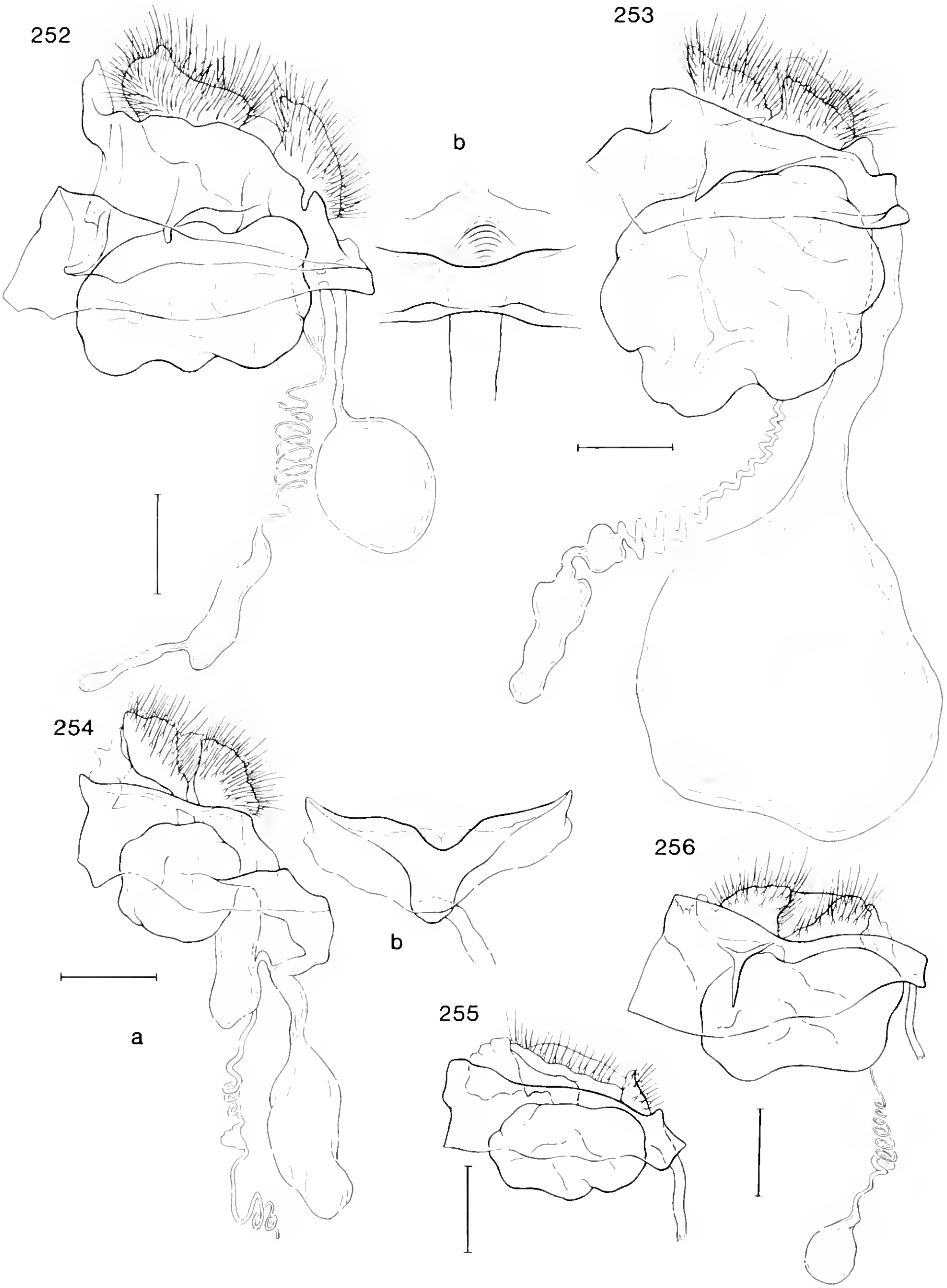
Figures 241–243. Female genitalia, lateral views. Figure 241. *Acraga melinda* (USNM 28051), with ventral view of sterigma (b) (scale = 1 mm). Figure 242. *Acraga citrinopsis* (USNM 28048) (scale = 1 mm). Figure 243. *Dalcerides alba* (USNM 28042) (scale = 0.5 mm).



