

PHYLOGENY OF OPILIONES (ARACHNIDA): AN ASSESSMENT OF THE “CYPHOPALPATORES” CONCEPT

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ABSTRACT. The arachnid order Opiliones has typically been divided into three suborders (Cyphophthalmi, Laniatores and Palpatores), but this system has been challenged in recent years. Based on scenarios of genitalic evolution, Martens and coworkers have argued that certain lineages within Palpatores are more closely related to Cyphophthalmi than to other palpatorean opilions and erected a new clade, Cyphopalpatores, to accommodate this proposal. However, this system is also problematic. Because most genitalic characters within Opiliones are unique to that order, genitalic characters cannot be polarized and opilion phylogeny cannot be rooted using objective outgroup comparison. Thus the Cyphopalpatores concept rests heavily on speculative scenarios of character evolution. The goal of the present study was to examine relationships among the major lineages of Opiliones using both genitalic and non-genitalic characters and thereby assess the Cyphopalpatores concept and associated scenarios of genitalic evolution. Maximum-parsimony analysis of a matrix composed of 17 terminal taxa (including two outgroups) and 26 binary and multistate characters recovered a minimal-length topology that was incompatible with the Cyphopalpatores concept but suggested that Cyphophthalmi is the sister group to a clade comprising a monophyletic Palpatores and monophyletic Laniatores. In contrast, the most-parsimonious distribution of characters within the minimal-length topology supported many of the character transformation series upon which the Cyphopalpatores concept was based. This result reaffirms the observation that a given hypothesis of character evolution can be consistent with several phylogenetic hypotheses and that an empirically robust phylogenetic analysis should include more than one character system.

For the last two decades, discussions of higher-level relationships within Opiliones have been heavily influenced by the phylogenetic hypotheses proposed by Martens and his coworkers (Martens 1976, 1980, 1986; Hoheisel 1980; Martens, Hoheisel & Götze 1981). Prior to these hypotheses, Opiliones had generally been divided into three principal clades, namely, Cyphophthalmi, Palpatores and Laniatores (Hansen & Sørensen 1904; Roewer 1923; Shear 1982; Hennig 1986; see Šilhavý 1961 for an alternative). However, based primarily on analysis of selected genitalic characters, Martens and coworkers argued that Palpatores is paraphyletic. Specifically, they proposed that the palpatorean superfamily Troguloidea is the sister group to a clade comprising Cyphophthalmi and the palpatorean superfamilies Phalangioidea, Caddoidea and Ischyropsalidoidea (Fig. 1) and erected a new clade (Cyphopalpatores) to accommodate the non-laniatorean opilions. Although the Cyphopalpatores concept has yet to undergo explicit numerical assessment, it was accepted by some opilionologists and influenced family- and genus-level revisions

within Troguloidea (Shear & Gruber 1983) and Ischyropsalidoidea (Shear 1986) (Fig. 2). The goal of the present study was to assess the Cyphopalpatores hypothesis by conducting maximum-parsimony analysis on representative opilions using genitalic and non-genitalic characters.

Several aspects of the original formulation of the Cyphopalpatores concept are open to question and must be considered when devising fair and appropriate tests of the hypothesis. First, Martens and coworkers based their conclusions on a small fraction of the taxonomic diversity known to exist within Opiliones (i.e., 21 out of more than 4500 species). Such an approach is valid and expected when data are derived from intensive morphology-based analyses, but the resulting data are strictly applicable only to resolving relationships among those terminal taxa actually observed. However, Martens and coworkers used their results to address relationships among eight superfamilies (i.e., Sironoidea, Travunioidea, Gonyleptoidea, Oncopodoidea, Phalangioidea, Caddoidea, Ischyropsalidoidea, Troguloidea) without demonstrating the mono-

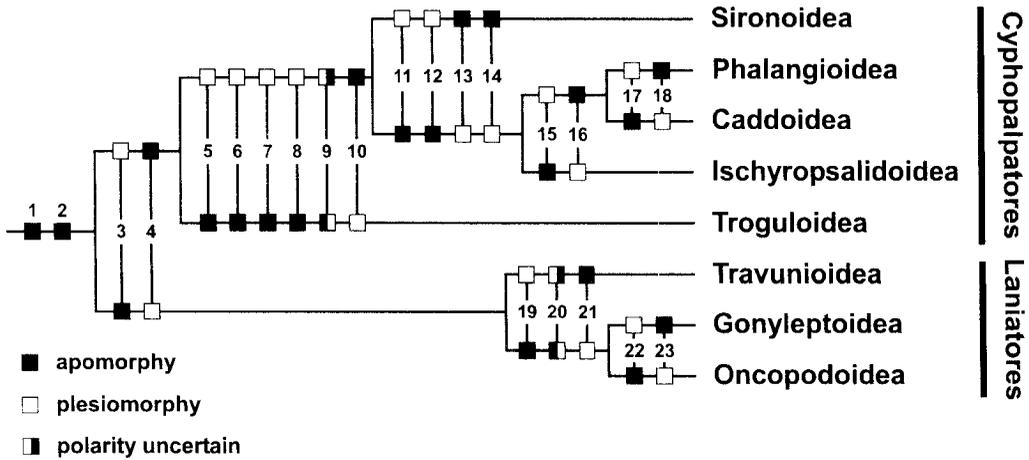


Figure 1.—Phylogeny of the superfamilies in Opiliones proposed by Martens (1980, 1986) and Martens et al. (1981). The first state of each character is the apomorphic state; the state in parentheses is the plesiomorphic state. 1, ovipositor; 2, penis; 3, x-shaped vagina present (absent), 4, ovipositor with segmentally arranged chitinous rings (ovipositor primitively unsegmented); 5, two penis muscles (three penis muscles); 6, ovipositor secondarily unsegmented (ovipositor with segmentally arranged chitinous rings); 7, sternum fused to leg coxae (not fused to leg coxae); 8, pedipalpal setae clavate, glandular (setae unspecialized); 9, outer circular muscles present in ovipositor (outer ring muscles absent); 10, colleterial glands of ovipositor compact, drained by large duct (glands aciniform, drained by many small ducts); 11, penis with one median muscle (three muscles); 12, pedipalpal setae plumose (pedipalpal setae not plumose); 13, genital operculum not covering genital opening (operculum covering genital opening); 14, tendency toward scutum completum (no such tendency); 15, ovipositor secondarily unsegmented (ovipositor with segmentally arranged chitinous rings); 16, inner surface of ovipositor sheath lined with cuticular hooks (not lined with cuticular hooks); 17, tendency toward reduction in number of chitinous rings in ovipositor (no such tendency); 18, leg tibia with accessory tracheal stigmata (no accessory stigmata); 19, median penis muscle reduced (one median longitudinal muscle); 20, ovipositor with 4 lobes (2 lobes); 21, ovipositor with inner longitudinal muscle (without inner longitudinal muscle); 22, tendency toward fusion of tergites into scutum completum (no such tendency); 23, cells of colleterial glands consolidated into a few functional units and concentrated in terminal lobes of the ovipositor (many functional units formed from small cells and distributed in the vaginal epithelium).

phyly of each superfamily or that the assigned states were synapomorphic for each superfamily as a whole. Second, Martens and coworkers chose to resolve opilion phylogeny using a character system unique to Opiliones, and thereby virtually eliminated the possibility of assigning character polarity or of rooting their phylogeny by objective reference to outgroups. Rather than offer an unrooted phylogenetic network, Martens and coworkers relied on speculative scenarios of genitalic evolution to polarize characters and to root their tree. Finally, comparisons of the character descriptions, tabulations and phylogenetic tree presented in Martens et al. (1981) revealed that these workers did not include all relevant genitalic characters in their analysis but offered no justification for their selection.

