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A Review of the Cyphophthalmi of the United States and Mexico, with a Proposed Reclassification of the Suborder (Arachnida, Opiliones)

WILLIAM A. SHEAR[1]

ABSTRACT

The species of cyphophthalmid opilionids known from the United States and Mexico are surveyed. The genus *Neosiro* is considered a synonym of *Siro*; *Siro sonoma* is described as new. The male genitalia of *S. exilis*, *S. kamiakensis*, and *S. acaroides* are illustrated for the first time, and the male of *Neogovea mexasca* is newly described. A new scheme of family-level classification is proposed for the suborder worldwide. The family Sironidae Simon is redefined to include the genera *Siro, Parasiro, Tranteeva, Odonotosiro, Metasiro, Paramiopsalis,* and *Suzukielus*. *Troglosiro* is placed here provisionally. The new family Pettalidae is proposed for *Pettalus, Purcellia, Parapurcellia, Neopurcellia, Speleosiro, Rakaia,* and *Chileogovea*. the subfamily Stylocellinae Hansen and Sörensen is raised to family rank and redefined to include only the genus *Stylocellus*. For the genera *Ogovea* and *Huitaca*, the new family Ogoveidae is proposed, and for the genera *Neogovea, Paragovia,* and *Metagovea*, the new family Neogoveidae. The new arrangement is based upon a cladistic analysis. Arguments against Savory's 1977 proposal to consider the Cyphophthalmi an order of Arachnida separate from Opiliones are presented.

INTRODUCTION

Opilionids of the suborder Cyphophthalmi are mitelike creatures inhabiting caves, forest litter, and soil crevices. Their short legs and armored, egg-shaped bodies are far from the usual concept of "daddy-long-legs" or "harvestmen." Because of their restrictive habits, these animals are not likely to distribute themselves with ease and therefore could be of considerable importance in biogeography (Juberthie and Massoud, 1976).

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At first considered among the rarest of arachnids, the cyphophthalmids have been the subject, in the last two or three decades, of a virtual explosion of knowledge and interest, which, paradoxically, has not been fully incorporated into their classification. Further, no comprehensive review of the group in America has been carried out.

The first cyphophthalmid opilionid known from the United States, *Siro acaroides* (Ewing) of Oregon, was described in 1923. During the next 20 years, only two new species were described: *Siro americanus* Davis from Florida (Davis, 1933) and *Neosiro kamiakensis* Newell from Washington (Newell, 1943). Only the work of Newell, including a redescription of *acaroides* published in 1947, can be said to meet modern standards for taxonomic work. By far the most valuable contribution on the suborder in America was that of Hoffman (1963), who described *Siro exilis* from the central Appalachian region, critically reviewed previous work, and set up a new genus, *Floridogovea,* for *S. americanus*. He also drew attention to the usefulness in classification of the sternal region of the cephalothorax, particularly the relationships of the coxal elements to the gonostome. Hoffman did not examine the male genitalia of any of the American species, although it had been known for some time that the form of the penis is of great importance in taxonomy. He was also evidently unaware of a paper by Juberthie (1960) redescribing *S. americanus* in detail, and giving it the new generic name *Metasiro*. Juberthie provided the first illustrations of the male genitalia of an American species. Finally, Shear (1977) described, from female specimens, the first troglobitic cyphophthalmid from the New World, *Neogovea mexasca,* collected in a cave in Oaxaca, Mexico.

The purpose of the first part of this paper is to review briefly our knowledge of a biogeographically important group of soil animals in North America, providing comprehensive data on distribution and illustrating taxonomic features not heretofore described. In addition, a remarkable new species from California has been discovered. During the course of this investigation and others on cyphophthalmids (Shear, 1977, 1979a, 1979b) it has become obvious that the present scheme of classification, especially at the level of the family, no longer reflects all that we have learned about the group. In particular, as Hoffman (1963) accurately predicted, the grouping of all forms into one family Sironidae, with two subfamilies Sironinae and Stylocellinae, is quite inadequate to represent the knowledge that has accumulated concerning the probable evolutionary relationships of the described genera and species. Therefore, the purpose of the second part of this paper is to propose a new family-level classification for the suborder Cyphophthalmi. In addition, the recent proposal of Savory (1977) that the suborder be raised to full ordinal status will be critically examined.

ACKNOWLEDGMENTS

I am grateful to Dr. Norman Platnick of the American Museum of Natural History for the loan of specimens and for his comments on the manuscript. Specimens were also lent by Dr. H. W. Levi, Museum of Comparative Zoology, Mr. Henry Dybas, Field Museum of Natural History, Dr. Paul Arnaud, California Academy of Sciences, Mr. Rod Crawford, University of Washington (Seattle) Museum, Dr. S. Tuxen, Universitets Museum, København, and Mr. F. Wanless, British Museum (Natural History). Dr. William B. Muchmore lent material from his personal collection, as did Dr. Richard L. Hoffman.

Knowledge of the distribution of *Siro acaroides* comes largely from a sampling program carried out by Dr. Ellen Benedict, Portland State University, Portland, Oregon. She generously allowed me to sort opilionids from her material.

Drs. Jochen Martens, Ray Foster, and Jurgen Gruber read the second section of the manuscript and made valuable comments, but the ideas expressed there are the full responsibility of the author. I am also most grateful to Mr. Theodore Savory for his correspondence.

Finally, I thank the Faculty Research

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ABBREVIATIONS

AMNH, American Museum of Natural History, New York
MCZ, Museum of Comparative Zoology, Harvard University, Cambridge
FMNH, Field Museum of Natural History, Chicago
CAS, California Academy of Sciences, San Francisco
UWM, University of Washington Museum, Seattle
WBM, personal collection of William B. Muchmore, Rochester
WAS, personal collection of William A. Shear, Hampden-Sydney

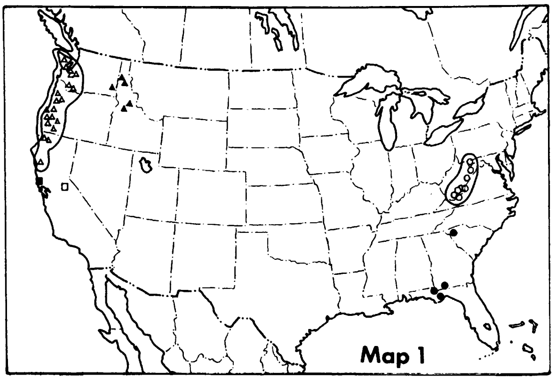
THE NORTH AMERICAN CYPHOPHTHALMID FAUNA

Hoffman (1963), Juberthie (1970) and Shear (1977) have discussed in some detail the usefulness of various taxonomic characters in the study of the Cyphophthalmi. To summarize, the characters most useful at the level of species seem to be the form and location of the adenostyle of the male, the shape and spination of the penis, the relationships of the elements of the ventral thoracic complex to the gonostome, and the proportions of the bodies of both sexes. These characters, if concepts are appropriately broadened, remain useful for distinguishing related groups of species as genera, but to these we must add the degree of fusion of the coxae to one another and to the dorsum, the presence or absence of teeth on the claws, modifications of the male anal region, the position of the ozophores, and the dentition of the cheliceral fingers.

FAMILY SIRONIDAE SIMON

SIRO LATRIELLE

Siro Latrielle, 1804, p. 329 (type species, *S. rubens* Latrielle, by original designation). Hansen and Sörensen, 1904, p. 88, p. 107. Roewer, 1923, p. 52; 1927, p. 266. Hinton, 1938, p. 331. Rosas Costa, 1950, p. 145 (complete references to 1948). Hoffman, 1963, p. 132. Juberthie, 1969, p. 1383. Martens, 1978, p. 60.



MAP 1. Distribution of cyphophthalmid opilionids in the United States. Open circle enclosed in solid line, *Siro exilis*. Filled circles, *Metasiro americanus*. Open triangles enclosed in solid line, *Siro acaroides*. Filled triangles, *Siro kamiakensis*. Filled square, *Siro sonoma*. Open square, single female specimen of undescribed probable new species.

Cyphophthalmus Joseph, 1868, p. 249 (type species, *C. duricorius*, Joseph by original designation). Rosas Costa, 1950, p. 145 (complete references).

Holosiro Ewing, 1923, p. 388 (type species, *H. acaroides* Ewing, by original designation). Roewer, 1927, p. 266. Hinton, 1938, p. 332.

Neosiro Newell, 1943, p. 416 (type species, *N. kamiakensis* Newell, by original designation). Rosas Costa, 1950, p. 142. Hoffman, 1963, p. 133. Juberthie 1969, p. 1383. New Subjective Synonymy.

DIAGNOSIS: *Metasiro* is the only other sironid genus found in North America; the males of its single species have a fimbriate adenostyle rim giving the appearance of a tuft of setae; in *Siro* species the adenostyle is lamelliform.

DESCRIPTION: See Juberthie (1967, 1969). The former reference is to a detailed redescription of *S. rubens*, the type species.

DISTRIBUTION: Europe; Appalachians in eastern North America, the Pacific coast from Washington to northern California; western Washington and adjoining regions of northern Idaho.

NOTES: Species of *Siro* are united by the form of the adenostyle, ventral complex, and penis, as well as some additional characters discussed by Juberthie (1969). *Neosiro* was set up by Newell (1943) largely because his new species, *kamiakensis,* had the fourth tarsus divided in males. I am not of the opinion that this difference justifies a separate genus, given that *Neosiro kamiakensis* fits in *Siro* in every other respect. In addition, as shown below, the fourth tarsus of male *S. acaroides* specimens is moderately to strongly constricted distal to the adenostyle, and the new species *S. sonoma* has the same segment strangely modified, suggesting a tendency in western North American members of the genus to strong modifications (and division) of the fourth tarsus.

EVOLUTIONARY RELATIONSHIPS: The American species of *Siro* are clearly related to the European species, and resemble them more or less closely in all respects. In particular, the male genitalia are of the same general type as regards setation pattern and the presence of two "movable fingers" near the genital opening. However, in the penis of *S. kamiakensis* (fig. 7), these are reduced. The adenostyles of all species are acuminate-lamelliform. With respect to modifications of the fourth tarsus in males, the American species show a tendency toward stronger, more unusual modifications, as seen in *S. sonoma* (fig. 16) and in *S. kamiakensis,* where the tarsus is actually divided just distal to the adenostyle.

Juberthie (1967) has pointed out the presence of anal glands in males of European species of *Siro*. These are generally coupled with some slight modifications of the anal plate, corona analis, and tergite 8 (see Martens, 1978, for illustrations of the variation of this character in *Siro rubens*). In some poorly sclerotized specimens of each of the American species, it is possible to make out one to three small pores in the cuticle of tergite 8. Dissection reveals a group of three cylindrical glands just under the dorsal cuticle, with ducts leading to these pores. The anal regions of each of the American species show slight modifications. In *exilis,* tergite 8 has a small, subtriangular median eminence, visible only in ventral view (fig. 3), in *S. kamiakensis* and *S. sonoma,* the anal plate has a median ridge (figs. 6, 11), and in *S. acaroides,* tergite 8 is broadly and shallowly excavate (fig. 18). It is also of interest to note that in females of the western species a trend exists, most strongly expressed in *sonoma* and *acaroides,* for the part of the abdominal sternite forming the posterior lip of the gonopore to be set off by a depressed line, almost suggesting a suture. This is not a characteristic of the European species, but I have also observed it in the South American ogoveid *Huitaca ventralis* Shear (Shear, 1979a).

Siro kamiakensis is something of a discordant element. The fourth tarsus is divided in the male, and the penis has some distinctive features, including different ventral setation and the reduction of the movable fingers. However, in several important characters it closely resembles *S. acaroides* and *S. sonoma,* and the form of the penis is no more divergent from the other American species than is already seen in the European species of *Siro*; compare Martens's (1978) illustrations of *S. rubens* and *S. carpathicus*. Also, a study of other groups in which the fourth male tarsus is divided suggests that this is (despite our possible prejudice) a fairly superficial modification and not indicative of great phyletic distance. Its functional significance is not known; evidently the distal segment is not movable with respect to the basal. The other leg tarsi are not divided in either males or females of any known cyphophthalmid.

Not surprisingly, the western species evidently are each other's closest relatives, with *sonoma* and *kamiakensis* diverging from *acaroides,* but in different ways. *Siro exilis* seems to have more in common, especially as regards the male genitalia and secondary sexual characters, with European forms such as *S. rubens*. This in turn suggests that the original divergence took place between the western species and *S. exilis* plus the European forms. The movement of North America away from Europe and Africa, which resulted in the opening of the present Atlantic Ocean, may account for the separation of *S. exilis* from its European relatives. The earlier event is problematic. A great seaway separated the eastern and western part of North America about 95 million years ago. We would have to postulate quite slow rates of evolution in order to infer that this seaway was responsible for the separation of the western American group of *Siro* from the Appalachian-European group. But it is worth pointing out that some arachinid orders still extant (Solpugida, Ricinulei, Amblypygi, Uropygi, Scorpionida) are present in Paleozoic North American sediments at least that old, represented by forms which, given imperfect preservation, are not very different from living ones (Petrunkevitch, 1913). There is thus a precedent for hypothesizing such slow evolutionary rates.

There is a clear connection in some elements of the opilionid fauna of the Pacific Coast of North America with that of Japan and temperate East Asia (Suzuki, 1972; Ljovuschkin, 1971). The only cyphophthalmid known from Japan is *Suzukielus sauteri* (Roewer). I examined the type specimens of this species and found it to be only distantly related to *Siro,* having a greater affinity with *Paramiopsalis ramulosus* Juberthie. No cyphophthalmids have been discovered as yet in northern China and western Siberia, but it is very likely they exist.

KEY TO MALES OF AMERICAN SPECIES

1. Tarsus 4 of males divided distal to adenostyle; Washington, Idaho .. *kamiakensis* (Newell)
   Tarsus 4 of males not divided 2
2. Male tarsus 4 modified as in figure 16, with ventral spur and excavated region; San Francisco Bay region .... *sonoma,* new species
   Male tarsus 4 not strongly modified, more or less cylindrical or somewhat constricted distal to the adenostyle 3
3. Tergite 8 of male evenly and shallowly excavate (fig. 18); Northern California, Oregon and Washington .... *acaroides* (Ewing)
   Tergite 8 of male with a small median knob (fig. 3); Virginia, West Virginia, Maryland .... *exilis* Hoffman

Siro exilis Hoffman

Figures 1–3, Map 1

Siro exilis Hoffman, 1963, p. 132, figs. 1–13.