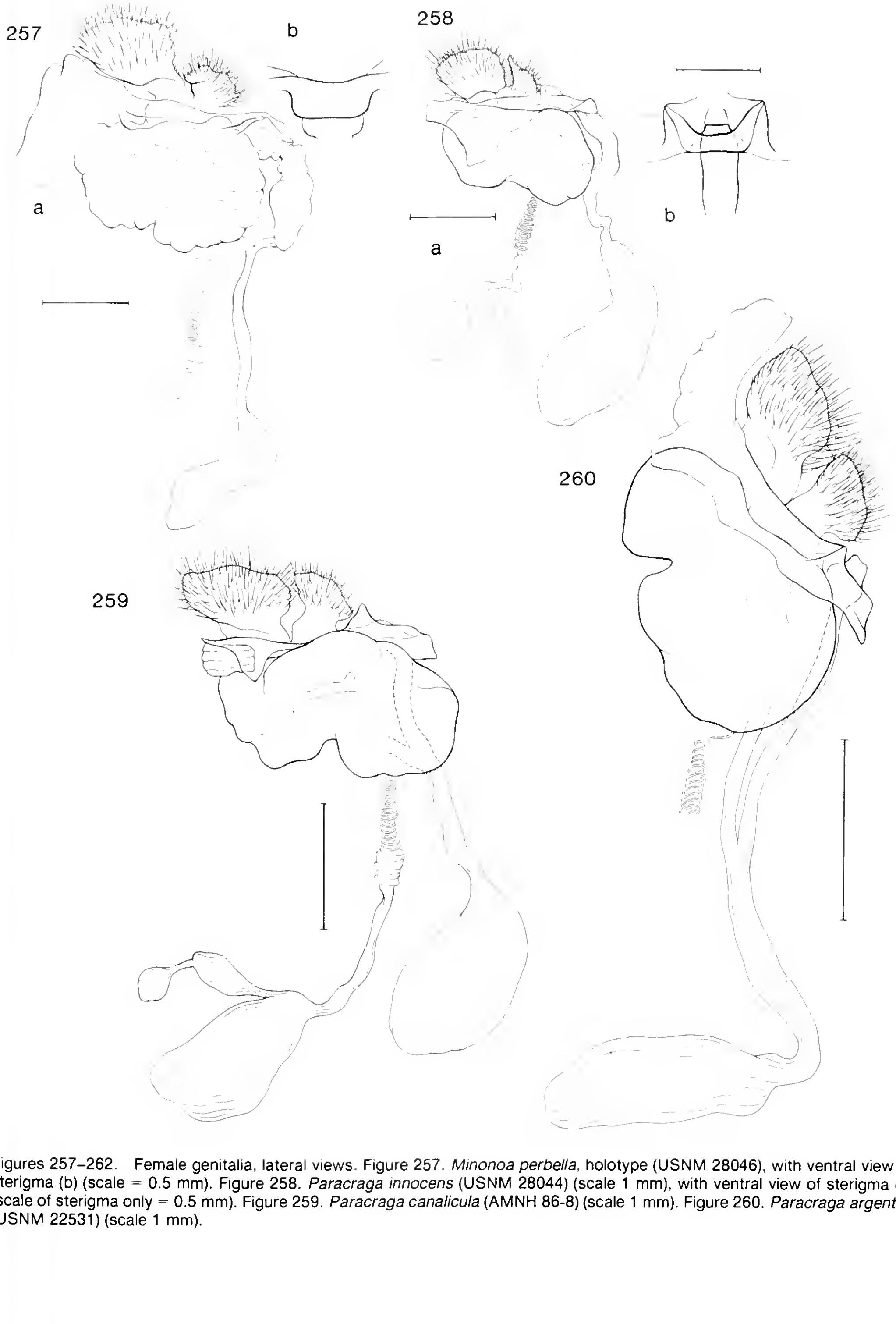
Figures 244–247. Female genitalia of *Acraga*, lateral views. Figure 244. *Acraga sexquicentenaria* (USNM 28054) (scale = 1 mm). Figure 245. *Acraga ochracea* (USNM 28047) (scale = 1 mm), with ventral view of sterigma (b) (scale for sterigma only = 0.5 mm). Figure 246. *Acraga citrina* (USNM 22484), with ventral view of sterigma (b) (scale = 0.5 mm). Figure 247. *Acraga leberna* (USNM 28052), with ventral view of sterigma (b) (scale = 1 mm).