Based on these observations, the Cypho-

palpatores concept was assessed in the following way. First, the taxon sample was essentially identical at the generic level to that used by Martens et al. (1981), and genera rather than superfamilies were used as terminal taxa. This approach ensured that differences between the results of Martens et al. and the present study would not be due to differences in taxon representation and also avoided problems associated with assigning "synthetic" character states to higher-level taxa of doubtful monophyly. Second, opilion phylogeny was rooted by including outgroups and variable somatic (non-genitalic) characters expressed in both Opiliones and the outgroups. To avoid the circularity inherent in basing phylogeny on preconceived notions of character evolution, polarities were inferred in the course of computerized maximum-parsimony

ber of Arachnida and is the sister group to a clade encompassing Scorpiones, Pseudoscorpiones and Solifugae. Several arachnologists have questioned this hypothesis (e.g., Selden 1990), but no evidence or analysis has been put forward to refute the proposed placement of Opiliones. Consequently, based on Shultz's proposal that Opiliones is an early divergent group of arachnids, Xiphosura and Scorpiones were selected as outgroups.

Ingroups: Opiliones is clearly monophyletic and united by many apomorphic characters, including an ovipositor, spermatopositor/penis, nine complete opisthosomal somites, a single pair of sternal tracheal stigmata, and prosomal glands opening on the carapace via ozopores. The order is here represented by 15 terminal taxa, which are discussed briefly below.

Superfamily Sironoidea: The sironoids are small, heavily sclerotized opilions characterized by many autapomorphies (e.g., elevated ozopores, unique coxosternal arrangement, male adenostyles) (Shear 1980, 1982), and the monophyly of the superfamily is unquestioned. The distinctiveness of sironoids has led them to be placed in their own suborder, Cyphophthalmi (Hansen & Sørensen 1904). Sironoidea is here represented by *Siro* Latreille 1796. Martens et al. (1981) based their characterization of the sironoid ovipositor on original observations of two species, *Siro duricorius* (Joseph 1868) and *S. rubens* (Latreille 1804), but Martens (1986) synthesized information from many species to obtain character states for the male genitalia. Somatic characters used in the present study were based on *Siro acaroides* (Ewing 1923) and other *Siro* species obtained from the literature and from original observations.

Superfamily Travunioidea: This superfamily comprises several families of laniatorean opilions distributed mainly in temperate regions in the northern and southern hemispheres. The travunoids are typically defined as laniatorean opilions with a muscularized penis, a character that may be primitive, and the group may be paraphyletic with respect to gonyleptoids and oncopodoids. The travunoids are represented in the present analysis by two genera, *Peltonychia* (Travuniidae) and *Holoscotolemon* Roewer 1915 (Cladonychiidae). Martens et al. (1981) examined the ovipositors of *Peltonychia clavigera* (Simon

1872), *Holoscotolemon unicolor* Roewer 1915 and *Theromaster brunnea* (Banks 1902) (Cladonychiidae). They found few differences between *Holoscotolemon* and *Theromaster*, none of which were important for purposes of the present study. Martens (1986) depicted the penes of a *Peltonychia* species and *H. unicolor*. Somatic characters for the two genera were obtained from the literature and original observations.

Superfamily Gonyleptoidea: The gonyleptoids are a morphologically diverse and species-rich assemblage of 18 or so families that range throughout most temperate and tropical regions but are especially diverse in the tropics. More families may be recognized as genitalic diversity within the group becomes better known (Martens 1988). There appears to be no well-documented synapomorphies for the superfamily. Shear (1982) noted that gonyleptoids have a penis that lacks intrinsic longitudinal muscles as well as paired claws on the posterior legs, but both traits are also present in Oncopodoidea (Roewer 1923; Martens 1986). Consequently, it is possible that Gonyleptoidea is paraphyletic with respect to oncopodoids. The gonyleptoids are represented here by three genera, *Scotolemon* Lucas 1860 (Phalangodidae), *Vonones* Simon 1879 (Cosmetidae) and *Gonyleptes* Kirby 1819 (Gonyleptidae). Martens et al. (1981) based their model of the gonyleptoid ovipositor on original observations of *Bishopella laciniosa* (Crosby & Bishop 1924) (Phalangodidae), *Scotolemon lespesi* Lucas 1860, *Vonones sayi* (Simon 1879) and an unspecified gonyleptid. There were no substantial differences between the ovipositors of *Bishopella* and *Scotolemon*, so the former was omitted from the present analysis. Somatic and male genitalic characters were determined for *Scotolemon lespesi*, *Vonones ornata* (Say 1921) and *Gonyleptes* spp. from the literature and from original observations.

Superfamily Oncopodoidea: The oncopodoids encompass several genera from southeastern Asia. They generally resemble gonyleptoids but are distinguished by a suite of autapomorphies (Roewer 1923; Shear 1982). The superfamily is represented here by the genus *Oncopus* Thorell 1876. Martens et al. (1981) examined the ovipositor of *Oncopus acanthochelis* Roewer 1915, and Martens (1986) based his model of the oncopodoid pe-

nis on examination of *Oncopus* and *Pelitus* Thorell 1891. Somatic characters were obtained from the literature.

Superfamily Phalangioidea: This species-rich superfamily encompasses several, often poorly delimited families with representatives present on all continents except Antarctica. Phalangioidea are frequently united on the basis of a single synapomorphy, the presence of tibial spiracles. The superfamily is here represented by *Phalangium* Linneus 1758 (Phalangiiidae). Martens et al. (1981) examined the ovipositor in the phalangiiids *P. opilio* Linneus 1761, three species of *Opilio* Herbst 1778, and *Lacinius ephippiatus* (C.L. Koch 1835). There were no substantial differences among these taxa. Phalangioid penial characters were obtained from Martens (1986). Somatic characters were derived from the literature and original observations of *P. opilio*.

Superfamily Caddoidea: The superfamily includes several genera from North America, southern South America, New Zealand, Australia, Japan and South Africa. They resemble small phalangioidea but differ in having large eye tubercles and apparently raptorial pedipalps (Shear 1982). Several workers recognize two caddoid families, Caddidae and Acropopilionidae (e.g., Cokendolpher & Maury 1990), but others advocate only one, Caddidae (e.g., Shear 1996). The superfamily is here represented by *Caddo* Banks 1892. Martens et al. (1981) based their character analysis of the caddoid ovipositor on one species, *Caddo agilis* (Banks 1892), although substantial variation in ovipositor structure is known to exist in the superfamily (Gruber 1974; Shear 1996). Likewise, Martens (1986) apparently used the penis of *C. agilis* (Gruber 1974) as representative, although the penis also shows considerable variation in the superfamily (e.g., Shear 1996). Somatic characters used in the present analysis were obtained from the literature and from original observations of *C. agilis* and *C. pepperella* Shear 1975.

