

CHAPTER

3

Phylogeny and Biogeography

Gonzalo Giribet and Adriano B. Kury

Opiliones are, together with Acari and Araneae, the most diverse group of arachnids, and they also present a great deal of body-plan disparity (see Chapters 1 and 2). Crown-group Opiliones were already around during the Devonian (see Chapter 5), which corroborates the idea of them being an old group of arachnids that has had time to evolve the enormous disparity observed in the extant harvestman fauna and to colonize all continents and major islands at all latitudes (see Chapter 7). The object of this chapter is to compile phylogenetic and biogeographic evidence to discuss the evolutionary relationships of Opiliones and to propose a working phylogenetic hypothesis.

PHYLOGENETIC STUDIES OF THE ORDER OPILIONES AND ITS RELATIONSHIPS TO THE OTHER ARACHNIDA

In order to understand the evolution and origin of the order Opiliones, its phylogenetic placement within the arachnid tree of life needs to be considered. However, the phylogenetic position of Opiliones has remained one of the most contentious issues in arachnid systematics and requires extensive discussion. Fortunately, progress has been made in recent times, in part because of the use of sound phylogenetic methodologies applied to the analysis of morphological data (Shultz, 1990; Wheeler & Hayashi, 1998; Giribet et al., 2002), the careful study of new character systems, including skeletomuscular anatomy (Shultz, 2000), and the incorporation of molecular evidence into the toolkit of arachnid systematists (Wheeler & Hayashi, 1998; Giribet et al., 1999, 2002; Shultz & Regier, 2001).

The issue of Opiliones monophyly and its components

Before revising the phylogenetic placement of Opiliones, the issue of Opiliones monophyly needs to be addressed. Since the early recognition of Opiliones, only the discovery of Ricinulei and Cyphophthalmi has challenged the monophyly of the group. Hansen and Sørensen (1904) defined the order and largely established the modern systematics of the group as we recognize it today. Before Hansen and Sørensen, Latreille (1796, 1806) established the family Phalangida for the genera *Galeodes* (Solifugae), *Phalangium* (Eupnoi), *Trogulus* (Dyspnoi), and *Siro* (Cyphophthalmi). Sundevall (1833) excluded the genus *Siro* from his order Opiliones and placed it together with his family Galeodides, in his order Solpugae, together with his families Phrynides (*Phrynus* and *Thelyphonus*), Scorpionides, and Obisides—an artificial clade containing members of the current orders Opiliones, Solifugae, Amblypygi, Uropygi, Scorpiones, and Pseudoscorpiones. Koch (1839) included all the harvestman families in his order Solpugae, which also comprised the family Galeodides, following Latreille. Later he excluded the family Sironidae from this order (Koch, 1850). Thorell (1876) recognized three main harvestman lineages (“sections”): Palpatores (including Cyphophthalmi), Laniatores, and the new group Ricinulei. Afterward he presented a new division of the order Opiliones into four suborders: Palpatores, Laniatores, Anepignathi (= Cyphophthalmi), and Ricinulei (Thorell, 1892). Karsch (1892) removed the family Cryptostemmatoidae from Opiliones, and Hansen and Sørensen (1904) recognized it as an arachnid order, adopting for it the name Ricinulei, proposed by Thorell for his suborder of Opiliones.

After this early period the order Opiliones was considered monophyletic and, to include what we currently recognize as its members, was generally arranged in three suborders: Cyphophthalmi, Laniatores, and Palpatores, the latter with the two tribes Dyspnoi and Eupnoi (e.g., Roewer, 1923). Only one historical note defied its monophyly. On the basis of phenetic criteria, Theodore Savory proposed that Cyphophthalmi be erected as a new arachnid order in a hilarious article reporting the results of an arachnological opinion poll, where the question of erecting the new order was asked. The results of this poll are not less amusing because of the sample size and responsiveness of the voting pool; two did not reply, two were uncertain “but favorably advised progress,” three were in disagreement, and four were strongly in favor (Savory, 1977). We were not told if the ones who disagreed were strongly against it or not. Unfortunately, democracy is no optimality criterion in systematics. The proposal was also justified phylogenetically: “Thus we come to look upon the Cyphophthalmi as the representatives of the ancestral group, from which have evolved the other orders of their subclass, namely the ‘Phalangida’ and the Ricinulei, both of which have passed beyond the stage of using a spermatophore” (Savory, 1977). No other researcher, to our knowledge, has followed such a proposal, and all phylogenetic analyses of harvestmen have corroborated the monophyly of Cyphophthalmi + Phalangida, even when including Ricinulei (e.g., Giribet, 1997; Giribet et al., 1999, 2002; Shultz & Regier, 2001). For a detailed explanation of the morphological characters found in the order, see Chapter 2.

The sister taxon of Opiliones

Although the monophyly of the order Opiliones is well accepted and corroborated by phylogenetic methodology, its sister-group relationships remain more contentious because of the number of phylogenetic trees that have been proposed for arachnids (see a summary of hypotheses in Wheeler & Hayashi, 1998). One of the most influential modern articles on chelicerate phylogenetics, the study of Weygoldt and Paulus (1979), proposed a sister-group relationship of Opiliones to a clade containing Acari and Ricinulei (Figure 3.1A). This system has been endorsed in some textbooks (Ax, 2000), but van der Hammen (1985), in the third part of his “Comparative Studies in Chelicerata” series, proposed the clade Myliosomata, grouping Opiliones, Xiphosura, and Scorpiones on the basis of their coxosternal feeding mode and the presence of a myliosoma. (A myliosoma is a more or less cone-shaped subdivision of the body with a complicated structure [van der Hammen, 1985: 26].) However, in the same article he also suggested an alternative relationship to Tetrapulmonata based on the development of the coxal glands and on the position of the spiracles (van der Hammen, 1985). A slight variation of that tree was published a year later (van der Hammen, 1986; Figure 3.1B). The current thinking until then was that the order Opiliones was related to Acari, as summarized by Shear (1982): “opilionids are evidently closest to some groups of mites.” The first numerical cladistic analysis of chelicerate relationships was the elegant study of Shultz (1990), who proposed a clade containing Opiliones, Scorpiones, Pseudoscorpiones, and Solifugae, which he named Dromopoda (see also Shultz, 1989). The specific position of Opiliones within Dromopoda was as a sister group to the clade Novogenuata (Scorpiones, Pseudoscorpiones, and Solifugae), also proposed by Shultz (1990; Figure 3.1C). The same result was obtained by Wheeler and Hayashi (1998) in the first total-evidence analysis of chelicerate relationships using morphological and molecular data. Some characters supporting this node are the extensor muscles and special articulations at the femoropatellar and patellotibial joints (Shultz, 1989, 1990), the transverse furrows of the prosomal carapace, a reduced intercoxal sternal region, the prosomal endosternite composed of two segmental elements, and perhaps the presence of a stomotheca later lost in Haplocnemata (Shultz, 1990). Another morphological analysis by Giribet et al. (2002) agreed with the monophyly of Dromopoda only when fossils were not taken into consideration, but the addition of relevant fossils such as Eurypterida, palaeophonid scorpions, *Proscorpius*, or Trigonotarbidia resulted in an unresolved pattern that contained three alternative topologies: Dromopoda, Opiliones + Haplocnemata, or Opiliones + nonscorpion arachnids (Giribet et al., 2002). Clearly the addition of the fossils—especially the eurypterids and the putatively marine Paleozoic scorpions—has an effect of pulling scorpions down the tree. The combination of those morphological data with molecular sequence data of the nuclear rRNA genes shows the monophyly of Dromopoda, but the internal resolution of Dromopoda is affected by the inclusion of the fossil taxa. The combined analysis without fossils shows Dromopoda *sensu* Shultz (1990), but the analysis with fossils shows a sister-group relationship of Opiliones to Haplocnemata (Figure 3.1D).

