• Chelicerae: Robust (Figure 4.6f), with basal segment with or without a dorsal crest. Distal segments of chelicerae mostly smooth, sometimes with scale-like ornamentation in the second segment. Mobile digit of chelicerae with a single type of dentition; teeth regular or irregular.
• Pedipalps: Without distinct modifications or a ventral process in trochanter.
• Legs: Tarsal claws I, III, and IV smooth; II with a row of teeth (Figure 4.6g). Tarsus IV of males entire. Adenostyle short, lamelliform (Figure 4.6h), near the tarsal base.
• Genitalia: Spermatopositor with four apical microtrichia fused in pairs and their bases much thickened; movable fingers enlarged; middle pair of dorsal microtrichia sometimes reduced or absent; with dentate/lamellate lateral margins. Ovipositor long, multisegmented, with two apical lobes, each with a long terminal seta, a short subterminal seta, and a bi- or trifurcated sensitive process.
• Color: Dark, brownish to black. Troglosiro raveni has a distinctive color pattern of black and brown. a rare characteristic among Cyphophthalmi.
• Sexual dimorphism: Besides the adenostyle and the gonostome area, the presence of the opisthosomal sternal gland pores, often accompanied by profound depressions of the sternal region, is the only sexual character. No modifications in the male anal plate (Figure 4.6b). Male anal glands absent.

**Distribution:** The genus Troglosiro is restricted to New Caledonia in the Coral Sea (South Pacific). Several species have been collected in localities around the island (Sharma & Giribet, 2005), including six undescribed species.

**Relationships:** Juberthie (1979) suggested a relationship of Troglosiro to the sironid genus Siro, although he noticed some affinities to the pettalid genus Parapurcellia. Uncertainty about the position of the genus Troglosiro followed (Shear, 1980, 1985; Juberthie, 1989), until Shear (1993b) proposed a sister-group relationship of Troglosiro to Sironidae + Pettalidae, justifying its familial rank. This result was not corroborated by a morphological cladistic analysis of most Cyphophthalmi genera (Giribet and Boyer, 2002), although the analysis by de Bivort and Giribet (2004) suggests that Troglosiro falls within a Sironidae + Pettalidae clade. The first molecular data presented for Cyphophthalmi (Giribet & Boyer, 2002) indicated a relationship of Troglosiro to Neogoveidae, which shares the presence of sternal opisthosomal gland openings and the toothed claw of leg II.

**Main references:**

- **Systematics:** Shear (1993b), Sharma & Giribet (2005).

**EUPNOI**

**Historical systematic synopsis**

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The harvestmen of the suborder Eupnoi are the most familiar Opiliones, not only because they are abundant and diversified almost worldwide but also because they are common in Europe and the USA. They were the first Opiliones to be recorded on paper, being illustrated by Aldrovandus in 1603. Despite the number of species, the group is somewhat homogeneous. Currently only six families are recognized, and the suprageneric relationships among them deserve more attention than they have received.

The first harvestman (Phalangium opilio) described with binomial nomenclature by Linnæus (1758) is now a member of Eupnoi. Linnæus listed Phalangium under the class Insecta, order Aptera. As other genera and species were described, the names of the classes, orders, and families changed back and forth. Some authors included whip spiders, solifuges, and mites with harvestmen. Latreille (1802a) included all harvestmen and a solifuge in the order Acera, family Phalangites. Latreille (1829) later moved the harvestmen to the order Tracheennes, family Hoketra, tribe Phalangiens. Even later, Sundevall (1833) recognized the then-known five genera in three families (Gonoleptides, Phalangides, Trogulides) of his new order Opiliones. Unfortunately, he placed the genus Caeculus (a mite) in Opiliones (Trogulides), while the genus Siro (Opiliones) was placed in the order Acari. Hansen and Sørensen (1904) described the tribe Eupnoi under the suborder Palpatores.