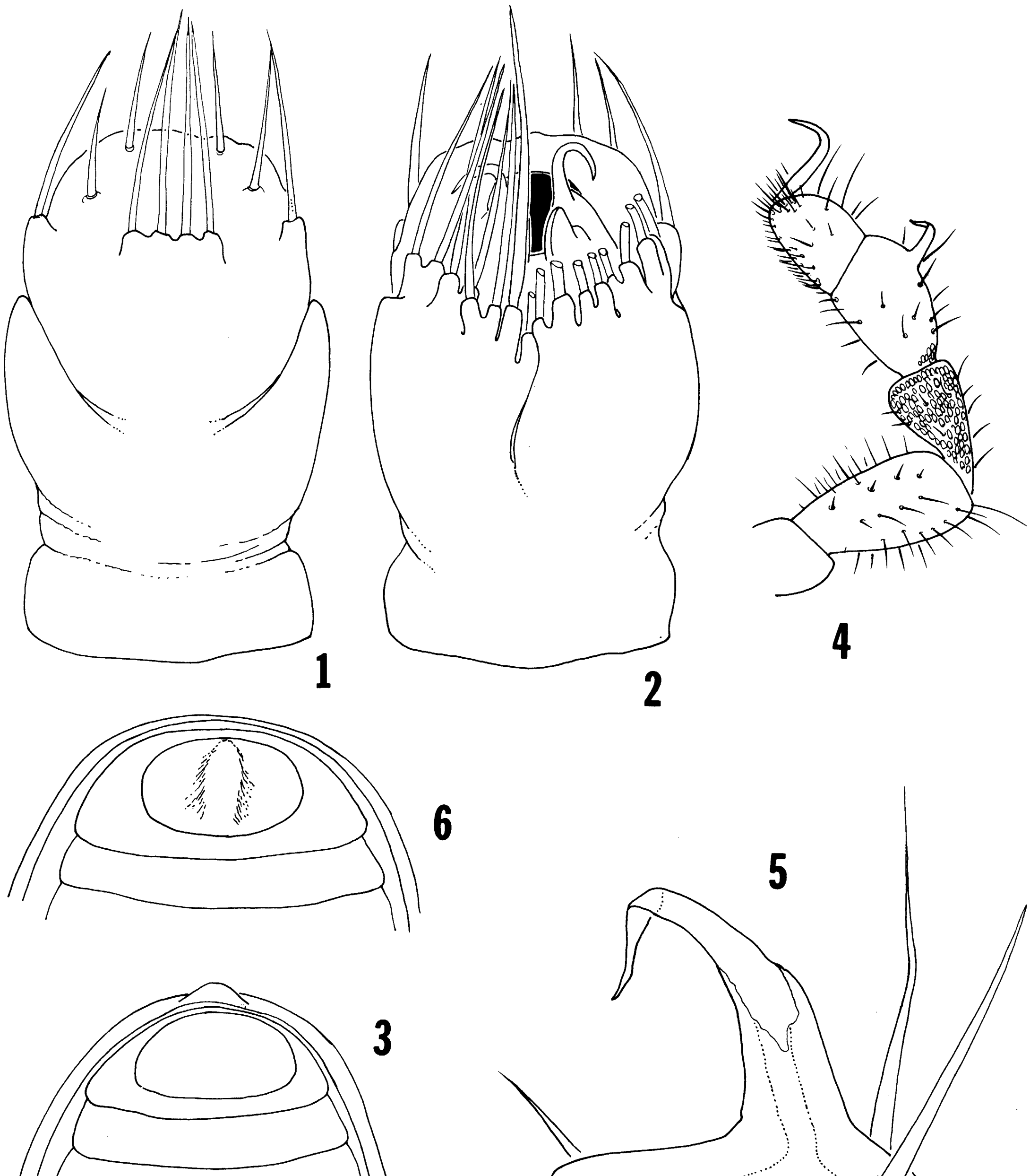
TYPES: Male holotype and male and female paratypes (Senckenberg Museum, Frankfurt) from Blacksburg, Montgomery Co., Virginia, collected November 3, 1961, by P. Holt and J. Lawson. Paratypes (which I examined) are also in USNM and AMNH.

DIAGNOSIS: There are no other cyphophthalmids in the range of this species; it may be separated from the western species of *Siro* by the characters given in the key.

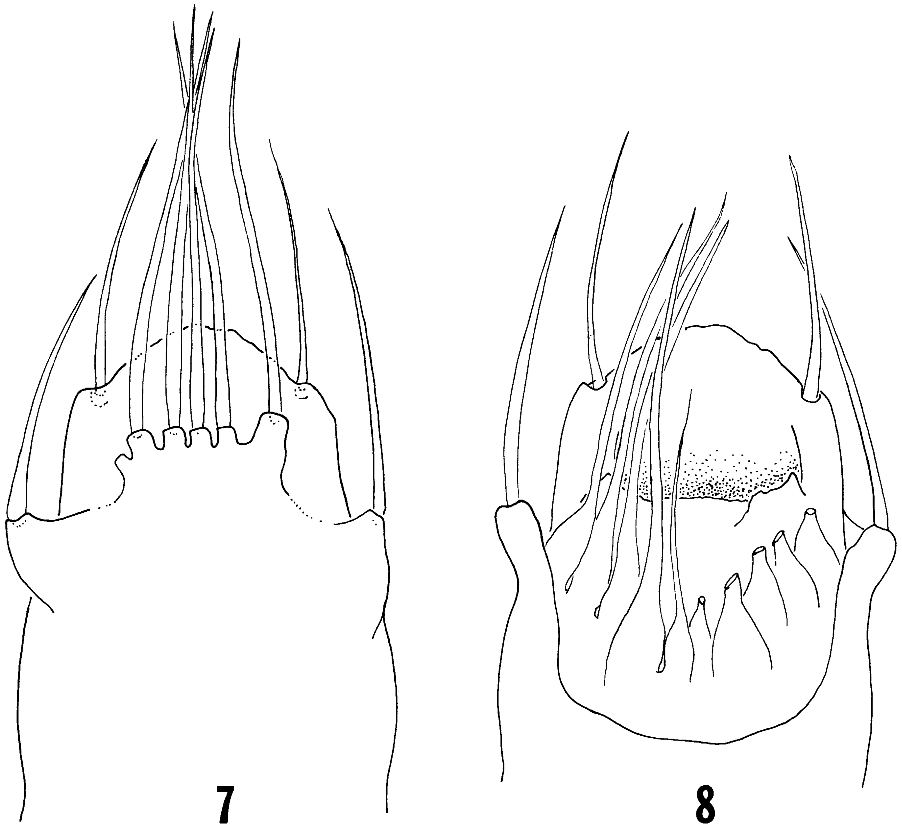
DESCRIPTION: See Hoffman (1963). Hoffman omitted to describe the penis of the male, which I illustrate here (figs. 1, 2); it is typical of *Siro* species. He also missed the sexually dimorphic features of tergite 8 (♂, fig. 3).

DISTRIBUTION: (Map 2) MARYLAND: *Garrett Co.,* Swallow Falls State Forest, W. B. Muchmore, June 30, 1968, ♀ (WBM). VIRGINIA: *Giles Co.,* outside Tawney's Cave, W. B. Muchmore, July 7, 1970, 2 ♂♂ (WBM). WEST VIRGINIA: *Pendleton Co.,* 5 mi. S of Witmer, 3000 ft. elev., S. B. Peck, July 8, 1971, 16 ♂♂ 13 ♀♀ (WAS); Spruce Knob, 3500 ft. elev., June 8, 1967, S. B. Peck and A. Fiske, ♀ (WAS). *Randolph Co.,* Bickle Knob, E of Elkins, 3800 ft. elev., S. B. Peck, June 19, 1968, juveniles (WAS, FMNH). *Mercer Co.,* Athens, W. Shear, July 5, 1967, ♀♀ (WAS); 0.75 mi. NE of Athens on Laurel Creek, December 8, 1967, ♀, juvs. (WAS). *Summers Co.,* Crump's Bottom, 10 mi. NE of Princeton, W. Shear, May 26, 1971, 8 ♂♂, 10 ♀♀ (WAS). *Tucker Co.,* Backbone Mountain, W. B. Muchmore, June 30, 1968, 7 ♂♂, 7 ♀♀ (WBM).

NOTES: This species is restricted to the montane district along the border of Virginia and West Virginia. Label notes and my personal collecting indicate that it is most likely to be found in litter from deciduous trees along stream banks or in other damp places. Hoffman (*in litt.*) noted an association with loose, stony debris beneath the litter, but my own experience suggests this is not a requirement. However, it does seem likely that the animals need a perpetually damp retreat into which they may move during dry periods. Adults have been collected at nearly every season. The Peck collection from Randolph Co., West Virginia, contained nearly 50 juveniles in several stages of development;



FIGS. 1–6. Anatomy of cyphophthalmids. 1, 2. Penis of *Siro exilis*. 1. Ventral view. 2. Dorsal view. 3. Anal region of male *S. exilis*, ventral view. 4–6. *S. kamiakensis*. 4. Leg 4 of male, lateral view. 5. Adenostyle, lateral view. 6. Anal region of male, ventral view.



FIGS. 7, 8. Penis of *Siro kamiakensis*. 7. Ventral view. 8. Dorsal view.

four more or less distinct instars could be detected.

Siro kamiakensis (Newell)

Figures 4–8, Map 1

Neosiro kamiakensis Newell, 1943, p. 416, figs. 1–12; 1947, p. 362. Rosas Costa, 1950, p. 142. Hoffman, 1963, p. 136.

TYPES: Series of males and females from Kamiak Butte, 9 mi. N of Pullman, Whitman Co., Washington, originally in Newell's personal collection, present whereabouts unknown. Newell provided no specific holotype designation in his original description.

DIAGNOSIS: *Siro kamiakensis* is the only American sironid in which the fourth tarsus of the males is divided.

DESCRIPTION: See Newell (1943). The specimens I examined agreed well with Newell's description of the types, except as noted below. Newell failed to illustrate or describe the penis, which I show here in figures 7 and 8. It is somewhat divergent in form from the other American species of *Siro,* but still well within the range of variation recognized in the genus. The apical setae of the ventral plate are reduced in number, and the movable fingers are shortened to small nubs.

The Idaho specimens were first thought to be a new species, because of their larger size (1.7 mm. long, 0.9 mm. wide) compared to the material described by Newell (1.29–1.43 mm. long, 0.73–0.76 mm. wide) and because the adenostyles of the males were shorter (fig. 5). However, an examination of other specimens, from the Mt. Spokane area of Washington, has convinced me that this is simply an expression of geographic variation.

DISTRIBUTION: (Map 1) WASHINGTON: *Spokane Co.*, base of Mt. Spokane, H. Dybas, June 22, 1957, 4 ♂♂, 4 ♀♀, juvs. (FMNH), Bald Knob of Mt. Spokane, 4500 ft. elev., same data, ♂. IDAHO: *Idaho Co.*, Clearwater National Forest, Apgar Campground, T. Briggs, July 12, 1967, ♂, ♀ (CAS); 17.7 mi. from Lolo Pass on Rt. 12, T. Briggs, K. Hom, A. Jung, ♂, ♀ (CAS). *Kootenai Co.*, Harrison Creek, east side of Hayden Lake, F. Raney, July 25, 1959, 3 ♂♂, ♀ (AMNH).

NOTES: This species seems to favor a habitat dominated by coniferous trees, primarily fir, pine, and cedar. At Mt. Spokane, specimens were taken in Berlese samples of duff and litter; the material from Idaho Co., Idaho, came from under surfaces of rotted logs. Newell's specimens were from beneath the bark of a decaying stump.

Siro sonoma, new species

Figures 9–17, Map 1

TYPES: Male holotype and female paratype from Jenner, Sonoma Co., California, collected April 11, 1969 by Thomas Briggs, deposited in the collection of the California Academy of Sciences. Further female paratypes from Jenner collected on various dates (1967–1969) are also in the California Academy of Sciences. An additional female paratype from the same locality, collected March 12, 1967, is deposited in the American Museum of Natural History.

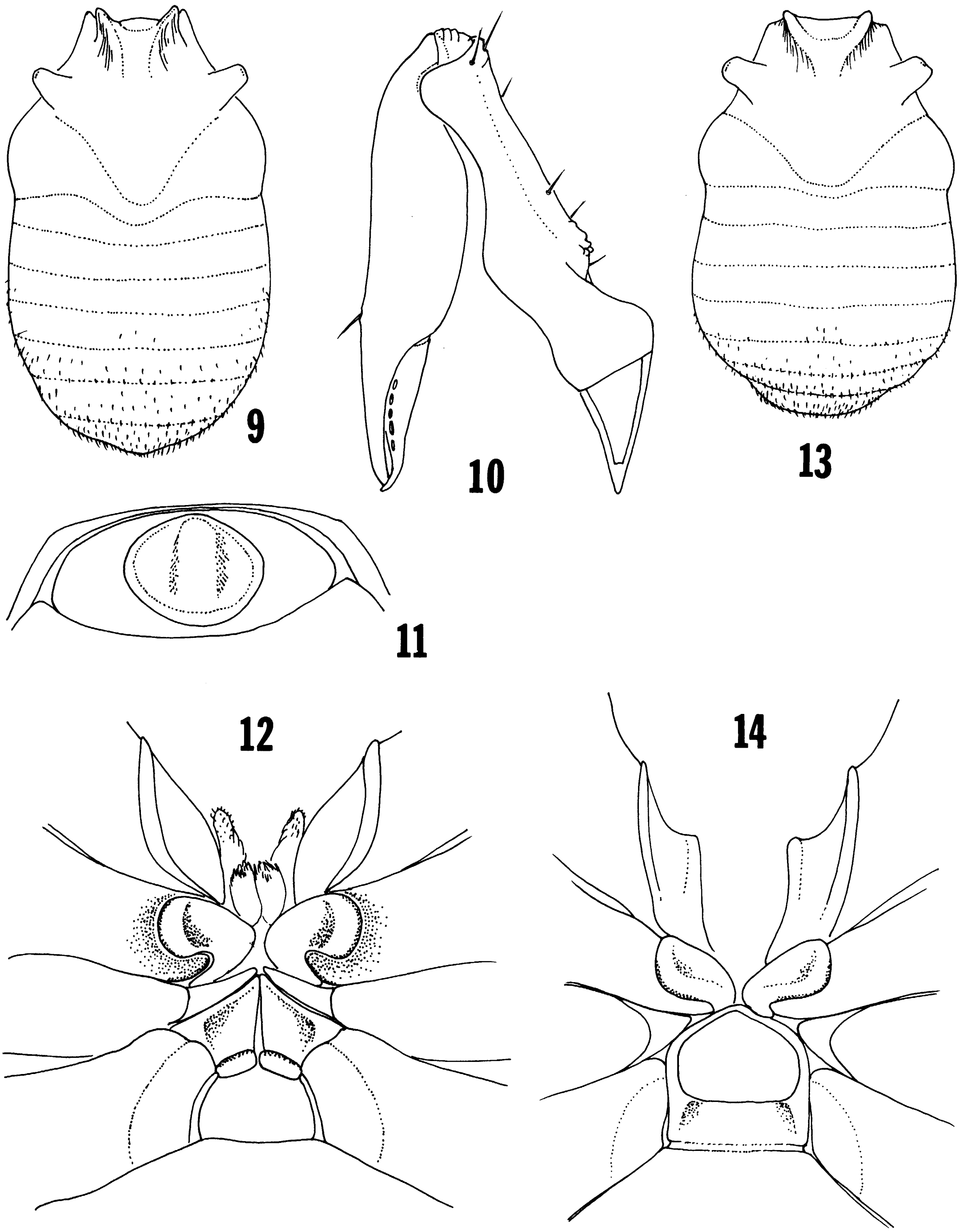
ETYMOLOGY: The species name is a noun in apposition referring to the type locality.