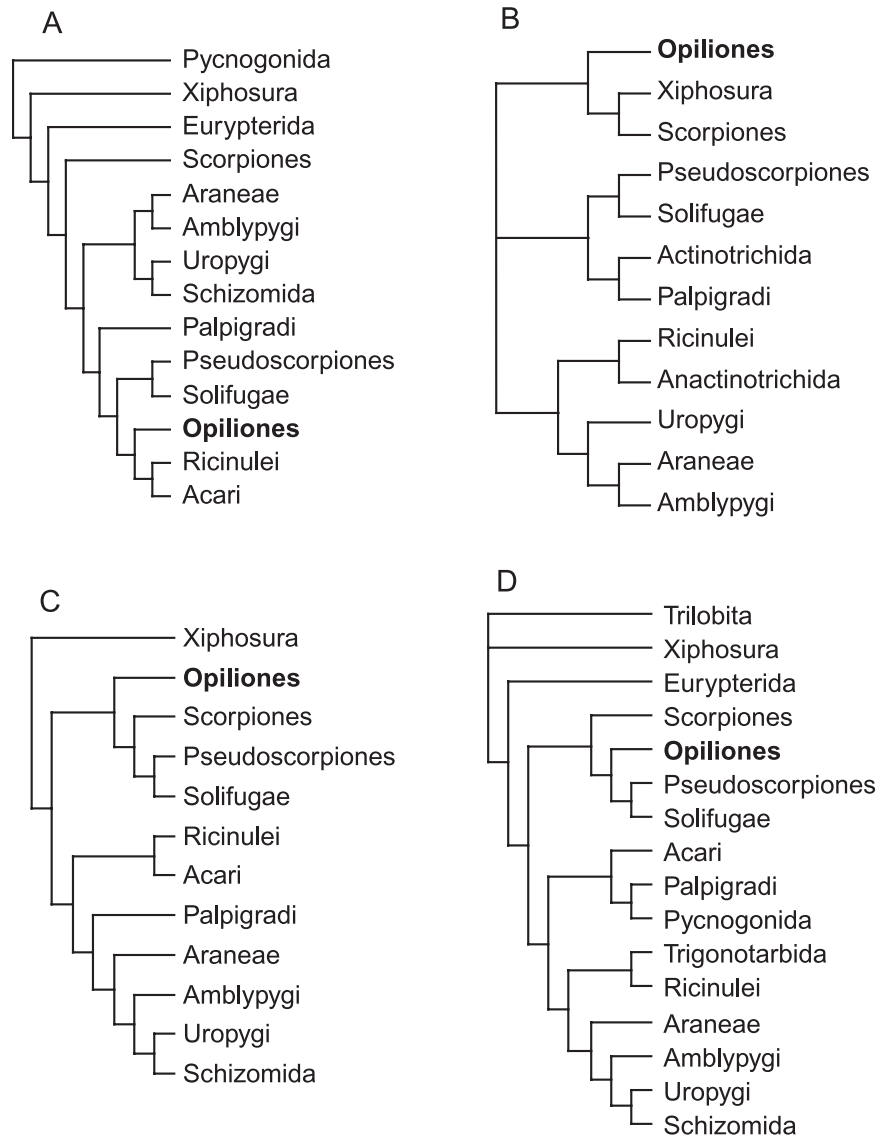


Figure 3.1. Hypothesis of relationships of Opiliones to other chelicerate groups as viewed by (A) Weygoldt and Paulus (1979), (B) van der Hammen (1986), (C) Shultz (1990), and (D) Giribet et al. (2002).

As the data (morphological and molecular) stand today, it seems that there is fairly good support for a Dromopoda clade that is also stable under model variation (see Giribet et al., 2002). However, the internal resolution of Dromopoda seems to change with the addition of fossil taxa, a possibility that had not been explored in Shultz (1990) or in Wheeler and Hayashi (1998). Furthermore, an explicit relationship of Opiliones and Scorpiones has been suggested on the basis of skeletomuscular anatomy (Shultz, 2000).

THE GROUPS OF OPILIONES AND THEIR INTERRELATIONSHIPS

An early attempt to produce a phylogenetic tree for the families of Opiliones was presented by Mello-Leitão (1944) on the basis of a few characters used in a hierarchical order (Figure 3.2). For Mello-Leitão there was a sister-group relationship between Cyphophthalmi and Palpatores, resembling the Cyphopalpatores hypothesis that Martens would propose decades later. Mello-Leitão considered Sironidae to be a sister group to a monophyletic group of extant Palpatores, but neither Eupnoi nor Dyspnoi were monophyletic in his scheme. Mello-Leitão also failed to recognize the dichotomy between Insidiatores and Grassatores, but it is interesting to note that he placed Onco podidae in a rather basal position, as Šilhavý (1961) would do decades later.

Since the publication of Hansen and Sørensen's (1904) monograph, the order

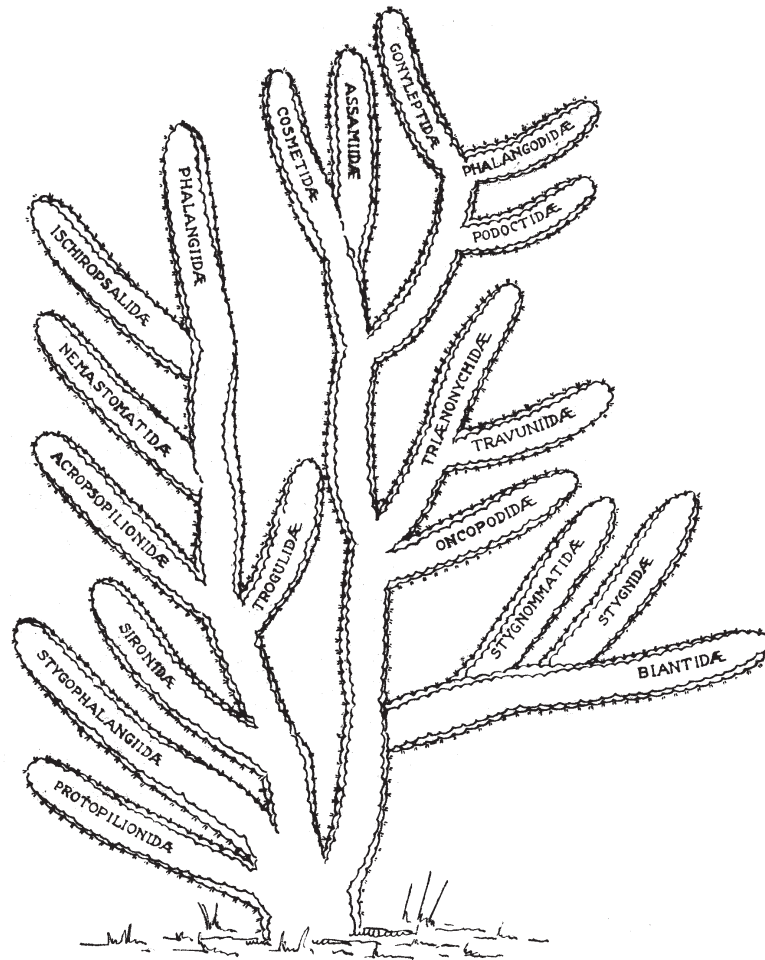


Figure 3.2. Evolutionary cactus of the Opiliones proposed by Mello-Leitão (1944).

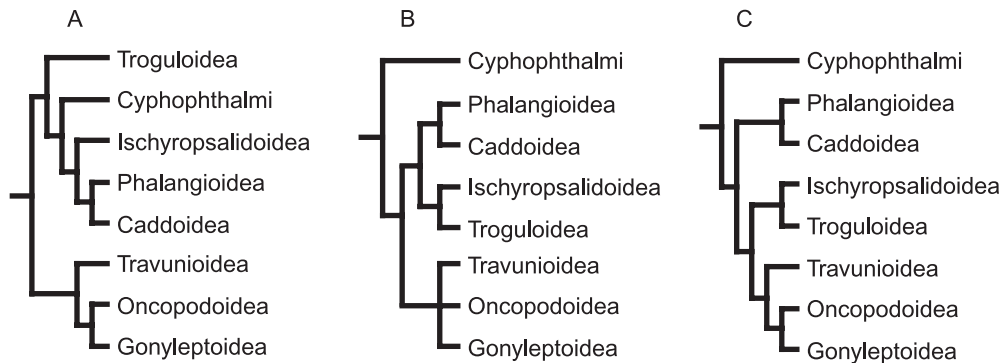


Figure 3.3. Alternative hypotheses for the evolution of Opiliones as envisioned by different authors. (A) Cyphopalpatores hypothesis of Martens (1976). (B) Classical hypothesis with Palpatores monophyletic, as in Hansen and Sørensen (1904) or Shultz (1998). (C) Dyspnolaniatores hypothesis of Giribet et al. (1999, 2002).

Opiliones has been recognized to contain three suborders: Cyphophthalmi, Palpatores, and Laniatores. They furthermore divided the Palpatores into two tribes, Eupnoi (containing the current Phalangioidae and Caddoidea) and Dyspnoi (containing the current Ischyropsalidoidea and Trogluoidae). While this system has been mostly in use until modern times (Shear, 1982), Šilhavý (1961) proposed to give Eupnoi and Dyspnoi a subordinal rank and proposed two new suborders for Laniatores, Gonyleptomorphi and Oncopodomorphi. Shear (1975a) explicitly rejected this system in order to preserve stability, especially in the case of Eupnoi and Dyspnoi. However, this system of classification was challenged by the prominent German arachnologist Jochen Martens, who proposed a radically new hypothesis of harvestman evolution based on the analysis of the genitalia (Martens, 1980). His Cyphopalpatores system (Martens, 1980, 1986; Martens et al., 1981) placed Cyphophthalmi within Palpatores, specifically as a sister group to Ischyropsalidoidea + Eupnoi, rendering Dyspnoi and Palpatores paraphyletic (Figure 3.3A). Since the Cyphopalpatores concept was proposed, it has been adopted in several arachnological studies and textbooks (e.g., Cokendolpher & Lee, 1993; Westheide & Rieger, 1996). Phylogenetic testing of the Cyphopalpatores system using modern cladistic techniques of both morphological and molecular data rejects Martens's idea and places Cyphophthalmi as the sister group of the remaining harvestmen, the Phalangida (Giribet, 1997; Shultz, 1998; Giribet et al., 1999, 2002; Giribet & Wheeler, 1999; Shultz & Rieger, 2001). All these studies found evidence for the monophyly of Phalangida, as well as for each one of the major lineages of Phalangida: Eupnoi, Dyspnoi, and Laniatores. However, disagreement emerged with regard to the status of Palpatores, which appear monophyletic in the studies of Shultz (1998; Shultz & Rieger, 2001; Figure 3.3B), but Dyspnoi appeared as the sister group to Laniatores in the studies of Giribet (1997; Giribet et al., 1999, 2002; Giribet & Wheeler, 1999; Figure 3.3C). The new name Dyspnolaniatores was pro-

posed on the basis of the stability of that clade to parameter variations in phylogenetic analyses (Giribet et al., 2002). A debate between both parties has been going on in recent literature, with critiques in both directions. However, both studies render very similar topologies for most lineages at all levels. The study of Shultz and Regier (2001) supports Palpatores on the basis of analysis of elongation factor-1 α and RNA polymerase II, as well as the combination of these genes with the ribosomal RNA sequence data of Giribet et al. (1999). The analysis of Giribet et al. (2002) supports Dyspnoaniatores on the basis of the ribosomal and morphological data and includes a larger taxon sampling both within and outside Opiliones. This study furthermore attempts to look at stability, finding that the Palpatores hypothesis is marginally supported. In order not to confound the reader, we decided to follow the well-corroborated evidence—the monophyly of Cyphophthalmi, Phalangida, Eupnoi, Dyspnoi, and Laniatores—and will present sections on the relationships of the four major harvestman clades. Whether Palpatores or Dyspnoaniatores is accepted should not matter in the following sections.

