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A CLADISTIC ANALYSIS OF THE CYPHOPHTHALMID GENERA (OPILIONES, CYPHOPHTHALMI)

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ABSTRACT. A phylogenetic analysis of the genera of Cyphophthalmi is undertaken by studying 32 morphological characters in 43 species representing all families and most genera. The analysis is complemented with a molecular analysis using 18S rRNA and 28S rRNA sequence data of twelve cyphophthalmid species representing ten genera. The Cyphophthalmi are monophyletic, as are the families Stylocellidae and Pettalidae. However, the families Sironidae, Ogoveidae, and Neogoveidae are not monophyletic. Relationships among families need more data, but molecular characters strongly support the monophyly of Troglosironidae + Neogoveidae. Rooting the cyphophthalmid tree by using sequence data of one Eupnoi, one Dyspnoi, and one Laniatores results in two alternatives, one proposing a sister group relationship of Stylocellidae to the remaining taxa, or alternatively Pettalidae (with *Suzukielus*?) as sister group of the remaining cyphophthalmids. The position of *Troglosiro*, *Suzukielus*, *Metasiro*, *Huitaca*, and the epigean ‘‘*Neogovea*’’ *mexasca* are re-evaluated and discussed.

Keywords: Cyphophthalmi, systematics, molecular data, morphological data, cladistics

The arachnid suborder Cyphophthalmi contains about 115 described species (Giribet 2000) of mostly inconspicuous opilionids. The suborder is the smallest of the four opilionid suborders (the other three being Eupnoi, Dyspnoi, and Laniatores according to Giribet et al. 1999, 2002. The taxonomy of the group has changed considerably in recent times, especially with the work of Shear (1980, 1993a). The first attempt to systematize the suborder was the monographic work of Hansen & Sørensen (1904), which divided the single family Sironidae into two subfamilies, named Stylocellini (sic) and Sironini (sic). The Stylocellini contained the genera *Stylocellus* Westwood 1874, *Ogovea* Hansen & Sørensen 1904, and *Miopsalis* Thorell 1890. The subfamily Sironini contained the genera *Pettalus* Thorell 1876, *Purcellia* Hansen & Sørensen 1904, *Siro* Latreille 1796, and *Parasiro* Hansen & Sørensen 1904. One of the main characters to establish this classification is the presence of mobile coxae II in Sironini, while it is fused to coxae III and IV in Stylocellini. This classification remained in place until the seminal studies of Shear (1980, 1993a) who established the new classification system of the Cyphophthalmi, with two infraorders, Temperophthalmi Shear 1980 and Tropicophthalmi Shear 1980 corresponding to the subfamilies Sironini and Stylocellini of Hansen & Sørensen (1904). The Temperophthalmi contain a single superfamily, Sironoidea Simon 1879 with three families, Troglosironidae Shear 1993, Sironidae Simon 1879 and Pettalidae Shear 1980. The Tropicophthalmi include two superfamilies, Stylocelloidea Hansen & Sørensen 1904 with the single family Stylocellidae, and the Ogoveoidea, with the families Ogoveidae Shear 1980 and Neogoveidae Shear 1980.

The new classification of Shear (1980) was based on a cladistic (non-numerical) analysis of all known cyphophthalmid genera. However, the use of generic characters in many cases, and the discovery of new cyphophthalmid species since the study of Shear (1980) made us reevaluate the relationships among cyphophthalmid taxa by selecting exemplar species (Prendini 2001). With this aim, we have coded a morphological matrix including representatives of most cyphophthalmid genera, with the exception of *Odontosiro* Juberthie 1961, *Tranteeva* Kratochvíl 1958, *Manangotria* Shear & Gruber 1996, and *Ankaratra* Shear & Gruber 1996, for which we were unable to examine material. The remaining genera were represented by one or more species, including the type species whenever possible. We have also included representatives of some new taxa such as two putative species of *Miopsalis*, a new species of *Fangensis*, one pettalid species from Western Australia (''Pemberton''), and a new species of *Ogovea*.

The morphological study has been complemented with a molecular analysis of twelve cyphophthalmid species, representing the families Stylocellidae, Neogoveidae, Troglosironidae, Pettalidae, and Sironidae. The sequence data consists of complete 18S rRNA sequences and the D3 region of the 28S rRNA gene. Representatives of the Eupnoi, Dyspnoi, and Laniatores are used as outgroups in the molecular analysis.

METHODS

Abbreviations.—Specimens are lodged in the following institutions: American Museum of Natural History, New York (USA) = AMNH. Australian National Insect Collection, Canberra (Australia) = ANIC. The Natural History Museum, London (UK) = BMNH. James Cockendolpher private Collection, Lubbock (USA) = CCol. Field Museum of Natural History, Chicago (USA) = FMHD. Field Museum of Natural History, Arachnid collection, Chicago (USA) = FMAC. Museo Civico di Storia Naturale 'Giacomo Doria', Genova (Italy) = MCSN. Museum of Comparative Zoology, Harvard University, Cambridge (USA) = MCZ. Muséum d'histoire naturelle, Genève (Switzerland) = MHNG. Natal Museum, Pietermaritzburg (South Africa) = NMSA. South African Museum, Cape Town (South Africa) = SAM. Senckenberg Museum, Frankfurt am Main (Germany) = SMF. Museum für Naturkunde, Zentralinstitut der Humboldt-Universität zu Berlin, Berlin (Germany) = ZMB. Zoological Museum, University of Copenhagen (Denmark) = ZMUC. Western Australian Museum, Perth (Australia) = WAM.

Morphological data.—Material of over 90 species of cyphophthalmids (some undescribed) has been examined, and 43 of these species have been chosen to represent the maximum diversity within the group. All the species included in the analysis have been checked directly from specimens except for *Fangensis leclerci* and *Metagovea disparunguis* for which we have not been able to locate the types from the Rambla collection, or the Rosas Costa collection respectively, and therefore they are based on literature sources (see Appendix 1).

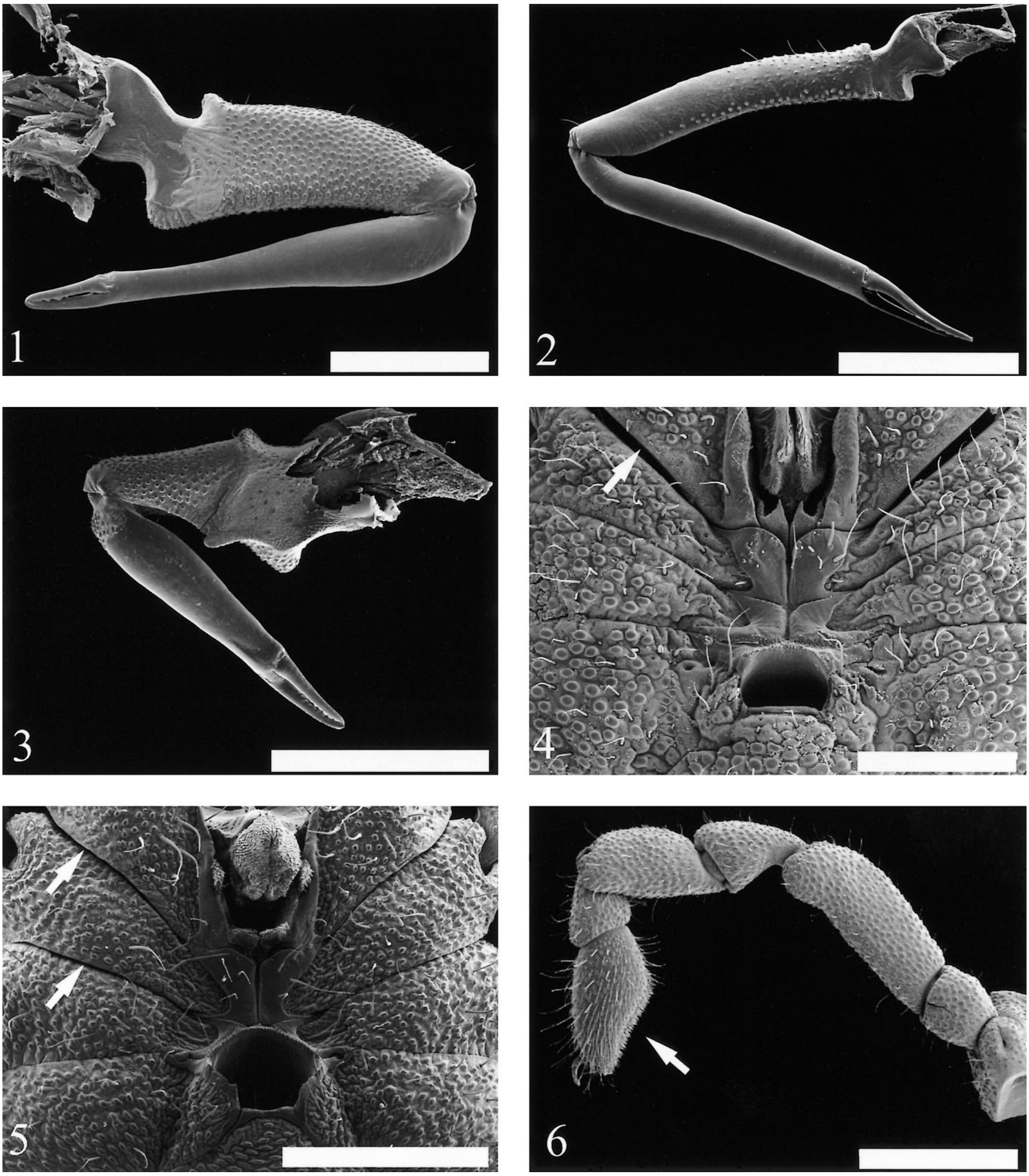
The morphological data matrix has been compiled in NDE v. 0.4.8 (Page 2000), and comprises 32 somatic and sexual characters. All characters are treated as unordered, and equally weighted. The character description and comments refer to the species used in this data matrix (Appendix 2). When relevant character states appear in species not represented in the matrix, those are discussed in the character description.