Superfamily Ischyropsalidoidea: The superfamily encompasses at least seven genera, namely, *Ischyropsalis* C.L. Koch 1839, *Sabacon* Simon 1879, *Taracus* Simon 1879, *Acuclavella* Shear 1986, *Ceratolasma* Goodnight & Goodnight 1942, *Hesperonemastoma* Gruber 1970 and *Crosbycus* (Crosby 1911), with a generally Holarctic distribution. The phylogenetic and taxonomic structure within the su-

perfamily is controversial and has been treated most recently by Shear (1986). Following Martens et al. (1981), Ischyropsalidoidea is represented here by *Ischyropsalis*, *Sabacon* and *Hesperonemastoma*. Martens et al. derived their model of the ischyropsalidoid ovipositor from original examinations of *Ischyropsalis luteipes* Simon 1879, *Sabacon viscayanum* Simon 1881 and *Hesperonemastoma kepharti* (Crosby & Bishop 1924). Ischyropsalidoid penial characters were obtained from Martens (1986). Somatic characters are based on observations of *Ischyropsalis luteipes*, *I. hellwigi* (Panzer 1796), *Sabacon cavicolens* (Packard 1884) and *Hesperonemastoma modestum* (Banks 1894) obtained from the literature and from original observations.

Superfamily Troguloidea: The superfamily consists of four families, that is, Nipponopsalididae, Nemastomatidae, Dicranolasmatidae and Trogulidae. Nipponopsalididae includes three described species within the genus *Nipponopsalis* Martens & Suzuki 1966 that occur in Japan and Korea. Nemastomatidae is a morphologically diverse family of about 50 species with a primarily Holarctic distribution (Shear & Gruber 1983; but see Schwendinger & Gruber 1992). The dicranolasmatids include several species within the genus *Dicranolasma* Sörensen 1873 which occurs in southern Europe, southwestern Asia and northern Africa. The trogulids include several genera distributed in Europe, the Caucasus, the Middle East and North Africa (Roewer 1923; Shear 1982). Dicranolasmatids and troguloids are similar in having heavily sclerotized bodies, an optic tubercle bearing two anteriorly projecting processes and, in most, in gluing soil particles to the exoskeleton.

Following Martens et al. (1981), the superfamily is represented here by three genera, namely *Paranemastoma* (Nemastomatidae), *Dicranolasma* (Dicranolasmatidae) and *Trogulus* (Latreille 1892) (Trogulidae). Martens et al. examined the ovipositor in four troguloid species, *Paranemastoma quadripunctatum* (Perty 1833), *Dicranolasma scabrum* (Herbst 1799), *Trogulus nepaeformis* (Scopoli 1763) and *T. coriciformis* C.L. Koch 1839. Martens (1986) did not list the species used in his characterization of the troguloid penis and treated this character in general terms at the super-

familial level. Somatic characters for the present analysis were determined for *Paranemastoma sillii* (Herman 1871), *Dicranolasma scabrum* and *Trogulus nepaeformis* from the literature and original observations.

Character analysis.—*Character 1:* Soil crypsis by glandular adhesion of particles: 0, absent; 1, present. Several litter- or soil-dwelling opilions have evolved chemical and/or mechanical specializations for covering their bodies with soil or detritus. *Dicranolasma* and *Trogulus* are unique among the terminal taxa examined here in using a gland-produced adhesive for coating their bodies with soil particles (Shear & Gruber 1983).

Character 2: Medial eye tubercle with anteriorly projecting bilobed hood equipped with marginal fringe of cuticular projections: 0, absent; 1, present. Hoodlike structures projecting anteriorly from the carapace and covering the feeding apparatus have evolved independently in several opilion lineages, e.g., ortholasmatine nemastomatids (Shear & Gruber 1983) and *Ceratolasma* (Gruber 1978). The hood in *Dicranolasma* and *Trogulus* is formed by bilobed processes projecting anteriorly from the eye tubercle and are fringed with leathery cuticular projections (Roewer 1923: figs. 800–806; pers. obs.) Some authors have suggested that the structures are not homologous in the two families, as the eyes are located basally on the hood in *Trogulus* and more distally in *Dicranolasma* (Shear & Gruber 1983). However, presence of basally located eyes in immature *Dicranolasma* (Roewer 1923: fig. 2; Gruber 1996: figs. 16–20) suggests that either the adult condition in *Dicranolasma* is an autapomorphic modification of a more general trogulid condition or that the trogulid state is a pedomorphic expression of the condition in *Dicranolasma*.

Character 3: Metapeltidial cones: 0, absent; 1, present. Metapeltidial cones are small projections that occur on the dorsal surface of the metapeltidium. A pair of metapeltidial cones is present in *Sabacon* (Roewer 1923: fig. 869; Martens 1988: figs. 16–18; pers. obs.) and in *Caddo agilis* and *C. pepperella* (pers. obs.). Metapeltidial cones in *Caddo* appear to have gone unrecognized by previous workers. The cones are readily seen in *C. agilis*, where they are small dark projections located at the lateral margins of the white band on the medial metapeltidial surface. The cones are easily over-

looked in *C. pepperella*, where they are small tubelike processes that are concolorous with the metapeltidium. *Ischyropsalis* species have a variable number of metapeltidial cones (Roewer 1923: figs. 849, 859, 860, 865; Shear 1986; pers. obs.). Shear (1986) described a pair of metapeltidial depressions in *Hesperonemastoma modestum* and hypothesized that these represent vestigial cones. The existence of these depressions could not be corroborated (pers. obs.) and, in any event, the attempt to homologize invaginated depressions with evaginated cones seems questionable.

Character 4: Prosomal intercoxal sternal region: 0, no apparent prosomal intercoxal region; 1, prosomal sternal region flexibly attached to pedal coxae; 2, prosomal sternal region sclerotized with firm attachment to pedal coxae. The ventral surface of the prosoma in Opiliones can be divided into three basic regions, namely, the labium, intercoxal sternal region, and *arculi genitales*. The labium is an apparent sternite associated with the coxae of the first leg pair (Winkler 1957), and the *arculi genitales* forms the dorsoanterior margin of the pre-genital chamber and probably corresponds to the sternite of the first opisthosomal somite (Hansen & Sørensen 1904). The intercoxal sternal region does not appear to be a distinct sclerite, or sternite, but is a region with different degrees of development and sclerotization in different lineages (Pocock 1902; Hansen & Sørensen 1904). The intercoxal sternal region is well developed in *Limulus* (Xiphosura) and is flexibly attached to the pedal coxae by soft cuticle (pers. obs.). The “labium” may correspond to a small sclerite associated with the coxae of leg I in scorpions (Shultz 1990). The “sternum” of scorpions may represent the first opisthosomal sternite (van der Hammen 1986) and, if so, would correspond to the *arculi genitales*. The coxae of legs I and II in scorpions meet along the midline obliterating the prosomal intercoxal sternal region (Shultz 1990).