Cyphophthalmi

Cyphophthalmi is clearly a monophyletic group comprising six recognized families of small to medium-sized Opiliones thought to retain several plesiomorphies of the order Opiliones, although they may be highly autapomorphic for other characters. The group was clearly defined by Hansen and Sørensen (1904), who presented its first monograph, which is still the most important study of Cyphophthalmi anatomy. They identified two main lineages, which they called subfamilies Sironini [*sic*] and Stylocellini [*sic*]. They differ in having a movable coxa I and fused coxae II, III, and IV in Stylocellini, or free coxae I and II in Sironini, among other features. That classification remained in place until the seminal cladistic analyses of Shear (1980, 1993b), who proposed a new system consisting of two infraorders, Temperophthalmi and Tropicophthalmi, which correspond mainly to the Sironinae and Stylocellinae of Hansen and Sørensen. Temperophthalmi currently includes the single superfamily Sironoidea with three families, Troglisironidae, Sironidae, and Pettalidae. Tropicophthalmi is comprised of the superfamilies Stylocelloidea and Ogoveoidea, the first with the family Stylocellidae, and the second with the families Ogoveidae and Neogoveidae. While the main characteristic used by Hansen and Sørensen and subsequent workers for separating the two main lineages is highly conserved, taxa with exceptional articulation of the coxae II have been described: the sironid genera *Paramiopsalis* and *Iberosiro* have the second coxae of the legs fused to the third, as in the members of the Tropicophthalmi. Furthermore, "*Neogovea*" *mexasca* has a free second coxa, unlike the members of Neogoveidae, but this species now seems to be unrelated to Neogoveidae (Giribet & Boyer, 2002).

Although a recent cladistic morphological analysis of most Cyphophthalmi genera (Giribet & Boyer, 2002) agrees with Shear's (1980) phylogeny in the monophyly of Pettalidae and of Stylocellidae, no support was found for the monophyly of Sironidae, Neogoveidae, or Ogoveidae *sensu* Shear (1980). Furthermore, the division

between Tropicophthalmi and Temperophthalmi does not seem to be supported by either morphological or molecular data. The analysis from Giribet and Boyer (2002) is unresolved in many aspects and, like that of Shear (1980), lacks a proper criterion for defining the root position within Cyphophthalmi. In that respect a molecular analysis of 18S rRNA and 28S rRNA sequence data, using other harvestmen as outgroups, suggests two alternative rooting positions for Cyphophthalmi: (a) between Stylocellidae and the remainder families or (b) between Pettalidae and the remainder families. The latter option is favored in recent unpublished analyses that include a much larger diversity of Cyphophthalmi sequences.

A major disagreement between the hypotheses of Shear (1993b) and Giribet and Boyer (2002) is the phylogenetic position of Troglosironidae. Shear (1993b) postulated that *Troglosiro* is the sister group to a clade formed by Sironidae + Pettalidae, hence assigning to it a familial status. However, since the discovery of the first *Troglosiro* species (Juberthie, 1979), it has been noticed that the opisthosomal sternal region of the male bears glandular pore openings, as in the Neotropical genus *Huitaca* and in the African genus *Ogovea*. These structures were not seen as homologous according to their different position in the opisthosomal sternites (Shear, 1979a). More recently, other types of glandular openings have been observed in the opisthosomal sternal areas of the males in several species of American and African Neogoveidae (Giribet & Boyer, 2002; Giribet & Prieto, 2003; Sharma & Giribet, 2005). The presence of opisthosomal sternal glands in the males of members of Troglosironidae, Ogoveidae, and Neogoveidae may reflect apomorphy. Although this remains to be tested morphologically, DNA sequence data suggest that Neogoveidae and Troglosironidae form a monophyletic group.

Given the current uncertainty about the position of the root in the Cyphophthalmi tree, it is not possible to discuss evolution of most characters in the group. However, at least two more character systems deserve special attention, although their polarity is essential to understand the evolution within the group. One character is the presence of eyes in most members of Stylocellidae and in several pettalid species from Sri Lanka, Chile, and Australia. The second character is the evolution of the anal pore glands in Sironidae, Pettalidae, and Stylocellidae.

Most Cyphophthalmi are blind, although many members of the family Stylocellidae bear a pair of eye lenses in lateral position, frontal to the ozophores. Likewise, members of the pettalid genera *Pettalus* and *Chileogovea* and some undescribed Australian pettalids bear eyes incorporated into the base of the ozophore (Juberthie, 1989; Sharma & Giribet, 2006). The identity of these eyes is still disputed. Some authors think that they are homologous to the median eyes of other harvestmen, median eyes that migrated to the edges of the dorsal scutum. However, the eyes of stylocellids appear almost completely transparent with a reflective tapetum, which led Shear (1993c) to postulate that the stylocellid eyes are homologous to the lateral eyes of other arachnids (see Sharma & Giribet, 2006). However, no ultrastructural study of the Cyphophthalmi eyes has been completed. Irrespective of their final status, the eyes of Cyphophthalmi seem to be a plesiomorphic condition lost in several lineages of the group.

Anal gland pores in opisthosomal tergites VIII and IX have been widely described for male members of Sironidae and Pettalidae (Juberthie, 1962, 1967; Shear, 1980; Giribet & Boyer, 2002; de Bivort & Giribet, 2004) but have not been recorded for the families Neogoveidae, Ogoveidae, or Troglосironidae. The finding of a similar gland pore in *Fangensis leclerci* from Thailand (Rambla, 1994) led her to classify this species in the family Sironidae. Examination of other *Fangensis* species led to the inclusion of *Fangensis* within the family Stylocellidae (Giribet, 2002; Giribet & Boyer, 2002). Anal gland pores have since been discovered in other stylocellids of the genera *Fangensis* and *Stylocellus*, including the species type of the family, *S. sumatranus* (Schwendinger et al., 2004; Schwendinger & Giribet, 2005). Interestingly, the Cyphophthalmi families that lack anal gland pores have other special glandular openings in the anterior opisthosomal sternal area, and these glands are now thought to be probable homologues of the gland opening in the anal region in pettalids, sironids, and stylocellids (Sharma & Giribet, 2005). Therefore, it may seem reasonable to think that the primitive Cyphophthalmi had eyes and a male with either anal or opisthosomal sternal gland pores and an adenostyle. With the exception of the ozophores, no other homologous glandular systems can be found in the other harvestman lineages.

With respect to the genitalia, Cyphophthalmi are supposed to have plesiomorphic conditions for many of the characters, with a muscular spermatopositor and a long segmented ovipositor with sensory structures at the tip. However, the lack of similar structures outside Opiliones does not allow testing this hypothesis further. The presence of spermatophores in some species of Sironidae and Stylocellidae (Karaman, 2005; Schwendinger & Giribet, 2005) may require detailed comparison with other arachnid spermatophores.

Phalangida

Variations of the name Phalangida have been commonly used as synonyms to Opiliones, especially in the North American literature since the late nineteenth century (e.g., Banks, 1900; Bristowe, 1949; Edgar, 1990). However, recently the term Phalangida has been applied to the clade formed by Eupnoi, Dyspnoi, and Laniatores, and we use it as such here.

Palpatores

Given that the higher taxon Palpatores has been used in numerous studies of harvestman taxonomy and systematics—irrespective of whether it is monophyletic (Hansen & Sørensen, 1904; Roewer, 1923; Shultz, 1998), paraphyletic to the inclusion of Cyphophthalmi (Martens, 1980, 1986; Martens et al., 1981), or paraphyletic to the inclusion of Laniatores (Giribet et al., 1999, 2002)—we are forced to discuss it. Although most of the discussion of its subgroups—Eupnoi and Dyspnoi—can be achieved independently, some of the early work, especially that before Hansen and Sørensen (1904), did not differentiate among these two groups and requires the use of the name “Palpatores.”