DIAGNOSIS: The peculiar modification of the fourth tarsus of the male is not matched by any other known *Siro* species; the dull black color is also diagnostic.

MALE: Total length, 1.16 mm., width across tips of ozophores 0.76 mm., greatest width 0.95 (measured at abdominal segment 3), L/W = 1.22. Dorsum as in figure 9, cuticle coarsely pebbled, setation sparse except on posterior abdominal segments; ozophore openings terminal, small, not valvulate. Ventral thoracic complex (fig. 12): endites of coxae I long, narrow, unusually prominent, smooth and shining. Mesosterna arcuate, larger anterior lobe strongly raised, heavily rimmed. Metasterna small, elongate-triangular. Posterior wall of gonostome formed by lobes of coxae IV, these lobes medially excavate, strongly produced into toothlike projections at gonostome lip. Lateral walls of gonostome formed by coxae IV, posterior wall by abdominal sternite I. Spiracular grooves indistinct, spiracle as usual for genus. Chelicerae (fig. 10) of typical form; basal article 0.77 mm. long, 0.17 mm. wide; distal article 0.69 mm. long, 0.14 mm. wide, movable finger 0.26 mm. long. Pedipalps typical, trochanter lacks ventral processes. Leg formula 1423. Claws not toothed. Tarsus 4 strongly modified (figs. 15, 16); in ectal view with a dorsal swelling just proximal to midlength and with more acute ventral process; mesally, an excavated region extends along side of ventral process. Adenostyle (fig. 17) with base partly concealed by dorsal swelling of tarsus, pore opening laterally about one-third of length from base; distal to pore, adenostyle suddenly attenuate, slightly sinuous, acute. Three anal gland pores clearly present, but tergite VIII not modified. Anal plate with distinct median ridge (fig. 11). Color dull black, legs slightly lighter, claws amber.

FEMALE: Total length, 1.10 mm., width across ozophores 0.55 mm. Greatest width (abdominal segment III) 0.84, L/W = 1.3. Dorsum as in figure 13. Ventral thoracic complex (fig. 14) similar to that of male, but gonostome larger, as usual. Margination of gonostome obscure, posterior margin probably formed by abdominal sternite I, but this portion very clearly set off by an impressed line. Chelicerae stouter than in male, basal article 0.64 mm. long, 0.15 mm. wide; distal article 0.68 mm. long, 0.12 mm. wide; movable finger 0.26 mm. long. Other nonsexual characters as in male. Ovipositor typical. Color dull black.

DISTRIBUTION: Known only from the type



FIGS. 9–14. *Siro sonoma*. 9. Dorsal view of male. 10. Male chelicera, mesal view. 11. Male anal region, ventral view. 12. Male ventral thoracic complex, ventral view. 13. Female, dorsal view. 14. Female ventral thoracic complex, ventral view.

locality (map 1). An immature specimen from 0.6 mi W of Soda Rock Lane from Alexander Valley Road, near Lytton, *Sonoma Co.,* California, was collected by T. Briggs on 25 February 1968. This specimen (CAS) is probably *S. sonoma.*

NOTES: Unfortunately, I am unable to illustrate or describe the penis of *S. sonoma* because I lost it during the dissection of single available male. I assume with confidence that it will prove to be typical of *Siro* species. The left fourth tarsus of the male (fig. 15) shows a faint, suture-like line just distal to the adenostyle which is not visible on the right tarsus. This may be an incipient division, illustrating further affinity between this species and *S. kamiakensis.*

A number of opilionid and diplopod families and genera (see Shear, 1975) illustrate the distributional pattern of isolated species or populations in the San Francisco Bay region, after having dropped out (as one goes south) in the area of the California/Oregon border. Sometimes this pattern also includes in isolate in the Sierra Nevada (Coyle, 1968; Shear, 1976), and a tantalizing female specimen in the collection of the California Academy of Sciences comes from this area (map 1; Calaveras Co., South Grove, Calaveras Big Tree, coll. B. J. Adelson, June 13, 1956). Clearly not *S. sonoma,* this specimen has quite a different ventral thoracic complex, is brown instead of black, more densely setose, and entirely different in body proportions (L/W = 2.06). It more closely resembles *S. acaroides,* but that species has a typical L/W ratio of 1.7. While I think that it is a separate species, it seems best not to describe it until males become available.

Siro acaroides (Ewing)

Figures 18–20, Map 1

Holosiro acaroides Ewing, 1923, p. 388, fig. 1, Pl. 39.

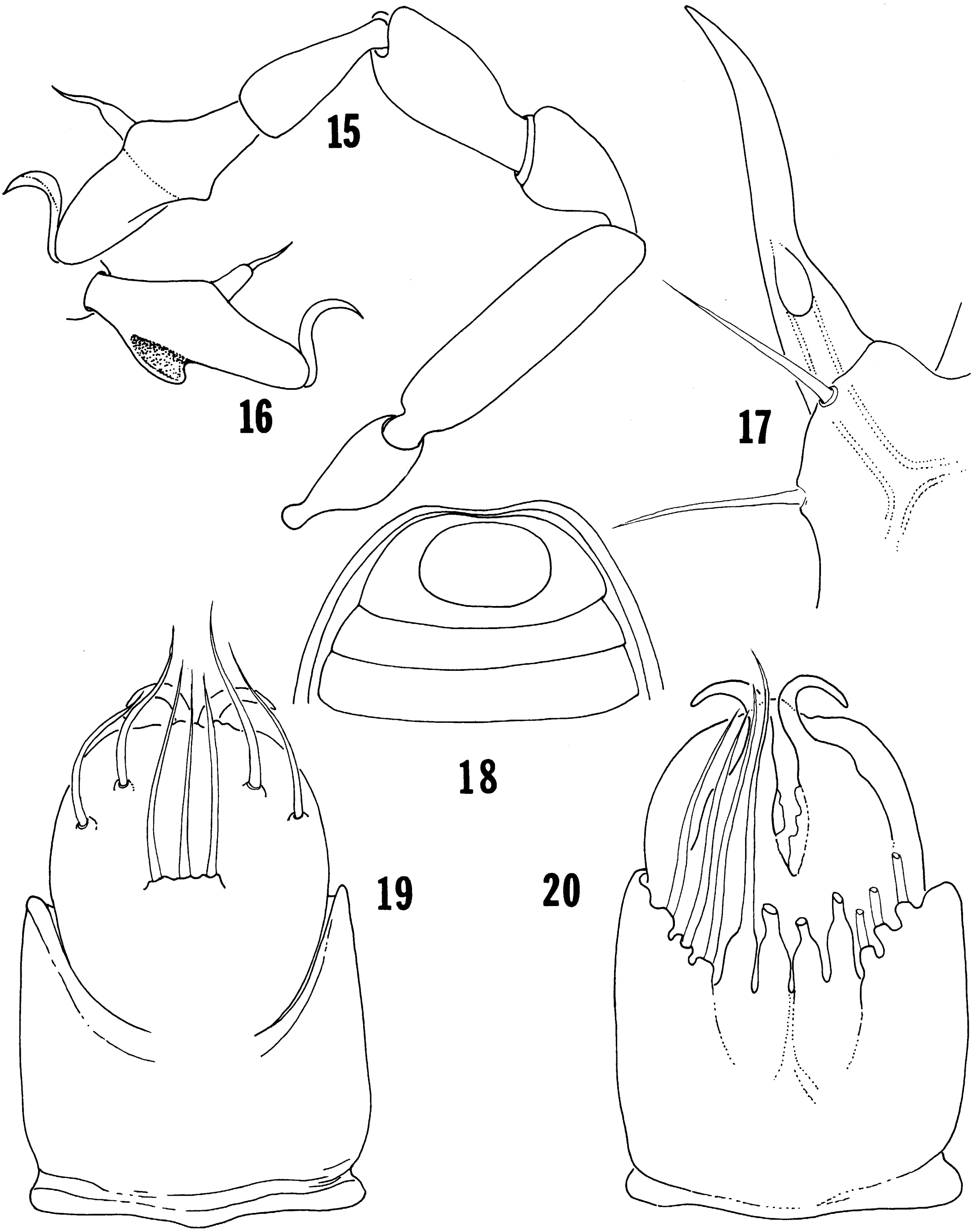
Siro acaroides: Newell, 1947, p. 354, figs. 1–31. Hoffman, 1963, p. 136, fig. 14.

TYPES: Female holotype from "foothills of Coast Range Mountains, Benton County, Oregon," present whereabouts unknown.

DIAGNOSIS: The adenostyle is longer and more sharply curved than in *S. exilis,* and the modifications of tergite 8 are different (fig. 18); the strong modifications of the fourth tarsi of the males separates *S. kamiakensis* and *S. sonoma* from this species.

DESCRIPTION: Newell (1947) has provided an excellent description of both sexes, to which I can add only illustrations of the penis (figs. 19, 20). It is typical of species of *Siro,* but with somewhat reduced ventral setation and extraordinarily large movable fingers.

DISTRIBUTION: (Map 1) CALIFORNIA: *Del Norte Co.,* Ft. Dick, December 2, 1966, C. W. O'Brien, ♂, 2 ♀♀ (CAS); near Ft. Dick, May 21, 1957, H. Dybas, juvs. (FMNH); Redwood State Park, June 25, 1966, V. Lee, 2 ♀♀ (CAS). OREGON: *Curry Co.,* 13 mi. E of Gold Beach, 600 ft. elev., March 10, 1972, E. Benedict, 5 ♂♂, ♀ (WAS); 5 mi. N of Brookings, October 1, 1959, V. Roth, 2 ♂♂, ♀ (AMNH); 13 mi. N, 5 mi. W of Brookings, 200 ft. elev., February 12, 1972, E. Benedict, 3 ♂♂, ♀ (WAS); 28 mi. E of Gold Beach on Snout Creek, March 10, 1972, E. Benedict, juv. (WAS); Loeb State Park, 7 mi. E of Brookings, May 22, 1957, H. Dybas, juvs. (FMNH); Pistol River, May 23, 1957, H. Dybas, 8 ♂♂, 3 ♀♀ (FMNH); 4.5 mi. S of Gold Beach, January 29, 1957, T. Briggs, ♂, ♀ (CAS); east end of Wedder Burn, January 29, 1957, T. Briggs, ♀ (CAS). *Coos Co.,* 10 mi. E and 1 mi. S, 9 mi. E and 5 mi. S, 6 mi. E and 2 mi. S, 10 mi. E and 2 mi. S, 8 mi. E and 2 mi. S, 14 mi. E and 2 mi. S of Allegany, Weyerhauser Millicoma Tree Farm, November 20–21, 1971, E. Benedict, 38 ♂♂, 27 ♀♀ (WAS); Charleston, May 24, 1957, H. Dybas, ♀ (FMNH). *Douglas Co.,* Loon Lake, July 1, 1959, V. Roth, 8 ♂♂, ♀, juvs. (AMNH); Elliot State Forest, 1 mi. S, 2.5 mi. W of Ash, December 11, 1971, E. Benedict, 10 ♂♂, 14 ♀♀ (WAS); 11 mi. E, 4 mi. S of Allegany, Millicoma Tree Farm, November 21, 1971, E. Benedict, 15 ♂♂, 22 ♀♀ (WAS); 3.2 mi. NE of Scottsburg, 400 ft. elev., December 11, 1971, E. Benedict, 9 ♂♂, 11 ♀♀ (WAS). *Lane Co.,* head of Hand Lake Trail, 22 mi. E of McKenzie Bridge, October 16, 1971, E. Benedict, 2 ♂♂, 7 ♀♀ (WAS); Honeyman State Park, June 20,



Figs. 15–20. Anatomy of cyphophthalmids. 15–17. *Siro sonoma*. 15. Male leg 4, ectal view. 16. Male tarsus 4, mesal view. 17. Adenostyle, ectal view. 18–20. *S. acaroides*. 18. Male anal region, ventral view. 19. Penis, ventral view. 20. Penis, dorsal view.

