

4.4 Opiliones

by

A.B. Kury & R. Pinto-da-Rocha

Dr. Adriano B. Kury, Museu Nacional (UFRJ), Quinta da Boa Vista, São Cristóvão, 20.940-040 Rio de Janeiro-RJ, Brazil;
e-mail: adrik@alternex.com.br

Dr. Ricardo Pinto-da-Rocha, Universidade Bandeirante de São Paulo, Caixa Postal 11161, 05422-970 São Paulo-SP, Brazil; e-
mail: ricrocha@usp.br

Introduction

Systematics

Harvestmen or Opiliones constitute the third largest arachnid order. They are characterized by having the five first opisthosomatic somites fused with the prosoma forming a dorsal scute (Fig. 1), a pair of prosomatic scent glands which open at lateral margin of carapace, presence of penis and ovipositor and one pair of median eyes (lateral eyes absent).

According to the hypothesis of phylogeny proposed by SHULTZ (1990), the order Opiliones is most closely related to the Scorpiones, Solifugae and Pseudoscorpiones, forming a monophyletic group called Dromopoda.

SHULTZ's is not the only hypothesis of arachnid relationships. Strong arguments have been given which suggest that scorpions and eurypterids (an order not taken into account by SHULTZ) are sister groups or, at least, that scorpions are basal in Arachnida (see DUNLOP & SELDEN 1997; DUNLOP 1998; DUNLOP & WEBSTER 1999).

The order Opiliones was traditionally divided in three suborders: Palpatores, Laniatores and Cyphophthalmi. An alternative division was proposed by MARIENS (1980), where the Palpatores were a paraphyletic taxon, and the Trogludidae were the sister group to the remaining Palpatores plus the Cyphophthalmi. However, recent reanalyses of the problem (SHULTZ 1998; GIRIBET et al. 1999) proposed a move back to the original arrangement: Opiliones = Cyphophthalmi + Phalangida; Phalangida = Palpatores + Laniatores.

Biodiversity and distribution

For convenience, the concept of Amazonia adopted in this chapter is restricted to: the Colombian States Amazonas and Uaupés; the Brazilian States Amapá, Amazonas, Pará and Roraima; the Peruvian States Loreto, Madre de Dios and Ucayali; and the Venezuelan State Amazonas (cf. List of genera and species).

Estimates on the diversity of the order Opiliones are still highly guesswork. The best known faunas are of some countries in Europe. In the New World, only recently is the diversity being more thoroughly assessed (PINTO-DA-ROCHA 1999). Brazil has a great diversity, with about 950 recorded species, contrasting with the Afrotropical Region with 707 species (STAREGA 1992) and with other South American countries which have a strikingly lesser diversity, such as Venezuela with a little more than 300 species, Chile, Peru and Ecuador with about 150 species each, Argentina with 115 species (ACOSTA & MAURY 1998), and Colombia with 77 species (FLOREZ & SANCHEZ 1997). In Great Britain 23 species are known (HILLYARD & SANKEY 1989), in the Netherlands 21 (SPOEK 1963) and in Europe, north of the Mediterranean Sea, 110 species (MARTENS 1978). Fewer than 500 species have been hitherto described from North America (Mexico, north) (EDGAR 1990; KURY & COKENDOLPHER 2000).

The knowledge about the Amazonian opiliofauna is noticeably less. Presently, there are only 173 species recorded, indicating how little is known about this fauna (Table 1). For the sake of comparison, from a much smaller area such as the state of São Paulo 232 species are described, most endemic to the Atlantic Forest (PINTO-DA-ROCHA 1999).

Table 1. Updated numbers of described genera and species in Opiliones (cf. ADIS & HARVEY 2000; Chapter 3).

Opiliones	World	Neotropics	Amazonia
Genera	2000	758	75
Species	5500	2609	173

One available survey from Amazonia was conducted at Reserva Ducke (cf. Chapter 2) near Manaus (Amazonas State, Brazil) where 16 species have been recorded over more than 10 years of sampling (HÖFER & BECK 1995). However, the Reserva Ducke represents a relatively small area of non-flooded upland (terra firme) forest. In other humid areas on terra firme and in floodplains of Central Amazonia with a different floristic variety (cf. Chapter 2), a greater diversity is to be expected. On the other hand, drier and open areas such as campinas and savannas are not expected to show high diversities. This is indicated by the material collected by ADIS and collaborators during the last 25 years in the environs of Manaus (PINTO-DA-ROCHA, unpubl.) which contains several undescribed species. The total number of morphospecies recorded was 21 on terra firme (Reserva Ducke), 9 in a blackwater inundation forest (igapó) at Rio Tarumã Mirim, 4 in whitewater floodplains (várzea) on Ilha de Marchantaria and 10 morphospecies in a mixedwater inundation forest (igapó & várzea) at Lago de Janauari. It should be stressed that the opilionid fauna of the floodplains has not been surveyed with the same intensity as that of Reserva Ducke.

The endemism of harvestmen in humid areas is often very high. In the Atlantic Rain Forest the species are distributed over areas of only a few hundred square kilometers (PINTO-DA-ROCHA 1999). In Amazonia it is hard to draw a general overview of the fauna and areas of endemism, because only scattered material has been collected and the localities sampled are strongly correlated with larger rivers like the Rio Amazonas, Xingu and Tocantins. Another factor, which prevents an initial estimate of the biogeography of Opiliones in that region, is the lack of revisionary work and of the phylogenetic hypotheses of relationships among species. The single review and phylogenetic analysis available only refers to the family Stygnidae (26 genera, 73 species). In spite of the examination of material of this family from most museums of the world, a large portion of the species are still only known from their type localities. The diversity of Stygnidae is still poorly known. GONZÁLEZ-SPONGA (pers. comm.) while studying vast Venezuelan material has found 35 undescribed species of this family. This situation must also occur in poorly studied and highly diverse families like the Manaosbiidae, Cosmetidae and Sclerosomatidae.

Bionomics

Reproduction: The opilionids are dioecious and have a direct sperm transfer, except for a few records of parthenogenesis in some species of Caddidae (SHEAR 1975). Few people have observed the copulatory behavior of Neotropical opilionids. The pre-copulatory behaviors are quite simple and are fast (just a few minutes). In some species the males can fight each other in order to get females (BERLAND 1949). The fertilization is internal and the females lay eggs some hours after mating (JUBERTHIE 1964). Eggs can be buried as in most harvestmen or deposited on stone walls (Gonyleptidae, Goniosomatinae) or under live leaves (Gonyleptidae, Progonyleptoidellinae). The number of eggs in each lay can vary from a few up to 200.

Developmental stages and molts: Opilionids generally have 4 to 7 molts required to reach adulthood in the Laniatores and afterwards the adults do not molt (JUBERTHIE 1964; GNASPINI 1995). There are one larval (L) and 4-8 nymphal stages (N1-8). The definitive number of tarsomeres only appears in adults. The larva molts just a few minutes after hatching and only the legs are functional appendages (MUÑOZ-CUEVAS 1971b). The larva is distinguished by absence of an arolium on tarsi I-IV and an apothele normally found on the pedipalps (reduced or absent in nymphal stages) (MUÑOZ-CUEVAS 1971a). All nymphs but the ultimate possess an arolium (spongy pad) beneath the tarsal claws, which assists in adhering to the substrate during molting. The ultimate nymph, also called "subadult", loses the arolium but still preserves the primitive division of tarsi in 2 (legs I-II) or 3 (legs III-IV) segments. To determine the nymphal stage the tarsal and tibial armature of the pedipalps can be used (MUÑOZ-CUEVAS 1971b), as well as the armature of leg IV in males (GNASPINI 1995). GNASPINI (1995) showed that the length of legs I-IV is more useful to distinguish nymphal stages. However, subadults and adults are morphometrically identical (GNASPINI 1995).

Sexual dimorphism: Females of Palpatores Gagrellinae have an enlarged second distinct prosomal sclerite and body. Among Laniatores, males usually have leg IV enlarged, with more pronounced spines and tubercles than on females (sometimes lacking on females), the femora IV can be sinuous. Males of Stygnidae, Cosmetidae, Agoristenidae, Cranidae

and Manaosbiidae usually possess enlarged chelicerae. Manaosbiidae males have a spindled basitarsus. Zalmoxidae usually have femur IV clavate and tibia IV incrassate with a row of spines.

Life span: The adults of *Daguerreia inermis* can live for more than 22 months (PINTO-DA-ROCHA 1996); more than 2 years were reported for *Goniosoma spelaeum* (GNASPINI 1995); 3-4 years for *Pachylus quinamãvidensis* (JUBERTHIE & MUÑOZ-CUEVAS 1971); 2-5 years for *Cynortoides cubanus* (JUBERTHIE 1972); and more than 3 years for *Vonones scyi* (COKENDOLPHER & JONES 1991). All the available data is for Laniatores and there is no data on the life span for Neotropical Palpatores and Cyphophthalmi. JUBERTHIE (1964) mentioned a life span of 2 years for European Sironidae (Cyphophthalmi) and 1 year for European Phalangiidae (Palpatores).

Life cycle and phenology: In blackwater inundation forests of Central Amazonia adults of two Laniatores species (*Auranus parvus*, Gonyleptidae; *Eucynortula lata*, Cosmetidae) move to the trunk/canopy region prior to flooding where they pass the 5-7 months lasting aquatic phase (FRIEBE & ADIS 1983). IRMLER (1981) showed in laboratory experiments, that these harvestmen are negatively phototactic during the terrestrial phase and positive phototactic during flooding. He suggested that annual inundation might cause an escape reaction, which triggers the vertical upward migration by changing phototaxis. Both species are univoltine and represent the terricolous migrating arthropod guild (ADIS 1997). Main reproduction occurs in the upper organic layer of the forest floor during the terrestrial phase (ADIS 1992). Phenological data from species inhabiting non-inundated upland (terra firme) forests in the Manaus area indicate that they are plurivoltine, i.e. reproduce throughout the year (ADIS & PINTO-DA-ROCHA, unpubl.). ADIS (unpubl.) observed submerged adults of *Eucynortula lata* covered with an air casing and foraging for prey on the flooded part of tree trunks in the blackwater inundation forest.