One of the earliest attempts to provide a phylogenetic classification for Palpatores was given by Pocock (1902b). He used the name Plagiostethi (= Palpatores), which was divided into Apagosterni and Eupagosterni, and this classification was followed by other authors (e.g., Roewer, 1910). Apagosterni included the current Phalangoidea and Ischyropsalididae (Phalangiidae and Ischyropsalidae of Pocock); and Eupagosterni included the families of the current Troguloidea (Nemastomidae, Dicranolasmatidae [*sic*], and Trogulidae of Pocock). Nonetheless, most authors of the late nineteenth and early twentieth centuries used taxonomic systems that reflected an understanding of the two palpatorean lineages (Sørensen, 1873; Thorell, 1876, 1877; Hansen & Sørensen, 1904; Roewer, 1923), about which Pocock (1902b: 504) stated that “these conceptions are unquestionably erroneous.”

Other authors preferred not to define suprafamilial taxa within Palpatores and used the four recognized families (Phalangiidae, Ischyropsalididae, Nemastomatidae, and Trogulidae, with variable spellings) without specifying their relationships (Simon, 1879a). Shear (1975a) proposed classifying Palpatores into three superfamilies, Troguloidea (Trogulidae, Nemastomatidae, Ischyropsalididae, Sabaconidae), Phalangoidea (Phalangiidae, Neopilionidae, Leiobunidae, Sclerosomatidae), and Caddoidea (Caddidae). His Troguloidea corresponds to Dyspnoi, while the other two superfamilies comprise the current Eupnoi. Since the widely used classification of Hansen and Sørensen (1904), the only influential articles that have questioned the monophyly of Dyspnoi are the studies of Martens and collaborators proposing the Cyphopalpatores hypothesis. But no phylogenetic testing has ever rendered Cyphopalpatores, and all studies have recognized the two main palpatorean lineages, Eupnoi and Dyspnoi. In fact, these two categories have been used in several taxonomic studies (e.g., Starega, 1976a).

Eupnoi

Eupnoi constitutes a clear monophyletic group containing the best-known harvestmen from the Northern Hemisphere, the members of the families Phalangiidae and Sclerosomatidae. Knowledge of the European Eupnoi species is exemplary, and most species were already included in the seminal monograph of Martens (1978b). Currently Eupnoi includes the two superfamilies Phalangoidea and Caddoidea (Shear, 1982). The monophyly of a selected group of members of Phalangoidea has been shown in current phylogenetic analyses (Giribet et al., 1999, 2002; Shultz & Regier, 2001), but the monophyly of Caddoidea remains yet to be tested phylogenetically.

Caddoidea includes the single family Caddidae with two subfamilies, Caddinae and Acropsopilioninae (Shear, 1975a). Phalangoidea is a much larger group, with five families recognized: Phalangiidae, Sclerosomatidae, Neopilionidae, Monoscutidae, and Protolophidae, as well as a few species of uncertain affinities (Cokendolpher & Lee, 1993). Although the monophyly of Phalangoidea has been assumed, only the families Phalangiidae and Sclerosomatidae and a genus of uncertain position, *Dalquestia*, have been analyzed phylogenetically (Giribet et al., 1999, 2002; Shultz & Regier, 2001). Taxonomic delimitation of the families and

subfamilies within Phalangioidea remains uncertain in many cases, and no attempt to study the phylogeny of the entire superfamily has been made, despite the fact that this group contains the most typical forms of Opiliones. Hunt and Cokendolpher (1991) presented a cladistic analysis of Phalangioidea restricted to Southern Hemisphere nonentapophysate species. Unfortunately, their results are difficult to interpret in a strict parsimony sense because preferred trees (and not the consensus of the shortest trees) were presented, rooting was done with a hypothetical ancestor, and several hypotheses were proposed after the analysis. Certainly Eupnoi is in urgent need of further systematic study.

Dyspnolaniatores

The taxon Dyspnolaniatores was formalized by Giribet et al. (2002) on the basis of phylogenetic evidence presented in this and previous studies combining morphological and molecular evidence (Giribet, 1997; Giribet et al., 1999; Giribet & Wheeler, 1999). The group is comprised of Dyspnoi and its sister group, Laniatores. As mentioned earlier, this was questioned by another phylogenetic analysis based on a different set of molecular characters (Shultz & Regier, 2001), although the analysis from Shultz and Regier is more restricted in terms of taxon sampling and did not include outgroup taxa outside the Opiliones. Both studies show alternative resolutions, and conflict among the loci employed cannot be ruled out, as shown in an analysis of centipede relationships (Giribet & Edgecombe, 2006). Overall, the ribosomal genes are more congruent with morphology than elongation factor-1 α or RNA polymerase II, as shown in the resolution within the superfamily Ischyropsalidoidea (Shultz & Regier, 2001). Dyspnolaniatores can be diagnosed by the lack of a jointed ovipositor.

Dyspnoi

Among the groups of Opiliones, Dyspnoi is perhaps the one that has received the most phylogenetic attention, from both a morphological and a molecular point of view. The group is restricted to the Northern Hemisphere, and its fauna has been worked extensively (Suzuki, 1965, 1974; Shear, 1975b, 1986; Martens, 1978b; Shear & Gruber, 1983). Dyspnoi is clearly monophyletic, despite Martens's polyphyletic proposal (Martens, 1980, 1986; Martens et al., 1981). Both morphological cladistic analyses and molecular studies (see previous references) have corroborated the monophyly of the group and clearly show that it is divided into two major lineages—Trogluloidea and Ischyropsalidoidea (Martens, 1976)—each receiving the rank of superfamily.

Relationships within Ischyropsalidoidea have been investigated in detail (Shear, 1986; Shultz & Regier, 2001; Giribet et al., 2002). It is comprised of three families: Ischyropsalididae, Ceratolasmatidae, and Sabaconidae. From the characters used by Shear (1986) to diagnose the superfamily (presence of metapeltidial sensory cones, loss of segmentation in the ovipositor, reduced or absent pedipalpal claws, and the presence of cheliceral glands in males), none are considered autapomorphic; they

are Dyspnoi characters, or they may be plesiomorphic or convergent with other Opiliones (see a discussion in Giribet et al., 2002). Disagreement exists over the status of Ceratolasmatidae and Sabaconidae, since molecular analyses tend to place the ceratolasmatid *Hesperonemastoma* with the sabaconid *Taracus*. Given the necessity of including members of the genera *Crosbycus* and *Acuclavella* in the molecular studies, taxonomic amendments should await more careful studies within the superfamily.

The second superfamily of Dyspnoi, Troguloidea, includes the families Trogulidae, Nemastomatidae, Dicranolasmatidae, and Nipponopsalididae, distributed in the Northern Hemisphere. The phylogeny of the nemastomatid subfamily Ortholasmatinae has been investigated by Shear and Gruber (1983). The monophyly of Troguloidea has also been corroborated by morphological and molecular studies (Shultz & Regier, 2001; Giribet et al., 2002) that mostly agree on the following scheme: (Nipponopsalididae (Nemastomatidae (Dicranolasmatidae + Trogulidae))) (Shultz, 1998; Giribet et al., 2002). This group is supported by a similar type of sternum (Hansen & Sørensen, 1904) and by genitalic characters: two muscles in the penis, aciniform vaginal glands in the ovipositor, and outer circular muscles in the ovipositor (Martens et al., 1981; Martens, 1986).

Given the evidence for the monophyly of Dyspnoi and the well-delimited number of families and genera, we expect that a more comprehensive phylogenetic study of Dyspnoi will be obtained in the near future. One item remains, though, which is the presence of certain characters, thought to be typical of Troguloidea, in some Cad-doidea: metapeltidial sensory cones (Shultz, 1998) and plumose pedipalpal setae with distal clusters of microtrichia (Shear, 1986; Shultz, 1998). The latter character has also been observed in juveniles of different species of Eupnoi (Hunt & Cokendolpher, 1991).

Laniatores

Thorell (1876) coined the names Palpatores (Latin *palpātor*, a stroker; a flatterer) and Laniatores (Latin *lāniātor*, butcher) as the first division of Opiliones. While Eupnoi and Dyspnoi were known for a long time and some species were included in the Linnaean classification (Linnaeus, 1758), the first laniatorean was not described until 1818 (*Gonyleptes horridus*), from Brazil. More Laniatores, especially from Brazil, started to be revealed through the work of Perty (1833). Hope (1837) described a Brazilian Mitobatinae (Gonyleptidae) as an example of an intermediate between "Palpatores" and Laniatores.

What we now call Travunioidea took many years to be discovered. European species were at first put in *Scotolemon* (Phalangodidae), as was the South African *Phalangium rugosum*. Simon's classification of Laniatores (Simon, 1879b) recognized three families, namely, Phalangodidae, Cosmetidae, and Gonyleptidae. Phalangodidae included future members of almost every family. It is noteworthy that Cosmetidae and Gonyleptidae are now deemed to be very closely related families, so Simon's system detached a specialized group, making a large paraphyletic Phalangodidae.

Loman (1902) first recognized the morphological gap between Travunioidea

(then all in a single family Triaenonychidae) and the other Laniatores and proposed a new suborder for this family—Insidiatores (Latin *insidiātor*, a soldier lying in ambush, one who lies in wait, a lurker)—but this change was mostly not incorporated by subsequent authors. Loman's concept did not extend to Travuniidae, whose few species known were then placed within Phalangodidae. The nominal family would still take 30 years to be discovered.