1966, T. Briggs et al., ♀♀ (CAS); 1.2 mi. E of Hwy. 101, Heceta Head, September 3, 1970, T. Briggs et al., ♀ (CAS); Neptune State Park, June 20, 1966, V. Lee, ♂ (CAS). *Linn Co.,* 13 mi. N, 18 and 23 mi. E of Sweet Home, April 23 and 29, 1972, E. Benedict, 3 ♂♂, 5 ♀♀ (WAS); Swamp Mtn. Road, 2 mi. S, 2 mi. E of Cascadia, April 29, 1972, E. Benedict, ♀ (WAS). *Tillamook Co.,* 1 mi. W, 0.5 mi. S of Lee's Camp, November 4, 1972, E. Benedict, 5 ♂♂, 3 ♀♀ (WAS); Kiwanda Viewpoint on Cape Lookout, 2.5 mi. N, 1.5 mi. W of Sandlake, 600 ft. elev., November 4, 1972, E Benedict, 11 ♂♂, 15 ♀♀ (WAS). *Clackamas Co.,* 30 mi. SE, 30 mi. S, 39 mi. SE, 44 mi. SE of Estacada, 2000–2500 ft. elev., May 26, 1972, E. Benedict, 57 ♂♂, 38 ♀♀ (WAS). *Clatsop Co.,* 3 mi. SE of Olney on Rt. 202, November 21, 1971, E Benedict, ♂, ♀ (WAS); 4 mi. SE of Olney, November 27, 1971, E. Benedict, ♀, 2 ♀♀ (WAS); 5 mi. N, 7 mi. W of Elsie, 700 ft. elev., March 15, 1972, E. Benedict, 2 ♂♂ (WAS); 2.6 mi. E of Astoria, April 4, 1976, H. Ramsey, 2 ♂♂ (UWM). *Lincoln Co.,* 1.4 mi. W of Nashville, December 20, 1971, E. Benedict, 4 ♂♂, 4 ♀♀ (WAS); 7.7 mi. NW of Eddyville, June 20, 1966, V. Lee, ♀ (CAS). *Benton Co.,* 0.5 mi. NW of Glenbrook on South Fork of Alsea River, 600 ft. elev., December 14, 1971, E. Benedict, 5 ♂♂, 6 ♀♀ (WAS). *Marion Co.,* 9 mi. S, 6 mi. E of Silverton, March 26, 1972, E. Benedict, ♂ (WAS). WASHINGTON: *Pacific Co.,* 5.9 mi. NE of Astoria Bridge, 100 ft. elev., August 26, 1969, T. Briggs, ♂ (CAS). *Olympic Nat. Pk.,* Olympic Hot Springs, June 18–19, 1957, H. Dybas, 2 ♂♂ (CNHM). *Skamania Co.,* 4.3 mi. ENE of Cougar, 1280 ft. elev., December 1, 1974, R. Crawford, 3 ♂♂, 6 ♀♀ (UWM); 1.5 mi. N Swift Reservoir, no date, T. Briggs et al., 4 ♂♂, 3 ♀♀ (CAS). *Thurston Co.,* 15 mi. S of Olympia, October 28, 1967, E. Benedict, 30 ♂♂, 32 ♀♀ (WAS); Millersylvania State Park, October 28, 1967, E. Benedict, 18 ♂♂, 15 ♀♀ (WAS). *Mason Co.,* 1.5 mi. S, 0.5 mi. W of Grapeview, January 21, 1968, E. Benedict, 10 ♂♂, 13 ♀♀ (WAS), 2.5 mi. N of Grant, January 21, 1968, E. Benedict, 22 ♂♂, 16 ♀♀ (WAS). *Pierce Co.,* Horseshoe Lake, 3.4 mi. N of Eatonville, November 25, 1975, A. Ruggles, 3 ♂♂, 3 ♀♀ (UWM); Mt. Ranier National Park, Carbon River at Chennis Falls, June 16, 1957, H. Dybas, 2 ♂♂, ♀ (CNHM); Fairfax, June 16, 1957, H. Dybas, 3 ♂♂, ♀ (CNHM).

NOTES: Both Ewing (1923) and Newell (1947) thought that *S. acaroides* had a very limited distribution: between Blodgett and Summit, Benton Co., Oregon. Extensive collecting by Berlese funnel methods has resulted in a totally different picture; we know now that the species is distributed from northern California north along the coast and through the foothills of the Coast Ranges to the Olympic Peninsula. It probably also occurs in southern British Columbia. Label notes do not suggest a consistent association with any forest type; usually material was recovered from mixed deciduous and conifer litter, or from conifer litter alone, or from rotten wood. A minority of specimens came from mosses. As the numbers of specimens in individual collections suggests, the species must be very common, and can no longer be regarded as rare. Rustin Godfrey, a student at Hampden-Sydney College, carried out a study of geographic variation in *S. acaroides.* No discontinuities were found. All the meristic characters studied showed overlap at one standard error of the mean, including samples from Del Norte Co., California and Mason Co., Washington. There was, however, a noticeable trend toward larger size and a greater length to width ratio from south to north. There was no significant variation in the shape of the adenostyle.

The evolutionary relationships of this species have already been adequately covered in the discussions of *S. kamiakensis, S. sonoma,* and *S. exilis.*

METASIRO JUBERTHIE

Metasiro Juberthie, 1960, p. 235 (type species, *Siro americanus* Davis, by original designation); Shear, 1977, p. 167.

Floridogovea Hoffman, 1963, p. 137 (type species, *Siro americanus* Davis, by original designation).

Siro: Davis, 1933, p. 49 (not *Siro* Latrielle, 1789).

Parasiro: Hinton, 1938, p. 332 (not *Parasiro* Simon).

DIAGNOSIS: The adenostyle of the male is close to the tarsal base and has a fimbriate rim (fig. 26); in *Siro* species the adenostyle is acuminate and near the midpoint of the tarsus; the ninth tergite in *Metasiro* is free, while in *Siro* species it is fused with the eighth and ninth sternites to form a corona analis.

DESCRIPTION: See Juberthie (1960) for a complete and accurate description.

DISTRIBUTION: Southeastern United States (map 1).

NOTES: *Metasiro* is difficult to place. The fimbriate rim of the male adenostyle recalls *Neogovea* species of northern South America, but the form of the ventral thoracic complex, the chelicerae and the male genitalia are all more like *Siro* and its relatives, even though I expressed doubts about this in my 1977 paper. Further, referring back to the old character of the movability of the first two coxae, *Metasiro* has them free from the dorsum and the other coxae, whereas in *Neogovea* we find species in which all four coxae are solidly fused. I was able to show (Shear, 1977) that in *Neogovea* the setae at the tip of the adenostyle arise from within the adenostyle rim, and are real setae. In *Metasiro,* the rim of the adenostyle is ornamented with cuticular fimbriae that are *not* real setae (fig. 26). But, again, *Metasiro* evidently lacks anal glands and modifications of tergite 8 in the males—this is like *Neogovea.*

Assuming the relationship between *Siro* and *Metasiro* which Juberthie (1960) originally postulated, we have a biogeographical puzzle. I stated above that *S. exilis* has evidently retained a close relationship with the European species despite a long period of separation, and with the western forms after an even longer (hypothetical) period. What, then, can we make of a species which is found in an area not particularly known for its biogeographical distinctness, yet which appears to be quite unique in its combination of evolved (adenostyle) and primitive (free tergite 9) characteristics?

Juberthie (1962) published a description of *Paramiopsalis ramulosus,* from Portugal, and [I believe] incorrectly assigned this species to the "stylocellinae" because the second coxae are fused to the third. However, if one does not accept this character as the absolute arbiter of taxonomic assignment, nearly all its other characteristics, including those of the penis, are "sironine." Juberthie illustrated (his fig. 6) an "orifice trachéen accessoire" found at the tip of the abdomen, which, as a result of later work (Juberthie, 1967) he recognized as an anal gland pore—something never found in the "stylocellines." Further, the anal plate has the median ridge modification found in *Siro* species. The adenostyle of this species is distant from the base of the tarsus and not much like that of *Metasiro* in general shape, but it does have some peculiar, fimbriate cuticular extensions projecting from its surface. The ninth tergite is free, as in *Metasiro.* The ventral complex is unusual, too, with fused mesosterna and metasterna. Table 1 summarizes the characters of the forms discussed above. Examining it suggests that both *Metasiro* and *Paramiopalis* are closer to the sironids than to *Neogovea* (or to any "stylocellines"), but both species have characters that are discordant with their assignment to that family, as well as unique ones of their own.

Let them both remain in the Sironidae for the present! However, it is tempting to suggest that both of these species are the remnants of old evolutionary lines that may have arisen before the ogoveids and neogoveids diverged from the incipient sironids and pettalids. The peculiar characteristics they have both developed are a result of long isolation and differentiation.

Metasiro americanus (Davis)

Figure 26, Map 1

Siro americanus Davis, 1933, p. 49, figs. 1–10.

Metasiro americanus: Juberthie, 1960, p. 235, figs. 1–12.

Floridogovea americana: Hoffman, 1963, p. 139, figs. 15–20.

TYPES: Male holotype and more than 50 male and female paratypes from Torreya Ravine, Liberty Co., Florida, collected by N. W. Davis, April 12, 1930, May 29, 1931, in Cornell University Collection at AMNH.

TABLE 1
Taxonomic Characters in Four Genera

Character	State in the genus: *Neogovea*	*Metasiro*	*Paramiopsalis*	*Siro*
Adenostyle	Group of setae at tip	Fimbriate rim	Fimbriae over distal surface	Smooth
Penis	Neogovea type	Siro type	Siro type	Siro type
Tergite 9	Fused in corona analis	Free	Free	Fused in corona analis
Anal glands	Absent	Absent	Present	Present
Modifications of tergite 8, anal plate	None	None	Anal plate with median ridge	Anal plate with median ridge, tergite 8 modified
Coxa I	Fused to coxa II in 3 of 4 species	Free	Free	Free
Coxa II	Fused to coxa III	Free	Fused to coxa III	Free

Male and female paratypes are also in the American Museum of Natural History and a male paratype is in the Senckenberg Museum (Hoffman, 1963).

DIAGNOSIS: The genus is monotypic; the forms of the adenostyle and corona analis clearly distinguish *M. americanus* from the American species of *Siro*.

DISTRIBUTION: (Map 1) FLORIDA: Jackson Co., Florida Caverns State Park, Blue Hole Campground, S. B. Peck, April 6–7, 1969, 3 ♂♂, 4 ♀♀, many juvs. (WAS, FMNH). GEORGIA: *Grady Co.*, swamp near Calvary, W. Suter, July 9, 1965, ♂ (FMNH). SOUTH CAROLINA: *Pickens Co.*, Sassafras Mtn., 2500 ft. elev., S. Peck and A. Fiske, July 21, 1967, 3 ♂♂, ♀, many juvs. (FMNH).

NOTES: I have some doubts about the South Carolina record, but am impressed with the record of careful curatorial work by the collectors and by the curators of the Field Musuem (see Shear, 1977). Needless to say, the area intervening between the records on the Gulf Coast plain and the South Carolina piedmont should be searched.

Collecting in Florida in the spring of 1930 and 1931, Davis obtained numerous mature specimens, while the later Florida collections consisted of very large numbers of juvenile specimens (as many as 150) and only a few adults. Perhaps Davis did not record the juvenile specimens he collected. Seasonality in life history is not suggested by this data, because the juveniles are in a variety of instars. All the later material was taken by Berlese sampling in hardwood litter or in rotten wood from logs and stumps.

NEOGOVEA HINTON

Neogovea Hinton 1938 (type species, *N. immsi* Hinton, by original designation), p. 333; Rosas Costa, 1950, p. 139; Hoffman, 1963, p. 137; Martens, 1969, p. 110; Shear, 1977, p. 166.

Sirula Goodnight and Goodnight 1942 (type species, *Siro kartabo* Davis, by original designation), p. 1.

Brasilogovea Martens 1969 (type species, *B. microphaga* Martens, by original designation), p. 112. New Subjective Synonymy.

DIAGNOSIS: The adenostyle of three of the four species ends in a brush of true setae, an appearance duplicated in other cyphophthalmids only in *Metasiro americanus*, a much smaller species. However, one species included here, *N. mexasca*, bears an adenostyle which is long and acute; its troglobitic adaptations distinguish it from any other New World species.

DESCRIPTION: A full description is found in Shear (1977) and Martens (1969). This description must be modified somewhat to include the species discussed below; see that account.

DISTRIBUTION: Brazil, Guyana, and two caves in Oaxaca, Mexico.

NOTES: *Brasilogovea,* with its only species, *microphaga* Martens, is newly synonymized here with *Neogovea*. There are some differences in the form and spination of the penis, but it is clearly of the unusual *Neogovea* type (see Martens's figs. 15–17). *Neogovea* is most closely related to *Metagovea,* but has a goodly number of specializations, especially in the form of the penis, with its extended ventral plate lacking apical setae, and in the setose brush present (except in *N. mexasca*) at the tip of the adenostyle. In some species, the first coxa, as well as the others, is fused into a ventral mass which itself is solidly attached to the dorsum. But the chelicerae are of the long, thin type associated with *Stylocellus,* a genus generally considered primitive. However, it is possible that these elongate chelicerae represent a parallel specialization in *Stylocellus* and *Neogovea*.

Neogovea mexasca Shear
Figures 21–25

Neogovea mexasca Shear, 1977, p. 172.

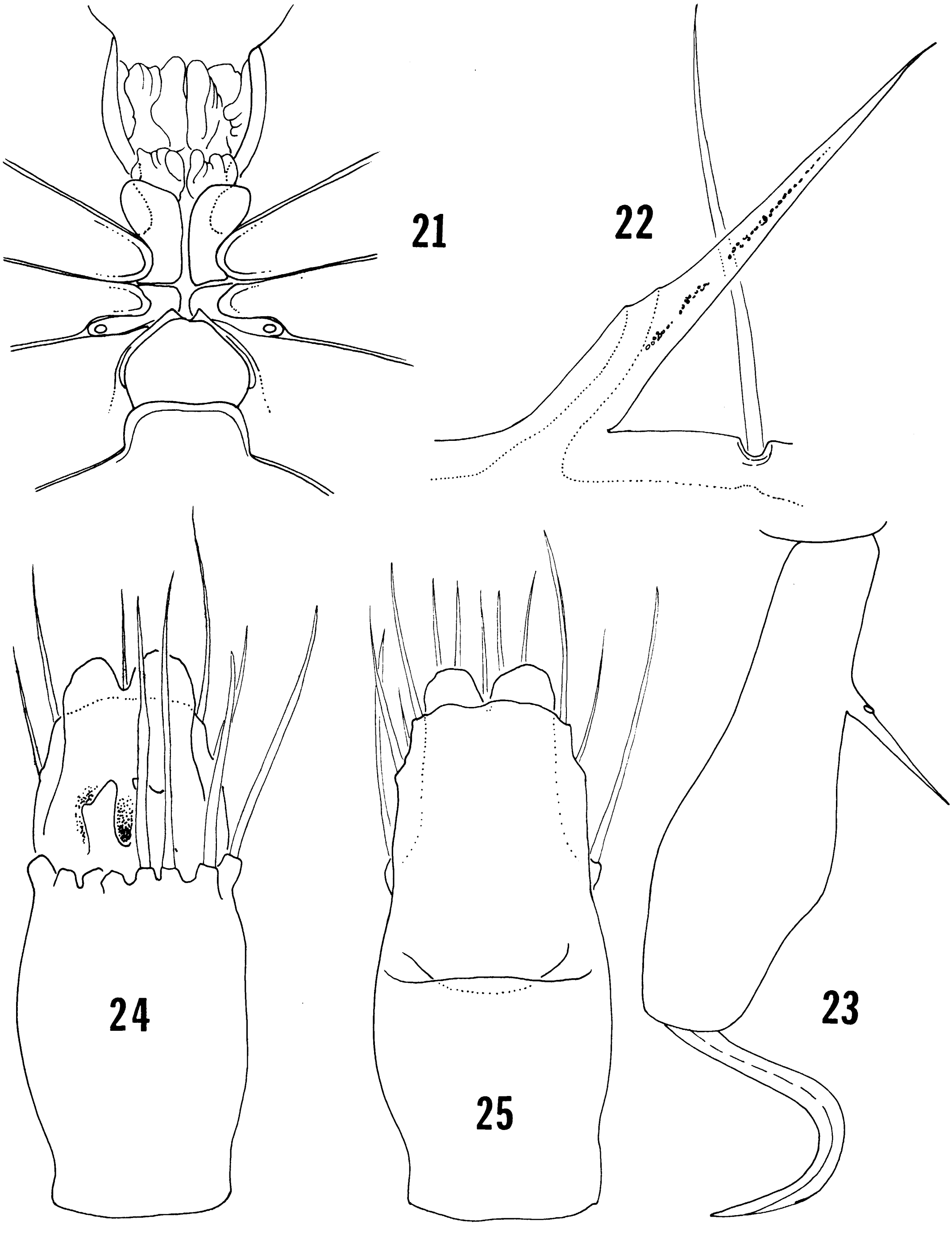
TYPES: Female holotype and paratypes from Cueva Nacimiento del Río San Antonio, 10 km. S of Acatlán, Oaxaca, Mexico, collected December 31, 1973 by James Reddell, William Elliott, and Roy Jameson, in the American Museum of Natural History.