Morphological characters.—*1. Eyes: absent (0), present (1):* The presence of eyes in cyphophthalmids of the genus *Stylocellus* has been recently discussed elsewhere (Giribet et al. 2002; Shear 1980, 1993b). No polarity has been assumed.

2. Ozophore position: type 1 (0), type 2 (1), type 3 (2): Juberthie (1970b) categorized three types of ozophores according to the position on the carapace, since it is commonly used for species descriptions. Type 3 shows a dorsal position, as exemplified by *Speleosiro*, while the other two types show a lateral position, with type 1 being completely lateral (Juberthie 1970b: fig. 2a) and type 2 being slightly raised on the carapace (Juberthie 1970b: fig. 2c). The position of the ozophore shows sexual dimorphism in certain species of the genus *Parapurcellia*, but not in the species here used.

3. Attenuate chelicerae: absent (0), present (1): Cyphophthalmid chelicerae are a set of complex characters, perhaps displaying two extreme forms, a robust type found in many sironids, and a very special type, called attenuate type, where the distal cheliceral segment tapers, and the movable finger is extremely small. This condition is found in the members of the genus *Neogovea*, in *Huitaca ventralis* (Fig. 1), and *Pettalus cimiciformis*. However, the cheliceral type of ''*Neogovea*'' *mexasca* (Fig. 2) is not considered attenuate; it is an elongated type of chelicerae, but does not fit the description here used for the attenuate type. A similar condition is found in some stylocellid chelicera, that even though tapering, they do not have a reduced mobile digit.

4. Distal segment of chelicerae ornamented: absent (0), present (1): The distal segments of the chelicerae are smooth in most cyphophthalmids, but it is completely or partially ornamented in *Stylocellus* (Fig. 3), *Fan-*



Figures 1–6.—1. Attenuate left chelicera of *Huitaca ventralis*; 2. Left chelicera of ‘‘*Neogovea*’’ *mexasca*; 3. External view of left chelicera of *Stylocellus ramblae* showing the dorsal crest and the two ventral protuberances of the basal segment, and the ornamentation near the base of the distal segment; 4. Male ventral thoracic complex of *Metagovea philipi*, with arrowhead showing separation between coxae I and coxae II; 5. Female ventral thoraci complex of ‘‘*Neogovea*’’ *mexasca* with arrowheads showing separation between coxae I, coxae II, and coxae III; 6. Leg I of *Paragovia sironoides* showing the subapical modification of tarsus I where sensory hairs concentrate. Scale bars = 200 μm (Fig. 4), 400 μm (Fig. 5), 500 μm (Figs. 1–3, 6).

gensis (Rambla 1994: Plate II, fig. 1), and *Miopsalis*.

5. Ornamentation of the distal cheliceral segment: only ornamented at the base (0), mostly ornamented (1): Within the members of the Stylocellidae, the ornamentation of the distal cheliceral segment (character 4) can be found only near the base of the distal segment in certain *Stylocellus* (Fig. 3) and in *Miopsalis*. Alternatively, the ornamentation may cover a larger portion of the distal segment, as in *Fangensis leclerci* (Rambla 1994: Plate II, figure 1), or in certain *Stylocellus* (*S. silhavyi* and *S. gryllospecus*; Rambla 1991; Shear 1993b). The type species of the genus has not been examined, but according to Hansen & Sørensen (1904: Plate II, fig. 4b), it may belong to this type of chelicerae with the distal segment mostly ornamented.

6. Dentition of the mobile digit of the chelicerae: uniform (0), two types of dentition (1): The dentition of the mobile digit of the chelicerae is uniform in most cyphophthalmids, but there are two distinct types of dentition in members of the Pettalidae (Juberthie 1970b: fig. 3) except in *Parapurcellia*.

7. Basal article of chelicerae with dorsal crest: absent (0), present (1): A dorsal crest (‘‘dorsal ridge’’ of Hansen & Sørensen (1904)) on the basal article of the chelicerae is present in most cyphophthalmids (e.g. Figs. 1–3), but not in those of the genus *Siro*, or in *Paramiopsalis*.

8. Basal article of chelicerae with a ventral process: absent (0), present (1): A ventral protuberance on the basal cheliceral article (‘‘processus basalis’’ of Hansen & Sørensen (1904)) is present in most cyphophthalmids (e.g. Figs. 1–3) but not in those lacking the dorsal crest, or in a few other sironids and pettalids.

9. Basal article of chelicerae with a second ventral process: absent (0), present (1): Most cyphophthalmids have a ventral process on the basal cheliceral segment (character 9; Figs. 1, 2). Within the Stylocellidae, *Fangensis* and most members of the genus *Stylocellus* have a second ventral process (‘‘processus inferior exterior’’ of Hansen & Sørensen (1904)), anterior to the typical ventral process and connected to the dorsal crest by an external keel (Fig. 3; see also Hansen & Sørensen 1904; Shear 1993b). This character is generally correlated with having the ornamentation of the distal segment near the base (but not in *Fangensis*), while *Stylocellus silhavyi* lacks this second cheliceral ventral process. From the two species of *Miopsalis* examined here only one has the second ventral process and it is unknown whether the type species of the genus has it or not.

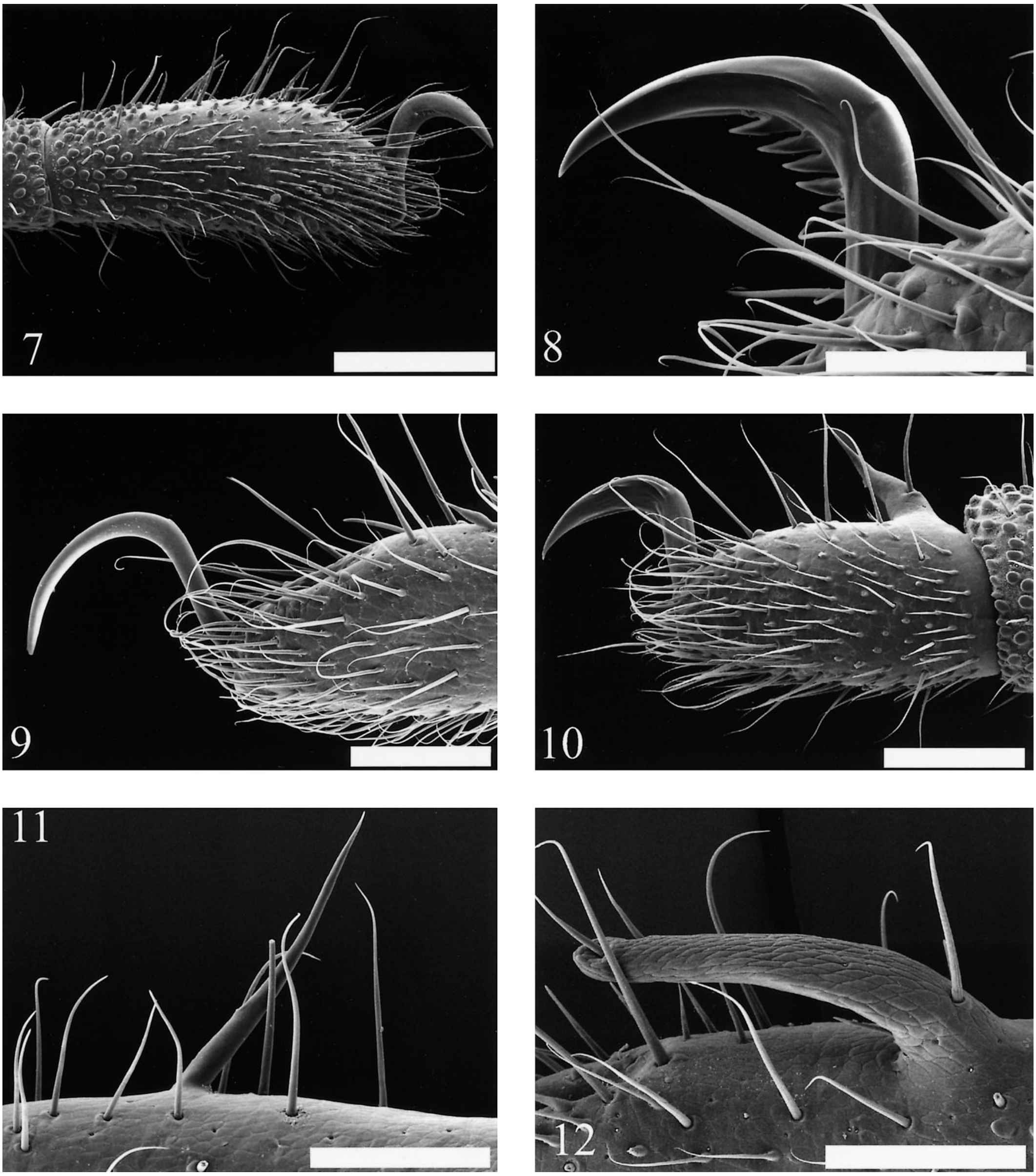
10. Palpal trochanter with ventral process: absent (0), present (1): A ventral process in the palp trochanter (Juberthie 1970b: fig. 11) is found in pettalids from Australia, New Zealand, and South Africa, but not in *Chileogovea*. A similar structure is found in *Paramiopsalis ramulosus* (Juberthie 1962: fig. 10).