Pocock (1902a) divided Simon's Mecostethi into Insidiatores (including his Triaenonychidae, Triaenobunidae, and Aadaeidae) and Laniatores, a classification system followed by Roewer (1910). In the beginning of the twentieth century, all previous work was obscured by the unwavering labor of Roewer (see Chapter 1). This indefatigable German author established the base of most future harvestman systematics by using an artificial system based on a few "rank-worthy characters." Roewer (1923) recognized six families with 32 subfamilies in Laniatores, without grouping any of these families in larger units. Other authors (e.g., Mello-Leitão, 1932, 1938, 1949) expanded some taxa, but did not propose suprafamilial groups in Laniatores.

Kratochvíl (1958a) proposed two superfamilies based on claw structure: Oncopodoidea (with six families) and Travunioidea [*sic*] (with three families). The incorrect derivation of the superfamily name was corrected by Shear (1977) to Travunioidea. Shortly after Kratochvíl's scheme, a new one was proposed by Šilhavý (1961), who split Laniatores into two suborders: Gonyleptomorphi (containing the superfamilies Gonyleptoidea and Travunioidea) and Oncopodomorphi. Both systems recognized three basic groups: (1) the small group Oncopodoidea from Southeast Asia, (2) the families with elaborately branched single claws in the hind legs and muscular penises (Travunioidea, from northern and southern [mostly temperate] latitudes), and (3) the large tropical Gonyleptoidea, with double claws in the hind legs and hydraulic penises lacking musculature. The fundamental difference between the two systems was the internal relationship of these groups: (Travunioidea (Oncopodoidea + Gonyleptoidea)) (Kratochvíl, 1958a) or (Oncopodoidea (Travunioidea + Gonyleptoidea)) (Šilhavý, 1961).

Martens (1980) published the first comprehensive phylogenetic analysis of Opiliones, dividing Laniatores into three superfamilies, following Kratochvíl's (1958a) scheme. However, Martens did not use numerical cladistics and relied on an evolutionary scenario to polarize his characters. He also extrapolated character states for some taxa (notably Travunioidea) on the basis of preconceived ideas of phylogeny. As usual at that time, terminals for the cladistic analysis were based on groundplans instead of species.

More recently (Martens, 1988; Starega, 1989, 1992; Kury, 1992a,b), certain familial diagnoses were questioned. Kury (1992a, 1993a, 1994a,b, 1997a,b) proposed phylogenetic hypotheses for some families of Gonyleptoidea, but there is no proposed phylogeny for the entire Laniatores. The monophyly of Travunioidea and Triaenonychidae was rejected by Dumitrescu (1975a, 1976) on the basis of detailed examination of the intestinal caeca (see Chapter 2). The tripartition of the *diverticulum tertium* into a *ramus medianus*, *ramus lateralis*, and *ramus exterior* stands as a pu-

tative synapomorphy of Gonyleptoidea (Cosmetidae + Phalangodidae + Assamiidae + Gonyleptidae + Stygnidae) plus *Synthetonychia* and the southern Triaenonychidae (*Adaeulum* + *Larifuga* + *Tasmanonyx* + *Paranuncia* + *Nuncia*). This contrasts with the plesiomorphic bipartite condition of most Travunioidea, namely, Travuniidae (*Peltonychia* + *Speleonychia*), Northern Hemisphere Triaenonychidae—for which Dumitrescu coined the name Sclerobuninae (*Sclerobunus* + *Zuma*)—*Paranonychus*, and *Pentanychus*. The quadripartite condition of the *diverticulum primum* is a putative apomorphy for the Southern Hemisphere Triaenonychidae.

The character used to distinguish families in Travunioidea—the claw structure—varies within a single genus (Hunt & Hickman, 1993). Maury (1988) also acknowledged a set of characters that make difficult the placement of a cave-dwelling Argentinean relict, *Pichunchenops spelaeus*, which ended up in Triaenonychidae.

According to the phylogeny proposed by Martens (1980), Oncopodoidea and Gonyleptoidea constitute a monophyletic group, defined mainly by the hydraulic penis lacking musculature (Martens, 1976). Kury informally called this group *Grasatores* (from Latin *grassator*, a disorderly person, one who goes rioting about, especially at night, whether for fun and enjoyment or for robbery), a name used by Giribet et al. (2002) and formalized in the catalogue of the New World Laniatores (Kury, 2003).

The three superfamilies of Martens (1980)—Travunioidea, Oncopodoidea, and Gonyleptoidea—were recovered in two recent combined molecular and morphological analyses (Giribet et al., 1999, 2002), although taxonomic coverage for Laniatores was restricted to a few species. Molecular-only-based analyses failed to recover monophyly of Triaenonychidae, the only family of travunioidea sampled so far (Shultz & Regier, 2001; Giribet et al., 2002). Kury (1993a) pursued the issue of the basic division within Laniatores and has shown further evidence for a diphyletic Travunioidea, refuting Martens's dichotomy of Oncopodoidea versus Gonyleptoidea (Kury, 2002).

Other preliminary conclusions indicate that the widely accepted Travunioidea (= infraorder Insidiatores) does not form a clade (nor do Triaenonychidae *sensu lato*). "Travunioidea" can be arranged in two clades, here called superfamilies Travunioidea and Triaenonychoidea. The Northern Hemisphere Triaenonychidae (except for the remarkable *Fumontana*) group with Travuniidae. All Southern Hemisphere Triaenonychidae plus the New Zealand Synthetonychiidae form a clade. Pentanychidae could well form the sister group to all other Laniatores because of the plesiomorphic retention of all opisthosomal sclerites, as in *Cyphophthalmi*, *Eupnoi*, and *Dyspnoi*, but this remains to be tested. So far, molecular analyses relying on nuclear ribosomal genes support monophyly of Gonyleptidae + Cosmetidae + Stygnopsideae + Phalangodidae and do not support Phalangodoidea (= Phalangodidae + Oncopodidae) (Giribet et al., 1999, 2002). Molecular analyses relying on nuclear protein-coding genes support monophyly of Gonyleptidae + paraphyletic Phalangodidae (Shultz & Regier, 2001), but this study did not include Oncopodidae. With such a limited familial sampling, conclusions based on molecular sequences should await further data.

Martens et al. (1981) provided a nice overview of the structure of ovipositors in representative harvestman species. Many of the phylogenetic conclusions on larger groups are based on those observations. However, their sampling for Travunioidea did not include any Southern Hemisphere species. The derived state of their character “loss of longitudinal inner musculature of ovipositor” supporting the monophyly of Travunioidea (Martens et al., 1981) is based on a state that occurs in three species only (*Holoscotolemon unicolor* and *Theromaster brunnea*, both Cladonychiidae, and *Peltonychia clavigera*, Travuniidae). These species surely form a monophyletic group, but the character state in Triaenonychidae *sensu lato* remains unknown. The cladistic analysis of Giribet et al. (2002) defended the monophyly of Travunioidea, coding this state in species where the character is unknown, two Southern Hemisphere and one North American Triaenonychidae (*Equitius*, *Triaenobunus*, and *Zuma*). Another problem is the number of apical lobes. This character was extrapolated for all Travunioidea, but it was known for three species of two families in Martens et al. (1981). Descriptions and illustrations of the Pentanychidae *Sclerobunus* and Paranonychinae (Briggs, 1971a,b) confirm the apomorphic number of four lobes. However, in *Picunchenops* it is explicitly said to be bilobed, the plesiomorphic state (Maury, 1988), and in all Southern Hemisphere Triaenonychidae (Kauri, 1961) and *Fumontana* (J.C. Cokendolpher, pers. comm.) it is also bilobed. Forster (1954) did not make any reference to the ovipositor in Synthetonychiidae.

Detailed study of the descriptions and illustrations of ovipositors in Martens et al. (1981) reveals a misinterpretation of Martens's character 23, which supports all nononcopodid Laniatores with penises lacking musculature (his “Gonyleptoidea”). The concentration of glands for oviposition is considered apomorphic, while the presence of diffuse glands in Oncopodidae (Martens et al., 1981) is considered plesiomorphic. Outgroup comparison illustrates that the condition found in Phalangodidae, Gonyleptidae, and other families is similar to the condition found in species of Dyspnoi and Travunioidea and therefore probably plesiomorphic, while the condition in Oncopodidae is apomorphic. These characters are unknown for the vast majority of Laniatores.

On the basis of Kury (1992a, 1993a, 1997a,b, 2002, and unpublished analyses), the phylogeny of Laniatores can be reconstructed with a first split between Travunioidea and Triaenonychoidea + Grassatores, the latter group including Zalmoxoidea, Biantoidea, Phalangodoidea, Epedanoidea, and Gonyleptoidea. In this scheme Travunioidea includes the Northern Temperate Insidiatores (Travuniidae, Cladonychiidae, Triaenonychidae, Pentanychidae); Triaenonychoidea includes the Southern Temperate Insidiatores (Triaenonychidae, Adaeini, Triaenobunini, Synthetonychiidae) + *Fumontana*; the other superfamilies are Zalmoxoidea (Icaleptidae, Guasiniidae, Zalmoxidae + Fissiphalliidae), Samooidea (Samoidae + Podoctidae + Biantidae + Minuidae + Stygnommatidae), Phalangodoidea (Phalangodidae + “Pyramidopidae”? + Oncopodidae?), Epedanoidea (Epedaninae + Acrobuninae + Sarasinicinae), and Gonyleptoidea (Assamiidae + Stygnopsidae + Agoristenidae + Manaosbiidae + Cranidae + Stygnidae + Cosmetidae + Gonyleptidae) (Figure 3.4).