DIAGNOSIS: The legs are elongate (the first leg nearly twice as long as the body) as a part of a suite of troglobitic adaptations not shown by any other American species.

DESCRIPTION: In my original account (Shear, 1977), I described the female in detail. Late in 1976, after my paper had gone to press, James Reddell and some of his colleagues from the Association for Mexican Cave Studies made a second collection of the species from a cave near the type locality (see Distribution section below). This collection contained males, and the description that follows is drawn from them. Total length of male, 2.00 mm., width across ozophores 1.02 mm., greatest width, 1.23 mm., L/W = 1.63. Dorsum and ozophores as described for female. Ventral complex (fig. 21) very similar to that of female, but gonostome smaller, with more regular margins, anterior lip of gonostome with raised, sometimes medially indented, rim. Chelicerae with basal article 1.19 mm. long. 0.14 mm. wide, distal article 1.02 mm. long. 0.13 mm. wide; movable finger 0.22 mm. long. Anal region not modified, anal glands absent. Fourth tarsus as in figure 23; significantly swollen just distal to midpoint; adenostyle (fig. 22) 0.43 mm. from distal end of tarsus, long, acuminate; pore opening on dorsal side in basal third. Penis (figs. 24, 25) of *Neogovea* type, but with reduced setation and shorter ventral plate than in other species. Color golden brown.

DISTRIBUTION: In addition to the type locality: MEXICO: OAXACA: Cueva de la Finca, 10 km. SW of Acatlán, December 31, 1976, J. Reddell, D. McKenzie, A. Grubbs, 9 ♂♂, 5 ♀♀ (AMNH, WAS, MCZ, coll. Assoc. Mex. Cave Studies).

NOTES: The new record is from a cave near the type locality. Nonetheless, there are some differences in the specimens. The new material from Cueva de la Finca seems slightly smaller and lighter in color, but the measurements of the body and appendages are very close to those I reported for the types (Shear, 1977). Interestingly, none of the claws of the new specimens are toothed. In the epigean species of *Neogovea,* all claws are toothed; in the type collection of *mexasca* teeth are found only on the claws of the last two legpairs. Perhaps the loss of claw teeth is a part of troglobitic adaptation, which has profoundly influenced the form of these animals. I reported that the first coxae of the specimens in the type collection were free; so are those in the new collection, but the second coxae are also easily detached! This contrasts strongly with the epigean species, in which even the first coxae are often solidly fused to the second. So here is a species that undoubtedly would be placed



FIGS. 21–25. Male *Neogovea mexasca*. 21. Ventral thoracic complex, ventral view. 22. Adenostyle, ectal view. 23. Tarsus 4, ectal view. 24. Penis, dorsal view. 25. Penis, ventral view.

in the old Stylocellinae, but which lacks the primary character used to define that subfamily. Similarly, *Paramiopsalis ramulosus* is definitely a sironine, but has the second coxae fused to the third.

The adenostyle of *N. mexasca* is not like that of the epigean species, but more like that found in species of *Siro*. I cannot say if this represents a specialization or the retention of an ancestral form. Certainly, *N. mexasca* is far separated from the South American species and could be a very ancient relict of an original *Neogovea* stock—predating both the origin of the brushlike adenostyle and the extensive coxal fusion of the South American species.

A NEW CLASSIFICATION OF THE CYPHOPHTHALMI

INTRODUCTION

Hansen and Sörensen (1904) were the first to recognize the existence of definable groups of genera within the cyphophthalmids. They divided the family Sironidae, which they recognized as the only family in the suborder, into two subfamilies. The Sironinae were characterized as having the coxae of legpairs one and two free from the posterior coxae, whereas Stylocellinae encompassed those forms in which the second coxae were fused to the third pair. Although other differences, having to do with the maxillary lobes of the first two pairs of coxae, were mentioned, these have turned out to be variable. Hansen and Sörensen (1904) wrote their diagnoses in Latin, using the word *mobilis* to describe the coxae not fused to their posterior neighbors; this has been rendered in English as "movable" by numerous authors. However, even Hansen and Sörensen pointed out that it seemed unlikely the second coxae could actually be moved by the animal to any extent, since the musculature and the close approximation of the second coxae to the third pair would make movement nearly impossible. The condition of the second pair of coxae which they described therefore can be detected by an observer only by manipulating the second coxae to see if they are fused to the third pair, or free from them.

Juberthie (1962) described *Paramiopsalis ramulosus* as a member of the Stylocellinae because the second pair of coxae were fused to the third, even though in every other important characteristic (see table 1) the animal is clearly a relative of *Siro* and *Parasiro,* typical members of Hansen and Sörensen's Sironinae. In 1977 I reviewed the genus *Neogovea,* traditionally placed in the Stylocellinae, and found that in some specimens of one species (*N. mexasca*) the second coxae were free, whereas in one or two other species in the genus even the first coxae had either severely limited mobility, or were in fact fused to the others. Although these exceptions may themselves be unimportant (*Neogovea mexasca,* for example, differs from typical *Neogovea* species in at least one other important way), they suggest that the fusion of the coxae in cyphophthalmids is an evolutionary trend which has proceeded in a parallel fashion in different phyletic lines at different speeds. The same can be said with greater clarity of the progressive fusion of the eighth and ninth abdominal sternites and the ninth abdominal tergite to form a complete corona analis—several degrees of fusion can be found in one phyletic line, and to place together those forms with similar degrees of coalescence is to ignore other characters which may be of greater evolutionary significance.

The division of a single family of cyphophthalmids into two subfamilies has been followed in an essentially unquestioning way by all subsequent workers who have reviewed the group (Hinton, 1938; Rosas Costa, 1950; Juberthie, 1970). In part this may have been due not only to the ease with which this character can be observed, but also to its biogeographical appeal: the stylocellines are all tropical forms, and the sironines occur in both the northern and southern temperate zones. But again, *Paramiopsalis* seems out of place, and Juberthie (1979) has found a "sironine" genus in tropical East Asia. Neither of these biogeographical novelties can be described as totally unexpected. But if a wide spectrum of characters is examined, I believe that three distinct phyletic lines can be distinguished in the world tropics, and that the northern and southern temperate zones each harbor distinct, though related, groups.

Finally, grouping of the species within the suborder into a single family with but two subfamilies fails to reflect the mass of new information on these animals that has accumulated since 1904. Many new species and genera have been discovered and described, and numerous characteristics of undoubted evolutionary importance have been found. In addition, doubt has been cast (see above) on the meaning of some of the traditionally recognized features used in taxonomy. A system of classification should "mirror evolution" and reflect, more or less at a glance, the hypotheses of relationship upon which it is based.

For these reasons, I propose below a new set of family-level taxa for the suborder Cyphophthalmi which I believe more fully illustrates the evolution of the group.

TAXONOMIC CHARACTERS

Rosas Costa (1950) and Juberthie (1970) have both presented excellent essays on the ranges of variation and degrees of utility at each level of taxonomic characters in the cyphophthalmids. This brief account is meant as a supplement to their treatments.

1. Eyes. Only one genus of cyphophthalmids, *Stylocellus,* has eyes, and in these animals they are near the margins of the cephalothorax slightly anterior to the ozophores. Outgroup comparison with opilioacarid mites suggests that this is a primitive characteristic. The exact nature of these eyes is difficult to ascertain, and some degrees of reduction are evident in several species of *Stylocellus,* with the eyes very difficult to make out in some animals. Even when these are well-developed, their structure seems such that they are probably very limited in function, although in the best of them there appears to be a tapetum behind the lens. In many features they recall the "ocelli" of ricinuleids, which scanning electron microscope studies show cannot be more than light-sensitive spots, if that (Platnick and Shadab, 1976).

2. Ozophore position. Juberthie (1970) clearly discerned three positions of the ozophores in the "sironine" genera he examined, and my study of "stylocelline" genera confirms that these animals present nothing new in this regard. In fact, all of them uniformly show Juberthie's type 2, as do most of the genera he studied. Type 1 ozophores are situated right at the margins of the cephalothorax, type 2 ozophores are removed from that margin by a distance about equal to the diameter of their bases, and type 3 ozophores are more fully dorsal than type 2. Although it may be tempting to arrange these in a transformation series in which they become progressively more dorsal, correlations with other characters suggest that type 1 and type 3 are separate derivations of type 2. Type 2 occurs in *Stylocellus,* with its numerous other plesiomorphic character states, whereas in the Southern Hemisphere pettalids, the presence of type 2 ozophores only in the genus *Parapurcellia* (the others all have type 3) is correlated with a primitive type of cheliceral dentition. Type 1 is found only in the genera *Parasiro* and *Odontosiro*; both have other apomorphic characters, especially *Odontosiro,* with its unusual body sculpture of sharp, toothlike tubercles.

3. Male fourth tarsus. Three features have been used here for taxonomic purposes: (1) form of the adenostyle; (2) position of the adenostyle, and (3) division (or not) of the tarsus into two segments. The form of the adenostyle varies in two ways. One represents a transformation series in which the adenostyle becomes progressively more attenuate and lamelliform, ranging from the short, stout, thornlike adenostyle of *Stylocellus* and *Ogovea* to the long, curved, pointed form found in some species of *Siro*. Evidently isolated specializations are the ornamentation of the adenostyle with cuticular fimbriae (*Metasiro, Paramiopsalis*) and the appearance in *Neogovea* (except for *N. mexasca*) of a terminal brush of setae. The position of the adenostyle on the fourth tarsus (basal, or near the tarsal midpoint) is of significance only at the species level. In the

TABLE 2

Male Genitalia of the Cyphophthalmi

Character state in penis of the five types

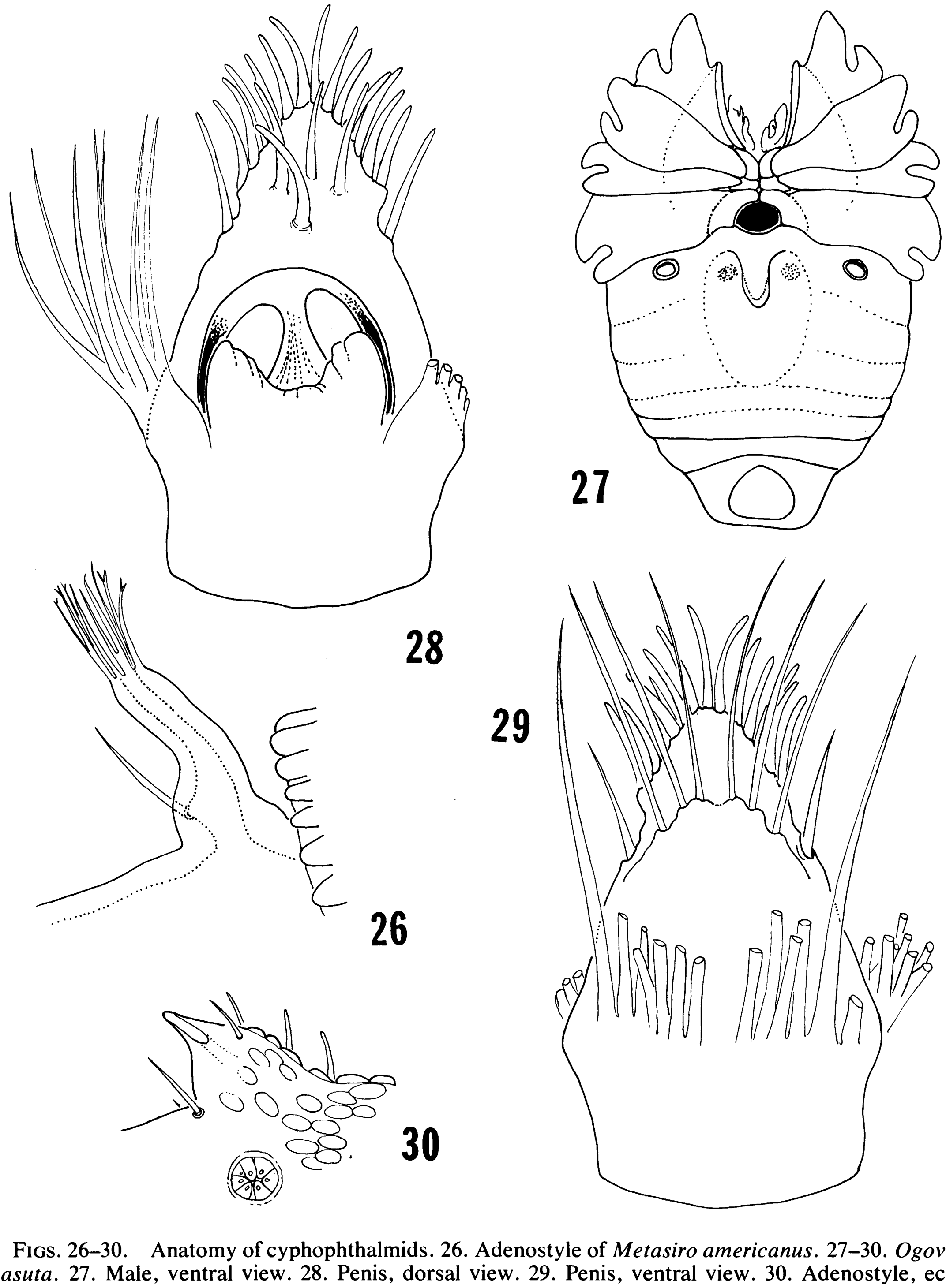
Character	*Siro*	*Stylocellus*	*Neogovea*	*Metagovea*	*Ogovea*
Structures around gonopore	One or two sets of movable fingers	Trilobed structure	Protective sclerotic plate	Not studied	Membranous structure
Ventral plate	Normal	Normal	Hyper-trophied	Normal	Normal
Apical setae of ventral plate	Long	Long	Absent or displaced	Short	Short, ensiform, sometimes accessory group on dorsal side
Ventral setae	Transverse row	Transverse row	Single or absent	Compact group	Compact group or transverse row
Dorsal setae	Single series	Setal bases fused, 3 groups vaguely indicated	Three groups	Three groups	Displaced to 2 groups or series on ventral plate

preceding section, I have shown that in at least one case, the division of the tarsus into two segments occurs in a species whose closest relatives have the tarsus entire. No other tarsal segments are divided in the cyphophthalmids, and, most importantly, the *females* of species in which the male fourth tarsus is divided have it entire. When correlated with other apomorphic characters, this can be of value, but ought not to be used on its own to group species into genera or families. The functional significance of the division is not understood.