Circadian rhythm: Most opilionids are active at night. At twilight they start activity and come back to their shelters by dawn. As a rule, they feed and mate at night. Activity periods have been studied for only a few species from southeastern Brazil (GNASPINI 1996; MACHADO et al. 2000). Some groups are not strictly nocturnal, such as the Caelopyginae, Progonyleptoidellinae and Sodreaninae (all south-southeastern Brazilian Gonyleptidae) whose species show nocturnal and diurnal activities. A species of Agoristenidae (*Trinella albiornata*) and some Cosmetidae have been observed to be active during daylight and at night in Trinidad & Tobago (RPR, pers. obs.).

Feeding: In general the opilionids are omnivores that feed on live and dead animals and plants. However, the trend is toward carnivory (GNASPINI 1996). The following alimentary items were observed for Neotropical opilionids: native fruits, Basidiomycetes fungi, flowers, Hirudinea, Oligochaeta, insects (Orthoptera, adults and larvae of Coleoptera, Lepidoptera, Diptera, Neuroptera, Hymenoptera and Homoptera), feces of birds and rodents (CANALS 1936; CAPOCASALE & BRUNO-TREZZA 1964; ACOSTA et al. 1995; GNASPINI 1996; PINTO-DA-ROCHA 1996; MACHADO, 2000). The predation of Laniatores Gonyleptidae on gagrelline Sclerosomatidae harvestmen was reported by MACHADO et al. (2000).

Defensive substances: Opilionids possess a pair of openings to the exocrine scent glands on the sides of the prosoma. These substances possess antibacterial properties and include ketones, quinones, alcohols and aldehydes (Palpatores) as well as phenols, benzoquinones and esters (Laniatores) and a mixture of other volatile compounds (ACOSTA et al. 1993; GNASPINI 1995). Their presumed function is defense, but they could also be involved in waste disposal, protection against microorganisms, sexual and intraspecific recognition, alarm and aggregation behavior (HOLMBERG 1986). To date, only the avoidance of predators (see experiment of EISNER et al. 1971) and formation of aggregations have been empirically verified (HOLMBERG 1986). In spite of the great variety of substances produced by scent glands, their composition has been studied in little more than 20 species (see complete references in ACOSTA et al. 1993; GNASPINI 1995). The administration of fluids is done from the mouth, passing through coxal apophyses by capillarity into the grooves of scute, later the fluid is mixed with that of scent glands where they are diluted and dispersed by evaporation or leg dabbing.

Fluorescence: Some opilionids can glow when exposed to ultraviolet (or "black") light (see ACOSTA 1983; ACOSTA et al. 1995). We believe that all species that have white patches on the scute (as Cosmetidae) can fluoresce. A variety of fungi and other arthropods also fluoresce and can be collected at night by using a portable UV light. The bulb should have a long wavelength in order to maximize the number of captures. It is interesting to note that black light bulbs work better during new moon when the light is minimal, but also the abundance of opilionids may be influenced by the moon. Some other arthropods are known to forage less on moonlit nights to reduce encounters with vertebrate predators that need some light to see.

Parasites and predators: An excellent review on the pathogens and parasites of harvestmen can be found in COKENDOLPHER (1993). It lists the following organisms living in or on opilionids: bacteria Enterobacteriaceae; fungi Eumycota, Clavicitaceae, Hypomyces, Entomophthoraceae; Protozoa; Microsporida; Apicomplexa Gregarinasina; flatworms Cestoda, Trematoda, worms Nematoda and Nematomorpha; dipterans Cyclorrapha and Nematocera; hymeno-

pterals Chalcididae and Pompilidae; mites Thrombidiidae and Erythraeidae. Opilionids do not possess specific predators but are eaten by other opilionids, spiders, heteropterans, frogs, lizards, birds and mammals (BRISTOWE 1949; EDGAR 1971; PINTO-DA-ROCHA 1994; GNASPINI 1996; MACHADO et al. 2000). EDGAR (1971) reported that spiders are the most important predators of opilionids.

Identification

The common morphological characters and terminology used in the key are given in figures 1-4, specific terms are explained in the glossary below.

Glossary of specific terms (cf. Figs. 1-4)

- Abdominal scute** - formed by the fusion of the first five opisthosomatic tergites.
- Apophysis** - an elongate non-articulate projection from the exoskeleton.
- Apothele** - 7th (terminal) article of leg, which bears the arolium, the tarsal process and the claws.
- Arolium** - spongy pad beneath the tarsal claws.
- Basitarsus** - the most proximal division of the leg tarsi of nymphs, which in adults is subdivided into more articles (typically 3 to 10).
- Carapace** - prosomatic part of the dorsal scute.
- Cheliceral hand** - in the tripartite chelicera of Opiliones, the hand is formed by the two distal segments which form a forceps, with a projection of the hand (second segment) forming the fixed finger and the third segment forming the movable finger.
- Distitarsus** - the most distal division of the tarsi in nymphs, in adults, subdivided into 2 to 3 (usually) articles.
- Dorsal scute** - entire plate formed by the fusion of the prosoma with the first five opisthosomatic tergites. The primitive segmentation can be seen as grooves. It comprises the carapace plus the abdominal scute, separated by the scutal groove.
- Eye mound** - medial elevation of the carapace on which the paired eyes occur. Opiliones do not have lateral eyes. In some families a common eye mound is lacking and the eyes are placed on two separate mounds. Eyes are absent from some cave living species as well most Cyphophthalmi.
- Free tergites** - the first three of the last opisthosomatic dorsal somites not fused in the scute.
- Legs** - the third to sixth pairs of appendages, formed of 7 segments. From proximal: coxa, trochanter, femur, patella, tibia, metatarsus, tarsus + claw.
- Mesotarsus** - intermediate division of tarsi of legs III and IV of nymphs. Tarsi of legs I and II only have basitarsus and distitarsus. It is never subdivided in adults.
- Mesotergum** - the scutal areas I to IV.
- Pedipalpus** - the second pair of appendages, usually more robust than the walking legs. The segment names as in the legs, except the metatarsus is lacking.
- Tarsal process** - unpaired process of the distalmost tarsal article which occurs on legs III and IV of some Laniatores (cf. Fig. 4); called the "pseudonychium" by earlier authors.

Handling specimens

Immature and adult stages should be sacrificed and stored in 70-80 % ethanol. The observations on color, granules and spines of dorsal scute are best made using dry specimens. Specimens can be dabbed dry on toweling for examination and then returned to alcohol. The number of tarsal articles is to be counted under liquid. The specimens should be kept in flat bottom vials together with identification and collection data labels. The vials should be stored in larger jars with 70-80% ethanol.

For detailed study, it is necessary to remove the genitalia. The ovipositor is not well studied and it is currently thought to be most informative only for higher level relationships. The study of Neotropical opilionids' penes began in the 1970's. To dissect the penis, parallel cuts must be made with a sharp scalpel from each side of the genital operculum to near the posterior margin. The detached region is lifted and the penis removed with forceps. Part of the tissues that

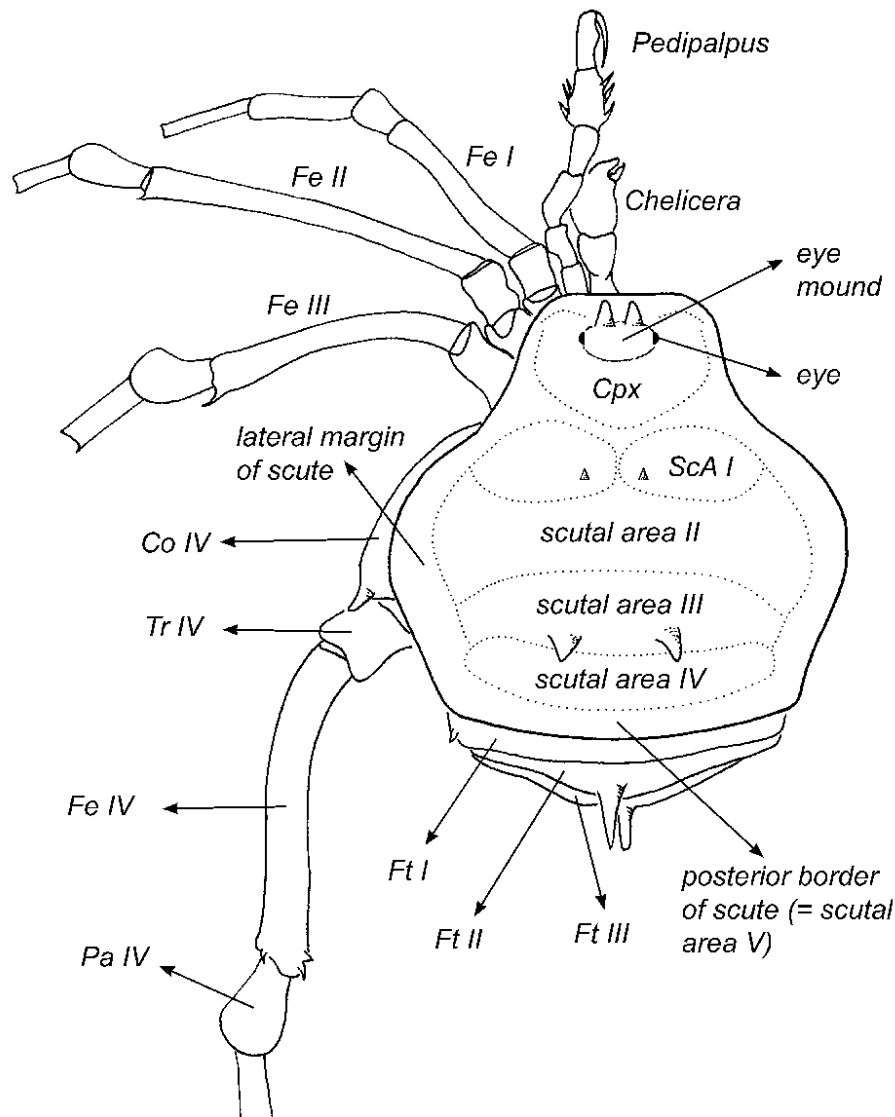


Fig. 1. Undescribed species of *Ampycus* (Gonyleptidae), schematic dorsal view of habitus. Co: coxa, Cpx: carapace, Fe I-IV: femora, Ft I-III: free tergites, Pa: patella, ScA I: scutal area I, Tr: trochanter. Note that scutal grooves (shown in dotted lines) may be absent in many species of some families.

cover the penis is removed and washed with 70 % ethanol. The penis can then be cleared in Creosote. The genitalic characters are to be examined on an excavated slide with lactophenol under an optic dissecting microscope. Human hairs or fine-tipped needles can be used for manipulation of the penis on the slide. The penis is preserved in microvials with 70 % ethanol and stored together with the specimen from which it was removed (ŠILHAVÝ 1969; PINTO-DA-ROCHA 1997). Specimens can be sexed by observation of the usual dimorphic features (cf. Sexual dimorphism, above) or in medium-large sized Laniatores species by raising the genital opercle and direct observation (under the stereomicroscope) of the ventral plate and stylus of the penis or the soft spines of the ovipositor.