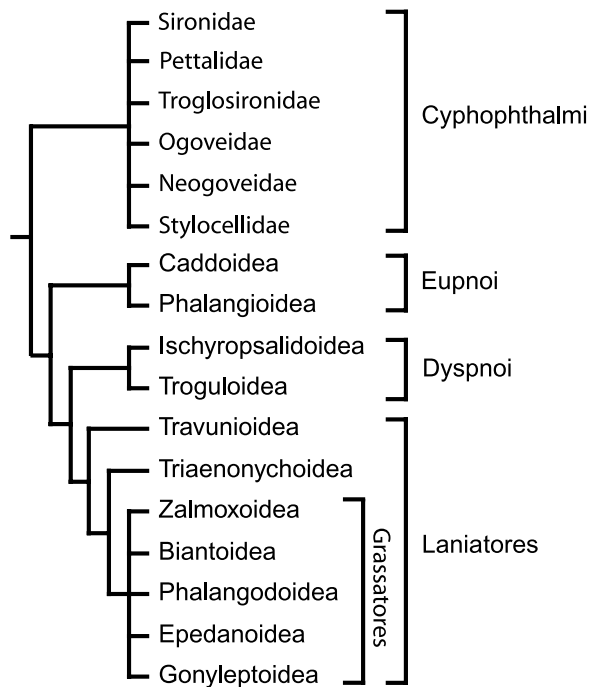


Figure 3.4. Summary tree of harvestman relationships with monophyly of Phalangida and paraphyly of Palpatores, as in Giribet et al. (2002), and with Laniatores reflecting the hypotheses of Kury (1992b, 1993a, 1997a,b, and unpub. data). Cyphophthalmi are shown mostly unresolved because of the conflictive hypotheses of Shear (1980), Giribet and Boyer (2002), and Giribet (unpub. data).

Phylogenetic conclusions

Elucidating the evolutionary history of the order Opiliones is an exciting research topic that has been explored in depth during the last two decades with the application of cladistic methodology, including parsimony analyses of morphology and molecular data. The number of phylogenetic analyses of Opiliones has grown steadily during this period, and we expect it to keep growing in the coming years. Areas that will need special attention are the relationships within Phalangioidea, relationships among the laniatorean families, and internal analyses of many families whose monophyly has been questioned (e.g., Sironidae, Ceratolasmatidae, Sabacnidae, Triaenonychidae). Having a sound phylogenetic hypothesis that includes representatives of most harvestman genera seems an achievable goal for the next decade or so. A summary phylogenetic account of Opiliones, as we currently recognize it, is provided in Figure 3.4.

THE GROUPS OF OPILIONES AND THEIR BIOGEOGRAPHY

Opiliones are rather unusual among arthropods in having limited dispersal ability, as a consequence of their low vagility (with the exception of some temperate Eupnoi). This limitation in colonizing new environments causes present-day distribu-

tions to reflect historical changes in addition to ecological constraints. Opiliones are therefore a prime candidate group for biogeographic studies.

Early workers on systematics had a rather casual approach to biogeography. This is especially true in reference to Carl F. Roewer, who erected taxonomic groups with disjunct distributions that make no sense phylogenetically—the most blatant example being the subfamily Tricommatinae (Roewer, 1935a), based on species from Europe, South America, and Malaysia. Current views place the species of Tricommatinae in at least three different families. Mello-Leitão took biogeography into consideration, but his taxonomic inaccuracy resulted in errors such as the southern Brazilian “podoctid” that happened to be a triaenonychid (Soares & Soares, 1979). Despite the high endemism of most Opiliones, Goodnight and Goodnight (1951, 1983) failed to recognize the diversity of the current Stygnommatidae and treated them as a single widespread species.

Few studies explicitly summarized or discussed species distributions. Loman (1900) presented a clear overview of the global distribution of all harvestman families. Mello-Leitão (1936) proposed a scenario to explain present-day distribution of Gonyleptidae (then including also Cranaidae and Manaosbiidae) and hypothesized a center of origin in the Colombian highlands. Forster (1954) provided detailed distributions of New Zealand Cyphophthalmi and Laniatores. Kratochvíl (1958a) provided distribution maps for the European Cyphophthalmi and relictual Laniatores. Lawrence (1959) discussed relationships among the Madagascan fauna. Kauri (1961) mapped the distribution of the South African species and explained their relationships. Suzuki (1967, 1972b, 1977a) assessed the Japanese biogeography. Šilhavý (1979) provided worldwide records for samoids. Starega (1984) offered a scenario to explain the dispersal of Phalangiinae in Africa and later (Starega, 1989) retook Kauri's discussion on the relationships of the South African fauna. Ringuelet (1959) offered an organization of the zoogeographic areas in Argentina, later refined by Acosta (2002a). For Cyphophthalmi, several authors have provided the distributional ranges for the families and genera (e.g., Juberthie, 1970b; Shear, 1980; Giribet, 2000).

The first biogeographic analysis in Opiliones presented a Brooks parsimony analysis of the Brazilian Atlantic forest using the distributions and phylogeny of Mitobatinae (Kury, 1991). Pinto-da-Rocha (2002) presented an analysis for Caelopyginae, Silva (2002) studied the biogeography of Goniosomatinae, and Pinto-da-Rocha et al. (2005) analyzed the records of occurrence of 84 species of Laniatores and Eupnoi in 11 areas of the Atlantic rain forest of Brazil.

Zoogeographic realms

In order to discuss the zoogeographic relationships of the different harvestman taxa, we employ the traditional zoogeographic realms: Afrotropical, Australian, Indo-Malayan, Nearctic, Neotropical, Palearctic, and Oceanian. Four areas that show overlap between major zoogeographic realms are China, Indonesia, Japan, and Mexico, and they require particular discussion. For example, regarding the har-

vestman fauna, the Japanese islands show a progressive predominance of Indo-Malayan versus Holarctic elements toward the south (Suzuki, 1967). Likewise, the Mexican states present more Neotropical-related fauna toward the south (Kury & Cokendolpher, 2000). A few current biogeographic terms are defined here:

- Amphipacific (= Amphiberingian, orthern transpacific disjunctions): North America and Japan/eastern Asia
- Temperate Gondwana: Southern South America, southern Africa/Madagascar, India/Sri Lanka, Australia, New Zealand, and New Caledonia
- Amphitotic (= Austral): Temperate Gondwana without southern Africa/Madagascar
- Tropical Gondwana: Neotropics, central Africa
- Wallacea and Sundaland: The continental and insular components of the Malayan Peninsula, including Sumatra, Borneo, Java, and Sulawesi

Cyphophthalmi

Cyphophthalmi have championed biogeographic explanations in harvestmen. Its members are found in all continents and major islands of continental origin, with the exception of Antarctica, where they are supposed to have become extinct (Figure 3.5). They have not been able to disperse to any oceanic islands, and instances of recent dispersal between separate landmasses have not been demonstrated. Each of the six recognized families has a well-characterized biogeographic distribution (Figure 3.5): Sironidae has a Laurasian distribution; Neogoveidae is restricted to cir-

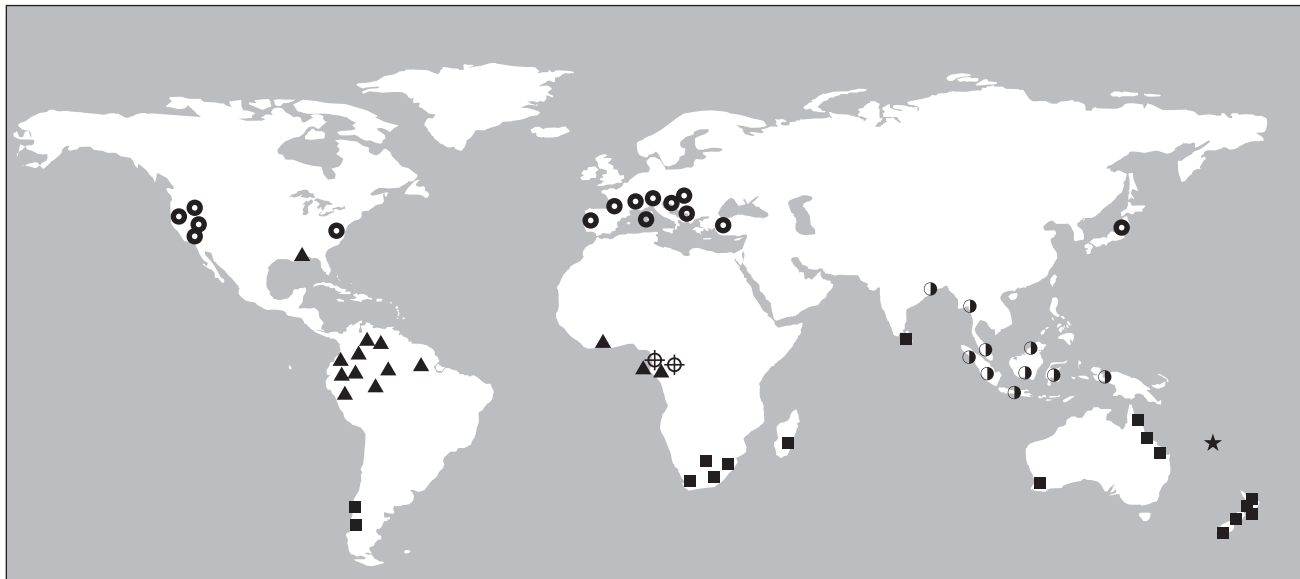


Figure 3.5. Geographic distribution of Cyphophthalmi: Neogoveidae (triangles), Ogoveidae (crossed circles), Pettalidae (squares), Sironidae (circles), Stylocellidae (half-colored circles), and Troglosironidae (star).

cumequatorial South America, Florida, and western Africa; Ogoveidae is restricted to the Gulf of Guinea in West Africa; Pettalidae has a typical temperate Gondwanan distribution; Troglonironidae is restricted to New Caledonia and is clearly unrelated to Pettalidae; Stylocellidae is found in Southeast Asia, including northern Thailand, Wallacea, Sundaland, and western New Guinea.