11. Second coxa: free (0), fused to coxa of leg III (1): The coxa of leg II is free in members of the Sironidae and Pettalidae, while it is fused to the coxae of legs III and IV in members of the Stylocellidae (including *Fangensis* and *Miopsalis*), Neogoveidae (Fig. 4) and Ogoveidae. The genus *Troglosiro* has free coxa II, as well as ‘‘*Neogovea*’’ *mexasca* (Shear 1977) (Fig. 5). In contrast, *Paramiopsalis ramulosus* has the coxa II fused to the coxa of legs III and IV (Juberthie 1962), as does *Marwe coarctata*.

12. Tarsus of leg I with a subapical modification where sensory hairs concentrate: absent (0), present (1): A subapical modification in tarsus of leg I (Fig. 6) is found in most cyphophthalmid species. The absence of such a process in ‘‘*Neogovea*’’ *mexasca* has been confirmed with the SEM, but the absence of such a structure in the sironids needs further study using SEM.

13. Leg II ornamentation: metatarsus and tarsus smooth (0), metatarsus partially ornamented (1), metatarsus ornamented (2), ornamentation in the dorso-basal part of the tarsus (3), tarsus almost entirely ornamented (4): Juberthie (1970b) gave an account of different types of ornamentation in the legs I and II in several Temperophthalmi. Due to the observation of differences in ornamentation in legs I and II in certain cyphophthalmids, we prefer to restrict the definition of the character to the ornamentation of leg II, where the tarsus is not modified subapically as may occur with leg I.

14. Claw of leg II with a row of ventral teeth: absent (0), present (1): While most cyphophthalmids have a smooth claw II (Fig. 7), a row of ventral teeth is characteristic of all the members of the genera *Neogovea*, *Huita-*



Figures 7–12.—7. Smooth tarsal claw II of *Chileogovea oedipus*; 8. Toothed tarsal claw II of *Metagovea philipi*; 9. Smooth tarsal claw II of ''*Neogovea*'' *mexasca*; 10. Male IV tarsus with posterior adenostyle of *Metagovea philipi*; 11. Adenostyle of ''*Neogovea*'' *mexasca*; 12. Adenostyle of *Paragovia sironoides*. Scale bars = 50 μm (Fig. 8), 100 μm (Figs. 9–12), 200 μm (Fig. 7).

ca, *Metagovea* (Fig. 8), *Paragovia*, *Troglosiro*, and *Metasiro*. ''*Neogovea*'' *mexasca* lacks this type of teeth (Fig. 9). These teeth are not considered homologous to the lateral pegs of certain *Parasiro*.

15. Male tarsus IV: entire (0), bisegmented (1): Tarsus of leg IV of males bears an adenostyle, and in *Suzukielus sauteri* and certain members of Pettalidae (*Austropurcellia*, *Neopurcellia*, *Purcellia*, *Speleosiro*, and *Parapurcellia*) is bisegmented (Juberthie 1970b: fig. 5b).

16. Adenostyle: lamelliform (0), with a tuft of setae (1), plumose (2): The adenostyle is generally lamelliform (Figs. 10–12), but in Stylocellidae, *Metasiro* (Shear 1980: fig. 26) and all the species of *Neogovea* (except ''*Neogovea*'' *mexasca*: Fig. 11) the adenostyle terminates in a tuft of setae (Shear 1977, 1980). The adenostyle of *Paramiopsalis ramulosus* is plumose (Rambla & Fontarnau 1984: fig. 5).

17. Adenostyle in the most-basal region of the tarsus: absent (0), present (1): The position of the adenostyle is highly variable, tending to be near the middle of the tarsus in members of the Stylocellidae. In members of the genera *Metagovea* (Fig. 10), *Huitaca*, *Paragovia* (Legg 1990: fig. 15), and *Metasiro* (Shear 1980: figure 26) the adenostyle emerges from the most-basal portion of the tarsus. However, *Paragovia sironoides* (Fig. 12) does not have an adenostyle at the most-basal region of the tarsus.

18. Ovoid plate on male tarsus IV: absent (0), present (1): An ovoid plate on the internal-lateral side of the male tarsus IV was described for *Fangensis leclerci* (Rambla 1994: plate III, figs. 1, 2), and is also found in a new species of *Fangensis* from Thailand collected by P. Schwendinger.

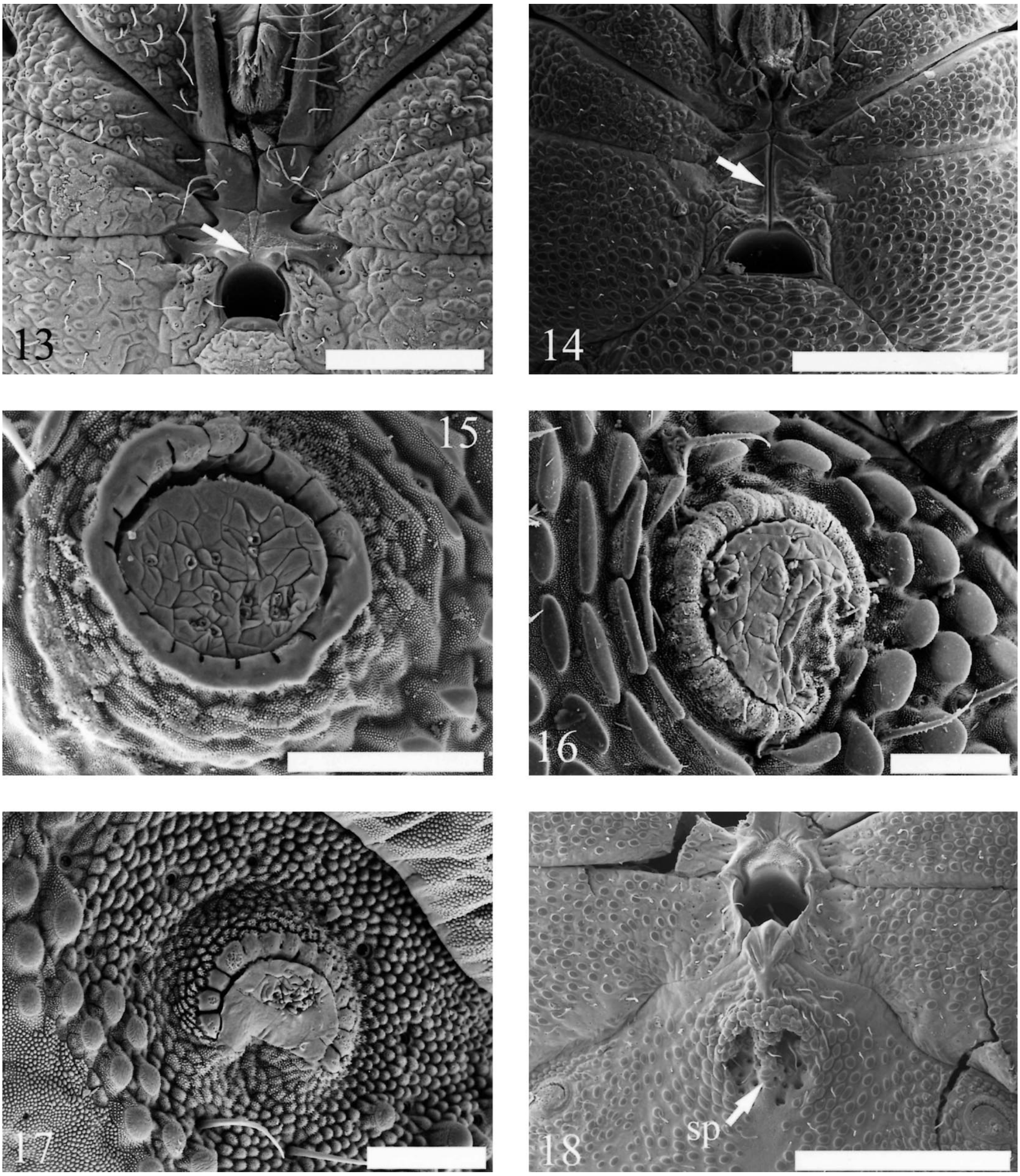
19. Male coxae IV meeting ventrally in the midline: absent (0), present (1): The coxae of leg IV generally meet in the midline in males (Fig. 13), but in certain species of the Ogoveidae and Neogoveidae, they form a tube-like structure for the penis, not meeting in the midline (Fig. 4).