Key to families and subfamilies of Amazonian Opiliones

1. Genital operculum absent, genital opening exposed. Scent glands placed in mounds (ozopores) on lateral margin of cephalothorax. Eye mound and eyes absent (Fig. 5).....Cyphophthalmi – Neogoveidae
- Genital operculum present (fused or as a distinct sclerite). Scent glands internal with openings on lateral sides of cephalothorax (without mounds). Eye mound and eyes usually present (Figs. 6-16) Phalangida (2)

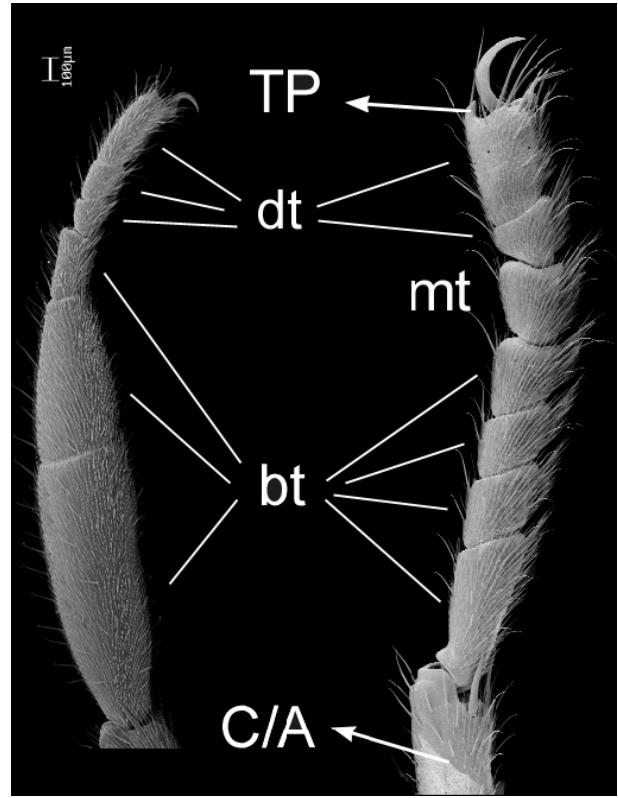
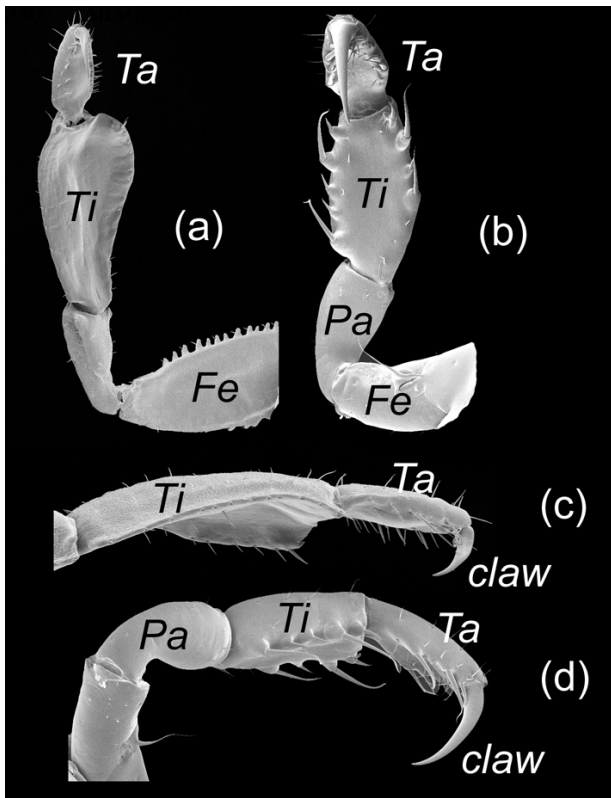
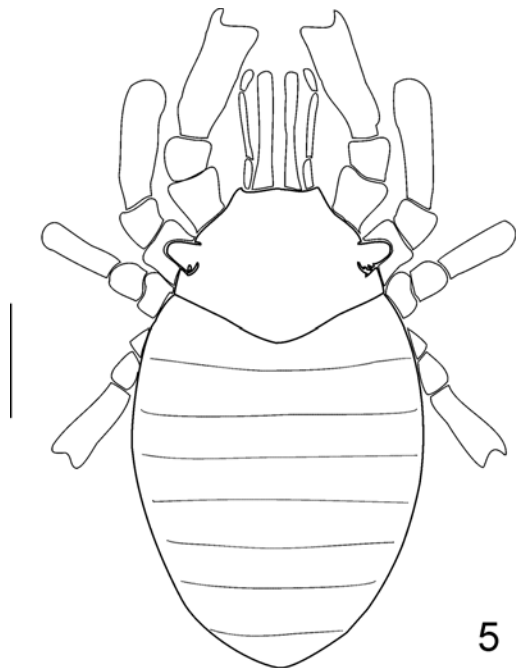
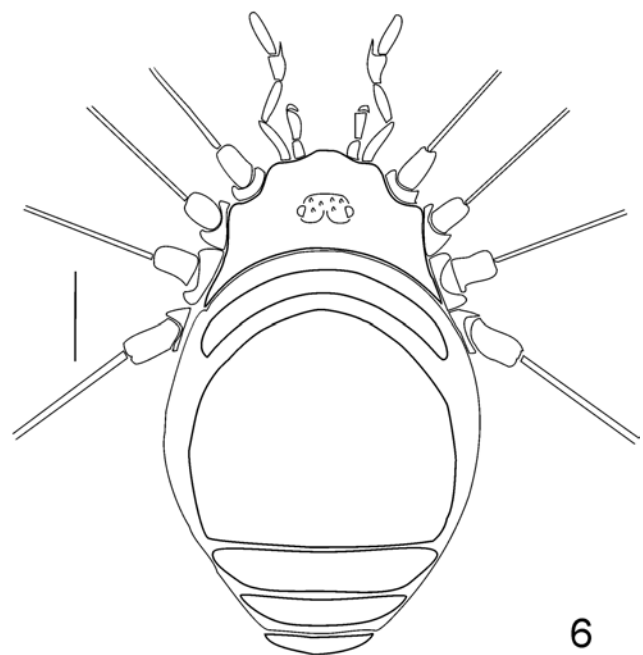


Fig 2 (left). Scanning electron micrographs of the pedipalps of Laniatores. a: Cosmetidae, ventral view; b: Manaosbiidae, ventral view; c: Cosmetidae, lateral view; d: Manaosbiidae, lateral view.

Figs. 3, 4 (right). Tarsi of Laniatores. 3 (left): Tarsus of leg I of a male Manaosbiidae. Note the swollen two basalmost basitarsomeres. The third basitarsomere is normal. 4 (right): Tarsus of leg IV of a pachyline gonyleptid. Note that in anterior legs (I and II) the tarsomeres are grouped in two, whereas in posterior legs (III and IV) they are grouped in three; bt: basitarsus (in this case with 3 and 4 articles), C/A: groove between calcaneus (distal) and astragalus (proximal), dt: distitarsus (2 articles), mt: mesotarsus (absent in legs I-II), TP: tarsal process (“pseudonychium”).



5



6

Fig 5. Cyphophthalmi family Neogoveidae gen. sp.: (MNRJ 5921), Brazil, Amapá.

Fig 6. Palpatores family Sclerosomatidae, subfamily Gagrellinae, *Geaya* sp.: (AMNH AK 97) Colombia.

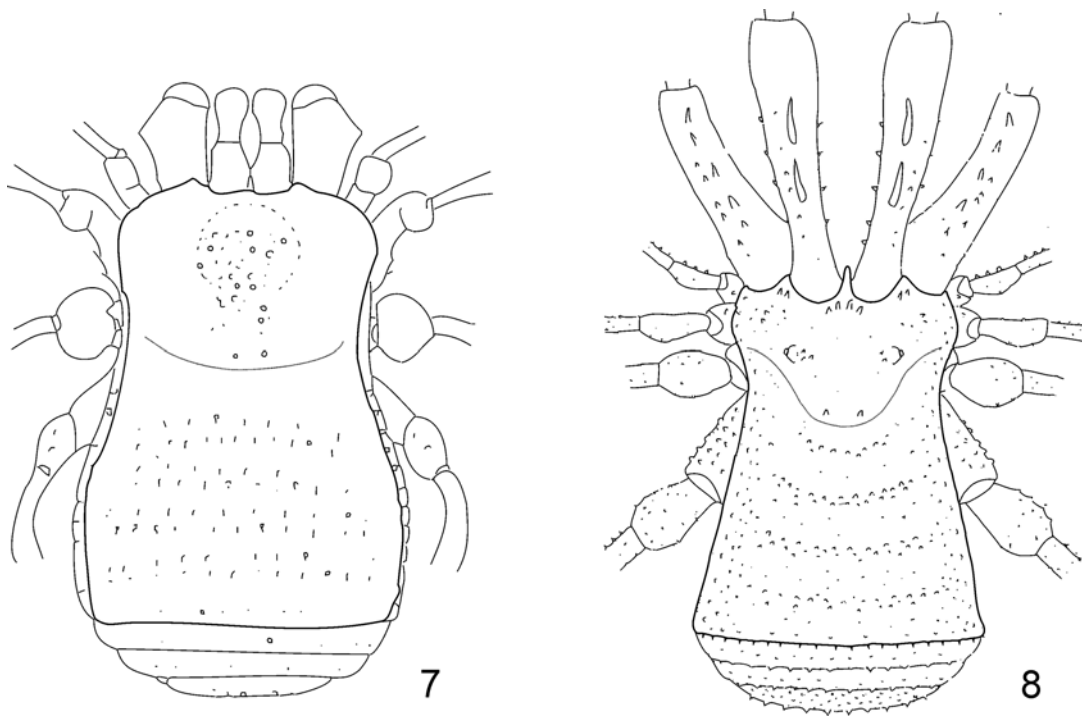


Fig 7. Laniatores family Guasiniidae, *Guasinia delgadoi* GONZÁLEZ-SPONGA, 1997, male, Venezuela; adapted from the literature.
Fig 8. Laniatores family Stygnommatidae, *Stygnomma monagasiensis* SOARES & AVRAM, 1981: male, Venezuela; adapted from the literature.