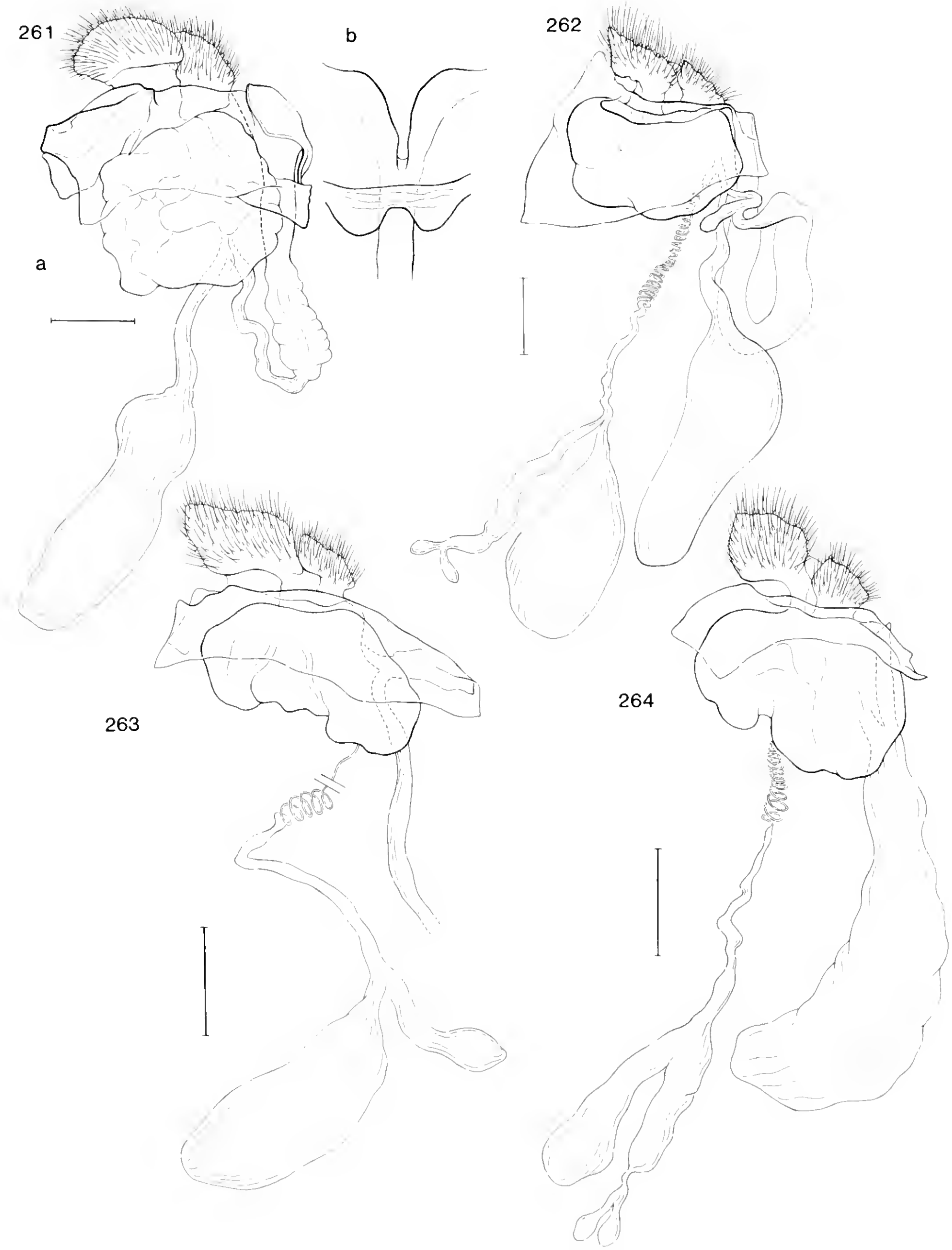
Figures 248–251. Female genitalia, lateral views (scale = 0.5 mm). Figure 248. *Dalcerides sofia* (USNM 28061), with inset of apophysis posteriores variation (USNM 28056, holotype of *D. phasma*). Figure 249. *Dalcerides flavetta* (USNM 28057). Figure 250. *Dalcerides mesoa* (USNM 28049). Figure 251. *Dalcerides radians* (USNM 28055).