20. Male gonostome small, with coxae IV meeting ventrally for a distance longer than the length of the genital opening: absent (0), present (1): In most members of the Pettalidae, the male genital opening is very small, with the coxae IV meeting in the midline forming the solid anterior wall of the gonostome. In this case the gonostome is always shorter than the length of the coxae IV that run parallel in the midline (Fig. 14).

21. Spiracle shape: circular (0), open circle (1), ''C'' shaped (2): Spiracle morphology has been overlooked in cyphophthalmid taxonomy, although it seems to be conserved at the familial level. Typical sironids, most neogoveids (including ''*Neogovea*'' *mexasca*, Fig. 15), *Ogovea*, *Troglosiro* and *Marwe* have circular spiracles. All pettalids, some neogoveids (*Neogovea microphaga* and two undescribed neogoveids from Trinidad and Venezuela), *Metasiro* and *Suzukielus* have spiracles that are an open circle (e.g. *Chileogovea oedipus*, Fig. 16). All the stylocellids (including *Fangensis* and *Miopsalis*) have spiracles shaped like the letter ''C'' (Fig. 17). *Speleosiro argasiformis* bears a special type of spiracles, resembling the open circular type of typical pettalids, but it is so open that it resembles the ''C'' type of stylocellids. However, the direction of the aperture corresponds to that of the pettalids and not that of the stylocellids, and therefore we have coded *Speleosiro* as belonging to the open circle type.

22. Male sternal glands: absent (0), present (1): Sternal secretory glands have been described for *Ogovea nasuta* and *Huitaca ventralis* (Fig. 18), and have been used to suggest a sister group relationship for these two genera (Shear 1979, 1980). Similar structures of possible secretory function have been recently found in *Metagovea philipi* (Figs. 19, 20), two undescribed *Metagovea* species from Ecuador, and *Paragovia sironoides* (Figs. 21, 22). Juberthie (1979) reported a type of secretory structures for the genus *Troglosiro* similar to the ones found in the Neogoveidae, although according to Shear (1980) these structures have questionable homology with those of *Ogovea* and *Huitaca* as they do not fulfill the criterion of positional homology. Here we have chosen to code the sternal glands of *Huitaca*, *Ogovea*, *Metagovea*, *Paragovia*, and *Troglosiro* as homologous structures.

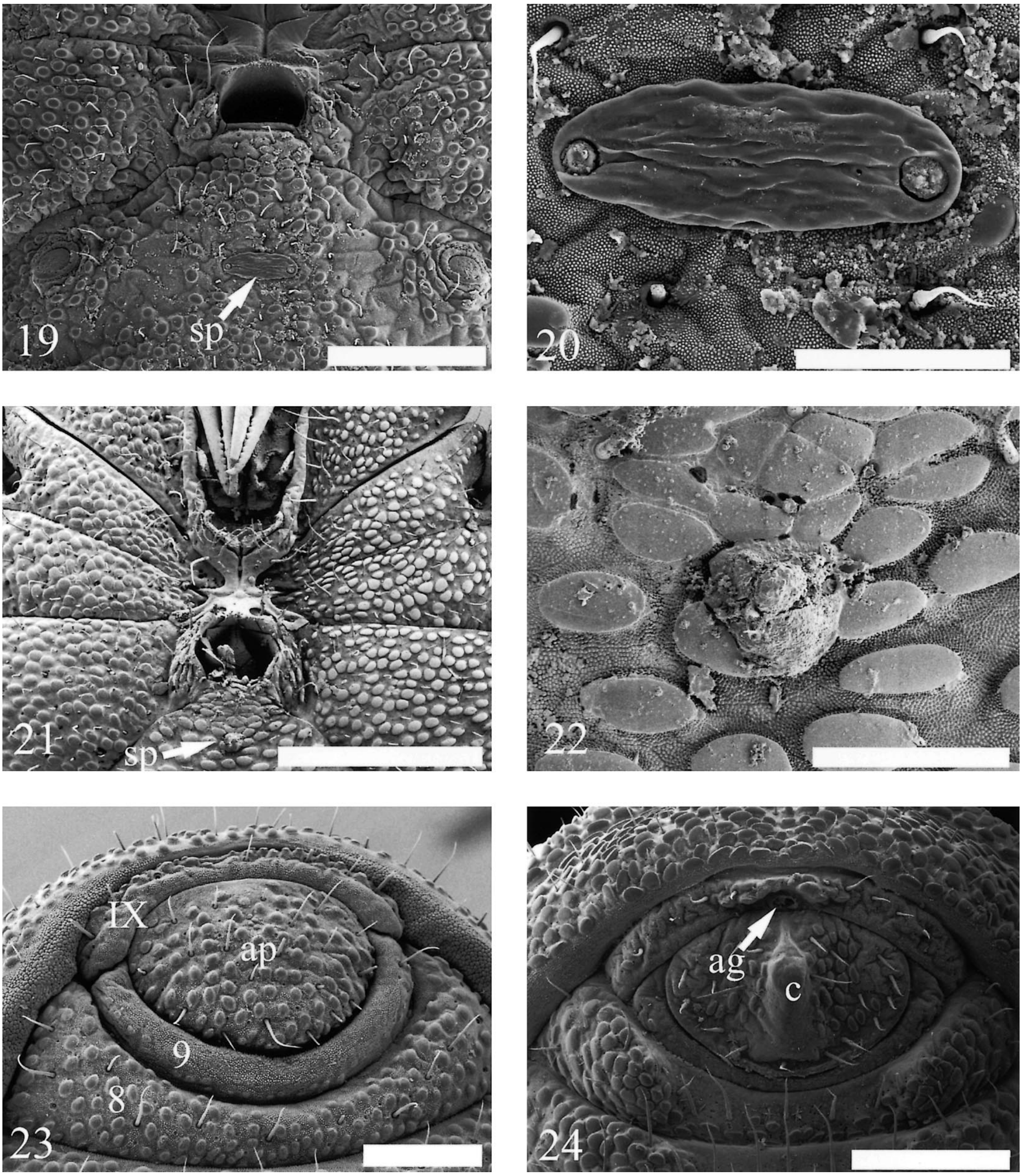
We have examined the types and all the material reported in the literature of *Brasilogovea microphaga* (synonymized by Shear 1980), ''?Gen.'' *enigmaticus*, and all the species of the genus *Neogovea*. ''*Neogovea*'' *mexasca* clearly lacks the sternal glands when studied with an SEM. Unfortunately, the male of ''?Gen.'' *enigmaticus* is unknown, and from the other species, all the known males except one specimen of *N. immsi* lack the sternal area after having been dissected to study the penis. The single complete male of *N. immsi* has the ventral area covered by a film of an unidentified substance that cannot be removed from the specimen. This substance seems to emerge from some ventral gland and a few pores seem to be apparent in the centre of the second sternite. However, this needs confirmation with fresh material of males of *Neogovea*, and we have chosen to code it as a '?'. Therefore, with the exception of ''*Neogovea*'' *mexasca*, all members of *Neogovea* and related genera



Figures 13–18.—13. Male ventral thoracic complex of and undescribed *Metagovea* species from Chiriboga (Ecuador) showing the short area of contact of the IV coxae; 14. Male ventral thoracic complex of *Chileogovea oedipus* showing the large contact area of the IV coxae; 15. Circular spiracle of ''*Neogovea*'' *mexasca*; 16. Open circular spiracle of *Chileogovea oedipus*; 17. Detail of the spiracular area of *Stylocellus ramblae* with the spiracle in the center; 18. Male sternal area of *Huitaca ventralis* showing the sternal pores (sp). Scale bars = 50 μm (Figs. 15–17), 200 μm (Fig. 13), 500 μm (Figs. 14, 18).

are coded as '?', although we believe that sternal organs may be found when fresh material is examined.

23. Sternal apophysis of male: absent (0), present (1): A sternal apophysis in the ventral region is found in males of the genus *Ogovea* (e.g. Shear 1980: fig. 27) but not in any other cyphophthalmids.