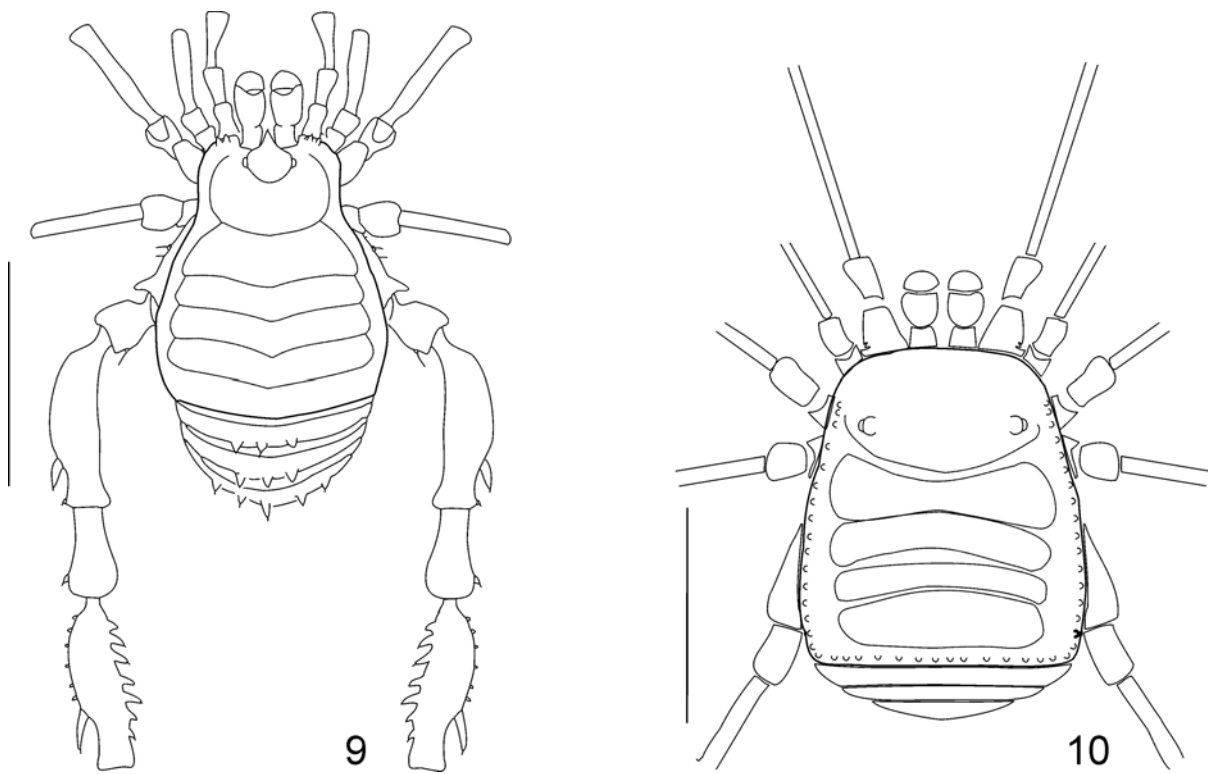


Fig 9. Laniatores family Zalmoxidae, *Tegipiolus* sp.: male (MNRJ 6997) Brazil, Espírito Santo.
Fig 10. Laniatores family Biantidae, *Stenostygnus pusio* SIMON, 1879: female, Brazil, Amazonas, adapted from PINTO-DARROCHA (1995).

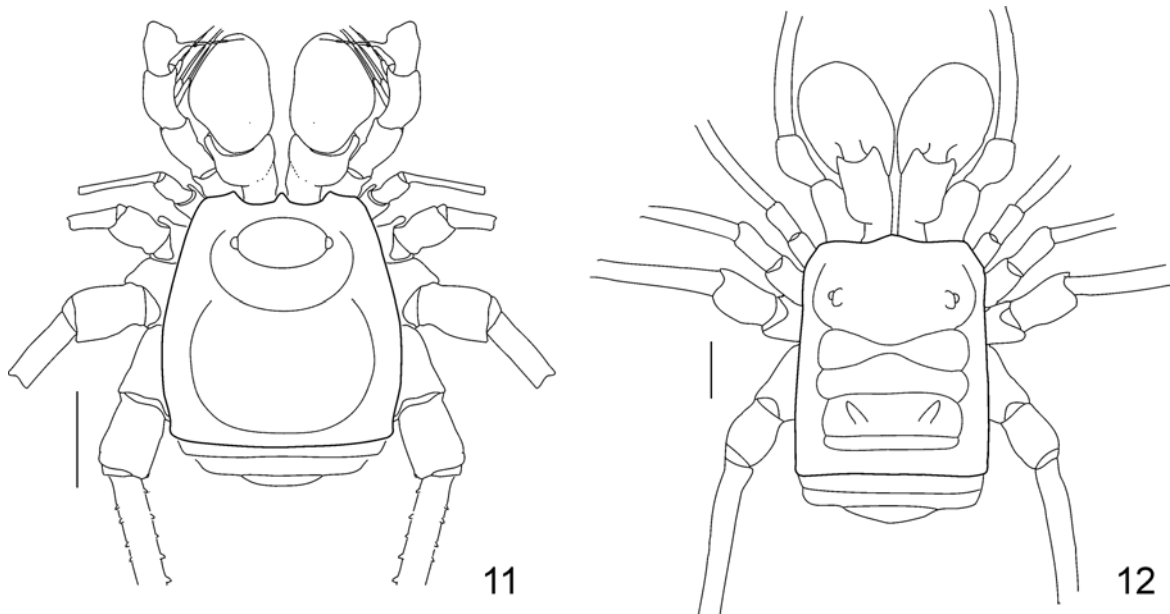


Fig 11. Laniatores family Agoristenidae, *Trinella* sp.: male (FMNH) Ecuador, Pastaza.

Fig 12. Laniatores family Stygnidae, *Protimesius longipalpis* (ROEWER, 1943): male (MNRJ 6226) Brazil, Amazonas, Manaus, Reserva Ducke.

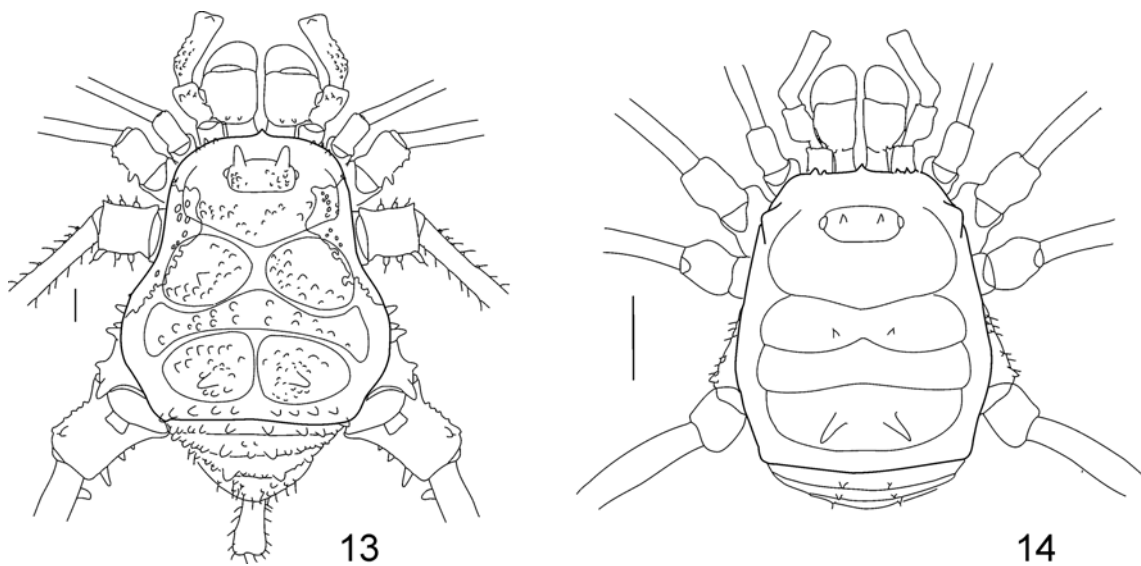


Fig 13. Laniatores family Cranidae, *Parkocraneus* sp.: male (FMNH) Ecuador, Pastaza.

Fig 14. Laniatores family Manaosbiidae, *Manaosbia scopulata* Roewer, 1943: male (MCN-RS 1223), Brazil, Amazonas, Manaus, Reserva Ducke.