The sternal region is connected to pedal coxae 2 and 3 by flexible cuticle in *Phalangium* (Hansen & Sørensen 1904: fig. B; pers. obs.), *Caddo* (pers. obs.), *Sabacon* (Hansen & Sørensen 1904; pers. obs.) and *Ischyropsalis* (Pocock 1902: fig. 1B; Roewer 1923: fig. 39; pers. obs.). The sternal region is sclerotized and fused to pedal coxae 2 and 3 in *Peltonychia* (pers. obs.), *Holoscotolemon* (Roewer

1923; Briggs 1969), *Scotolemon* (van der Hammen 1985: figs. 2, 11), *Vonones* (pers. obs.), *Gonyleptes* (Roewer 1923), *Hesperonemastoma* (pers. obs.), *Paranemastoma* (pers. obs.), *Dicranolasma* (Pocock 1902: fig. 3A; pers. obs.) and *Trogulus* (Pocock 1902: fig. 3B; pers. obs.).

Character 5: Diaphanous cheliceral teeth: 0, absent; 1, present. The opposing margins of the cheliceral fingers are emarginate and lined with diaphanous to subdiaphanous teeth in *Sabacon* (Roewer 1923: fig. 867; Suzuki 1965: fig. 4; pers. obs.), *Ischyropsalis* (Roewer 1923: fig. 849b; Eisenbeis & Wichard 1987: plate 22; pers. obs.), *Hesperonemastoma* (pers. obs.), *Paranemastoma* (Eisenbeis & Wichard 1987: plate 18; pers. obs.), *Dicranolasma* (pers. obs.) and *Trogulus* (Eisenbeis & Wichard 1987: plates 20, 21; pers. obs.).

Character 6: Male cheliceral glands: 0, absent; 1, present. Glands open on the basal cheliceral article in males of *Sabacon* (Martens & Schawaller 1977: fig. 9), *Ischyropsalis* (Martens & Schawaller 1977: figs. 7, 8), *Paranemastoma* (Martens & Schawaller 1977: fig. 6), and most *Dicranolasma* species (Martens & Schawaller 1977: fig. 1).

Character 7: Glandular pedipalpal setae: 0, absent or simple; 1, plumose; 2, clavate. Plumose pedipalpal setae are present in *Phalangium* (pers. obs.), *Caddo* (Gruber 1974: fig. 20a), *Hesperonemastoma* (Shear 1986: fig. 8) and *Sabacon* (Shear 1986: figs. 7, 9). Clavate glandular setae are expressed at some time during postembryonic development in nemastomatids and *Dicranolasma* (Gruber 1978).

Character 8: Pedipalpal apotelic claw: 0, present, readily observed; 1, extremely small or apparently absent. The opilion pedipalp is primitively equipped with a terminal apotelic claw, a condition retained in *Phalangium* (Edgar 1990: figs. 57, 105; pers. obs.), *Caddo* (pers. obs.), *Peltonychia* (pers. obs.), *Holoscotolemon* (Briggs 1969: fig. 7), *Scotolemon* (van der Hammen 1985: fig. 23), *Vonones* (pers. obs.), *Gonyleptes* (Roewer 1923) and *Oncopus* (Bristowe 1976: plate 1). The claw is greatly reduced or absent in *Siro* (Eisenbeis & Wichard 1987: plate 27; van der Hammen 1985: fig. 23; pers. obs.), *Sabacon* (Martens 1989: figs. 5, 6, 11; pers. obs.), *Ischyropsalis* (pers. obs.), *Hesperonemastoma* (pers. obs.), *Paranemastoma* (pers. obs.), *Dicranolasma* (pers. obs.) and *Trogulus* (pers. obs.).

Character 9: Leg II: 0, not longer than adjacent legs; 1, longer than adjacent legs. Leg II is typically longer than adjacent legs in non-sironoid opilions, including *Peltonychia* (pers. obs.), *Holoscotolemon* (Roewer 1923: p. 102), *Scotolemon* (Roewer 1923: p. 97; Berland 1949: fig. 589), *Vonones* (Shear 1982: plate 102; pers. obs.), *Gonyleptes* (Roewer 1923), *Oncopus* (Bristowe 1976: plate 1), *Phalangium* (Berland 1949: fig. 597; pers. obs.), *Caddo* (pers. obs.), *Ischyropsalis* (Berland 1949: fig. 596; pers. obs.), *Sabacon* (pers. obs.), *Hesperonemastoma* (pers. obs.), *Paranemastoma* (Berland 1949: fig. 595; pers. obs.), *Dicranolasma* (Gruber 1993: figs. 9, 12; pers. obs.) and *Trogulus* (Berland 1949: fig. 594; pers. obs.). Leg II is shorter or not notably longer than adjacent legs in *Siro* and other sironoids (Hansen & Sørensen 1904; pers. obs.).

Character 10: Coxapophysis, leg II: 0, absent; 1, present, not conelike; 2, present, conelike; ?, Xiphosura. Coxapophyses are projections occurring on the medial surface of the pedipalpal and certain pedal coxae (especially legs I and II) in scorpions and many opilions, where they assist in forming a preoral chamber, the stomotheca (Hansen & Sørensen 1904). These structures are typically termed "endites" in the literature, which implies homology with the endites of xiphosurans and eurypterids. However, recent comparative skeletal muscular studies (unpubl. data) indicate that the coxapophyses are more similar to immovable coxal processes of *Limulus* (Xiphosura) than to the endites. Given the uncertainties in homology, van der Hammen suggested that the more neutral term coxapophysis be used in describing these structures, and this usage is adopted here.

The coxapophyses are frequently reduced or lost on the posterior legs in Opiliones, but variation in their expression on leg II may have significance for resolving higher-level relationships. Coxapophyses are present on leg II in *Siro* (Shear 1980: figs. 12, 14, 21; pers. obs.), *Phalangium* (pers. obs.), *Caddo* (Roewer 1923: fig. 847; pers. obs.), *Ischyropsalis* (Pocock 1902: fig. 1B; Martens & Suzuki 1966: fig. 1; pers. obs.) and *Hesperonemastoma* (pers. obs.). Coxapophyses are also present but variously developed in *Peltonychia* (pers. obs.), *Holoscotolemon* (Roewer 1923: fig. 37), *Scotolemon* (van der Hammen 1985:

figs. 2, 11), *Vonones* (pers. obs.), *Gonyleptes* (Roewer 1923) and *Oncopus* (Roewer 1923: figs. 60–62, 64). Coxapophyses are absent on leg II in *Paranemastoma* (Roewer 1923: fig. 40; pers. obs.), *Dicranolasma* (Pocock 1902: fig. 3A; pers. obs.), *Trogulus* (Pocock 1902: fig. 3B; Roewer 1923: fig. 41; pers. obs.) and most *Sabacon* species (Hansen & Sørensen 1904; pers. obs.). However, Hansen & Sørensen (1904: p. 32) describe *Sabacon* (*Tomicomerus*) *bryanti* (Banks 1898) as having coxapophyses (“low rounded tubercles or thick cones”) on leg II. *Sabacon* is coded here as being polymorphic for this character, a decision that assumes Shear (1986) was justified in synonymizing *Tomicomerus* with *Sabacon*. Conelike coxapophyses are also present in *Ischyropsalis* (Pocock 1902: fig. 1B; Martens 1969: fig. 27; pers. obs.) and *Hesperonemastoma* (pers. obs.).