Phylogenetic analysis of Cyphophthalmi relationships suggests a sister-group relationship of Pettalidae to the remaining families (G. Giribet, unpub. data). Relationships within Sironidae (Boyer et al., 2005) and Pettalidae (Giribet, 2003; Boyer & Giribet, unpub. data) have been explored in detail, and both global and local biogeographic patterns help understand current distributions of species. Within Neogoveidae, both the American and the African species form reciprocally monophyletic groups. Clearly, Cyphophthalmi species show a great potential for becoming a model for biogeographic studies.

Eupnoi

Caddis are typically found in temperate zones of both hemispheres—with Amphipacific and temperate Gondwanan distributions (Shear, 1975a)—with the remarkable exception of a record from Venezuela (González-Sponga, 1992b). Apart from Japan, the single record from the Palearctic region is from Baltic amber. *Acropsopilio* has a large disjunct distribution: northeastern USA, southeastern Canada, Mexico, southern South America (Argentina, Brazil, and Chile), northern South America (Venezuela), Japan (the same species found in the USA and Canada), New Zealand, and Australia. *Caddo* shows a disjunct Amphipacific distribution: northeastern USA, southeastern Canada, and Japan. *Austropsopilio* and *Tasmanopilio* show an Amphinotic distribution: Australia/Tasmania/southern South America (Argentina, Brazil, and Chile). *Caddella* is found in South Africa, while *Hesperopilio* is restricted to western Australia. Although these patterns are suggestive of several well-explained distribution patterns, no phylogenetic analysis has been attempted in the group.

The members of the family Neopilionidae are typically distributed across temperate Gondwana, in Chile, Argentina, southern Brazil, South Africa, and Australia. Protolophids are restricted to the western USA. The *Metopilio* group occurs in the western USA, reaching as far south as Costa Rica.

Sclerosomatidae include several subfamilies, from which Gagrellinae are distributed in Indo-Malaya and the Neotropics but absent elsewhere. Gyinae occur at high elevations in the Caucasus, Alps, and Nepal. Leiobuninae are distributed throughout the Palearctic region, as well as in the Nearctic, with a peak of diversity in Mexico, Guatemala, and Costa Rica. Sclerosomatinae are restricted to the Palearctic region.

Phalangiidae also include several subfamilies. Phalangiinae are most diverse in the Mediterranean region, having radiated to coastal Africa (Starega 1984), where many endemic genera are recognized. The few Nearctic Phalangiinae are all introduced. Opilioninae are mainly Palearctic, with a few representatives in continental

Southeast Asia. Oligolophinae are Holarctic, with their peak of diversity in central and western Europe. Finally, Platybuninae occur in central and southeastern Europe, the Balkans, Anatolia, and the Caucasus, with an odd record from Sumatra. There are records of introduced *Nelima* in Australia and New Zealand (Gruber & Hunt, 1973).

Dyspnoi

Dyspnoi are restricted to the Northern Hemisphere, often with restricted distribution patterns. Nemasomatidae have a disjunct Holarctic distribution, with its peak of diversity in the western Palearctic (from the Iberian Peninsula and the Atlas to the Caucasus), reaching as far as Thailand (Schwendinger & Gruber, 1992). Ortholasmatinae have a few species in the eastern Palearctic (Japan) and the Nearctic (western USA). Dicranolasmatidae are recorded from Spain to the Caucasus, Iraq, and Turkey. Nipponopsalididae are restricted to the eastern Palearctic (Japan and Korea). Trogulidae are found in the western Palearctic, with their peak of diversity in the eastern and central Mediterranean region. Ischyropsalididae are found in the western Palearctic, from central Europe to the Iberian Peninsula. Sabaconidae are Holarctic, found from the Iberian Peninsula to Japan and the USA. Finally, Ceratolasmatidae are Nearctic, restricted to the USA.

Laniatores

The Northern Temperate Insidiatores probably form a monophyletic group, Travunioidea. They are endemic to the Holarctic realm and occur in both coasts of the USA, Japan, Korea, and Europe, but are absent from central Asia (Briggs, 1969, 1971a, b; Martens, 1978a). Cladonychiidae have a disjunct relictual Holarctic distribution in Europe (*Holoscotolemon*) and both coasts of the continental USA. Travuniidae have a disjunct and relictual distribution in southern Europe, Japan, Korea, and the western USA. Pentanychidae/Paranonychinae are endemic to the northwestern USA. Sclerobuninae are endemic to the western USA.

A group of Southern Temperate Insidiatores (Triaenonychidae and Synthetonychiidae) and the eastern North American *Fumontana* form the Triaenonychoidea. They occur in the classical Austral realm along the former temperate Gondwana. Although a few genera are reported to occur in more than one continent (Lawrence, 1931; Forster, 1954; Kauri, 1961; Maury & Roig Alsina, 1985), phylogenetic testing of the genera has not been attempted.

Grassatores constitute the largest group of Laniatores. Phalangodidae are Nearctic and western Palearctic, especially circum-Mediterranean. Oncopodidae and Epedanidae are found in the Indo-Malayan province, the latter also occurring in China, Nepal, and Japan. Gonyleptoidea occur in tropical Gondwana, Wallacea, and Sundaland, with an interesting area relationship (Kury, 1997c): Assamiidae—the putative sister group to the rest—occur in tropical Asia and central Africa, while the others are endemic to the Neotropics. Of these, Stygnopsidae—which are the possible sister group to other gonyleptoid families—are restricted to Mexico, Belize, and

Guatemala. The remaining families are distributed from Costa Rica to subAntarctic Chile and Argentina. An exception is Cosmetidae, which reaches the southern USA.

“Samoidea” is an informal group that includes a number of families of small Laniatores that inhabit leaf litter, including Podoctidae, Biantidae, Escadabiidae, Samoidae, Minuidae, and Stygnommatidae. They occur in tropical Gondwana, Wallacea, and Sundaland, plus Madagascar and India. “Zalmoxoidea” is another pantropical group. The nominal family occurs in tropical Asia, tropical Africa, and the Neotropics, while the other families (Fissiphalliidae, Guasiniidae, and Icaleptidae) are endemic to South America. Some zalmoxoid species are additionally found in Australia and New Caledonia.

Areas and their harvestman taxa

The interesting biogeographic patterns shown by the different harvestman families have been summarized in Table 3.1. Here we provide a description of the taxa that occur in each area.

Afrotropical

- Madagascar: The dominant group is Triaenonychidae, although Biantidae are also diverse, including the typical genera (e.g., *Metabiantes*) and strange forms such as *Hovanoceros*. Cyphophthalmi are represented by two species, one pettalid and one of uncertain familial affinity.
- Seychelles: This region is poorer than Madagascar. It shows a strong presence of Podoctidae, with some Biantidae and Zalmoxidae. Alleged Samoidae (*Benoitinus*, *Mitraceras*) do not belong with typical Samoidae.
- South Africa: Triaenonychidae is the dominant group, followed by Biantidae. Cyphophthalmi of the family Pettalidae are also quite diverse. Assamiidae are poorly represented in this area.
- Central Africa: Phalangiinae, Assamiidae, and Podoctidae are well represented. Within Cyphophthalmi, Ogoveidae is endemic to the Gulf of Guinea. Neogoveidae is well represented in West Africa. *Marwe coarctata* is a Cyphophthalmi species of uncertain affinity from Kenya.

Neotropical/Andean (definitions of areas follow Morrone, 2001)

- Caribbean: This region is rich in numerous families of Laniatores (Table 3.1). Within Eupnoi, Gagrellinae are well represented.
- Amazonian: This region presents numerous laniatorean families, including some endemic families, a few Eupnoi, and a large diversity of Cyphophthalmi of the family Neogoveidae.
- Chacoan: Neogoveidae, Gonyleptidae Metasarcinae, Stygnidae, and Cosmetidae.
- Paraná: Predominance of Gonyleptidae and Gagrellinae.
- Andean: Mostly Cranaidae and also Agoristenidae Leisteninae, Stygnidae, Stygnommatidae, Gagrellinae, and Neogoveidae.

Neartic

Cosmetidae and Leiobuninae penetrate southeastern and southwestern USA, probably dispersing from the Neotropical regions. Members of both families include large Opiliones. Leiobuninae are recorded to be good dispersers. The same distribution is found for *Stygnomma spinifera* (presently in Stygnommatidae, but probably Samoidae) from southern Florida and a doubtful record from Ohio.