2. Genital operculum fused with stigmatic area. Pedipalps weak and short without ventral spines on tibia and tarsus. Tarsi of legs III-IV with only one claw. Body rounded with all legs filiform (Fig. 6).....Palpatores – Sclerosomatidae – Gágrellinae
- Genital operculum forming a distinct sclerite. Pedipalps with ventral spines on tibia and tarsus (excepted Guasiniidae and Cosmetidae). Tarsi of legs III-IV with two distinct claws. Body more or less flattened with legs short or long, but usually not filiform (Figs. 7-16).....Laniatores (3)

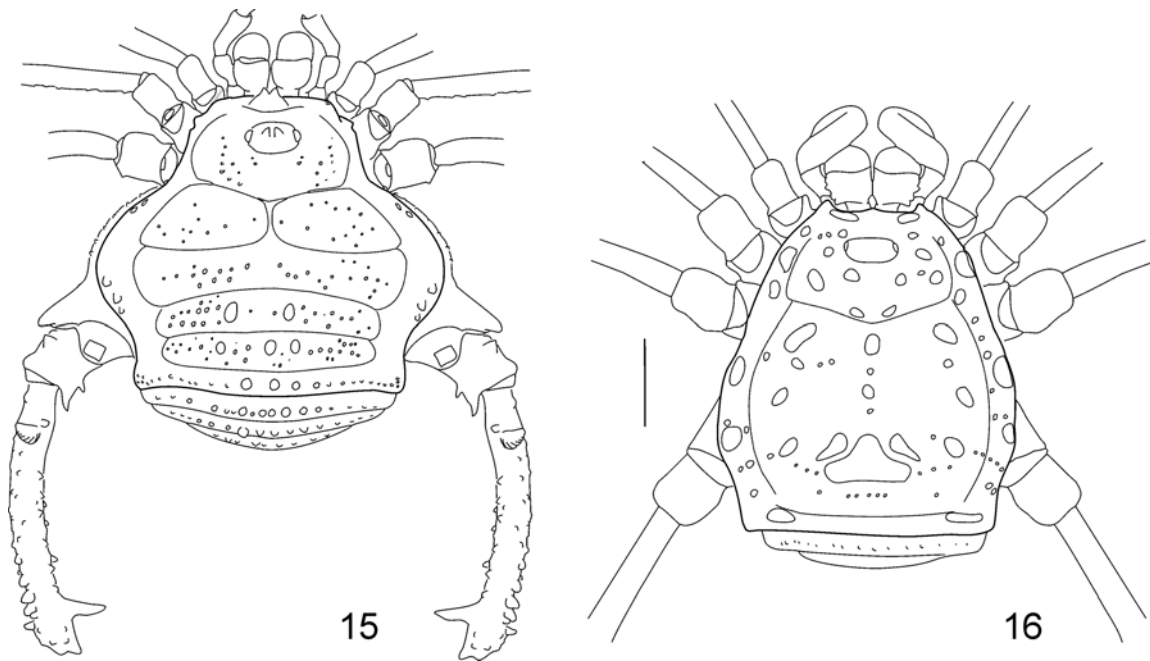


Fig 15. Laniatores family Gonyleptidae *Cearinus corniger* ROEWER, 1929: male (MNRJ 5229) Brazil, Pará, Serra do Ererê.
Fig 16. Laniatores family Cosmetidae, *Cynorta conspersa* (PERTY, 1833): male (MNRJ 6318) Brazil, Pará, Tucuruí.

- 3. Body outline hourglass shaped. Pedipalpal tarsus plus tibia together longer than femur.....4
- Body outline pyriform or subrectangular. Pedipalpal tarsus plus tibia together shorter than femur.....5
- 4. Chelicerae short and weak. Pedipalpal tarsus and tibia subequal, without spines; eyes absent (common eye mound may be present) (Fig. 7).....Guasiniidae
- Chelicerae swollen, basal segment very long armed with powerful spines in both sexes. Pedipalpal tibia much longer than tarsus and armed with spines; eyes usually present on separate mounds (Fig. 8).....Stygnomatidae
- 5. Common eye mound absent, eyes placed on two separate mounds.....6
- Common eye mound present, with or without median depression and carrying both eyes.....7
- 6. Tiny [scute up to 3 mm long] and rare animals. Chelicerae weak (similar in both sexes). Without tarsal process in claws III-IV. Dorsal scute smooth and unarmed (Fig. 10).....Biantidae (Stenostyginae)
- Medium-sized and fairly common animals. Chelicerae strongly swollen in males. With tarsal process in claws III-IV. Dorsal scute usually armed with paired spines in area III and one unpaired in carapace (Fig. 12).....Stygnidae (15)
- 7. Small animals (scute less than 2 mm). Sexual dimorphism more pronounced with femur IV being clavate and tibia IV incrassate with row of spines. Scutal areas well marked and pointed backwards. Area I generally longer than each of the other areas (Fig.9).....Zalmoxidae
- Medium-sized to large animals [scute more than 3 mm long]. Sexual dimorphism, if present, typically with coxa IV bearing apophyses and femur IV being sinuous and/or with spines, tibia rarely spined. Scutal areas sometimes effaced, never pointing backwards. Area I comparable to the others.....8
- 8. Opisthosomatic area I divided into left and right halves by longitudinal groove or by the intrusion of the area II (in some species the condition is indistinguishable because all the grooves are obscure); animals medium or large sized (scute larger than 4 mm); basitarsal spindle absent.....9
- Opisthosomatic area I generally undivided; mesotergal grooves typically obscure; medium sized animals (scute 3 to 4 mm), male always with basitarsal spindle in leg I.....Manaosbiidae
- 9. Pedipalpal femora compressed, spoon-shaped, concavity overlapping the chelicerae, pedipalpal tarsi and tibiae also flattened with very weak armor consisting of marginal array of similar tubercles (Fig. 2 a, c); eye mound very low; mesotergal grooves generally inconspicuous.....Cosmetidae (17)
- Pedipalpal femora cylindrical more or less elongate; pedipalpal tarsi and tibiae with powerful armature (Fig. 2 b, d); eye mound generally elevate; mesotergal grooves generally visible.....10

10. Leg I much shorter and thinner than other legs; eye mound saddle-shaped; pedipalpal patella with apical inner spineAgoristenidae (Leiosteninae)
- Leg I shorter than the others but of comparable thickness; eye mound variable, rarely saddle-shaped; pedipalpal patella usually unarmed.....11
11. Male coxa IV larger than the others, but only a small portion of it appears in dorsal view under scute, in general armed with small external apical spine; area I frequently armed with a pair of spines.....12
- Male coxa IV much developed, almost always broadly surpassing the scute in dorsal view, generally armed with strong apophysis; area I generally unarmed or with weak armature.....Gonyleptidae (13)
12. Only the first or the two first of the three basitarsomeres of male's leg I spindle-like inflated (Fig. 4), pedipalpal patella and tibia dorsally smooth; coxae III and IV united by array of pointed granules; pedipalpal femur ventrally unarmed; cheliceral hand of male never inflatedManaosiidae
- All basitarsomeres of male's leg I more or less thickened compared to the distitarsomeres, never inflated in spindle form; pedipalpal patella and tibia dorsally with coarse granulations; coxae III and IV not connected by pointed granules, unarmed; pedipalpal femur often with strong ventral armature; cheliceral hand of male often inflated....
-Cranidae
13. Eye mound with unpaired armature. Coxa IV with recurved apical inner apophysis.....Pachylinae
- Eye mound armed with two paramedian cones. Coxa IV without apical inner armature.....14
14. All free tergites unarmed. Body smooth or with setiferous granules.....Gonyleptinae
- Free tergite III with stout spine. Body covered with protuberances.....Undescribed subfamily [*Ampycus*, *Bullaepus*, *Hutamaia*, *Itequahy*, *Sibollus*]
15. Eye mounds halfway between carapace margin and scutal groove I (= scutal groove); pedipalpal femur and patella short and thick.....Nomoclastinae
- Eye mounds much closer to scutal groove than to the frontal border; pedipalpal femur and patella long and slender16
16. Claws III and IV opposite, pectinate; distitarsi III and IV slightly flattened.....Heterostygninae
- Claws III and IV parallel or subparallel, smooth; distitarsi III and IV cylindrical.....Stygninae
17. Claws of legs III and IV smooth.....Cosmetinae
- Claws of legs III and IV pectinate.....Discosomaticinae

Present status of knowledge of each family

Agoristenidae: 24 genera and 70 species, also occurs in the Caribbean and Andes. Phylogenetic analysis of genera in KURY (1997b).

Biantidae: Distribution pantropical, 29 genera and 123 species. Status of subfamilies uncertain: one Afrotropical, other Oriental, one Neotropical, a forth subfamily Palaeotropical. The Neotropical subfamily until recently was known as Caribbiantinae, but PINTO-DA-ROCHA (1995) observed that there was the older available name Stenostygninae. This taxon includes only 9 genera and 17 species, most from the Caribbean.

Cosmetidae: Third largest family of Opiliones in the world (118 genera, 719 species), generic classification undefined. Distributed from USA to Argentina.

Cranidae: 79 genera, 167 species. Family recently dismembered from Gonyleptidae, most diverse in the Andes (KURY 1992).

Gonyleptidae: Second largest family of Opiliones in the world (280 genera, 850 species). Very abundant in the Atlantic Forest realm, represented in Amazonia by only a few genera in two subfamilies.

Guasiniidae: The correct name of a family based on the type genus *Guasimia* is Guasiniidae and not "Guasinidae" as originally described. This small family has only three species, all from Venezuela, and consists of small Zalmoxoidea from leaf litter.

Manaosiidae: 26 genera, 39 species. Diagnosis of family and list of included genera in KURY (1997a). Distributed from Panama to Central Brazil.

Neogoveidae: Apart for the species cited here, which was not included in any known genus, this family possesses 2 genera and 12 species, distributed in Mexico, northern South America and West Africa. Hypothesis for relationships among families of Cyphophthalmi in SHEAR (1980).

Phalangodidae: see Zalmoxidae.

Sclerosomatidae: Largest family of Opiliones in the world, with more than one thousand species. The Gagrellinae are far more abundant in the Oriental Region, where they are represented by nothing less than 90 genera and 710 species. There are 26 genera and 250 species in the Neotropics. Current generic classification uses only number of nodules of femora I-IV and the ratio between femora I-III and body. Generic diagnoses are unsatisfactory and groups are unnatural. Catalog with keys for genera and species available in ROEWER (1953), list of type species and all genera in CRAWFORD (1992). Together with Zalmoxidae and Biantidae they are the only families to occur also in the Old World (but see Stygnomatidae).

Stygnidae: 26 genera, 77 species. PINTO-DA-ROCHA (1997) presented a cladistic analysis, descriptions and illustrations for genera and species.

Stygnomatidae: 1 genus, 27 species. There is only a record of an undescribed species from Amazonas, Brazil, cited in a congress abstract (KURY 1996). There is another highly doubtful genus *Stygnomimus* ROEWER, 1927 from Malaysia, but its familial placement is controversial.

Zalmoxidae: 46 genera, 130 species. Most genera are traditionally included in the catch-all family Phalangodidae. This family is also well represented in the Oriental and Australian Region.

List of Amazonian genera and species

Below is a list of species, organized by families and subfamilies, which occur in the States herein considered to belong to Amazonia.