Character 11: Pedal telotarsi: 0, without tarsomeres; 1, with tarsomeres. The telotarsi are undivided in most chelicerates, but they are typically subdivided into numerous tarsomeres in opilions. However, among the terminal taxa examined here, *Siro* (Hansen & Sørensen 1904; pers. obs.) and *Oncopus* (Roewer 1923: fig. 60; Bristowe 1976: plates I, II) have undivided pedal telotarsi. *Trogulus* is polymorphic for the character (Hansen & Sørensen 1904; Roewer 1923: figs. 794–799).

Character 12: Pairs of midgut diverticula: 0, no comparable structures; 1, three; 2, four. Midgut diverticula are found in many arachnids, although those of Opiliones appear to have a unique arrangement or are not readily homologized with those of the outgroups. Dumitrescu (1975) has conducted a comparative survey of these structures in Opiliones, and most of the information presented here is derived from that work. Four pairs of midgut diverticula are present in *Siro*, *Caddo*, *Ischyropsalis*, *Sabacon*, *Hesperonemastoma*, *Paranemastoma*, *Dicranolasma*, *Trogulus* (Dumitrescu 1975) and *Phalangium* (Loman 1903: fig. 20; Berland 1949: fig. 571). All laniatorean opilions examined by Dumitrescu had three pairs of midgut diverticula. However, except for *Peltonychia*, his generic taxon sample did not overlap the one used here. However, as Dumitrescu found three pairs of midgut diverticula in all laniatorean opilions (including a cladonychiid, phalangodid, cosmetid and gonyleptid), the genera *Holoscoto-*

lemon, *Scotolemon*, *Vonones* and *Gonyleptes* were coded as having this state, as well. Similarly, Dumitrescu did not include an oncopodoid in his analysis, but *Oncopus* was coded here as having three pairs of midgut caeca, as observed in the oncopodoid *Gnomulus* Thorell 1890 (Loman 1903: fig. 19).

Character 13: Sternite of opisthosomal somite 9: 0, present, well developed; 1, very small or apparently absent. Opisthosomal sternite 9 is present and readily observed in *Siro* (Roewer 1923: fig. 22; pers. obs.), *Peltonychia* (pers. obs.), *Holoscotolemon* (Briggs 1969: fig. 7), *Scotolemon* (van der Hammen 1985: fig. 2), *Vonones* (pers. obs.), *Gonyleptes* (Roewer 1923) and *Oncopus* (Roewer 1923: fig. 60a), although it is generally fused with sternite 8. It is greatly reduced or absent in *Phalangium* (pers. obs.), *Caddo* (pers. obs.), *Sabacon* (pers. obs.), *Ischyropsalis* (pers. obs.), *Hesperonemastoma* (pers. obs.), *Paranemastoma* (Hansen & Sørensen 1904: fig. H; pers. obs.), *Dicranolasma* (pers. obs.) and *Trogulus* (pers. obs.).

Character 14: Opisthosomal tergite 9 divided dorsally: 0, absent; 1, present. Following the interpretation of Hansen & Sørensen (1904), the dorsal surface of the opilion opisthosoma is generally regarded as having nine tergites and an anal operculum. Tergite 9 is variously modified in Opiliones in association with specializations of the anal complex. It is undivided in *Siro* and other sironids, whether distinct or consolidated in various ways with adjacent tergites and sternites (Hansen & Sørensen 1904; Roewer 1923: fig. 22; Shear 1980; pers. obs.). It is also undivided in *Peltonychia* (pers. obs.), *Holoscotolemon* (Briggs 1969: fig. 7), *Scotolemon* (van der Hammen 1985: fig. 2, but numbering is not precise), *Vonones* (pers. obs.) and *Gonyleptes* (Roewer 1923), but, again, is generally fused to tergite 8. In contrast, tergite 9 in most other opilions is divided dorsally with the two parts widely separated by the anal operculum and, in some cases, by tergite 8. This condition is present *Phalangium* (pers. obs.), *Caddo* (pers. obs.), *Sabacon* (pers. obs.), *Ischyropsalis* (pers. obs.), *Hesperonemastoma* (pers. obs.), *Paranemastoma* (Eisenbeis & Wichard 1987: plate 19; pers. obs.), *Dicranolasma* (pers. obs.) and *Trogulus* (pers. obs.).

Character 15: Genital operculum: 0, no comparable structure; 1, small, not forming

complete floor to pre-genital chamber; 2, well developed, forming complete floor to pre-genital chamber. The structure of the genital operculum in Opiliones is apparently unique and cannot be readily homologized with genital features in other arachnids. The genital operculum in most opilions is an oblong plate or dorsoventrally flattened process that projects anteriorly from the sternite of postoral somite IX and forms the floor to the genital opening or, more precisely, the opening to the pre-genital chamber. A similar situation is present in *Siro* and other sironoids, but the operculum itself is much shorter and only covers the extreme posterior part of the pre-genital opening (Hansen & Sørensen 1904; Eisenbeis & Wichard 1987: plate 27; pers. obs.). Some workers do not regard *Siro* as having a genital operculum (e.g., Shear 1982; Hennig 1986).

Character 16: Differentiation of shaft and glans within spermatopositor/penis: 0, no spermatopositor/penis; 1, shaft and glans absent; 2, shaft and muscle-operated glans; 3, shaft and hydraulically operated glans (Martens 1986). The term "spermatopositor" follows van der Hammen (1985) and refers to the homolog of the penis in sironoids. There is no evidence that the structure in sironoids serves as an intromittent organ.

Character 17: Intrinsic spermatopositor/penis muscles: 0, no spermatopositor/penis; 1, spermatopositor/penis without muscles; 2, spermatopositor/penis with one muscle; 3, spermatopositor/penis with two muscles; 4, spermatopositor/penis with at least three muscles. (Martens 1986).

Character 18: External morphology of ovipositor: 0, no ovipositor; 1, cuticular annuli, setae along shaft, terminal sensory organs; 2, without cuticular annuli, setae along shaft, no terminal sensory organs; 3, without cuticular annuli, few or no setae along shaft, no terminal sensory organs (Martens et al. 1981).

Character 19: Number of distal lobes on ovipositor: 0, no ovipositor; 1, two; 2, four (Martens et al. 1981).

Character 20: Inner sheath of ovipositor lined with cuticular hooks: 0, no ovipositor; 1, absent; 2, present (Martens et al. 1981).