4. Abdominal exocrine glands of the males. Juberthie (1962, 1967) has described a complex of glands found in the anal region of males of certain species. These glands are correlated with varying degrees of specialization in the posterior tergites. In the Northern Hemisphere, sironids generally show only modest modifications of the posterior end of the body. Characterisitcally, these modifications involve the anal plate (tergite 10) and the eighth tergite; the anal plate may possess a median groove or crest (fig. 6) and the tergite may be shallowly excavate, or have a small protuberance (fig. 3). In the Southern Hemisphere species, these modifications are much stronger, and of a different appearance. In the most extreme cases, the anal plate and tergites 8 and 9 are deeply grooved or even divided in two (tergite 9 only). In addition, the grooves are fitted with brushes of fine setae which probably function in dispensing a pheromone. It is not known if the pheromone is of a gustatory nature, as in some other opilionid groups (see Martens, 1970); it may be airborne. These glands and their associated modifications are obviously highly specialized, and are lacking in the Stylocellidae, Ogoveidae, and Neogoveidae.

The Ogoveidae possess glands on the second sternite, which open in the midline (Shear, 1979). In *Ogovea,* these are associated with a posteriorly projecting sternal apophysis. I consider these glands an autopomorphy for the Ogoveidae. Juberthie (1979) has described *Troglosiro aelleni* from New Caledonia with two sternal gland pores opening one behind the other in the midline of the third and fourth sternites; the relationships of this genus are not entirely clear, but it seems to be a sironid, so its sternal glands probably represent a separate development.

5. Male genitalia. I can discern five basic types of male genitalia among the cyphophthalmids; the characteristics of these are



FIGS. 26–30. Anatomy of cyphophthalmids. 26. Adenostyle of *Metasiro americanus*. 27–30. *Ogovea nasuta*. 27. Male, ventral view. 28. Penis, dorsal view. 29. Penis, ventral view. 30. Adenostyle, ectal view.

TABLE 3
Character States in Male Genitalia

Character	Plesiomorphic state	Apomorphic state
Dorsal setae	1. Three groups	Single series
	2. Dorsal position	Displaced ventrally
	3. Bases distinct	Bases fused
Ventral setae	4. Transverse row	Compact group
	5. Present	Reduced to absent
Ventral plate	6. Normal	Hypertrophied
Ventral plate apical setae	7. Present	Absent or displaced
	8. Long	Short, ensiform
	9. Accessory group absent	Accessory group present
Gonopore structures	10. Membranous or poorly formed structure	"Movable fingers"
	11. Membranous or poorly formed structure	Sclerotic plate

summarized in table 2 and in the paragraphs below.

a. Sirǒ type. One or two sets of "movable fingers" around the gonopore; ventral plate of normal size and shape, with long apical setae and ventral setae in a transverse row; dorsal setae tend to be in a single series, but may show signs of being in three groups. See figures 1, 2.

b. Stylocellus type. Membranous trilobed structure dorsal to the gonopore; ventral plate of normal size and shape, with long apical setae and ventral setae in a transverse row; dorsal setae with bases fused, three groups (two lateral, one median) vaguely indicated. See Shear (1979b) for an illustration.

c. Neogovea type. Protective sclerotized plate dorsal to gonopore; ventral plate hypertrophied, thickened apically and often dorsoventrally bifurcate, with apical setae absent or displaced to dorsal side of plate; ventral setae absent, or a single ventral setae present; dorsal setae in three groups (two lateral, one median). See Shear (1977) for illustrations.

d. Metagovea type. Structures around gonopore not studied, probably membranous, ventral plate normal, apical setae short, ventral setae in a compact group; dorsal setae in three groups (two lateral, one median). See Martens (1969) for illustrations.

e. Ogovea type. Membranous structure around gonopore; ventral plate normal, apical setae numerous and ensiform, sometimes with accessory group of short setae on dorsal side; ventral setae in a compact group or single series; dorsal setae displaced to two groups or to a series on the basal part of the *ventral* plate. See figures 28, 29.

Apomorphic vs. plesiomorphic character states of the male genitalia are summarized in table 3; the apomorphic states were arrived at by correlation with other apomorphic characters.

The function of the penis and its various parts in cyphophthalmids is not fully understood; this will be further discussed in the section dealing with Savory's proposal of the group as a new order of Arachnida. Morphologically, the small size of the penis suggests that it functions differently from the penis of other opilionids. Although the very short organ has no obvious division into truncus and glans, I think that the dorsal setae are apical on the part of the penis homologous to the truncus in other opilionids, because of the ease with which they can be displaced to the ventral side of the ventral plate base. Other homologies cannot be suggested with confidence.

6. Chelicerae. Two relatively distinct types of chelicera are found in the suborder.

TABLE 4
Character States in the Cyphophthalmi

Character	Plesiomorphic state	Apomorphic state
Eyes	12. Present	Absent
Ozophores	13. Type 2	Type 3
Anterior coxae	14. Free	Tendency to fusion
Chelicera	15. Distal segment narrowed	Distal segment robust
Cheliceral teeth	16. Uniform, large	Large and small
Adenostyle	17. Short, thornlike	Otherwise
Anal sclerites	18. S8, S9, T9 free	Partially or entirely fused
Anal glands	19. Absent	Present
Modified anal region	20. Absent	Present
	21. Without setal groups	With setal groups
Sternal glands	22. Absent	Present

In the robust type found in the Ogoveidae, Sironidae, and Pettalidae the distal article is about three times as long (or less) than the movable finger. An attenuate type is found in the Stylocellidae and Neogoveidae, in which the distal article is five or more times as long as the movable finger and is noticeably narrowed distally. The attenuate type is "mimicked" by troglobitic adaptation in *Tranteeva* and *Speleosiro,* which belong to robust-chelicera families. In these two genera the basal article of the chelicera is also narrowed.

If the attenuate type is considered apomorphic, we must accept parallelism in the Stylocellidae and Neogoveidae or, alternatively, reversal in the Ogoveidae. If it is plesiomorphic, then we must suggest either parallelism in the Ogoveidae and Sironidae and Pettalidae, or reversal in the Neogoveidae. It seems that there is little to choose between these alternatives, but in the Stylocellidae the attenuate chelicera is correlated with several plesiomorphic characters, so I prefer the first choice. Juberthie (1970) discussed the presence or absence of a dorsal crest on the basal article. The crest is absent in only a few genera (*Siro, Tranteeva*) in the Sironidae and its absence is regarded as apomorphic for those genera.

As suggested by Juberthie (1970), the type of cheliceral dentition is significant. I found three types: in all species of the Stylocellidae, Ogoveidae, and Neogoveidae I examined, the teeth were widely separated, somewhat nodular, and of subequal size. In the Sironidae, the teeth are all large, but are more numerous, more closely set, and triangular. In the Pettalidae two types of cheliceral teeth, large and small, are readily seen; this is a specialization.

7. Posterior abdominal sclerites. Sternites eight and nine and tergite nine may be either entirely free from one another, tergite nine may be entirely free or partially fused to sternite nine, or all three may be fused into a ring around the anal plate (tergite 10) called a complete corona analis. Comparisons with similar situations in other groups of opilionids suggest that the various degrees of fusion represent a transformation series in which the most primitive state is having all sclerites completely free and the most evolved the presence of a complete corona analis. I believe this transformation series has proceeded independently, because in each line we find several conditions associated with the distinguishing characters of that line. In the Sironidae, for example, *Siro* species have a complete corona analis, tergite nine is free in *Metasiro,* and all three sclerites are free in *Suzukielus*. The latter condition is the case in the Pettalidae, except for *Speleosiro,* which has a complete corona analis.

8. Anterior coxae. This character has already been discussed in the Introduction to this section. To recapitulate: just as in the anal sclerites, a tendency exists for the coxae

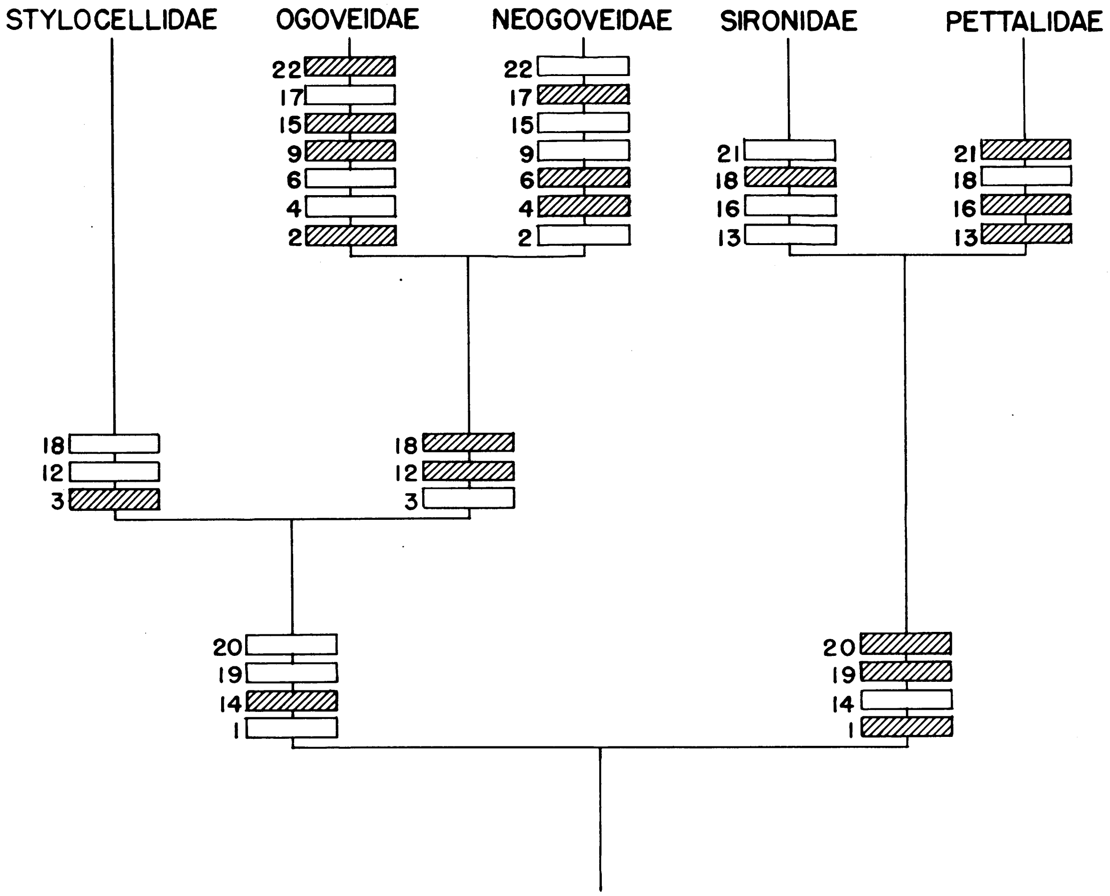


FIG. 31. Cladistic analysis of the families of Cyphophthalmi. See text for explanation.

to fuse, and this is expressed to varying degrees in different forms, though with less opportunity for variation than in the case of the posterior sclerites.

The apomorphic–plesiomorphic positions of these characters are shown in table 4, arrived at by correlation, outgroup comparison, or by their uniqueness.

CLADISTIC ANALYSIS

The results of a cladistic analysis of the suborder Cyphophthalmi are presented in figure 31; the analysis was not carried to the level of genus and species, so that characters 5, 7, 8, 10, and 11 are not included in figure 31. As the cladogram illustrates, I consider the genera formally grouped below into the Sironidae and Pettalidae to form a sister group to those in the other three redefined families; the Stylocellidae (genus *Stylocellus* only) is then shown to be the sister-group of the Ogoveidae and Neogoveidae taken together. The new arrangement of genera suggested by this analysis is formalized in the next section.

A strictly subordinated classification, such as that recently proposed for spiders by Platnick (1977), would result in infraordinal names for taxa with roughly the same content as the Hansen and Sörensen subfamilies Stylocellinae and Sironinae; it is reassuring to recognize that while the rank of these taxa would change radically, we still recognize them as monophyletic groups, with only minor changes in composition (next section). Because the category of infraorder is not generally used in arachnology, I have placed the infraordinal names I suggest below in brackets.

- Suborder Cyphophthalmi
  - [Infraorder Tropicophthalmi]
    - Superfamily Stylocelloidea Hansen and Sörensen, new rank
      - Family Stylocellidae Hansen and Sörensen, new rank
    - Superfamily Ogoveoidea, new
      - Family Ogoveidae, new
      - Family Neogoveidae, new
  - [Infraorder Temperophthalmi]
    - Superfamily Sironoidea Simon, new rank
      - Family Sironidae Simon, new rank
      - Family Pettalidae, new

This analysis has revealed that the ogoveids and neogoveids are not as closely related to the stylocellids as previous schemes implied, and the Sironidae and Pettalidae, while sister groups, are quite distinct.