Brazil — Amapá

Neogoveidae

Genus? *enigmaticus* MARTENS, 1969

Cosmetidae

Metarhaucus ohausi (ROEWER, 1912)

Paecilaema sigillatum ROEWER, 1912

Stygnidae Stygninae

Protimesius gracilis ROEWER, 1913

Stygnus luteus (MELLO-LEITÃO, 1931)

Brazil — Amazonas

Neogoveidae

Metaogovea oviformis MARTENS, 1969

Neogovea microphaga (MARTENS, 1969)

Sclerosomatidae Gagrellinae

Amazonesia pulchra H. SOARES, 1970

Geaya aenescens ROEWER, 1953

Geaya aureolucens ROEWER, 1910

Geaya centralis ROEWER, 1953

Geaya goodnighti ROEWER, 1953

Geaya tibialis ROEWER, 1953

Krusa amazonica ROEWER, 1953

Prionostemma aureomaculatum H. SOARES, 1970

Prionostemma bidens ROEWER, 1953

Prionostemma magnificum ROEWER, 1953

Prionostemma richteri ROEWER, 1953

Prionostemma transversale ROEWER, 1953

Agoristenidae Leiosteninae

Trinella matintaperera PINTO-DA-ROCHA, 1996

Trinella soaresorum PINTO-DA-ROCHA, 1996

Biantidae

Stenostygnus pusio SIMON, 1879

Cosmetidae

Eucynortula lata (BANKS, 1909); cf Plate 3 [identification doubtful]

Cocholla simoni ROEWER, 1927

Cynorta albiadpersa ROEWER, 1927

Cynorta clavipus ROEWER, 1927

Cynorta insperata H. SOARES, 1970

Cynorta itacoaiensis H. SOARES, 1970

Cynorta litterata H. SOARES, 1970

Cynorta mira H. SOARES, 1970

Cynorta notabilis H. SOARES, 1970

Cynorta propria ROEWER, 1947

Cynorta scripta SIMON, 1879

Cynorta vestita ROEWER, 1912

Cynorta zonata ROEWER, 1947

Cynortopyga h-album ROEWER, 1947

Discosomaticus cinctus (PERTY, 1833)

Eucynorta amazonica PIZA, 1938

Eucynortella duapunctata GOODNIGHT & GOODNIGHT, 1943

Eucynortella pauper PIZA, 1938

Eucynortula pentapunctata ROEWER, 1947

Eupoecilaema perducens ROEWER, 1947

Eupoecilaema quadrioctale ROEWER, 1947

Flirtea picta (PERTY, 1833)

Gryne amazonica ROEWER, 1947

Gryne orensis (SØRENSEN, 1879)

Gryne pustulata ROEWER, 1927

Paecilaema argentinoides H. SOARES, 1970

Paecilaema carvalhoi H. SOARES, 1970

Paecilaema graphicum ROEWER, 1947

Paecilaema leucomelas SIMON, 1880

Paecilaema limbatum KOLLAR, in KOCH 1839

Paecilaema lobipictum ROEWER, 1947
Paecilaema manifestum ROEWER, 1927
Paecilaema marajoara H. SOARES, 1970
Paecilaema withi HENRIKSEN, 1932
Paraprotus quadripunctatus ROEWER, 1947
Protus insolens SIMON, 1879

Cranidae Cranainae

Digalistes signata ROEWER, 1932
Ladantola aspersa ROEWER, 1932
Mecritta filipes ROEWER, 1932
Parkocraneus bimaculatus MELLO-LEITÃO, 1949
Santinezia manauara PINTO-DA-ROCHA, 1994
Santinezia singularis (H. SOARES, 1970)

Cranidae Prostyginae

Ostracidium fuscum PERTY, 1833

Gonyleptidae Undescribed subfamily

Ampycus telifer (BUTLER, 1873)
Bullaepus granulatus H. SOARES, 1970
Hutamaia caramaschii SOARES & SOARES, 1977
Itequahy ensiferus MELLO-LEITÃO, 1949

Gonyleptidae Pachylinae

Huralvioides hoeferi KURY, 1995
Parahuederwaldtia caramaschii SOARES & SOARES, 1979

Manaosbiidae

Clavicraneus tarsalis ROEWER, 1915
Manaosbia scopulata ROEWER, 1943
Paramicrocraneus difficilis H. SOARES, 1970
Rhopalocraneus apiculatus ROEWER, 1932
Saramacia lucasae (JIM & SOARES, 1991)

Stygidae Heterostyginae

Eutimesius simoni ROEWER, 1913
Stygnidius inflatus (GUÉRIN-MENEVILLE, 1843)

Stygidae Styginae

Auranus hoeferescovitorum PINTO-DA-ROCHA, 1997
Auranus parvus MELLO-LEITÃO, 1941
Protimesius albilineatus (ROEWER, 1957)
Protimesius amplichelis (ROEWER, 1931)
Protimesius coxalis (ROEWER, 1931)
Protimesius gracilis ROEWER, 1913
Protimesius longipalpis (ROEWER, 1943)
Protimesius palpalis (ROEWER, 1931)
Stygnus armatus PERTY, 1833
Stygnus lesserti (ROEWER, 1943)
Stygnus pectinipes (ROEWER, 1943)

Brazil — Pará

Neogoveidae

Neogovea immsi HINTON, 1938

Sclerosomatidae Gagrellinae

Corderobunus vittatus MELLO-LEITÃO, 1939
Geaya atrolutea ROEWER, 1910
Geaya bicornuta MELLO-LEITÃO, 1939
Geaya crucicolorata ROEWER, 1953
Geaya inermis MELLO-LEITÃO, 1939

Geaya marginata ROEWER, 1953
Geaya nigricoxa ROEWER, 1910
Geaya variegata MELLO-LEITÃO, 1939
Holcobunus tocantinus ROEWER, 1953
Holcobunus trochanteralis ROEWER, 1953
Paruleptes coronatus H. SOARES, 1970
Prionostemma aureum ROEWER, 1928
Prionostemma fulvibrunneum ROEWER, 1928
Taperina nigripes ROEWER, 1953

Laniatores - family uncertain

Belemarua nitens (SOARES & SOARES, 1946)

Agoristenidae Leiosteninae

Trinella bicoloripes (ROEWER, 1949)

Cosmetidae

Cynorta albanalis ROEWER, 1947
Cynorta albicurvata ROEWER, 1947
Cynorta albipicta ROEWER, 1947
Cynorta conspersa (PERTY, 1833)
Cynorta coxaepunctata ROEWER, 1947
Cynorta juruensis (MELLO-LEITÃO, 1923)
Cynorta mayi MELLO-LEITÃO, 1931
Cynorta ramulata ROEWER, 1947
Cynorta variegata ROEWER, 1947
Eupoecilaema perducens ROEWER, 1947
Flirtea picta (PERTY, 1833)
Gryne leprosa SØRENSEN, 1932
Gryne marginalis (PERTY, 1833)
Gryne oreensis (SØRENSEN, 1879)
Metalibitia fuscomaculata H. SOARES, 1970
Neocynorta m-inscripta MELLO-LEITÃO, 1939
Paecilaema paraense H. SOARES, 1970
Paecilaema triseriatum ROEWER, 1947
Roquettea singularis MELLO-LEITÃO, 1931

Gonyleptidae Gonyleptinae

Cearinus corniger ROEWER, 1929

Gonyleptidae Pachylinae

Huralvioides parauensis H. SOARES, 1970

Manaosbiidae

Belemnodes scaber (ROEWER, 1932)
Belemulus annulatus ROEWER, 1932
Rhopalocraneus apiculatus ROEWER, 1932
Rhopalocraneus aspersus ROEWER, 1932
Rhopalocraneus crulsi MELLO-LEITÃO, 1932
Rhopalocraneus marginatus ROEWER, 1913
Saramacia annulata (MELLO-LEITÃO, 1931)
Saramacia lucasae (JIM & SOARES, 1991)
Synceraneus cribrum ROEWER, 1913

Stygidae Heterostyginae

Stygnidius inflatus (GUÉRIN-MENEVILLE, 1843)

Stygidae Styginae

Auranus parvus MELLO-LEITÃO, 1941
Protimesius evelinae (SOARES & SOARES, 1978)
Protimesius laevis (SØRENSEN, 1932)
Protimesius trocaraincola PINTO-DA-ROCHA, 1997

Sickesia usta (MELLO-LEITÃO, 1941)
Stygnus armatus PERTY, 1833
Stygnus heliae PINTO-DA-ROCHA, 1997
Stygnus luteus (MELLO-LEITÃO, 1931)
Stygnus tocantinensis PINTO-DA-ROCHA, 1997
Verrucastygnus caliginosus (PINTO-DA-ROCHA, 1990)

Zalmoxidae

Ethobunus brasiliensis (MELLO-LEITÃO, 1941)

Brazil — Roraima

Sclerosomatidae — Gágrellinae

Romerella punctata GOODNIGHT & GOODNIGHT, 1943

Stygnidae

Paraphareus tatei GOODNIGHT & GOODNIGHT, 1943
Planophareus pallidus GOODNIGHT & GOODNIGHT, 1943
Stenophareus roraimus GOODNIGHT & GOODNIGHT, 1943
Stygnus pectinipes (ROEWER, 1943)

Zalmoxidae

Crosbyella roraima GOODNIGHT & GOODNIGHT, 1943

Colombia — Amazonas

Biantidae

Stenostygnus pusio SIMON, 1879

Colombia — Uaupés

No record

Peru — Loreto

Cosmetidae

Cynorta cancellata ROEWER, 1947
Metacynorta bimaculata ROEWER, 1947
Paecilaema guttigerum SØRENSEN, 1932
Paecilaema vittatum (SØRENSEN, 1932)
Pebasia singularis ROEWER, 1947
Poecilaemula peruviana ROEWER, 1947

Cranaidae Cranainae

Phalangodus poecilus (ROEWER, 1943)
Phareicranus albigyratus ROEWER, 1932

Gonyleptidae Undescribed subfamily

Sibollus margaritatus ROEWER, 1929

Manaosbiidae

Tegyra cinnamomea SØRENSEN, 1932

Stygnidae Heterostygninae

Eutimesius simoni ROEWER, 1913

Stygnidae Stygninae

Stygnus klugi (GOODNIGHT & GOODNIGHT, 1943)
Stygnus simonis (SØRENSEN, 1932)
Stygnus simplex (ROEWER, 1913)