Figures 19–24.—19. Male sternal area of *Metagovea philipi* showing the sternal pores (sp); 20. Detail of the sternal pores of *Metagovea philipi*; 21. Male sternal area of *Paragovia sironoides* showing the sternal pores (sp); 22. Detail of the sternal pores of *Paragovia sironoides*; 23. Female anal region of *Stylocellus ramblae* showing the anal plate (ap) and the unfused sternites 8, 9, and tergite IX; 24. Male anal region of *Chileogovea oedipus* showing the longitudinal carina of the anal plate (c), and the opening of the anal glands (ag). Scale bars = 50 μm (Figs. 20, 22), 100 μm (Fig. 23), 200 μm (Figs. 19, 24), 400 μm (Fig. 21).

24. Sternite 8, 9, and tergite IX: all free (0), sternites 8 and 9 fused (1), sternite 9 and tergite IX fused, but sternite 8 free (2), all fused into corona analis (3): The different degrees of fusion of sternites 8 and 9, and tergite IX have been extensively discussed in the literature (Juberthie 1970b; Shear 1980). All segments are free in the Stylocellidae and in most members of the Pettalidae, but not in *Pettalus cimiciformis*, in which sternite 9 is fused to tergite IX, but sternite 8 remains free. Sternites 8 and 9 may show different degrees of fusion leaving tergite IX free as in at least some *Parasiro* (only fused in the midpart) or in *Metasiro* and *Paramiopsalis* (almost completely fused), but until more detailed study of these conditions is conducted using SEM, we prefer not to separate these two states. *Ogovea*, *Troglosiro*, *Siro*, *Marwe*, and the Neogoveidae all have a complete corona analis (all segments fused).

25. Relative position of sternite 9 and tergite IX: stylocellid type (0), pettalid type (1): In those Cyphophthalmi without a complete corona analis, the relative position of sternite 9 and tergite IX shows two typical configurations. A first configuration, here named ‘‘stylocellid type’’ is illustrated in Fig. 23, in which both sclerites meet towards the midline of the anal plate, and sternite 8 does not contact tergite IX. This is found in all stylocellids and those sironids without a complete corona analis. In *Suzukielus* and the females of all the pettalids (the males may have modified anal regions), a ‘‘pettalid’’ type occurs (e.g. Fig. 24), in which tergite IX covers laterally sternite 9, and clearly meets sternite 8.

26. Male tergite IX: entire (0), divided (1): Tergite IX is divided in the males of *Suzukielus sauteri* and in several Pettalidae, such as certain species of *Austropurcellia*, *Neopurcellia*, *Rakaia*, and *Parapurcellia*.

27. Male anal plate: without modifications (0), with longitudinal carina (1), with concentration of setae (2): Male anal plates are similar to those of females, without modifications in all the Tropicophthalmi and in some sironids, *Troglosiro*, *Pettalus*, and in some undescribed pettalids from Western Australia (here represented by the terminal ‘Pemberton’). Some members of the Sironidae (*Paramiopsalis*, *Siro*, and *Suzukielus*), and *Chileogovea* (Fig. 24) have a longitudinal carina. Finally, most members of the Pettalidae have anal plates extremely modified with all kinds of concentrations of setae such as tufts of setae in a groove in the anal operculum (e.g. *Purcellia*, *Parapurcellia*, *Speleosiro*), a ‘‘scopula’’ on the dorsal surface of the anal plate (e.g. *Rakaia*, *Neopurcellia*), or an ‘‘anterior scopula’’ (*Austropurcellia*).

28. Male tergite VIII bilobed: absent (0), present (1): Tergite VIII becomes bilobed in the males of several pettalid species.

29. Male abdominal exocrine glands (anal glands): absent (0), present (1): The presence of a special type of abdominal exocrine glands associated with the anal complex of males (Juberthie 1962, 1967) has been observed in several species of the families Sironidae and Pettalidae, and its function is probably for dispensing a pheromone (Shear 1980). Although the anal glands may be directly associated to some of the modifications of the anal plate and tergite IX, at least in the genus *Fangensis*, the anal glands do not entail other specific modifications. For this reason, we have coded this character independently. Anal glands have been specifically reported in *Fangensis leclerci* (Rambla 1994), *Paramiopsalis ramulosus* (Juberthie 1962), *Siro rubens* (Juberthie 1967), *Suzukielus sauteri* (Juberthie 1970a), and *Austropurcellia scoparia* (Juberthie 1988). Anal glands have also been observed in *Chileogovea oedipus* (Fig. 24), *Metasiro americanus*, *Siro duricorius*, *Siro exilis*, *Neopurcellia florensis*, *Rakaia arcticosa*, *Purcellia illustrans*, *Speleosiro argasiformis*, and in the new species of *Fangensis* from Thailand. However, the tufts of setae did not allow detailed examination of *Pettalus cimiciformis* or *Parapurcellia silvicola*, and have been coded as ‘?’. The undescribed pettalid from Pemberton lacks anal glands.

30. Ventral plate of penis hypertrophied: absent (0), present (1): The ventral plate of the penis is hypertrophied in members of the genus *Neogovea* (*N. immsi*, *N. kamakusa*, *N. kartabo*, and *N. microphaga*), thickened apically and dorsoventrally bifurcate (Martens 1969; Shear 1977, 1980).

31. Ventral setae of penis: absent (0), present (1): Ventral setae are found in the penis of most cyphophthalmid, and certain lineages show a tendency towards reduction of the number of setae. Ventral setae are absent in *Paragovia sironoides* (Legg 1990: fig. 8), *Neogovea immsi*, and ‘‘*Neogovea*’’ *mexasca* (Shear 1980: fig. 5).

32. Ovipositor with sense organs: absent (0), present (1): The ovipositor of *Parasiro* lacks the sense organs commonly found in the ovipositors of the Cyphophthalmi (Juberthie 1970b: fig. 12).

Molecular data.—The molecular data comprise twelve cyphophthalmid species belonging to five families (Stylocellidae, Neogoveidae, Troglosironidae, Pettalidae, and Sironidae) and ten genera (*Stylocellus*, *Fangensis*, *Paragovia*, *Troglosiro*, *Chileogovea*, *Purcellia*, *Parapurcellia*, *Siro*, *Parasiro*, and *Paramiopsalis*) (see Table 1). Outgroups representing the other three major lineages of Opiliones, Eupnoi, Dyspnoi, and Laniatores, have been employed to root the cyphophthalmid trees. Sequence data for the 18S rRNA and D3 region of the 28S rRNA loci have been obtained following standard protocols for DNA extraction and amplification for Opiliones (Giribet et al. 1999, 2002), and sequenced in an ABI PRISM® 3100 Genetic Analyzer following manufacturer protocols.

Phylogenetic analysis.—The phylogenetic analysis of the morphological data set has been executed with the parsimony-based computer program NONA v. 2.0 (Goloboff 1998), using a heuristic search strategy with 1000 random addition replicates using tbr (tree bisection-reconnection) branch swapping, and retaining up to 10 trees per replicate (hold10000; hold/10; mult*1000). The results of this first round of searches were submitted to tbr swapping without limiting the number of trees (max*). Bremer support (BS) values (Bremer 1988) and relative Bremer supports (RFD) (Goloboff & Farris 2001) were calculated with the computer program TNT (Goloboff et al. 2000) holding 10,000 trees. Bremer support generates absolute values of the degree to which a tree is suboptimal compared to another. A defect of that method is that it does not always take into account the relative amounts of evidence contradictory and favorable to the group. This problem is diminished if the support of the group is calculated as the ratio between the amounts of favorable and contradictory evidence, as proposed by Goloboff & Farris (2001). Potential advantages of the relative supports over normal Bremer support are that they vary between 0 and 1 and they provide an approximate measure of the amount of favorable/contradictory evidence (for example, if the RFD is 0.25, the amount of contradictory evidence is 75% the amount of favorable evidence, so it is equivalent to the conflict of 4 characters versus 3).

The molecular data have been analyzed following the direct optimization method (Wheeler 1996) as implemented in the computer program POY (Wheeler & Gladstein 2000). The analyses have been executed in a Linux parallel cluster of 11 nodes running pvm (Parallel Virtual Machine) at Harvard University (darwin.oeb.harvard.edu), each node consisting of two Pentium III processors at 1000 MHz, and 1 Gbyte of RAM. An analysis of multiple parameters (different insertion/deletion to change ratios, and transversion to transition ratios) was performed following a sensitivity analysis sensu Wheeler (1995). Basically, the two molecular partitions have been analyzed independently and in combination for nine combinations of parameters (gap:transversion:transition 111, 121, 141, 211, 221, 241, 411, 421, 441), choosing the parameter that minimizes overall incongruence when the partitions are analyzed in combination, following a normalized ILD metrics (Farris et al. 1995; Wheeler 1995) (Table 2). For more detailed explanations of the analyses refer to previous work by one of the authors (Edgecombe et al. 1999; Giribet et al. 2001, 2002).

RESULTS AND DISCUSSION

The search strategy implemented in NONA yielded trees of minimal length in 404 out of the 1000 replications performed. Six hundred minimum-tree length trees were found after swapping to completion the trees found on each replicate, at 83 steps (CI = 0.50; RI = 0.83). The strict consensus of the morphological trees (Fig. 25) can be rooted in three alternative positions, according to the molecular results obtained (see below). Basically, the root is placed between the Stylocellidae and the remaining taxa (rooting option 1), or between the Pettalidae and the remaining taxa (rooting option 2). Since molecular data are not available for *Suzukielus*, the root could also potentially be placed between *Suzukielus* and the sironids (rooting position 3).