DIAGNOSIS OF NEW FAMILIES

FAMILY SIRONIDAE SIMON, EMENDED

TYPE GENUS: *Siro* Latrielle.

DIAGNOSIS: Eyes absent. Ozophores type 1 or 2. First and second coxae free, except in *Paramiopsalis,* where second coxae are fused to third coxae, sternites eight and nine and tergite nine fused to form complete corona analis, or all three sclerites free (*Suzukielus*), or only tergite 9 free (*Metasiro*). Chelicerae of the robust type, with or without dorsal crest, cheliceral teeth all large and uniform. Ovipositor with apical sense organs or special branched setae. Anal glands present in male, anal region slightly modified, modifcations when present usually involve midline crest or groove on anal plate. Adenostyle acuminate-laminar; male tarsus 4 divided or entire. Penis of Siro type (see table 2).

INCLUDED GENERA: *Siro* Latrielle, *Parasiro* Simon, *Tranteeva* Kratchovil, *Odontosiro* Juberthie, *Metasiro* Juberthie, *Paramiopsalis* Juberthie, *Suzukielus* Juberthie, and possibly *Troglosiro* Juberthie.

DISTRIBUTION: Europe, Japan, North America, ?New Caledonia.

DISCUSSION: This family is most closely related to the family Pettalidae. I suspect that *Tranteeva,* with a single troglobitic species, is a synonym of *Siro* (Juberthie [1970] consistently spells the name "Trenteeva"). In the first section of this paper, *Neosiro* is synonymized with *Siro.*

The most significant evolutionary trends in the Sironidae are the development of a complete corona analis (seen progressively in the series *Suzukielus–Metasiro–Siro*), the Siro-type penis, the presence of type 1 ozophores (*Parasiro*), and the suppression of the dorsal crest of the chelicera. See the discussions above on the genera *Siro* and *Metasiro.*

After most of the work for this paper had been concluded, Juberthie (1979) published a description of a remarkable new cyphophthalmid from a cave in New Caledonia, *Troglosiro aelleni.* I have not had the opportunity of examining specimens of this species, but according to Juberthie, coxae 1 and 2 are free, the ozophores are of type 2, the cheliceral teeth are subequal, the chelicerae lack a dorsal crest, and the corona analis is complete. These characteristics suggest placement in the Sironidae. However, the claws of leg 2 are toothed, the adenostyle is thornlike, the penis (see Juberthie's fig. 6) is very unusual, with large, well-sclerotized movable fingers and a pair of enormous apical compound setae. A unique set of sternal glands opening on the third and fourth sternites is present. Juberthie (1979) evidently believes that the genus can be placed in the group designated here as the Sironidae, but singles out *Parapurcellia,* a somewhat aberrant member of the Pettalidae (see below) as a possible close relative. Detailed study of both genera may in fact lead to the designation of a new family including both of them, or for *Troglosiro* alone. The finding of this unusual new species as well as the description of *Huitaca ventralis* (Shear, 1979a) of Colombia, hints that numbers of important and remarkable cyphophthalmids may yet be found in the tropics.

FAMILY PETTALIDAE, NEW

TYPE GENUS: *Pettalus* Thorell.

DIAGNOSIS: Eyes absent. Ozophores type 3 (type 2 in *Parapurcellia*). First and second coxae free. Abdominal sternites eight and nine and tergite nine free (complete corona analis in *Speleosiro*). Chelicerae of the robust type, dorsally crested, two kinds of cheliceral teeth, large and small. Ovipositor (when studied) with apical sense organs. Anal glands present in male, anal region strongly modified, modifications taking form of deep grooves on anal plate, ninth tergite (which may be divided) and eighth tergite (which may appear strongly bilobed), these grooves often with tufts of setae. Adenostyle acuminate-laminar; male tarsus 4 divided or entire. Penis of Siro type (see table 2).

INCLUDED GENERA: *Pettalus* Thorell, *Purcellia* Hansen and Sörensen, *Speleosiro* Lawrence, *Parapurcellia* Rosas Costa, *Rakaia* Forster, *Neopurcellia* Forster, *Chileogovea* Roewer.

DISTRIBUTION: South Africa, Sri Lanka, New Zealand, Australia, and Chile.

DISCUSSION: The genera included in this family are obviously all closely related, and I expect that future revisionary studies of them will result in some synonymies. *Rakaia* seems to differ from *Purcellia* only in the division of the male fourth tarsus in the latter genus; I see no significant differences between *Neopurcellia* and *Purcellia,* aside from the smaller size of species of the former. For that matter, the differences between *Pettalus* and *Purcellia* are largely ones of degree, centering on the modifications of the anal regions of the males; these are more striking in *Pettalus.*

Parapurcellia and *Chileogovea* are the most divergent elements. *Parapurcellia* has type 2 ozophores, and the cheliceral teeth are all of the large type, whereas the division of tergite nine along the midline in males provides an autapomorphy. I regard the genus as pettalid, but with plesiomorphic links to the sironids. *Chileogovea oedipus* is unique in the suborder in the two pairs of knobs on the sixth and seventh abdominal sternites. These knobs do not appear to be glandular. The male anal region has modifications more typical of the sironids (a midline crest on the anal plate), providing another link to that group, albeit plesiomorphic.

The distribution of the family is characteristically Gondwanan.

FAMILY STYLOCELLIDAE HANSEN AND SÖRENSEN, EMENDED

TYPE GENUS: *Styocellus* Westwood.

DIAGNOSIS: Eyes present. Ozophores type 2. First coxae free, second coxae fused to third. Abdominal sternites eight and nine and tergite nine all free. Chelicerae distally attenuate, with dorsal crest, cheliceral teeth uniformly large. Ovipositor (when studied) with sense organs. Male lacking anal glands and modifications of the anal region. Adenostyle short, triangular, thornlike; male tarsus 4 entire. Penis of Stylocellus type (see table 2).

INCLUDED GENUS: *Stylocellus* Westwood.

DISTRIBUTION: See the map provided by Shear (1979b); East Indies (Sumatra, Java, Borneo, Celebes) and Malay Peninsula. Jochen Martens (*in litt.*) has a few female specimens from northeastern India which may belong to *Stylocellus.*

DISCUSSION: The presence of eyes, the lack of anal glands and modifications, the large size, uniform cheliceral teeth, and free posterior abdominal sclerites are characters that mark this family as primitive. However, the form of the penis, particularly the fusion of the bases of the dorsal setae, and the degree of coxal fusion, are apomorphic characters.

FAMILY OGOVEIDAE, NEW

TYPE GENUS: *Ogovea* Roewer.

DIAGNOSIS: Eyes absent. Ozophores of type 2. First coxae free, second coxae fused to third. Corona analis complete. Chelicerae robust, dorsally crested, cheliceral teeth all large and nodular. Male lacking anal glands and modifications of the anal region. Exocrine glands present on second abdominal sternite of male, sometimes associated with a large apophysis (fig. 27). Adenostyle short, triangular, thornlike; male tarsus 4 entire. Penis of Ogovea type (see table 2).

INCLUDED GENERA: *Ogovea* Roewer, *Huitaca* Shear.

DISTRIBUTION: West Africa (Fernando Poo, Gabon), northern South America (Colombia).

DISCUSSION: Apomorphies linking the two genera of this family are the presence of the unique glands on the second abdominal sternite, and the ensiform setae of the apical group. The presence of distinct, but related genera in South America and Africa is entirely acceptable to biogeographers. I include here some new illustrations of *Ogovea nasuta* Hansen (figs. 27–30). The female holotype of *O. grossa* Hansen and Sörensen has been restudied by Juberthie (1969).

FAMILY NEOGOVEIDAE, NEW

TYPE GENUS: *Neogovea* Hinton.

DIAGNOSIS: Eyes absent. Ozophores type 2. First coxae free or fused to pancoxal group; second coxae free or fused to third coxae. Corona analis complete. Chelicerae distally attenuate, with dorsal crest; cheliceral teeth all large and nodular. Ovipositor with sense organs or branched setae. Males lacking anal glands and modifications of anal region. Adenostyle acuminate-laminar (*Metagovea, Paragovia*) or cylindrical, with a distal brush of setae (*Neogovea*); male tarsus 4 entire. Penis of Neogovea or Metagovea type (see table 2); but see discussion below of *M. gabonica*.

INCLUDED GENERA: *Neogovea* Hinton, *Paragovia* Hansen, *Metagovea* Rosas Costa.

DISTRIBUTION: West Africa, South America, Mexico.

DISCUSSION: I consider *Brasilogovea* Martens (type and only species *B. microphaga* Martens 1969) to be a synonym of *Neogovea* Hinton; see the discussion of *Neogovea* in the first part of this paper.

Juberthie (1969) described *Metagovea gabonica* from West Africa. Juberthie's species differs from the South American members of the genus in having a very unusual penis, described by Juberthie as ". . . plus simple et semble-t-il le plus primitif de tous les pénis de Cyphophthalmes. . . ." His reason for suggesting this is the absence of ventral setae, or their inclusion in the apical group. However, the dorsal setae are coalesced in a single series, a character I consider evolved. The ventral setae may just as well have been lost or incorporated in the apical group as an apomorphy, in fact the evidence from other characteristics of the animal favors this latter interpretation, and I so indicate it in table 3. Juberthie does not mention Hansen's genus *Paragovia,* described from West Africa with the single species *P. sironoides* (Hansen, 1921). *Metagovea gabonica* has the smooth claws Hansen described for *Paragovia.* Given the discordance between *M. gabonica* and the South American forms (see especially Martens, 1969), I suggest that the species actually belongs in *Paragovia.* This arrangement leaves us with the genera *Neogovea* and *Metagovea* as Mexican and South American, and the family represented in Africa by two species of *Paragovia.* However, without comparing the types of the two species, I do not wish to formally change the generic assignment of *Metagovea gabonica.*

SAVORY'S PROPOSAL

Savory (1977) proposed that the Cyphophthalmi be considered as an order of Arachnida separate from the Opiliones. In fact, he implied that the cyphophthalmids were "the representatives of the ancestral group, from which have evolved the other orders of their sub-class, namely the 'Phalangida' and the Ricinulei. . . ." Savory based his argument on the presence in cyphophthalmids of a "mass of distinctiveness" and listed a number of autapomorphies present in the group, asserting that each order of arachnids could be characterized by peculiar features, and that, therefore, any arachnid group possessing peculiar features should be considered an order. This implies that the task of the systematist is to recognize and emphasize distinctness as opposed to relatedness, but on any level other than that of species recognition, this is an anti-evolutionary position.

As a final bit of evidence supporting his proposal, Savory presented the results of a survey of 11 arachnologists working in Opiliones, of whom two did not reply to his letter, two were uncertain but suggested further study, three disagreed with his proposal, and four favored it. From this Savory somehow constructed a majority of six to three, and concluded his paper: "Since, as has been made clear, the establishment of any higher taxon is governed by individual opinions, and since of the authorities consulted a majority of 6 to 3 have expressed agreement, the 'opposition' has no case to answer and there remains no more to be said."

As one of those in oppostion to Savory's proposal, I find I must extend my disagreement to the remarkable proposition that in science, majority rules (if indeed a majority really exists), and that once the majority has spoken, no further debate can be countenanced. This is not only inimical to scientific progress but also implies that science is not based on objective criteria of truth, only on opinions.

Further, *any* taxon is distinguished from others by autapomorphies. The information content of a system of classification lies precisely in the opposite direction, the indication of relationships by synapomorphies. Reducing groups which are united by obvious synapomorphies to a series of smaller and smaller units of higher and higher taxonomic rank rapidly depletes the amount of information which can be recovered from the classification. In this regard, one need only cite the telling criticism of Mayr (1969, p. 239) of Roewer's *Weberknechte der Erde* (1923). Roewer arranged about 1700 known species of opilionids in about 500 genera, more than three-fifths of which were monotypic. Anyone who has attempted to work with Roewer's book, particularly in the families Cosmetidae and Gonyleptidae, realizes how impossible such a system becomes; it fails to indicate relationships and perpetuates itself endlessly as a sequence of small or monotypic taxa. This is, of course, an extreme example, and I do not mean to imply that monotypic (or small) higher taxa are never appropriate. I do mean to suggest that they should be reserved for cases in which two sister groups contain greatly different number of taxa. If Savory's reasoning were carried to its conclusions, a case could be made, and made rather strongly, for each superfamily and even many families of Opiliones to be raised to ordinal rank.

One could argue that it makes little differences if a taxon is regarded as an order or a suborder, but this argument is based again on the assumption that a classification is a device that depends entirely on consensus. The present trend in taxonomy is away from this view. If a group is ranked as a suborder under an ordinal name which it shares with one other taxon, the system clearly states by this arrangement that the two are believed to be each other's closest relatives. The information content of the classification is diminished if more than two suborders are present under an order, or if one or both of the suborders are raised to the level of order when the class has at least two other orders, and intermediate categories are lacking. This latter case is *part* of Savory's hypothesis; the former is a statement of the present condition of the system in Opiliones (there are three generally accepted suborders).

I believe that most modern arachnologists would find Savory's suggestion that the Cyphophthalmi represent an ancestral group from which both the Ricinulei and other Opiliones have evolved to be contrary to the bulk of the evidence (see Firstman, 1973; Kraus, 1976; Van der Hammen, 1977; and others), but as this part of the proposition is not explicitly argued by Savory, I will not deal with it further.

TESTING THE HYPOTHESIS

Let us examine what Savory's hypothesis explicitly states, and contrast it with other hypotheses. From Savory's paper we can abstract the following classification[2]:

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[2] Savory has, over the years, published several quite different classifications of the Arachnida. I wish to deal here only with the one presented in his 1977 paper.

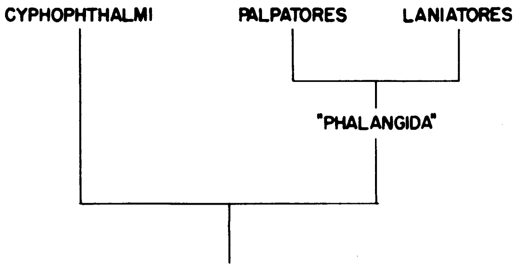

FIG. 32. A hypothesis contained in Savory's classification of the Opiliones.