Peru — Madre de Dios

Stygnidae Stygninae

Protimesius albilineatus (ROEWER, 1957)

Peru — Ucayali

Laniatores - family uncertain

Micriscaeus gracillimus ROEWER, 1957
Pucallpana pullex AVRAM & SOARES, 1983

Cosmetidae

Cosmetus peruvicus (AVRAM & SOARES, 1983)
Cynorta bassleri GOODNIGHT & GOODNIGHT, 1943
Cynorta bordoni AVRAM & SOARES, 1983
Cynorta thoraxpicta ROEWER, 1957

Cynortellana peruviana ROEWER, 1963

Cynortula alejandra ROEWER, 1957

Cynortula figurata ROEWER, 1957

Discosomaticus distinctus AVRAM & SOARES, 1983

Cranaidae Cranainae

Águaytiella maculata GOODNIGHT & GOODNIGHT, 1943

Stygnidae Heterostygninae

Protimesius albilineatus (ROEWER, 1957)

Stygnidae Stygninae

Stygnus peruvianus (ROEWER, 1957)

Venezuela — Amazonas

Agoristenidae Leiosteninae

Trinella glabrata (GONZÁLEZ-SPONGA, 1998)

Cosmetidae

Baria neblinensis GONZÁLEZ-SPONGA, 1993
Cynorta dearuwa GONZÁLEZ-SPONGA, 1992
Paecilaema amazonica GONZÁLEZ-SPONGA, 1992

Stygnidae Heterostygninae

Minax tetraspinosus PINTO-DA-ROCHA, 1997

Yapacana tibialis PINTO-DA-ROCHA, 1997

References

- ACOSTA, L.E. (1983): Sobre la fluorescencia del tegumento en opiliones (Arachnida). - *Historia. nat. (Corrientes)* **3**(23): 193-195.
- ACOSTA, L.E. & E. MAURY (1998): Opiliones. - In: J.J. MORRONE & S. COSCARÓN (eds.): *Biodiversidad de artrópodos argentinos*: 569-580. Ediciones Sur, La Plata, 599 pp.
- ACOSTA, L.E., PEREYRA, F.E. & R.A. PIZZI (1995): Field observations on *Pachyloidellus goliath* (Opiliones, Gonyleptidae) in Pampa de Achala, province of Córdoba, Argentina. - *Bull. Br. arachnol. Soc.* **10**(1): 23-28.
- ACOSTA, L.E., PORETTI, T.I. & P.E. MASCARELLI (1993): The defensive secretions of *Pachyloidellus goliath* (Opiliones, Laniatores, Gonyleptidae). *Bonn. zool. Beitr.* **44**(1-2): 19-31.
- ADIS, J. (1992): Überlebensstrategien terrestrischer Invertebraten in Überschwemmungswäldern Zentralamazoniens. - *Verh. naturwiss. Ver. Hamburg (NF)* **33**: 21-114.

- ADIS, J. (1997): Terrestrial invertebrates: Survival strategies, group spectrum and activity patterns. – In: JUNK, W.J. (ed.): The Central Amazon floodplain. Ecology of a pulsing system: 299-317. Ecological Studies 126, Springer, Berlin: 525 pp.
- ADIS, J. & M.S. HARVEY (2000): How many Arachnida and Myriapoda are there world-wide and in Amazonia? - Stud. Neotrop. Fauna and Environm. **35**(2): 139-141.
- BERLAND, L. (1949): Ordre des Opilions. - In: GRASSÉ, P. (ed.): Traité de Zoologie **6**: 761-793. Masson, Paris: 979 pp.
- BRISTOWE, W.S. (1949): The distribution of harvestmen (Phalangida) in Great Britain and Ireland, with notes on their names, enemies and food. - J. Anim. Ecol. **18**: 100-114.
- CANALS, J. (1936): Observaciones biológicas en arácnidos del orden Opiliones. - Rev. Chilena Hist. Nat. **40**: 61-63.
- CAPOCASALE, R. & L. BRUNO TREZZA (1964): Biología de *Acanthopachylus aculeatus* (Kirby, 1819) , (Opiliones; Pachylinae). - Revta Soc. uruguaya Ent. **6**: 19-32.
- COKENDOLPHER, J.C. (1993): Pathogens and parasites of Opiliones (Arthropoda: Arachnida). - J. Arachnol. **21**(2):120-146.
- COKENDOLPHER, J.C., & S.R. JONES (1991): Karyotype and notes on the male reproductive system and natural history of the harvestman *Vonones sayi* (SIMON) (Opiliones, Cosmetidae). - Proc. Ent. Soc. Wash. **93**(1): 86-91.
- CRAWFORD, R.L. (1992): Catalogue of the genera and type species of the harvestman superfamily Phalangioidea (Arachnida). - Burke Mus. Contrib. Anthropol. Nat. Hist. **8**:1-60.
- DUNLOP, J. (1998): The origin of tetrapulmonate book lungs and their significance for chelicerate phylogeny. - Proc. 17th Europ. Coll. Arachnol. (Edinburgh 1997): 9-16.
- DUNLOP, J. & P. SELDEN (1997): The early history and phylogeny of the chelicerates. – In: FORTEY, R.A. & R.H. THOMAS (eds.): Arthropod relationships: 221-235. Systematics Association Special Volume Series 55, Chapman & Hall, London: 650 pp.
- DUNLOP, J. & M. WEBSTER. (1999): Fossil evidence, terrestrialization and arachnid phylogeny. - J. Arachnol. **27**: 86-93.
- EDGAR, A.L. (1971): Studies on the biology and ecology of Michigan Phalangida (Opiliones). - Misc. Publ. Mus. Zool. Univ. Michigan **144**: 1-64.
- EDGAR, A.L. (1990): Opiliones (Phalangida). - In: D.L. DINDAL (ed.): Soil biology guide: 529-581. Wiley, New York: 1349 pp.
- EISNER, T., KLUGE, A.F., CARREL, J.E. & J. MEINWALD (1971): Defense of phalangid: liquid repellent administered by leg dabbing. - Science **173**: 650-652.
- FLOREZ D.E. & H. SANCHEZ C. (1997): La diversidad de los arácnidos en Colombia — aproximación inicial. - In: O. RANGEL (ed.): Colombia, Diversidad Biótica: 327- 372. Inst. Ciencias naturales, UN, Inderena, Fes, Fen. Santafé de Bogotá, vol. I: 442 pp.
- FRIEBE, B. & J. ADIS. (1983): Entwicklungszklen von Opiliones (Arachnida) im Schwarzwasser- Überschwemmungswald (Igapó) des Rio Tarumã Mirim (Zentralamazonien, Brasilien). - Amazoniana **8**(1): 101-110.
- GIRIBET, G, M. RAMBLA, S. CARRANZA, J. BAGUÑA, M. RIUTORT & C. RIBERA. (1999): Phylogeny of the Arachnid order Opiliones (Arthropoda) inferred from a combined approach of complete 18S and partial 28S ribosomal DNA sequences and morphology. - Molec. Phylogen Evol. **11**(2): 296-307.
- GNASPINI, P. (1995): Reproduction and postembryonic development of *Goniosoma spelaum*, a cavernicolous harvestman from south-eastern Brazil (Arachnida: Opiliones: Gonyleptidae). - Invert. Repr. Devel. **28**(2): 137-151.
- GNASPINI, P. (1996): Population ecology of *Goniosoma spelaum*, a cavernicolous harvestman from south-eastern Brazil (Arachnida: Opiliones: Gonyleptidae). - J. Zool. Lond. **239**: 417-435.
- GONZÁLEZ-SPONGA, M.A. (1997): Arácnidos de Venezuela. Una nueva familia, dos géneros y dos nuevas especies de Opiliones Laniatores. - Acta Biol. venez. **17**(3): 51-58.
- HILLYARD, P.D. & J.H.P. SANKEY (1989): Harvestmen. - Synopses Br. Fauna (n.s.) 4 (2nd ed.): 1-120.
- HÖFER, H. & L. BECK (1995): Die Spinnentierfauna des Regenwaldreservats "Reserva Ducke" in Zentralamazonien I. - Natur und Museum **125**(12): 389-401.
- HOLMBERG, R.G. (1986): The scent glands of Opiliones: a review of their function. – Proc. 5th Int. Congr. Arachnol. 1983: 131-133.
- IRMLER, U. (1981): Überlebensstrategien von Tieren im saisonal überfluteten amazonischen Überschwemmungswald. - Zool. Anz. **206**: 26-38.
- JUBERTHIE, C. (1964): Recherches sur la biologie de Opilions. - Ann. Spéléol. **19**(1): 5-238.
- JUBERTHIE, C. (1972): Reproduction et développement d'un opilion Cosmetidae, *Cynorta cubana* (BANKS) de Cuba. - Ann. Spéléol. **27**(4): 773-785.
- JUBERTHIE, C. & A. Muñoz-Cuevas (1971): Sur la ponte de *Pachylus quinamævidensis*. - Bull. Soc. Hist. Nat. Toulouse **107**(3-4): 468-474 pl. 1.
- KURY, A.B. (1991): Análise filogenética de Mitobatinae (Opiliones, Laniatores, Gonyleptidae). - M.Sc.-thesis, Museu Nacional/UFRJ, Rio de Janeiro, Brazil: 161 pp.
- KURY, A.B. (1992): The genus *Spinopilar* MELLO-LEITÃO (1940, with notes on the status of the family Tricommatidae (Arachnida, Opiliones). - Steenstrupia **18**(5): 93-99.
- KURY, A. B. (1996): Novo registro de Stygnommatidae para o Brasil (Arachnida, Opiliones). - Resumos do XXI Congresso Brasileiro de Zoologia, Porto Alegre: 69.
- KURY, A.B. (1997a): The genera *Saramacia* and *Syncranaus* ROEWER, with notes on the status of the Manaosbiidae (Opiliones, Laniatores, Gonyleptoidea). - Bolm. Mus. nac. Rio de Janeiro **374**: 1-22.