Roewer revised all Phalangiidea in his “Revision der Opiliones Plagiostethi” (Roewer, 1910, 1912c) and presented summary redescriptions of all known Eupnoi in Roewer (1923). The classification of Opiliones used by Roewer (1923) was as follows:

- Suborder Cyphophthalmi
- Suborder Laniatores
- Suborder Palpatores
  - Tribe Dyspnoi
    - Acropsopilionidae (not including Caddinae) and other families
  - Tribe Eupnoi
    - Phalangiidae
      - Liobuninae
      - Gagrellinae
      - Leptobuninae
      - Oligolophinae (including Caddinae)
      - Phalangiinae
      - Sclerosomatinae

- Crawford (1992) presented a new classification and a catalogue of all genera and type species of the superfamily Phalangiidea. He also established the synonym of Argyrasterinae Nakatsudi, 1942—previously synonymized with Leiobuninae by Suzuki (1971)—with Gagrellinae. A synopsis of his classification is as follows:

- Superfamily Phalangiidea
  - Neopilionidae
Caddids were first recorded by Banks (1892), who described a small harvestman with a prominent ocularium and large eyes occupying most of the propeltidium (*Caddo agilis*) in Phalangiidae. In 1893 he established for it the tribe Caddini. Silvestri (1905) described *Acropsopilio chilensis* but did not assign it to a family, noting that it showed characters of both Eupnoi and Dyspnoi. Roewer (1912c, 1923) placed *Caddo* in the subfamily Oligolophinae (Phalangiidae), a rather heterogeneous group as conceived by him. Roewer (1923) established Acropsopilionidae for Silvestri’s species only on the basis of the original description and placed it in Dyspnoi on the basis of the character “palp tarsus shorter than tibia,” disregarding contradictory evidence. When he later studied Silvestri’s type, he united *Caddo* and Acropsopilionidae in the subfamily Caddinae in Phalangiidae (Roewer, 1957b). Kauri (1961) and Ringuelet (1962) criticized this move; the latter regarded the similarities as convergent and adhered to placement in two families/superfamilies, while the former suggested a possible union within Acropsopilionidae. In the 1970s the “unified” group became accepted as a family (Cekalovic, 1974: as Acropsopilionidae, presumably following Kauri, 1961; Gruber, 1975, and Shear, 1975a: as Caddidae). Gruber (1975) discussed some systematic problems, such as the position of Caddidae in relation to Dyspnoi and Eupnoi. In the same year Shear (1975a) reviewed the family Caddidae and established for it the superfamily Caddoidea, containing Caddinae and Acropsopilionidae.

The second superfamily, Phalangioidae, includes the families Monoscutidae, Neopilionidae, Phalangiidae, Protolophidae, and Sclerosomatidae. Monoscutidae has previously been referred to as Megalopsalidinae. However, Crawford (1992) pointed out that the subfamily Monoscutinae had priority over Megalopsalidinae.

Neopilionidae was originally described by Lawrence (1931) in Phalangiidae to include the monotypic genus *Neopilio* from South Africa. The subfamily was primarily based upon the reduced or absent pedipalpal claw and equal-sized teeth on the chelicerae. South American members were added when Mello-Leitão (1933b) synonymized Enantiobuninae (Mello-Leitão, 1931, June) with the Neopilioninae (Lawrence, 1931, April). Roewer (1957b) retained the placement in Phalangiidae. Ringuelet (1959) synonymized the South American genera *Thrasychirus* with *Enantiobunus* and transferred them to the Leiobuninae (Phalangiidae). Kauri (1961) added the monotypic genus *Vibone* from South Africa and raised Neopilioninae to family status. Šilhavý (1970) recognized three subfamilies within the Neopilionidae: Neopilioninae, Megalopsalidinae, and Enantiobuninae. Shear (1982) and Hunt and Cokendolpher (1991) redescribed the family, with Megalopsalidinae excluded. Hunt and Cokendolpher (1991) also added the first Australian members and described another subfamily (Ballarrinae), primarily on the basis of differences in the pedipalps (setation and reflexed junction of patella and tibia). Although Hunt and Cokendolpher (1991) suggested raising Enantiobuninae to full family status, this has still not been formally done.

Phalangiidae is the longest- and best-known group of harvestmen for people living in temperate to subarctic regions of Eurasia (especially Europe) and North America. They have a soft or leathery body (rarely heavily sclerotized, as in *Scleropilio*) and relatively long legs. The dorsum of the body lacks large tubercles, cones, or long spines (such as those often found in members of Asian Gagrellinae, or Sclerosomatinae) but has sparse short spines. Pedipalps and legs are also often spiny, and legs are generally angulate in cross section in proximal segments (from femora to tibiae). The spiny habitus, leg coxae without marginal rows of denticles, smooth, nonpectinated tarsal claw of the pedipalp, and nonalate penis with a well-delimited glans dorsally bent at an acute angle in resting position and a distinct, more or less movable stylus serve to identify this family, though there are a few exceptions.