Character 21: Vaginal glands in ovipositor: 0, no ovipositor; 1, aciniform glands; 2, aggregate glands; 3, glands opening without ducts via vaginal pore fields. Martens et al. (1981) noted small glands draining into the

vaginal lumen via small ducts (aciniform glands) in *Paranemastoma*, *Dicranolasma* and *Trogulus*. Similar glands were drained collectively by larger ducts (aggregate glands) in *Siro*, *Phalangium*, *Caddo*, *Ischyropsalis*, *Hesperonemastoma* and *Sabacon*. The glands were found to empty directly into the vaginal lumen via pore fields in the vaginal wall in *Peltonychia*, *Holoscotolemon*, *Scotolemon*, *Vonones* and the gonyleptid. The condition in *Oncopus* appears to be intermediate between the aciniform and pore field conditions and is coded here as polymorphic.

Character 22: Seminal receptacles in vaginal lumen of ovipositor: 0, no ovipositor; 1, simple blind sacs or diverticula; 2, encased within structure protruding into vaginal lumen (Martens et al. 1981).

Character 23: Outer longitudinal muscles of ovipositor: 0, no ovipositor; 1, with segmental pattern of insertion; 2, without segmental pattern of insertion (Martens et al. 1981).

Character 24: Outer circular muscles: 0, no ovipositor; 1, absent; 2, present (Martens et al. 1981).

Character 25: Inner longitudinal muscles of ovipositor: 0, no ovipositor; 1, absent; 2, present. Martens et al. (1981) found longitudinal muscles immediately external to the vagina and internal to the circumvaginal muscles in *Scotolemon*, *Vonones*, *Oncopus* and a gonyleptid. They noted that the muscles were absent in *Peltonychia* and *Holoscotolemon*, and their figures indicated that inner longitudinal muscles were absent in *Phalangium*, *Caddo*, *Ischyropsalis*, *Hesperonemastoma*, *Sabacon*, *Paranemastoma*, *Dicranolasma* and *Trogulus*. Martens et al. did not report or illustrate the condition in *Siro*, but original examinations of the ovipositor in *Siro acaroides* indicated that inner longitudinal muscles are absent.

Character 26: Ovipositor with X-shaped vaginal lumen and circumferential fold: 0, no ovipositor; 1, absent; 2, present (Martens et al. 1981).

Tree construction.—The phylogenetic program PAUP, v. 3.1.1 (Swofford 1993) was used for all phylogenetic analyses. The data matrix shown in Table 1 was analyzed using the branch-and-bound algorithm, which ensures recovery of all minimal-length trees. All characters were unordered and weighted equally. Entries for multistate taxa were treat-

ed as polymorphisms. Phylogenetic analysis of unweighted data was followed by successive weighting in which each character was initially weighted with the consistency index assigned in the unweighted analysis. Successive weighting was repeated using the retention index.

Evidential support for internal relationships within minimal-length trees was assessed with the decay index (Bremer 1988) and bootstrap analysis (Felsenstein 1985; Hillis & Bull 1993). The decay index was determined for each phylogenetic relationship within a most-parsimonious tree by finding that minimal-length tree that does not contain the relationship. This was accomplished by importing a constraint tree that defined only the proposed relationship and then conducting a branch-and-bound search to discover the shortest tree that does not have the specified relationship. The decay index was calculated by subtracting the length of the most-parsimonious tree from that of the minimal-length constraint-enforced tree. The bootstrap is a nonparametric statistical procedure in which multiple character matrices are assembled by sampling characters from the original with replacement. The new matrices are treated as "independent" samples of the "population" of characters from which the original data were drawn. Bootstrap values were obtained from PAUP and were based on 1000 replicates using simple heuristic searches.

The effect of character class on phylogenetic reconstruction was examined by separate analysis of somatic characters (Table 1: characters 1–15) and genitalic characters (Table 1: characters 16–26). Again, these analyses were conducted using the branch-and-bound algorithm, but decay indices and bootstrap values were not determined. Rather, relationships were depicted as 50% majority-rule consensus trees, which show the relationships recovered in 50% or more of the minimal-length trees recovered.

RESULTS

Parsimony analysis of the data matrix in Table 1 yielded two minimal-length trees (tree length = 61; consistency index = 0.82, retention index = 0.90) which differed only with respect to their placement of *Hesperonemastoma*, which was either 1) the sister group to *Ischyropsalis* and *Sabacon* or 2) the sister

group to ((*Ischyropsalis*, *Sabacon*), (*Paranemastoma*, (*Dicranolasma*, *Trogulus*))). Only the former alternative is illustrated in Fig. 1 because it is the single most parsimonious topology resulting from successive weighting using consistency index (tree length = 50502, consistency index = 0.88, retention index = 0.94) and retention index (tree length = 51765, consistency index = 0.86, retention index = 0.93).

Analysis of somatic (non-genitalic) characters (Table 1: characters 1–15) produced six minimal length trees (tree length = 30, consistency index = 0.73, retention index = 0.86) and the 50% majority-rule consensus tree is illustrated in Fig. 3. Relationships among terminal taxa within Laniatores (*Peltonychia*, *Holoscotolemon*, *Scotolemon*, *Vonones*, *Gonyleptes*, *Oncopus*) were unresolved. The remaining relationships were consistent with those recovered by the full data set, except that *Hesperonemastoma* was consistently reconstructed as the sister to ((*Ischyropsalis*, *Sabacon*), (*Paranemastoma*, (*Dicranolasma*, *Trogulus*))). Successive-weighting analysis produced the same six minimal-length trees as the unweighted data using both consistency and retention indices.

Analysis of genitalic characters (Table 1: characters 16–26) produced 82 minimal-length trees (tree length = 29, consistency index = 0.97, retention index = 0.98). The 50% majority-rule consensus tree (Fig. 3) showed that genitalic characters recovered superfamilies in over 50% of the minimal-length trees and reconstructed *Siro* as sister to a clade containing *Phalangium* and *Caddo*. The strict consensus tree can be visualized by collapsing those relationships not observed in 100% of the minimal-length trees. Consequently, a strict consensus of the 82 trees would show no phylogenetic resolution within Opiliones. Successive weighting using consistency and retention indices produced trees identical to those recovered by the unweighted data.

DISCUSSION

Opilion phylogeny.—Results from this analysis are inconsistent with the Cyphopalpatores concept, which regards Cyphophthalmi as the sister group to a subset of palpatores and considers Palpatores to be a paraphyletic assemblage. Specifically, parsimony reconstructed the cyphophthalmid *Siro*

Table 1.—Character matrix used in the present analysis. Polymorphisms (e.g., "1/2") were assigned to genera that express two relevant states in different species. The uncertainty ("?") assigned to *Limulus* is explained in the text.