The morphological trees (irrespective of where they are rooted) show the monophyly of Stylocellidae and Pettalidae, but the strict consensus of all the shortest trees shows irresolution for the Sironidae and Neogoveidae. The Stylocellidae clearly includes the genera *Fangensis* and *Miopsalis* (RFD = 100), a result also corroborated by the molecular data, which support monophyly of *Fangensis* and the two species of *Stylocellus* included for all parameter sets for the combined molecular (Figs. 26A & B), and 18S rRNA (Fig. 26C)

Table 1.—Opilionid taxa employed in the molecular analysis, country of origin, collector, and molecular partition represented.

Eupnoi: Phalangiidae				
Opilio parietimus	Canada	R. Holmberg	18S rRNA	28S rRNA
Dyspnoi: Nipponopsalididae				
Nipponopsalis abei	Japan	N. Tsurusaki	18S rRNA	28S rRNA
Laniatores: Oncopodidae				
Oncopus cfr. *alticeps*	Malaysia	P. Schwendinger	18S rRNA	28S rRNA
Cyphopphthalmi				
Family Stylocellidae				
Stylocellus sp. BL	Malaysia	P. Schwendinger	18S rRNA	28S rRNA
Stylocellus sp. JP	Malaysia	P. Schwendinger	18S rRNA	28S rRNA
Fangensis sp.	Thailand	P. Schwendinger	18S rRNA	28S rRNA
Family Neogoveidae				
Paragovia sironoides	Equatorial Guinea	J. Lapuente & C. E. Prieto	18S rRNA	28S rRNA
Family Troglosironidae				
Troglosiro sp.	New Caledonia	G. B. Monteith	18S rRNA	28S rRNA
Family Pettalidae				
Chileogovea oedipus	Chile	J. Miller, F. Alvarez, J. Coddington	18S rRNA	
Purcellia illustrans	South Africa	G. Giribet & L. Prendini	18S rRNA	28S rRNA
Parapurcellia silvicola	South Africa	G. Giribet & L. Prendini	18S rRNA	28S rRNA
Family Sironidae				
Parasiro coiffaiti	Spain	E. Mateos	18S rRNA	28S rRNA
Paramiopsalis ramulosus	Spain	G. Giribet & M. K. Nishiguehi	18S rRNA	28S rRNA
Siro rubens	France	G. Giribet	18S rRNA	28S rRNA
Siro valleorum	Italy	Ferrario, Pantini, Pellizzoli, Valle	18S rRNA	28S rRNA

Table 2.—Tree length for the individual (18S: 18S rDNA; 28S: 28S rDNA) and combined (mol: molecular [18S + 28S]) datasets at different parameter values, and ILDs for the combined analyses. ILD number in bold reflects the minimum incongruence among data sets.

	18S	28S	MOL	ILD
111	308	175	497	0.0282
121	438	260	718	0.0279
141	690	422	1147	0.0305
211	325	198	537	**0.0261**
221	465	301	793	0.0340
241	741	503	1295	0.0394
411	350	232	607	0.0412
421	513	364	930	0.0570
441	837	628	1563	0.0627

analyses. This clade is clearly delimited biogeographically and is easily diagnosed by two unambiguous autapomorphies: an ornamented distal cheliceral segment (character 4), and ‘‘C’’-shaped spiracles (character 21). Other characters showing some degree of homoplasy are the presence of eyes (character 1) and the presence of tarsi almost completely ornamented (character 13). The monophyly of the genus *Fangensis* is supported by the presence of ovoid plate in the male tarsus IV (character 18) and by the presence of anal glands in the male (character 29), a feature that placed them originally within the Sironidae (Rambla 1993), but is now known for members of the families Sironidae, Pettalidae and Stylocellidae, and hence a putative synapomorphy of the Cyphophthalmi lost in several lineages.

The families Neogoveidae, Ogoveidae, Troglosironidae, and the clade containing the Sironidae + Pettalidae form a polytomy in the strict consensus of the morphological analysis (Fig. 25). The 18S rRNA data (Fig. 26C) show a similar pattern, with monophyly of the non-stylocellids for all parameter sets, but with irresolution between *Parasiro*, Pettalidae, (*Siro* + *Paramiopsalis*), and (*Troglosiro* + *Paragovia*). However, certain parameters for the combined analysis of 18S rRNA + 28S rRNA show an alternative rooting position, with Pettalidae being the sister group of the remaining cyphophthalmids (Fig. 26A). Irrespective of the rooting option, all molecular data (all partitions and combination of partitions, as well as all parameter sets) show monophyly of (*Troglosiro* + *Paragovia*) (Fig. 26). A putative synapomorphy for Troglosironidae + Neogoveidae is the sternal glands in the males, although their presence needs to be confirmed in members of the genus *Neogovea* (see discussion of character 22). If this relationship of *Troglosiro* and Neogoveidae, a stable result based on molecular data, is confirmed by further data, the position of *Troglosiro* as the sister group of Sironidae + Pettalidae (Shear 1993a) could be discarded.

The genus *Ogovea* is monophyletic, although its relationships to other genera are ambiguous, and molecular data are not available. Its relationship with *Huitaca* previously suggested based on the sternal secretory organs (Shear 1979) is not supported in this analysis since the character appears to be more widely distributed than previously thought. Sternal secretory organs are present in all males of the genus *Metagovea* examined so far (Figs. 19, 20), as well as in *Paragovia* (Figs. 21, 22). The morphology of *Huitaca* is also similar to that of other undescribed species of *Neogovea* from Trinidad and Venezuela, sharing the same cheliceral type (character 3), and differs considerably from the genus *Ogovea*. Neogoveid genera (*Paragovia*, *Huitaca* and *Metagovea*), and the ‘‘true’’ *Neogovea* (*Neogovea*, *Brasilogovea*, ‘‘?Gen.’’) are not resolved by the present morphological data, and they form a polytomy with Ogoveidae, Troglosironidae, and Sironidae—Pettalidae in the morphological tree. We will deal with these specific relationships in a forthcoming article revising the South American Neogoveidae.

The position of ‘‘*Neogovea*’’ *mexasca* is not consistent with previous classifications (Shear 1977, 1980). ‘‘*Neogovea*’’ *mexasca* clusters within the clade containing sironids and pettalids, due to many morphological characters. For example, coxae II are not fused to coxae III; the second leg claw lacks the ventral teeth (Fig. 9); and the chelicerae are elongated (Fig. 2) but with a large claw (not of the attenuate type typical of *Neogovea*). ‘‘Sironids’’ are here represented by two clades, one clade containing the genus *Parasiro*, and another clade containing the genera *Siro*, *Paramiopsalis* and *Marwe*, as sister group to *Suzukielus* + Pettalidae. Most of the relationships suggested for the clade containing the sironids are based on ambiguous optimizations, and character conflict may be very important. The sister