All the external characters traditionally used to delimit species and genera of Phalangiidae (e.g., armature of dorsal integument of body or appendages) are often highly variable between populations of the same species, or sometimes even within a
single population of a species. Because of this difficulty, taxonomy of this family has been rather chaotic. The situation has been much improved recently by extensive revisions emphasizing penial morphology made mainly by Martens (for European and Himalayan species), Starega (for Europe, Asia, and Africa), and Cokendolpher (for America), though many genera and species still await further revision.

Subfamilial classification of Phalangiidae has not yet been settled because no character can clearly define each subfamily so far proposed. Most widely accepted is a dichotomy of the family into the subfamilies Oligolophinae and Phalangiinae sensu lato, mainly by the presence or absence of a ventral spur on the chelicera (Martens, 1978b). However, the two character states are found in two congeneric species (Paroligolophus agrestis and P. meadii) whose close relationship is well supported by all the other characters (Martens, 1978b), and in some cases it is exemplified as sexual dimorphism or as intraspecific variation (e.g., Metaplathybunus hispanicus, Liopilio yukon). Starega (1973) synonymized Dentizacheinae Silhavý, 1961 with Phalangiinae. Starega (1976a,b) split Phalangiinae s. lat. further into three subfamilies (Phalangiinae sensu stricto, Platybuninae, and Opilioninae), and this system has been followed by some researchers. The monophyly of each of these subfamilies has not yet been tested (it is highly probable that at least Phalangiinae s. str. is not monophyletic), and there are many species that do not conform well to the keys.

Protolophidae, endemic to western North America, was originally described as a tribe (Protolophini) of the family Phalangiidae by Banks (1893). Later, Roewer (1911) transferred the type and only genus (Protolophus) to the subfamily Leptobunini (Roewer, 1923, corrected the ending to Leptobuninae), where it remained until the subfamily was dismantled by Cokendolpher (1985b). He suggested raising the group to subfamily status and emended the ending to Protolophinae within the family Gagrellidae. Edgar (1990) listed the genus in the Sclerosomatidae, and Crawford (1992) retained the group at the subfamily level within an unspecified family, but remarked that the group may be justified as a family. Cokendolpher and Lee (1993) raised the group to family status and recognized only the single monogenic subfamily Protolophinae.

Sclerosomatidae was traditionally included in the family Phalangiidae (Loman, 1903b, 1906), but modern classifications (Crawford, 1992; Cokendolpher & Lee, 1993; Giribet et al., 2002) recognize it as a separate family, albeit unclearly delimited. Sclerosomatidae is the largest family in the order Opiliones, with more than 1,300 species distributed in the New and Old Worlds. The family is currently composed of Sclerosomatinae, Gagrellinae, Gyinae (= Gyantinae), Leiobuninae, and the Metopilio genus group of Cokendolpher (1984b) (Crawford, 1992). The more appropriate rank status of these entities is a subject still under discussion. The first four are assigned status of either family or subfamily depending on the author, while the Metopilio assemblage may be an unnamed family or subfamily (Cokendolpher, 1984b). Because of its genital morphology, the assemblage has been listed within Sclerosomatidae by Crawford (1992), later followed by Cokendolpher and Lee (1993). Starega (1976a,b) proposed raising Gagrellinae, Gyinae and Sclerosomatinae to family status, with Leiobuninae in-
cluded in Gagrellidae. Martens (1978b, 1982, 1987) refused Starega's proposal and also included the genera *Dicranopalpus* and *Amblyopus* in Gyinae. Crawford (1992) disagreed with these inclusions and transferred the genera to what he called the *Dicranopalpus* group, an assemblage of seven genera considered by him as a family *incertae sedis*. Crawford also suggested that Leiobuninae and Gagrellinae should be separated for zoogeographic reasons and by the harder opisthosomal scutum present in Gagrellinae. The boundaries among the four accepted subfamilies are obscure, and the inclusion of the *Metopillie* group as part of Sclerosomatidae has been followed only by Cokendolpher and Sissom (2000). The distinctions between Gagrellinae and Leiobuninae are not clear, and there is morphological continuity at the supraspecific level. The characters supporting the taxa are poorly defined. For the most part, the formerly raised groups of species are artificial and lack phylogenetic meaning. A modern catalogue of the whole group is needed since the only available one is outdated and only covers Neotropical Gagrellinae (Roewer, 1953). Overall, this suborder of common harvestmen needs major phylogenetic studies.