Taxa	Xiphosura	Scorpiones	Siro	<i>Peltonychia</i>	<i>Holoscolemmon</i>	<i>Scotolemmon</i>	<i>Vonones</i>	<i>Gonyoleptes</i>	<i>Oncopus</i>	<i>Phalangium</i>	<i>Caddo</i>	<i>Ischyropsalis</i>	Hesperotoma			<i>Trogulus</i>
													<i>perotoma</i>	<i>nemasoma</i>	<i>stoma</i>	
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
3	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
4	1	0	0	2	2	2	2	2	2	1	1	1	2	2	2	2
5	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
6	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0
7	0	0	0	0	0	0	0	0	0	1	0	0	1	1	2	0
8	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	1
9	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
10	?	1	1	1	1	1	1	1	1	1	1	2	0/2	0	0	0
11	0	0	0	1	1	1	1	1	0	1	1	1	1	1	1	0/1
12	0	0	2	1	1	1	1	1	1	2	2	2	2	2	2	2
13	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
14	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
15	0	0	1	2	2	2	2	2	2	2	2	2	2	2	2	2
16	0	0	1	2	2	3	3	3	3	2	2	2	2	2	2	2
17	0	0	4	2	2	1	1	1	1	2	2	2	2	2	3	3
18	0	0	1	3	3	3	3	3	3	1	1	3	3	2	2	2
19	0	0	1	2	2	1	1	1	1	1	1	1	1	1	1	1
20	0	0	1	1	1	1	1	1	1	2	2	1	1	1	1	1
21	0	0	2	3	3	3	3	3	1/3	2	2	2	2	1	1	1
22	0	0	1	1	1	1	1	1	1	1	1	2	2	2	2	2
23	0	0	1	2	2	2	2	2	2	1	1	2	2	1	1	1
24	0	0	1	1	1	1	1	1	1	1	1	1	1	2	2	2
25	0	0	1	1	1	2	2	2	2	1	1	1	1	1	1	1
26	0	0	1	2	2	2	2	2	2	1	1	1	1	1	1	1

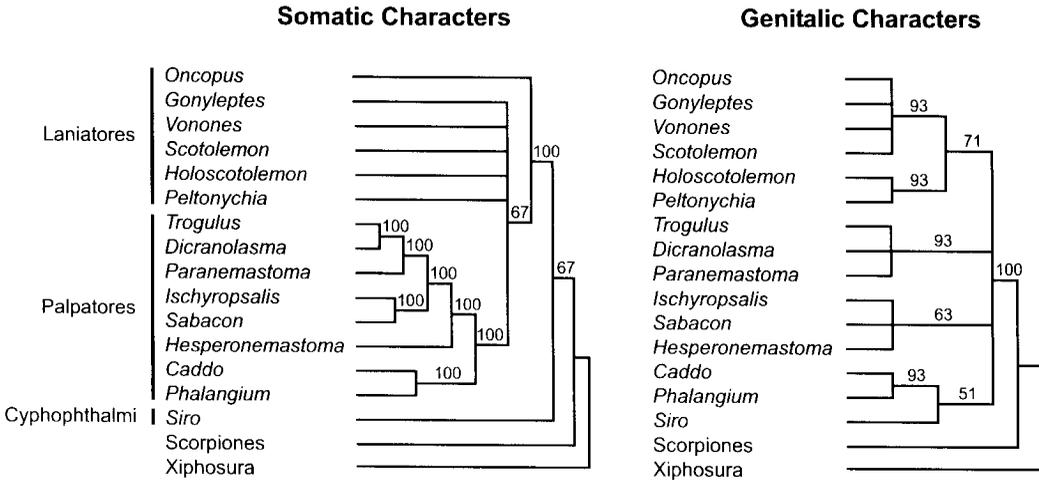


Figure 3.—Comparison of 50% majority-rule consensus trees based on 26 characters (Table 1), including 15 somatic characters (Table 1: characters 1–15) and 11 genitalic characters (Table 1: characters 16–26). Somatic characters resolved non-sironoid opilions and Palpatores in 100% of the eight minimal-length topologies but did not resolve Laniatores or relationships among laniatoreans. Genitalic characters recovered Opiliones in 100% of 82 minimal-length trees, and most superfamilies were resolved in over 50% of equally parsimonious trees. Strict consensus trees can be visualized by collapsing those internodes not found in 100% of minimal length trees.

as the sister group to the other opilions and Palpatores as the monophyletic sister group to Laniatores. A further implication of the Cyphopalpatores concept is that Ischyropsalidoidea and Troguloidea do not form a monophyletic group (Dyspnoi) that other opilion systematists have recognized (e.g., Juberthie & Manier 1978). However, results from the present analysis are concordant with the Dyspnoi hypothesis. The degree to which the Cyphopalpatores concept differs from the topology generated here can be illustrated by finding the minimal-length tree that contains all superfamily relationships proposed by Martens et al. This was accomplished by enforcing a “Cyphopalpatores” constraint tree during branch-and-bound analysis of the full data matrix (Table 1). The analysis produced two minimal-length topologies that differed only with respect to generic relationships within Troguloidea (Length = 68, consistency index = 0.73, retention index = 0.84). The minimal-length Cyphopalpatores tree was seven steps longer than the most-parsimonious solution and represents only two of the over 4000 possible solutions of the same length.

While the minimal-length tree favored here is clearly in conflict with the Cyphopalpatores concept, it does not represent a com-

elling solution to higher-level relationships within Opiliones. A much larger sampling of taxa and characters is needed. Still, these results are congruent with those from other studies. For example, ultrastructural analyses have shown that spermatozoa of the cyphophthalmid *Siro rubens* retain non-motile axonemes but that virtually all flagellar elements are absent in the palpatorean and laniatorean opilions that have been examined (Juberthie & Manier 1978). Because presence of a flagellum is undoubtedly primitive in Chelicerata (Shultz 1990), absence of this structure may be a synapomorphic feature of Palpatores and Laniatores. Further, the epistome-pharynx apparatus has been examined in representatives of the three opilion suborders and results are concordant with that derived from sperm ultrastructure (unpubl. data). Specifically, the epistomes in scorpions and *Siro* (Cyphophthalmi) have one dorsal and two lateral arms that serve as attachments for pharyngeal dilator muscles. However, the epistome essentially surrounds the pharynx in *Leiobunum aldrichi* (Weed 1893) (Palpatores: Phalangioidae) and *Acromares banks* Goodnight & Goodnight 1942 (Laniatores: Gonyleptoidea) such that fibers of the pharyngeal