- Mexico: Abundant Nearctic and Neotropical fauna merge in this area, with presence of Stygnopsidae, Zalmoxidae, Gagrellinae, and “*Neogovea*” *mexasca*, a Cyphophthalmi of uncertain familial affinity.
- USA: Numerous groups are found along both coasts of the USA (Table 3.1), while others have more restricted distributions. Ortholasmatinae, Sclerobuninae, Travuniidae, and Pentanychidae/Paranonychinae are restricted to the western USA coast. Caddidae is restricted to the eastern USA. A member of Neogoveidae are restricted to the southeastern USA coast.

Palaearctic

The Palaearctic region has been well studied. Three main regions are considered, and their familial composition is shown in Table 3.1.

- Europe: From the 10 families found in the area, two are endemic, Ischyropsalididae and Dicranolasmatidae.
- Central Asia: This region is poor in Opiliones diversity, and only members of two Eupnoi families and one Dyspnoi family have been recorded.
- Japan/Korea: This is an especially rich area that includes, among many other families, the endemic Nipponopsalididae.

Indo-Malayan

This area is divided into several regions with independent geological origins, making difficult the distinction of ancestral vicariant patterns from more recent ones explained by dispersal.

- Indian subcontinent: Biantidae, Assamiidae, Gagrellinae, and Podoctidae are abundant. Pettalidae are common in Sri Lanka, and Stylocellidae (or close relatives) have been reported from the Arunachal Pradesh province of India, near Burma.
- Southeast Asia: Although divided into a continental and an insular zone, this biogeographic region is homogeneous and includes the endemic families Oncopodidae and Stylocellidae. Biantidae are probably not in the region, despite two doubtful records.

Australian/Oceania

- Australian continent: Triaenonychidae and Pettalidae are the dominant groups, but several other temperate Gondwanan families occur. A few strange Gras-

Table 3.1 Summary of distribution of Opiliones in the geographic units of the world

Taxa	<i>Temperate Gondwana</i>								<i>Wallacea/Sundaland</i>				<i>Palaearctic</i>					<i>Mexican</i>	<i>Tropical Gondwana</i>					
	IND	MAD	SEY	SAF	CHI	NZE	NCA	AUS	PAP	MEL	MIC	POL	PHI	THA	CAS	EUR	NAF	JAP	WUS	EUS	MEX	SAM	CAR	CAF
Pettalidae	X	X		X	X	X		X																
Troglosironidae																								
Trienonychoidea		X		X	X	X	X	X																
Neopilionidae				X	X			X																
Acropsopilioninae				X	X	X		X									X		X		X			
Biantidae	X	X	X	X																		X	X	X
Stylocellidae									X				X	X										
Gagrellinae	X												X	X							X	X		
Monoscutidae						X		X																
Oncopodidae													X	X										
Epedanidae	X												X	X			X							
Assamiidae	X							X	X				X	X										X
Podoctidae	X	X	X					X	X	X	X		X	X										X
Zalmoxidae			X					X	X	X	X	X	X								X	X	X	?
Samoidae								X		X		X									X	X	X	
Sironidae															X		X	X	X	X				
Sclerosomatidae															X	X	X	X	X	X	X			
Phalangiidae			X												X	X	X	X	X	X				X
Nemastomatinae														X										
Dicranolasmatidae															X									
Trogulidae															X	X								
Ischyropsalididae															X									
Sabaconidae														X	X	X	X	X	X	X				
Travunioidea															X	X	X	X	X					
Phalangodidae															X	X			X	X				
Caddinae																	X			X				
Ortholasmatinae																	X	X						
Nipponopsalididae																	X							
Ceratolasmatidae																			X	X				

Taxa	<i>Temperate Gondwana</i>								<i>Wallacea/Sundaland</i>				<i>Palaearctic</i>				<i>Mexican</i>	<i>Tropical Gondwana</i>						
	IND	MAD	SEY	SAF	CHI	NZE	NCA	AUS	PAP	MEL	MIC	POL	PHI	THA	CAS	EUR	NAF	JAP	WUS	EUS	MEX	SAM	CAR	CAF
Stygnopsidae																					X			
Gonyleptoidea					X																	X	X	
Stygnommatidae																						X	X	
Minuidae																						X	X	
Escadabiidae																						X		
Zalmoxoidea																						X		
Neogoveidae																				X		X		
Ogoveidae																								X
Lacurbsinae																								X

Temperate Gondwana: IND=India/Sri Lanka/Nepal; MAD=Madagascar; SEY=Seychelles; SAF=South Africa; CHI=Chile/Argentina; NZE=New Zealand; NCA=New Caledonia (Melanesia); AUS=Australia/Tasmania.

Wallacea/Sundaland: PAP=Papua New Guinea; MEL=Melanesia (except New Caledonia); MIC=Micronesia; POL=Polynesia; PHI=Malay Peninsula/Indonesia/Philippines; THA=continental southeastern Asia (Thailand, Vietnam).

Palaearctic: CAS=central Asia; EUR=Europe; NAF=northern Africa; JAP=Japan; WUS=western USA; EUS=eastern USA.

Mexican: MEX=Mexico-Guatemala.

Tropical Gondwana: SAM=circumequatorial South America; CAR=Caribbean (insular); CAF=central Africa.

satores, which may be Phalangodidae, and some Zalmoxidae and Samoidae are found. Podoctidae are restricted to a single species.

- Tasmania: Triaenonychidae are the dominant group, but there are Monoscutidae and Acropsopilioninae. Pettalidae are surprisingly absent from Tasmania.
- New Zealand: Triaenonychidae and Pettalidae predominate. Acropsopilioninae, Monoscutidae, and one species of Assamiidae also occur. Synthetonychiidae are endemic to New Zealand.
- New Caledonia: Includes the endemic family Troglosironidae, several Podoctidae, Zalmoxidae, and a few Triaenonychidae.
- Pacific Islands: Their opiliofauna is typically impoverished because of the low dispersal ability of Opiliones. Samoidae are the dominant group. Melanesia presents the most diverse fauna, with a number of Podoctidae and Zalmoxidae.

Opilionofaunal relationships

It appears that the pattern of Laurasia versus Gondwana was replicated several times during the evolutionary history of Opiliones. The widespread purely Holarctic (= Laurasian) taxa include Sironidae, Sclerosomatidae, Sabaconidae, and Travunioidea (the possible sister group to all other Laniatores). Holarctic taxa with more restricted distributions include most Dyspnoi families, Caddinae, and Phalangodidae. Phalangiidae are a typical Laurasian component with dispersal ability; hence their presence in Africa and the Seychelles may be explained by dispersal from the Mediterranean, as postulated by Starega (1984).

Evidence for the monophyly of Gondwanan taxa is weak. Within Gondwanan Cyphophthalmi, Pettalidae does not form a clade with Neogoveidae, and it seems that Gondwana is a paraphyletic area from which the Cyphophthalmi diversity originated. In other groups the phylogenetic evidence is so precarious that we prefer to leave the topic open to future discussion. However, it is clear that very few groups encompass the totality of the Gondwanan landmasses.

Well-characterized temperate Gondwanan groups are Pettalidae, Triaenonychoidea, and Neopilionidae. The pertinence of India, Seychelles, and Madagascar to the temperate Gondwanan opiliofauna is not unambiguously supported. Although the presence of Triaenonychidae supports unity of Madagascar with the typical temperate Gondwana, Biantinae are present in India, Nepal, Madagascar, Seychelles, South Africa, and central Africa, and there are a few records from Indonesia. Assamiidae (absent from Madagascar and the Seychelles) suggest a relationship of India to central Africa.

The monophyly of tropical Gondwana is weakly supported, but again it should be noted that cladistic hypotheses are still needed for most groups, and Cyphophthalmi analyses clearly support monophyly of Neogoveidae, with representatives in both Africa and South America (including Florida, which originated from a Gondwanan fragment). Gonyleptoidea would be another candidate for this support, but Assamiidae are present in India and Australia.

Biogeographic conclusions

Opiliones are excellent candidates for biogeographic studies because of their limited distribution ranges and low dispersal abilities, as shown especially in Cyphophthalmi, Dyspnoi, and many Laniatores. Endemicity of Opiliones is found to be near 97.5% in the Brazilian Atlantic rain forest, whose fauna is predominantly composed of gonyleptids (Pinto-da-Rocha et al., 2005). The fact that some members of a few families are prominent dispersers (e.g., Leiobuninae) should not preclude researchers from continuing to analyze harvestman biogeographic data. However, before meaningful progress can be made in this area, quantitative and qualitative progress needs to be made in the phylogenetic relationships among families and other lower ranks. To date, major progress has been made in solving the relationships among the four suborders of Opiliones. Substantial progress has also been made within Cyphophthalmi and the relationships among their major lineages (e.g., Giribet & Boyer, 2002; Giribet, 2003; de Bivort & Giribet, 2004; Boyer et al., 2005). Although the temperate Gondwanan family Pettalidae seems to be the sister group to all other Cyphophthalmi, relationships among the remainder groups are still poorly understood.

Another interesting pattern, assuming monophyly of Dyspnolaniatores, is that Cyphophthalmi and Eupnoi are distributed globally, while Dyspnoi species are restricted to the former Laurasia, and Laniatores are mostly found in the Southern Hemisphere. This pattern may indicate that the separation between Dyspnoi and Laniatores followed the split of Pangea.

Clearly, more work needs to be done before harvestman distributional data can be placed into a global biogeographic context for inferring patterns using congruence as an optimality criterion. We anticipate major progress in this neglected area of harvestman research in forthcoming years as the phylogenetic relationships among the harvestman families are elucidated.

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