### Key to Eupnoi families (subfamilies)

1. Eyes enormous and ocularium occupies most of the prosoma (Figures 4.7a,b); legs II shorter than legs IV. ........................................... *Caddidae*... 2  
2. Cheliceral segment I with ventral spur; pedipalpal tarsus longer than tibia (Figure 4.7b). ........................................... *Caddidae* (Caddinae)  
3. Cheliceral segment I without ventral spur; pedipalpal tibia longer than tarsus (Figure 4.7a) ........................................... *Caddidae* (Acropsopilioninae)  
4. Penis with paired lateral bristle groups at articulation of glans and shaft (Figure 4.8d); Australia and New Zealand. ................................. *Monoscutidae*... 5  
5. Body rounded; only carapace sclerotized; opisthosoma smooth. Legs relatively long. Chelicerae sexually dimorphic; those of male enormously enlarged (Figure 4.8g) ........................................... *Monoscutidae* (Megalopsalidinae)  
6. Pedipalpal patella very long (patella about twice as long as tibia); tibia reflexed on the patella so that dorsal angle is less than 180° (Figure 4.9b); Australia, Chile ........................................... *Neopilionidae* (Ballarrinace)
. Pedipalpal patella shorter (patella less than 15% longer than tibia); tibia not re-
flexed upward on patella (Figure 4.9e).

7. Pedipalpal patella and tibia with dense pile of setae; patella slightly longer than
tibia; pedipalpal claw reduced and smooth (Figure 4.9e,f); South Africa.

                      Neopilionidae (Neopilioninae)

. Pedipalps without dense pile of setae; patella much shorter than tibia; claw large
and toothed (Figure 4.9c); Chile, Argentina, Brazil.

                      Neopilionidae (Enantiobuninae)

8. Male pedipalp almost always greatly thickened (Figure 4.8h); tarsus shorter than
tibia; western North America.

                      Protolophidae

. Pedipalpal tarsus longer than tibia.

                      Neopilionidae (Neopilioninae)

9. Pedipalpal patella and tibia with dense pile of setae: patella slightly longer than
tibia; pedipalpal claw reduced and smooth (Figure 4.9e,f); South Africa.

                      Neopilionidae (Enantiobuninae)

10. Basal segment of chelicera with ventral spur (Figure 4.10f); chelicerae not strik-
ingly different between the sexes.

                      Phalangiidae (Oligolophinae)

. Basal segment of chelicera without ventral spur; chelicerae sometimes differ be-
tween the sexes (Figure 4.10h).

                      Phalangiidae (Phalangiinae sensu lato)

11. Pedipalpal femur (often also remaining segments) thorned ventrally (Figure
4.10j); chelicerae of both sexes similar; penis rodlike, with slightly widened base.

                      Phalangiidae (Platybuninae)

. Pedipalp lacks ventral thorns; male chelicera tends to be modified (Figure
4.10h).

12. Pedipalpal patella and tibia of adults without distomesal apophyses; chelicerae
of both sexes basically the same in structure, though often enormously ex-
panded in male; leg I of male enormously swollen in some species; shaft of penis
dorsally flattened (Figure 4.10k).

                      Phalangiidae (Opilioninae)

. Pedipalpal patella and tibia with distomesal apophyses; male chelicera tends to
be modified in morphology (especially in the distal segment); femur of male pedi-
palp usually with ventral rows of denticles; shaft of penis generally more
rounded.

                      Phalangiidae (Phalangiinae sensu stricto)

13. Coxae II showing distally blunt lobes.

                      Sclerosomatidae (Gyinae)

. Coxae II not as above.

14. Leg femora with noduli (at least one on femur II, Figure 4.11p); dorsum sclero-
titized.

                      Sclerosomatidae (Gagrellinae)

. Leg femora usually without noduli.

15. Dorsum heavily sclerotized, often with spines or humps (Figure 4.11c); penis ta-
pering toward tip (Figure 4.11l).

                      Sclerosomatidae (Sclerosomatinae)

. Dorsum less sclerotized, usually smooth; penis not tapering, often with alate
part.

                      Sclerosomatidae (Leiobuninae)