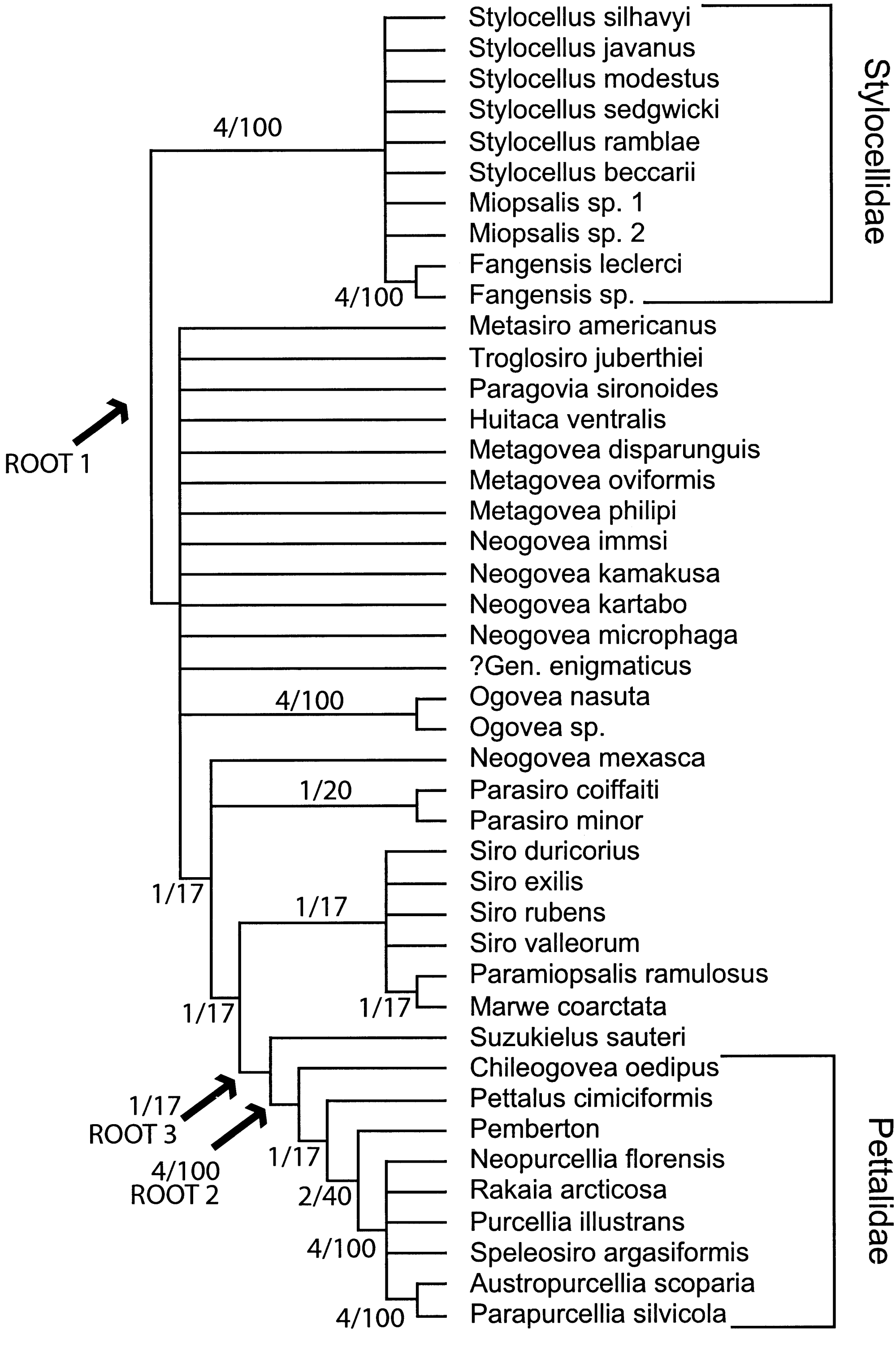


Figure 25.—Strict consensus of 600 trees of 83 steps (CI = 0.50; RI = 0.83) representing three alternative rooting positions as derived from the molecular analyses. Numbers in branches represent BS/RFD (Bremer support/Relative support).

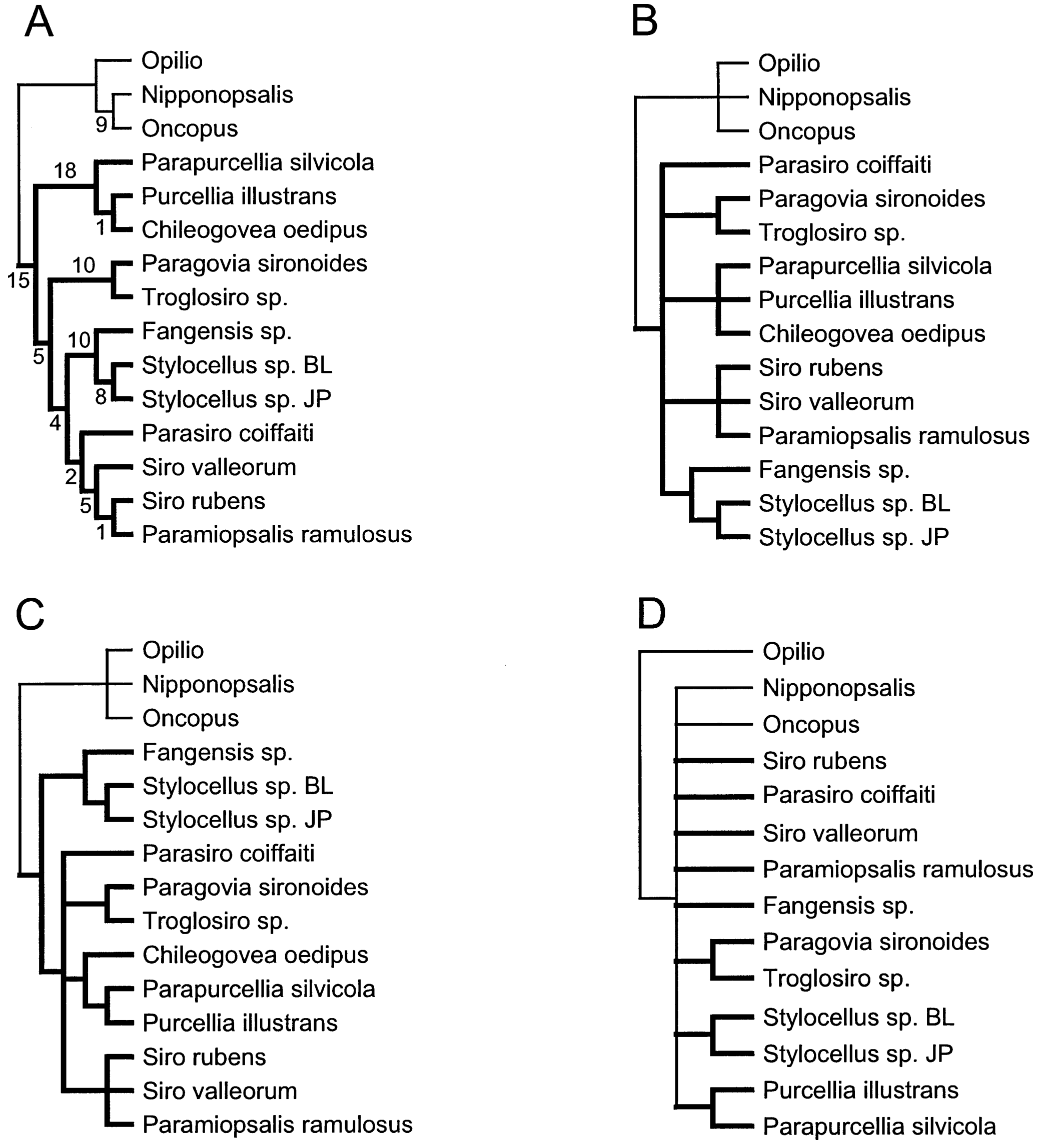


Figure 26.—Molecular trees with the cyphophthalmid taxa represented by thick branches. (A) Most parsimonious tree at gap cost = 2, transversion cost = transition cost = 1 (parameter set 211) for the combined analysis of 18S rRNA and 28S rRNA sequence data (537 steps; ILD = 0.0261). Numbers on branches represent absolute Bremer support values. (B) Strict consensus of all parameter sets examined (gap:transversion:transition 111, 121, 141, 211, 221, 241, 411, 421, 441) for the combined analysis of 18S rRNA and 28S rRNA sequence data. (C) Strict consensus of all parameter sets examined for the analysis of 18S rRNA sequence data. The split between Stylocellidae and the remaining cyphophthalmids is obtained for all parameter sets. (D) Strict consensus of all parameter sets examined for the analysis of 28S rRNA sequence data.

group relationship of *Marwe* and *Paramiopsalis* is based on the presence of fused second coxae, a character only shared by these two species within the ‘‘Sironidae’’. We suspect that this relationship will not withstand future analyses incorporating unknown penile and molecular characters of *Marwe*.

The position of *Metasiro* is uncertain, and more data are necessary to place this taxon unambiguously, although the claw of leg II with a row of ventral teeth (character 14) or the basal position of the adenostyle (character 17) may indicate a relationship with Neogoveidae, while some trees place it as the sister group to Sironidae + Pettalidae (if rooting position 1 is used).

Pettalidae is a clear monophyletic group in both morphological (Fig. 25; RFD = 100; BS = 4) and molecular analyses for all partitions and parameter sets (Fig. 26A, BS = 18; Figs. 26B–D) with most of its members having dorsal ozophores (character 2), two types of dentition in the mobile digit of the chelicerae (character 6), and a small type of male gonostome (character 20). All pettalids also share with a few *Neogovea*, *Metasiro*, and *Suzukielus* an open circular type of spiracles (character 21). *Suzukielus sauteri* appears in fact to be the sister group to Pettalidae (or sister to the remaining Cyphophthalmi if rooting position 3 were correct), both taxa sharing the distinct relative position of tergite IX and sternites 8 and 9 (character 25). This character, together with the open circular spiracle only found in *Metasiro* among the classical sironids (all other sironids that we have examined have a circular spiracle) makes doubtful the phylogenetic position of *Suzukielus* as a true sironid as suggested by other authors.

Sironidae are in fact non-monophyletic irrespective of the rooting position selected. If the rooting position 1 were correct, then Sironidae would be paraphyletic with respect to Pettalidae, reflecting the idea of a ‘‘more complex phylogeny’’ of Sironidae-Pettalidae than that proposed by Shear (1980) (Juberthie 1989). Monophyly of *Siro* and *Paramiopsalis* is found in most molecular analyses for all parameters (Fig. 26), however, *Parasiro* does not cluster with the other sironids under certain parameter sets (Figs. 26B–C).