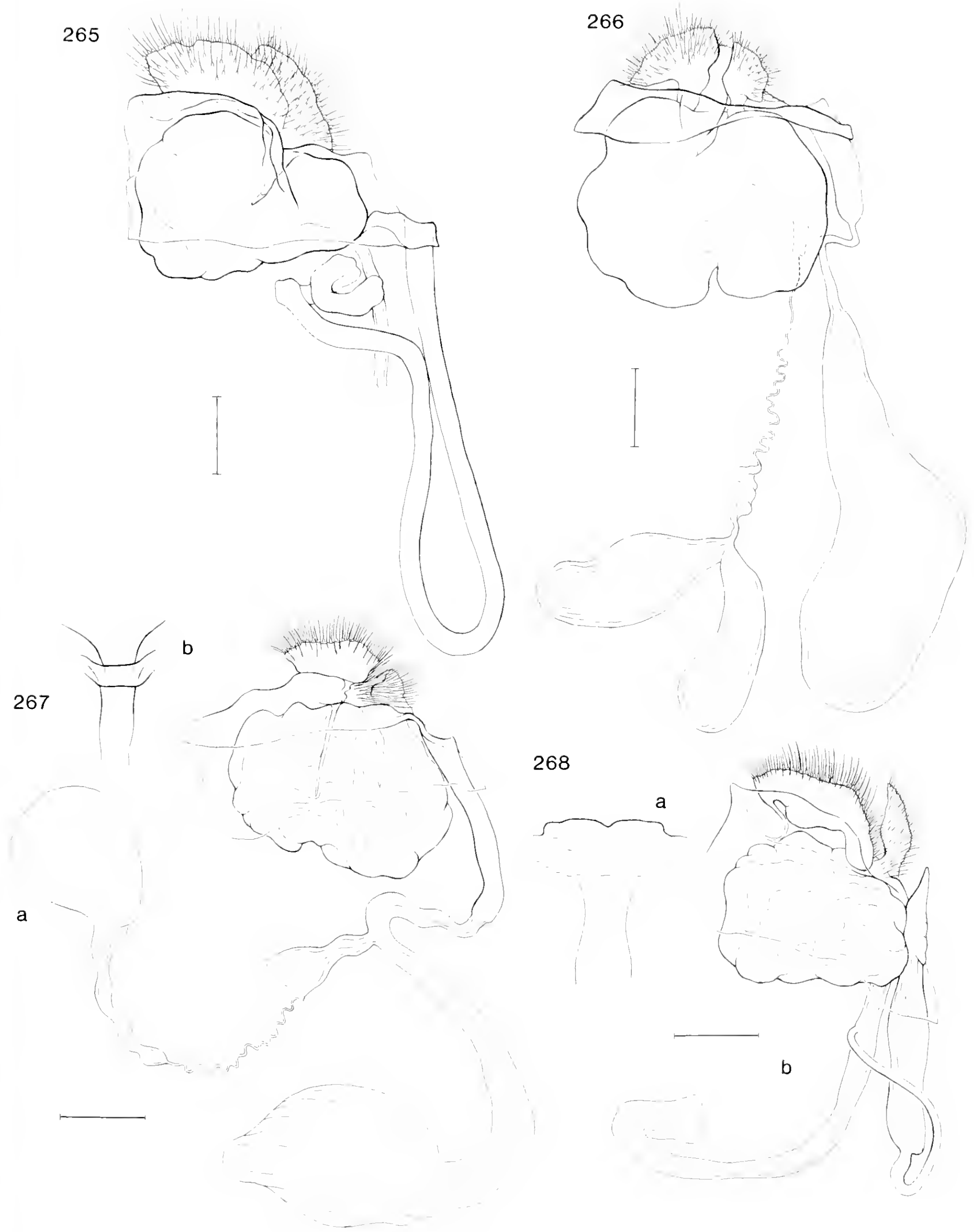
Figures 252–256. Female genitalia, lateral views (scale = 0.5 mm). Figure 252. *Dalcerides bicolor*, holotype (USNM 28066). Figure 253. *Dalcerides ingenita* (USNM 22505), with ventral view of sterigma (b). Figure 254. *Zikanyrops dubiosa*, holotype (ZMHB 3459), with ventral view of sterigma (b). Figure 255. *Minonoa pachitea*, holotype (ZSBS 86-9). Figure 256. *Minonoa elvira*, paralectotype (USNM 28067).



Figures 257–262. Female genitalia, lateral views. Figure 257. *Minonoa perbella*, holotype (USNM 28046), with ventral view of sterigma (b) (scale = 0.5 mm). Figure 258. *Paracraga innocens* (USNM 28044) (scale 1 mm), with ventral view of sterigma (b) (scale of sterigma only = 0.5 mm). Figure 259. *Paracraga canalicula* (AMNH 86-8) (scale 1 mm). Figure 260. *Paracraga argentea* (USNM 22531) (scale 1 mm).



Figures 261–264. Female genitalia, lateral views. Figure 261. *Dalcera abrasa* (USNM 22489), with ventral view of sterigma (b) (scale = 1 mm). Figure 262. *Minacragides*(?) new species B (USNM 28099) (scale = 0.5 mm). Figure 263. *Paracraga halophora* (BMNH 86-7), corpus bursae and section of duct of spermatheca missing (scale = 1 mm). Figure 264. *Paracraga necoda* (BMNH 86-6) (scale = 1 mm).



Figures 265–268. Female genitalia, lateral views (scale = 1 mm). Figure 265. *Minacraga itatiaia,* paratype (BMNH 86-1), corpus bursae missing. Figure 266. *Minacraga aenea* (ZSBS 86-4), reconstructed from flattened specimen. Figure 267. *Dalcerina tijucana* (USNM 22495), with ventral view of sterigma (b). Figure 268. *Minacraga disconitens* (USNM 22584), with ventral view of sterigma (b).

INDEX

Includes names of Lepidoptera only. Specific names are listed only by current genus. Foodplants are summarized in Table 1, and insect parasites and parasitoids are summarized in Table 2.

(US ISSN 0027-4100)

Bulletin OF THE Museum of Comparative Zoology

Volume 153

1992–1994

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS 02138 U.S.A.

DATE DUE

APR 1 2007