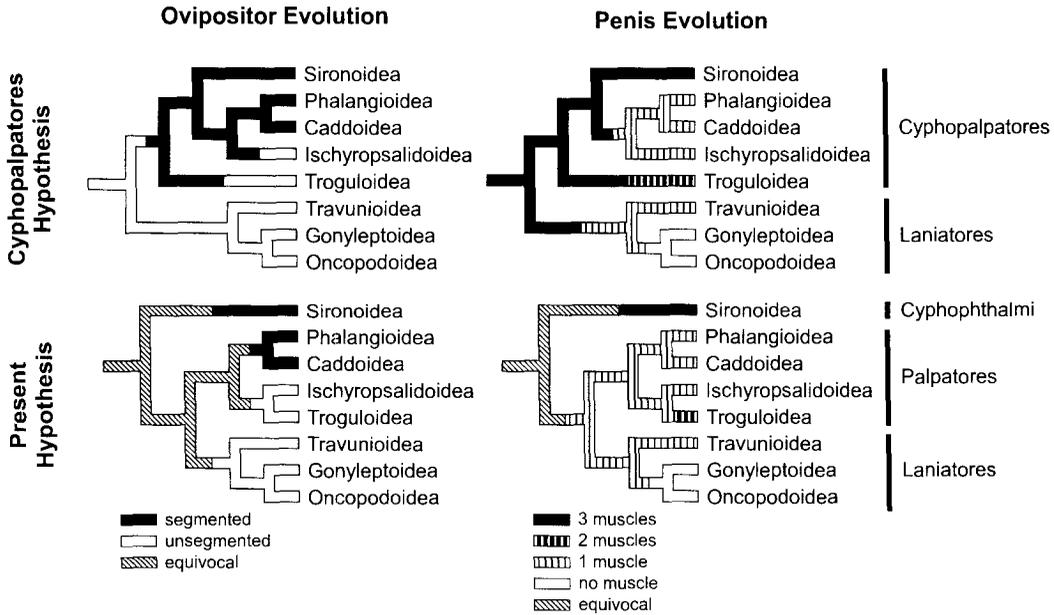


Figure 4.—Evolution of ovipositor segmentation and intrinsic spermatophore/penis muscles according to two scenarios.

dilators radiate from the full circumference of the pharynx.

Genitalic evolution.—The analysis of opilion phylogeny offered by Martens et al. was based almost exclusively on speculative transformation series of genitalic characters. The first cladogenetic event in the Cyphopalpatores hypothesis (Figs. 1, 4) resulted in the separation of Laniatores and Cyphopalpatores, with Laniatores retaining a “primitively unsegmented” ovipositor and Cyphopalpatores developing an ovipositor with cuticular annuli (Fig. 4). Martens et al. suggested that Troguloidea was the first clade to diverge within Cyphopalpatores, even though Troguloidea is characterized by ovipositors that *lack* cuticular segmentation. Martens et al. cited presence of a segmental pattern of muscle insertions in troguloids as evidence for primitive cuticular segmentation in the troguloid ancestor and thereby attempted to justify the use of the segmented ovipositor as a synapomorphy of Cyphopalpatores. Martens et al. argued further that the segmented ovipositor was also lost secondarily in the Ischyropsalidoidea but this time along with all internal evidence of segmentation, as well. This evolutionary scenario begs two questions. First, how did Martens et al. discriminate *a priori* between an ovipositor

that lacks all evidence of segmentation due to primitive absence (Laniatores) from one that lacks all evidence of segmentation due to secondary loss (Ischyropsalidoidea)? Second, how can one know that segmentally arranged muscle attachment must accompany or follow cuticular segmentation rather than precede this condition? Convincing answers to both questions were necessary in formulating their transformation series and their phylogenetic conclusion, but Martens et al. did not offer them.

In reconstructing the evolution of the spermatopositor/penis, Martens et al. reasoned that the short, three-muscle condition in sironoids was primitive for Opiliones, apparently because it alone had the potential to generate other conditions by the loss of muscles. Specifically, the one-muscle penis could have evolved through loss of the two lateral muscles of sironoids, and the two-muscle penis could have arisen through loss of the median muscle (Fig. 4). Because Martens et al. regarded sironoids as a late-divergent group, the one-muscle condition must have arisen from the three-muscle condition at least twice; once in basal laniatoreans and once in the common ancestors of phalangioids, caddoids and ischyropsalidooids.

An alternative and more objective strategy for understanding genitalic evolution is to reconstruct phylogeny using as many characters as possible, except the character of interest, and then to superimpose the character on the resulting topology to determine its course of evolution. This analysis was undertaken here for the characters of ovipositor segmentation and numbers of intrinsic penial muscles.

To reconstruct evolution of the ovipositor, character 18 was excluded from the matrix in Table 1 and analyzed in PAUP using the branch-and-bound algorithm. The resulting trees were identical to those achieved using the full matrix (tree length = 57, consistency index = 0.82, retention index = 0.91). The program MacClade, 3.1 (Maddison & Maddison 1992) was used to determine the most-parsimonious distribution of the binary character "ovipositor segmentation." The results indicate that the primitive state of the opilion ovipositor is unclear given current information. It is equally parsimonious to conclude that, 1) the opilion ovipositor was originally segmented and that segmentation was lost twice or, 2) that the ovipositor was originally unsegmented and evolved segmentation twice. Current evidence would tend to favor the former, given the other complex similarities between the ovipositors of sironoids, phalangoids and caddoids (e.g., terminal lobes and sensory organs, colleterial glands) and the segmental patterns of muscle insertions in troguloids.

The evolution of intrinsic penial muscles was examined in a similar way, but, in this case, character 17 was omitted from the analysis. As in the analysis of ovipositor segmentation, the analysis produced two minimal-length trees identical to those recovered from analysis of the full data set (tree length = 57, consistency index = 0.81, retention index = 0.90). Character 17 was then superimposed on the topology in Fig. 2 using MacClade. The primitive state of the intrinsic penial muscles is unclear from this analysis; it may have been a three-muscle or one-muscle penis. In either case, one need only invoke a single origin for the one-muscle penis, with the two-muscle penis of troguloids and the non-muscular penis of laniatoreans having evolved from the one-muscle condition.

It is interesting to note that the transformation series in ovipositor and spermatopos-

itor/penis evolution favored by Martens et al. are largely compatible with those found by parsimony analysis. The hypothesis that the unsegmented ovipositors of ischyropsalidoids and troguloids evolved from a segmented ovipositor is one of the two equally parsimonious transformation series suggested by the present analysis. However, while Martens et al. regarded the unsegmented condition in Laniatores as primitive, the present analysis would suggest that it represents a secondary loss of segmentation. One could also argue that Laniatores has a primitively unsegmented ovipositor, but this position would require independent origin of segmentation in Sironoidea and the ancestors of the Phalangioidea-Caddoidea clade. The transformation series that Martens et al. proposed for the evolution of intrinsic penial muscles is also largely congruent with results derived from parsimony. The hypotheses that the one-muscle penis evolved from a three-muscle penis and that the nonmuscular penis evolved from a one-muscle penis are consistent with results of the present analysis, the principal difference being the frequency of the three-muscle to one-muscle transformations. In contrast, the two scenarios differ in explaining the origin of the two-muscle penis of troguloids. Martens et al. propose that it evolved from reduction in the three-muscle penis, and parsimony suggests that it originated from the one-muscle condition.

These results suggest that a given character transformation series can be compatible, or largely compatible, with two or more phylogenetic topologies. In the absence of information from other characters, it would be difficult to recognize or discriminate among these alternative topologies. The principal conclusion of this analysis is that the Cyphopalpatores concept was based on reasonable interpretations of genitalic character evolution but that these interpretations were used to support only one of several possible topologies that were broadly consistent with the proposed transformation series. Parsimony-based analysis of genitalic and non-genitalic characters recovered a topology that was largely concordant with the transformation series upon which the Cyphopalpatores concept was erected but recovered a different phylogenetic topology that was based on a more objective and empirically robust analysis.

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