According to the molecular analyses, Cyphophthalmi are monophyletic (Fig. 26A–C), with the exception of certain parameter sets for the 28S rRNA partition (Fig. 26D), as shown in previous molecular analyses (Giribet & Wheeler 1999; Giribet et al. 1999, 2002), although two possibilities exist for rooting the morphological tree. One possibility suggests a root separating the Stylocellidae from the remaining cyphophthalmids (root 1 for all parameter sets for the 18S rRNA partition, and for parameter sets 111 and 241), or alternatively in the branch separating Pettalidae from the remaining cyphophthalmids (root 2 or root 3 for parameter sets 111, 121, 211, 221, 411, 421, 441). These are the only two rooting possibilities suggested by the molecular analyses, and both are equally parsimonious under certain parameter sets (111, 241). These alternative rooting positions may have very different morphological and biogeographical implications. A split between the Pettalidae and the remaining cyphophthalmids, as suggested by most combined 18S rRNA + 28S rRNA trees would imply a split between Gondwanan and Laurasian cyphophthalmids, while an interesting morphological implication of the split between Stylocellidae and the remaining families (as suggested by 18S rRNA data alone) would have to do with the homology of the stylocellid eyes. With the data in hand, we cannot choose among either one of these two rooting positions. What seems clear at this point is that neither one of the two rooting alternatives is compatible with the classification of Hansen & Sørensen (1904) or Shear (1980), rooting between the Tropicophthalmi and the Temperophthalmi.

The molecular trees are highly congruent with the morphological analysis here presented, and recognize the monophyly of major families such as Stylocellidae, Pettalidae, and more ambiguously, Sironidae. These results are encouraging for pursuing further morphological and molecular research for internal cyphophthalmid phylogeny.

In general, the phylogenetic relationships here presented mainly agree with the classification system for the Cyphophthalmi proposed by Shear (1980), although alternative rooting positions would make Tropicophthalmi or Temperophthalmi paraphyletic. Both in Shear’s and in the present analysis, the limitation in characters may result in weakly supported relationships. As an example, many nodes in the morphological tree here presented are unresolved for lack of information, or possess conflict of characters (low RFD). Only seven nodes have no conflicting characters (RFD = 100). From those, one supports the family Stylocellidae (*sensu* Giribet 2002), and another supports the family Pettalidae. However, the other families of Cyphophthalmi, Sironidae, Neogoveidae, and Ogoveidae (Troglosironidae is only represented by one species) *sensu* Shear (1980) are non-monophyletic. Hopefully, the addition of more characters through the generalized use of SEM and DNA sequence data will help to refine our knowledge of the evolutionary history of this interesting arachnid group.

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Appendix 1.—Morphological data matrix.

Species	Characters
	00000000011111111112222222222333
	12345678901234567890123456789012
Stylocellus beccarii	11010011101140010010200000000001?
Stylocellus javanus	1101001110114 0??00??2??00???????
Stylocellus modestus	110100111011400?00??2?000000????
Stylocellus ramblae	1101001110114001001020000000 0???
Stylocellus sedgwicki	110100111011400?00?020000000?01?
Stylocellus silhavyi	11011011001140010010200000000011
Fangensis leclerci	0101101110114001011020000 0?01011
Fangensis sp.	?1011011101140010110200000101???
Miopsalis sp. 1	0101001100114 0??????2??00???????
Miopsalis sp. 2	010100111011400 10?102?000000????
Metasiro americanus	0100-0110001210110101001000 01011
Troglosiro juberthiei	0100-0110001210000100103-0000011
Paramiopsalis ramulosus	0100-000-11000020010?00100101??1
Parasiro coiffaiti	0000-010-00010000010000100000010
Parasiro minor	0000-0110000100000100001000000 10
Siro duricorius	0100-000-000000000100003-0101011
Siro exilis	0100-000-000000000100003-010101?
Siro rubens	0100-000-000000000100003-0101011
Siro valleorum	0100-000-000000000100003-01010??
Suzukielus sauteri	0100-0110000000100010100011101 0?1
Pettalus cimiciformis	0210-111000130000011 1002-001????
Chileogovea oedipus	0200-1110001300000111000 10101011
Austropurcellia scoparia	0100-110-1012010001110001121 1011
Neopurcellia florensis	0200-1110101201000111000 11211???
Rakaia arcticosa	0200-1110101100000111000 11211??1
Pettalidae sp., Pemberton	0200-1110101100000111000 10000???
Parapurcellia silvicola	0100-010-101101000111000 1121????
Purcellia illustrans	0200-1110101101000111000 10211011
Speleosiro argasiformis	0200-1110101101000101000 10211011
Ogovea nasuta	0100-0110011400000000113-000001?
Ogovea sp.	0100-0110011400000000113-0000???
Paragovia sironoides	0100-0110011410000?00103-000000?
Huitaca ventralis	0110-0110011210010000103-000001?
Metagovea disparunguis	0100-0110011?1001000??03-0000???
Metagovea oviformis	0100-01100112?0010100?03-0000011
Metagovea philipi	0100-0110011210010000103-0000??1
Neogovea immsi	0110-0110011210100000?03-000010?
Neogovea kamakusa	0110-0110011210100000?03-00001??
Neogovea kartabo	0110-0110011410100?00?03-00001?1
Neogovea microphaga	0110-0110011410100101?03-000011?
?Gen. *enigmaticus*	0110-011001141??????0??3-??????1
Neogovea mexasca	0100-0110000200000100003-0000001
Marwe coarctata	0000-000-01050000?100?03-000????

Appendix 2.—List of species studied indicating if males (♂) and/or females (♀) have been examined, and depository institutions of the studied material.

Stylocellus beccarii (Thorell 1882) (♂ & ♀, ZMB, ZMUC)
Stylocellus javanus (Thorell 1882) (♀, AMNH)
Stylocellus modestus Hansen & Sørensen 1904 (♀, ZMUC)
Stylocellus ramblae Giribet 2002 (♂ & ♀, FMAC, MCZ, WAM)
Stylocellus sedgwicki Shear 1979 (♀, MCZ)
Stylocellus silhavyi Rambla 1991 (♂ & ♀, CCol)
Fangensis leclerci Rambla 1994 (Material not examined)
Fangensis sp. (♂ & ♀, MHNG)
Miopsalis sp. 1 (♀, BMNH)
Miopsalis sp. 2 (♂, FMAC)
Metasiro americanus (Davis 1933) (♂ & ♀, AMNH, FMAC)
Troglosiro juberthiei Shear 1993 (♂ & ♀, AMNH)
Paramiopsalis ramulosus Juberthie 1962 (♂ & ♀, MCZ)
Parasiro coiffaiti Juberthie 1956 (♂ & ♀, MCZ)
Parasiro minor Juberthie 1958 (♂ & ♀, MHNG)
Siro duricorius (Joseph 1868) (♂ & ♀, CCol, MCZ, ZMB)
Siro exilis Hoffman 1963 (♂ & ♀, AMNH, FMAC, SMF)
Siro rubens Latreille 1804 (♂ & ♀, ZMB)
Siro valleorum Chemini 1989 (♂ & ♀, MCZ)
Suzukielus sauteri (Roewer 1916) (♂ & ♀, CCol, MHNG, SMF, ZMB)
Pettalus cimiciformis (Cambridge 1875) (♂, BMNH)
Chileogovea oedipus Roewer 1961 (♂ & ♀, AMNH, FMAC, MCZ)
Austropurcellia scoparia Juberthie 1988 (♂, & ♀, ANIC)
Neopurcellia florensis Forster 1948 (♂ & ♀, NMSA)
Rakaia arcticosa Cantrell 1980 (♂ & ♀, ANIC)
Pettalidae sp. from Pemberton, Western Australia (♂ & ♀, FMAC)
Parapurcellia silvicola (Lawrence 1939) (♂ & ♀, MCZ, SAM, NMSA)
Purcellia illustrans Hansen & Sørensen 1904 (♂ & ♀, MCZ, SAM, NMSA, ZMUC)
Speleosiro argasiformis Lawrence 1931 (♂ & ♀, SAM, NMSA)
Ogovea nasuta (Hansen 1921) (♂, ZMUC)
Ogovea sp. from Abong Mbang, Cameroon (♂ & ♀, BMNH)
Paragovia sironoides Hansen 1921 (♂ & ♀, C. Prieto, leg., MCZ)
Huitaca ventralis Shear 1979 (♂, MCZ)
Metagovea disparunguis Rosas Costa 1950 (Material not examined)
Metagovea oviformis Martens 1969 (♂ & ♀, SMF)
Metagovea philipi Goodnight & Goodnight 1980 (♂ & ♀, AMNH)
Neogovea immsi Hinton 1938 (♂ & ♀, BMNH)
Neogovea kamakusa Shear 1977 (♂, AMNH)
Neogovea kartabo (Davis 1937) (♂ & ♀, AMNH)
Neogovea mexasca Shear 1977 (♂ & ♀, AMNH)
Neogovea microphaga (Martens 1969) (♂, SMF)
?Gen. *enigmaticus* Martens 1969 (♀, SMF)
Marwe coarctata Shear 1985 (♀, AMNH)