Class Arachnida
  Order Cyphophthalmi
  Order Phalangida
    Suborder Laniatores[3]
    Suborder Palpatores
  (Other orders)

For the moment, I wish to set aside Savory's contention that the Cyphophthalmi are ancestral to the "Phalangida" and the Ricinulei. Expressing the information contained in his classification as a cladogram, I present figure 32. One of the hypotheses contained in this cladogram is that the Cyphophthalmi form the sister group of Phalangida, with its two suborders, and that no synapomorphies exist to allow us to choose either Laniatores or Palpatores alone as a sister group of Cyphophthalmi.

The commonly accepted grouping of opilionids into three suborders (Cyphophthalmi, Laniatores, Palpatores) does not discriminate sister groups, and so encompasses at least four hypotheses of relationship including one similar to Savory's (fig. 32, fig. 33) except that the three groups are united as one order. Indeed, by implicitly endorsing this specific hypothesis, Savory's classification has a greater information content than the present classification, and is therefore more scientific in that it is subject to more rigorous testing (Popper, 1962). The hypothesis can be rejected, however, if it can be shown that the cyphophthalmids have more synapomorphies with one or the other of the two remaining groups. I believe this to be the case; the cyphophthalmids share with the Palpatores at least two important apomorphies.

The most significant of these is the long, segmented ovipositor with a bifurcate tip bearing sense organs of a special type. That this is an apomorphy may be determined by outgroup comparison with the opilioacarid mites, which group is generally accepted as being the most primitive of the Anactinotrichida. Van der Hammen (1968) illustrated the ovipositor of *Paracarus hexophthalmus*; it is short, unsegmented, and lacks special sensory organs at its tip. An ovipositor of a similar type is found in the Laniatores, but with an added apomorphy in that the tip has *four* asymmetrical lobes. Two superfamilies of Palpatores, Ischyropsalidoidea and Troguloidea, have a short, unsegmented *bilobed* ovipositor which may have scattered terminal sensory setae (see Martens, 1978, figs. 43, 44, 46–48) but the superfamilies Caddoidea and Phalangioidea have an annulate ovipositor with a specially organized sensory structure (replaced in very small species by unusual branched setae). The striking similarities between this ovipositor and the cyphophthalmid ovipositor are evident in Marten's (1978) figures 36–41. Functionally, this ovipositor may be connected with the deposition of eggs in deep soil crevices. No phalangioids or cyphophthalmids are known to exhibit parental care, and so achieve a clear reproductive advantage by hiding their eggs in this way. A number of laniatorid species do show parental care; if this habit is widespread, then having a long ovipositor to place eggs deep in the soil would be unnecessary. In the latter case, an autapomorphic behavioral character may have allowed the retention of a pleisiomorphic morphological one.

The second synapomorphy is found in the digestive system. Dumitrescu (1975a, 1975b) has studied the midgut diverticula of the opilionids. He found that cyphophthalmids resemble the Palpatores in having four sets of diverticula, whereas the Laniatores all have

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[3] Savory (in another place) favors the elevation of Šilhavý of Oncopodidae to subordinal rank; this has not been generally accepted (see Martens, 1976).

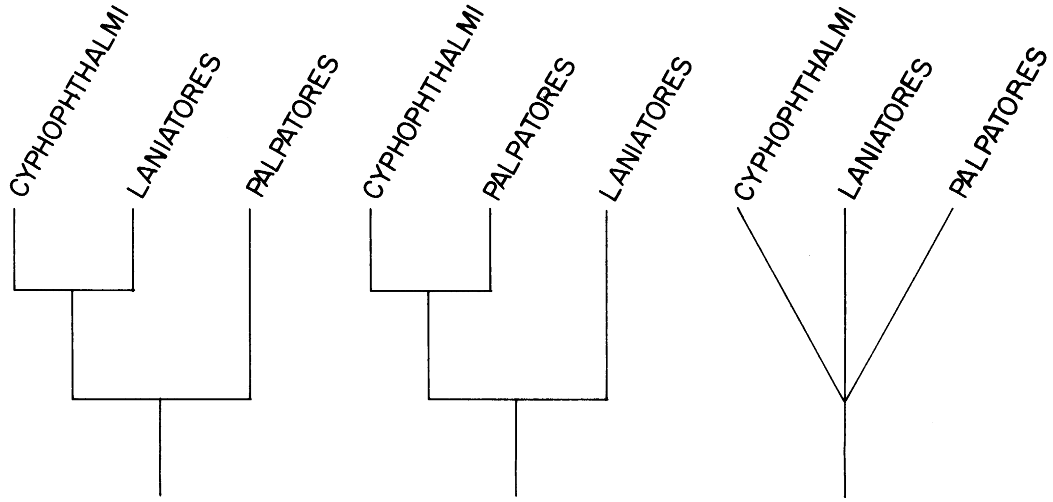

FIG. 33. Three hypotheses of relationship contained in the traditional classification of the Opiliones. A fourth hypothesis is depicted in figure 32.

three sets. That the direction of evolution is toward the multiplication of diverticula is shown by the presence of the most elaborated condition in species of the Trogulidae, where it is correlated with numerous other apomorphies.

In contrast, it is not possible at this time to show that *any* meaningful synapomorphies are shared by the Cyphophthalmi and any laniatorid group, or by palpatorid and laniatorid groups. Savory (1977) provided none of the latter in support of his hypothesis. If any opilionid suborder could be a candidate for ordinal status, it is thus the Laniatores.

Because so much more remains to be learned about the opilionids, I prefer not to propose a strictly subordinated classification for the entire order. But we can examine hypotheses of relationship and heuristically reject them if *what we know now* fails to support them. I believe this to be the case with Savory's hypothesis.

ARGUMENT FROM "UNIQUENESS"

But setting this crucial argument aside for the moment, what if we accept at face value that a "mass of distinctiveness" would constitute evidence for separating the Cyphophthalmi from the other opilionids? Has Savory demonstrated this is the list of unusual characteristics he presents? I believe not, and for two reasons. First, the characters he adduces fail to meet a reasonable criterion of uniqueness, in that similar clusters of apomorphies appear in other opilionid groups, and secondly, because errors of fact and interpretation have crept into his account. I will deal in turn with each of the features he lists.

1. Repugnatorial glands. Characteristic of all opilionids (and an excellent synapomorphy for uniting them) are a pair of lateral repugnatorial glands on either side of the cephalothorax. Savory, as others have, has drawn attention to the fact that these glands in the cyphophthalmids are located at the bases of protrusions (the ozophores), which bear the gland pores at their tips. This is a synapomorphy which unites the Cyphophthalmi, but it is actually part of a transformation series in which the glands become more dorsal. In the Laniatores and the two "Dyspnoi" superfamilies, the pores often open in soft cuticle below the margin of the carapace. But in the Phalangioidea and Caddoidea, the pore is definitely more dorsal, is

visible from above, and in many cases is completely surrounded by the hard cuticle of the carapace. This not only takes away some of the "uniqueness" of the cyphophthalmid arrangement, but also further suggests a relationship to the Phalangioidea and Caddoidea. The use by the cyphophthalmids of the secretion of the glands is indeed a further synapomorphy (they dab the secretion on attackers with their legs), but again its "uniqueness" is diluted by the presence of the same habit in the laniatorid family Cosmetidae (Eisner, Kluge, Carrell and Meinwald, 1971), an undoubted parallelism.

2. Eyes. The lateral eyes of the stylocellids (and Savory errs here by attributing eyes to the entire old subfamily Stylocellinae; only one genus of which has them) are not an apomorphic characteristic, but a plesiomorphic one for arachnids.

3. Exocrine glands. Savory rightly considers the adenostyle glands of the cyphophthalmids an autapomorphy for them, but again his argument hinges on the *uniqueness* of these glands. Indeed, they are unusual in that few other opilionids have exocrine glands in that position. But, even within the cyphophthalmids themselves, the presence of other exocrine gland complexes in the anal region and on the abdominal sternum is uniqueness of the same sort. In the troguloids and ischyropsalidoids, we find exocrine glands of a proven sexual function in the basal articles of the chelicerae—another unique arrangement. Certain laniatorids, most significantly the members of the family Stygnommatidae, have swollen, glandular metatarsi on the third legs of the males, and these, too, can be called unique. And, indeed, Martens (1972) has described a tarsal adenostyle on tarsus 2 of the males of the phalangodid *Ausobskya athos*! To me, the *quality* of the uniqueness of this characteristic falls off when more or less closely related groups have similarly unique characteristics—in other words, the position of the glands *is* unique, but their presence *somewhere* is almost to be expected among opilionids! Should we recognize each arrangement of exocrine glands in opilionids with ordinal status?

4. Legs. Here Savory makes reference to the uniarticulate tarsi and smooth claws of the cyphophthalmids. Actually, about half the described species have toothed claws, and in any case, smooth tarsal claws are commonplace in the other opilionid suborders. Uniarticulate tarsi are found in a genus of Laniatores (*Oncopus*, Oncopodidae) and are in the Trogulidae (*Anarthrotarsus*) together with, as in the Cyphophthalmi, numbers of other highly evolved characteristics. Further, the fourth tarsi of males of about half the species of cyphophthalmids are divided into two segments. Therefore, this is a character from which few conclusions can be drawn.

5. Genitalia. The presence of a penis and ovipositor is yet another synapomorphy uniting the subgroups of opilionids (Savory finds this to be of "negligible significance"). Martens (1976) studied the musculature of the penis and found evidence that the muscularization of the penis is primitive and that a transformation series proceeds in the direction of reducing these muscles, until in the Gonyleptoidea and Oncopodoidea the penis is operated entirely by hemolymph pressure. Cyphophthalmids have three penial muscles, the largest number found, and thus according to Martens are primitive in this respect. Therefore, the penial musculature is a plesiomorphy in the group and cannot safely be used to separate them. Further, the distinctiveness of having three penial muscles is greatly reduced when the progessive loss of the muscles in more evolved groups becomes clear.

The ovipositor has already been discussed; it shows that the Cyphophthalmi and Phalangioidea are related.

Savory also mentions the lack of a genital operculum (an extension of the first abdominal segment completely closing the gonostome) in the cyphophthalmids. Only in some ischyropsalidoids and troguloids, and in all laniatorids, is the genital operculum regularly present as a separate sclerite. In most phalangioids, the operculum is not hinged to the abdominal sternite, but simply an extension of it which serves both a protective function and to orient the gonostome anteriorly for the "face to face" copulation of the animals. This is simply a somewhat more developed form of the first abdominal sternite in cyphophthalmids, where the structure indeed does not cover the gonostome, but where it does extend between the fourth coxae, and is sometimes furnished with a deep transverse groove in its apical part, a suggestion of a nascent operculum. If anything, this character suggests a relationship between the Cyphophthalmi and Phalangioidea, not uniqueness. Further, if the separate operculum is considered apomorphic, then not having it is primitive and cannot be used to determine relationships.

6. Spermatophore. In a thesis completed in 1948, R. R. Forster demonstrated that the sperm of a species of *Rakaia* move from the testes in the direction of the penis in the form bundles, which he called spermatophores. Dr. Forster kindly sent me a series of 35 mm. photographs taken from microscope slides prepared more recently and they clearly show these sperm bundles. But can they be called spermatophores in the same sense as, for example, the spermatophores of the Pseudoscorpionida, Uropygi, and Amblypygi? The observation has been repeated in more detail by Juberthie, Manier, and Boissin (1976). They found, by means of electron microscope studies, that *Siro rubens* produces both functional sperm and nonfunctional, degenerate sperm. In the distal part of the tract, the functional sperm arrange themselves around a core of secreted material, and the nonfunctional sperm form a concentric layer around them; the whole mass is only 30 μm in diameter. They explicitly state: "*La 'boule spermatique' n'est pas l'equivalent d'un spermatophore car tous ses constituants proviennent due testicule; l'envelope des spermatophores, quand elle existe, est, en effet, sécréteé par d'autre composants de l'appariel génital* (Juberthie, Manier and Boissin, 1976)." Although Bacceti (1979) thinks that the type of sperm found in cyphophthalmids is primitive compared to that in other opilionids, he seems to overlook the fact that during spermatogenesis, *Siro* sperm retract their flagella. Flagellated sperm are found in *Ischyropsalis* species (Juberthie, 1964), surely a more primitive condition. In *Ischyropsalis* there is no evidence of the formation of a spermatic mass, nor has such an adaptation been found in the few other opilionids studied. Is this a specialization, or the retention of a primitive feature? Being coupled with a peculiar, evidently highly evolved type of spermatogenesis suggests that this is not a plesiomorphic feature. But it is entirely possible that in the course of evolution away from the primitive method of depositing a spermatophore on the substrate, the cyphophthalmids, as in some ticks, first form an "endospermatophore," which is transferred without being deposited.[4]

In any case, the presence of a sclerotized genital penis and direct copulation in all opilionids is very nearly unique in the Arachnida (paralleled only in a few mites), and certainly overshadows any minor differences in spermatogenesis. The presence of a penis in cyphophthalmids, regardless of the details of sperm transfer, refutes Savory's contention that they form "one of the early ancestral arachnid groups."

7. Life History. The lifespan of nine years or so is the longest recorded for any opilionid, approached only by the trogulids, which may live for three or four years. However, Savory is wrong when he asserts that no other opilionids live underground: many do, especially in the families Trogulidae, Nemastomatidae, Triaenonychidae, Phalangodidae, Erebomastridae, and Stygnommatidae. Is there really a distinction between living in the various layers and kinds of organic litter and in the soil? *Siro* species have been collected in both situations. Savory also claims that the Cyphophthalmi alone pass developmental stages that differ strongly from the adult ("nymphs"), but this is incorrect. Juvenile cosmetids differ a great deal from the adults (Goodnight and Goodnight, 1976). The characteristic appearance of *Ortholasma pictipes* (Nemastomatidae) is assumed only

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[4] Legendre and Lopez (1978) have demonstrated a true spermatophore in the spiders *Apneumonella* sp. and *Telema tenella*. They did not suggest that a new order of Arachnida be set up for these species.

at the last molt; in fact young and adults in this genus are so different from one another that Goodnight and Goodnight (1945) described a juvenile *Ortholasma* as a new genus in a completely different family (Shear, 1975).

Judged even by his own criteria, I believe that Savory has failed to show that the "mass of distinctiveness" claimed for the cyphophthalmids exists when they are accurately compared to the other opilionids, viz.: the characters claimed are in many cases similar in kind to those found in other opilionid groups, and nearly all are simply parts of transformation series that serve to relate and join Cyphophthalmi to the other Opiliones, rather than to separate them.

Such debates as these invigorate our science: there *is* more to be said. More thorough investigation of any hypothesis of relationship can only result, ultimately, in a truer picture of the course of evolution.

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