- KURY, A.B. (1997b): A new subfamily of Agoristenidae, with comments on suprageneric relationships of the family (Arachnida, Opiliones, Laniatores). – *Trop. Zool.* **10**(2): 333-346.
- KURY A.B. & J.C. Cokendolpher (2000): Opiliones. – In: J.E., LLORENTE B., E. GONZÁLEZ S. & N. PAPAVERO (eds.). Biodiversidad, taxonomía y biogeografía de artrópodos de México: Hacia una síntesis de su conocimiento: 137-157. Universidad Nacional Autónoma de México, México, vol. 2: 676 pp.
- MACHADO, G., R.L.G. Raimundo & P.S. Oliveira. (2000): Daily activity schedule, gregariousness, and defensive behaviour in the Neotropical harvestmen *Goniosoma longipes* (Opiliones: Gonyleptidae). - *J. Nat. Hist.* **34**(4): 587-596.
- MARTENS, J. (1978): Spinnentiere, Arachnida: Weberknechte, Opiliones. - In: Die Tierwelt Deutschlands **64**: 1-464. G. Fischer, Jena.
- MARTENS, J. (1980): Versuch eines phylogenetischen Systems der Opiliones. - *Verh. 8. Int. Arachnol. Kongr. Wien*: 355-360.
- MUÑOZ-CUEVAS, A. (1971a): Étude du tarse, de l'apotele et de la formation des griffes au cours du développement post-embryonnaire chez *Pachylus quinamævidensis* (Arachnides, Opilions, Gonyleptidae). - *Bulln Mus. Nat. Hist. Nat.*, 2 serie, tome **42**: 1027-1036.
- MUÑOZ-CUEVAS, A. (1971b): Contribution à l'étude du développement postembryonnaire de *Pachylus quinamævidensis* MUÑOZ-CUEVAS (Arachnides, Opilions, Gonyleptidae). - *Bulln Mus. Nat. Hist. Nat.*, 3 serie, tome **12**: 629-641.
- PINTO-DA-ROCHA, R. (1994): Invertebrados cavernícolas da porção meridional da província espeleológica do Vale do Ribeira, Sul do Brasil. - *Revta Bras. Zool.* **10**(2): 229-255.
- PINTO-DA-ROCHA, R. (1995): Redescription of *Stenostygnus pusio* SIMON and synonymy of Caribbiantinae with Stenostygninae (Opiliones: Laniatores, Biantidae). - *J. Arachnol.* **23**: 194-198.
- PINTO-DA-ROCHA, R. (1996): Description of the male of *Daguerreia inermis* SOARES & SOARES, with biological notes on population size in the Gruta da Lancinha, Paraná, Brazil (Arachnida, Opiliones, Gonyleptidae). - *Revta bras. Zool.* **13**(4): 833-842.
- PINTO-DA-ROCHA, R. (1997): Systematic review of the Neotropical family Stygnidae (Opiliones, Laniatores, Gonyleptoidea). - *Arq. Zool., S. Paulo.* **33**(4): 163-342.
- PINTO-DA-ROCHA, R. (1999): Opiliones. - In: C.R.F. BRANDÃO, & E.M. CANCELLO, (eds.): Invertebrados terrestres: 35-44. Biodiversidade do Estado de São Paulo. Síntese do conhecimento ao final do século XX (Joly, C.A. & Bicudo, C.E.M., orgs). FAPESP/USP, São Paulo, vol. 5: 279 pp.
- ROEWER, C.F. (1953): Neotropische Gagrellinae (Opiliones, Arachnidae). - *Mitt. zool. Mus. Berlin* **29**: 180-264.
- SHEAR, W.A. (1975): The opilionid family Caddidae in North America. With notes on species from other regions (Opiliones, Palpatores, Caddoidea). - *J. Arachnol.* **2**: 65-88.
- SHEAR, W.A. (1977): The opilionid genus *Neogovea* HINTON, with a description of the first troglotic cyphophthalmid from the Western Hemisphere (Opiliones, Cyphophthalmi). - *J. Arachnol.* **3**: 165-175.
- SHEAR, W.A. (1980): A review of the Cyphophthalmi of the United States and Mexico, with a proposed reclassification of the suborder (Arachnida, Opiliones). - *Am. Mus. Novit.* **2075**: 1-34.
- SHULTZ, J.W. (1990): Evolutionary morphology and phylogeny of Arachnida. - *Cladistics* **6**: 1-38.
- SHULTZ, J.W. (1998): Phylogeny of Opiliones (Arachnida): an assessment of the Cyphopalpatores concept. - *J. Arachnol.* **26**(3): 257-272.
- ŠILHAVÝ, V. (1969): Über die Präparation der Genitalien der Weberknechte. – *Deut. Ent. Z. NF* **16**(1-3): 141-145.
- SPOEK, G.L. (1963): The Opilionida (Arachnida) of the Netherlands. - *Zool. Verh. Leiden*, **63**: 1-70.
- STAREGA, W. (1992): An annotated check-list of harvestmen, excluding Phalangiiidae, of the Afrotropical Region (Opiliones). - *Ann. Natal Mus.* **33**(2): 271-336.

Appendix: Check-list of Amazonian Opiliones

Sampling sites in the environs of Manaus given in brackets; abbreviations as in Map of Chapter 2)

1. Genus? *enigmaticus* MARTENS, 1969 - Neogoveidae
2. *Aguaytiella maculata* GOODNIGHT & GOODNIGHT, 1943 – Gonyleptidae, undescribed subfamily
3. *Amazonesia pulchra* H. SOARES, 1970 – Sclerosomatidae, Gagrellinae
4. *Ampycus telifer* (BUTLER, 1873) – Gonyleptidae, new subfamily
5. *Auranus hoeferscovitorum* PINTO-DA-ROCHA, 1997 – Stygnidae, Stygninae (G)
6. *Auranus parvus* MELLO-LEITÃO, 1941 – Stygnidae, Stygninae – cited by ADIS & FRIEBE as *Stygnidius inflatus* (D, F, G)
7. *Baria neblinensis* GONZÁLEZ-SPONGA, 1993 - Cosmetidae
8. *Belemarua nitens* (SOARES & SOARES, 1946)- Laniatores – family uncertain
9. *Belemnodes scaber* (ROEWER, 1932) - Manosbiidae
10. *Belemulus annulatus* ROEWER, 1932 - Manosbiidae
11. *Bullaepus granulatus* H. SOARES, 1970 – Gonyleptidae, undescribed subfamily
12. *Cearinus corniger* ROEWER, 1929 – Gonyleptidae, Gonyleptinae

13. *Claviceranaus tarsalis* ROEWER, 1915 – Manosbiidae (Manaus)
14. *Cocholla simoni* ROEWER, 1927 - Cosmetidae
15. *Corderobunus vittatus* MELLO-LEITÃO, 1939 – Sclerosomatidae, Gagrellinae
16. *Cosmetus peruvicus* (AVRAM & SOARES, 1983) - Cosmetidae
17. *Crosbyella roraima* GOODNIGHT & GOODNIGHT, 1943 - Zalmoxidae
18. *Cynorta albanalis* ROEWER, 1947 - Cosmetidae
19. *Cynorta albiadspersa* ROEWER, 1927 - Cosmetidae
20. *Cynorta albicurvata* ROEWER, 1947 - Cosmetidae
21. *Cynorta albipicta* ROEWER, 1947 - Cosmetidae
22. *Cynorta bassleri* GOODNIGHT & GOODNIGHT, 1943 - Cosmetidae
23. *Cynorta bordoni* AVRAM & SOARES, 1983 - Cosmetidae
24. *Cynorta cancellata* ROEWER, 1947 - Cosmetidae
25. *Cynorta clavipus* ROEWER, 1927 - Cosmetidae
26. *Cynorta conspersa* (PERTY, 1833) - Cosmetidae
27. *Cynorta coxaepunctata* ROEWER, 1947 - Cosmetidae
28. *Cynorta dearuwa* GONZÁLEZ-SPONGA, 1992 - Cosmetidae
29. *Cynorta insperata* H. SOARES, 1970 - Cosmetidae
30. *Cynorta itacoaiensis* H. SOARES, 1970 - Cosmetidae
31. *Cynorta juruensis* (MELLO-LEITÃO, 1923) - Cosmetidae
32. *Cynorta litterata* H. SOARES, 1970 - Cosmetidae
33. *Cynorta mayi* MELLO-LEITÃO, 1931 - Cosmetidae
34. *Cynorta mira* H. SOARES, 1970 - Cosmetidae
35. *Cynorta notabilis* H. SOARES, 1970 - Cosmetidae
36. *Cynorta propria* ROEWER, 1947 – Cosmetidae (Manaus)
37. *Cynorta ramulata* ROEWER, 1947 - Cosmetidae
38. *Cynorta scripta* SIMON, 1879 – Cosmetidae (Manaus)
39. *Cynorta thoraxpicta* ROEWER, 1957 - Cosmetidae
40. *Cynorta variegata* ROEWER, 1947 - Cosmetidae
41. *Cynorta vestita* ROEWER, 1912 – Cosmetidae (Manaus)
42. *Cynorta zonata* ROEWER, 1947 – Cosmetidae (Manaus)
43. *Cynortellana peruviana* ROEWER, 1963 - Cosmetidae
44. *Cynortopyga h-album* ROEWER, 1947 – Cosmetidae (Manaus)
45. *Cynortula alejandra* ROEWER, 1957 - Cosmetidae
46. *Cynortula figurata* ROEWER, 1957 - Cosmetidae
47. *Digalistes signata* ROEWER, 1932 – Cranidae, Cranainae
48. *Discosomaticus cinctus* (PERTY, 1833) - Cosmetidae
49. *Discosomaticus distinctus* AVRAM & SOARES, 1983 - Cosmetidae
50. *Ethobunus brasiliensis* (MELLO-LEITÃO, 1941) - Zalmoxidae
51. *Eucynorta amazonica* PIZA, 1938 - Cosmetidae
52. *Eucynortella duapunctata* GOODNIGHT & GOODNIGHT, 1943 - Cosmetidae
53. *Eucynortella pauper* PIZA, 1938 - Cosmetidae
54. *Eucynortula lata* (BANKS, 1909) – Cosmetidae (D, G)
55. *Eucynortula pentapunctata* ROEWER, 1947 – Cosmetidae (Manaus)
56. *Eupoecilaema perducens* ROEWER, 1947 - Cosmetidae
57. *Eupoecilaema quadrioctale* ROEWER, 1947 – Cosmetidae (Manaus)
58. *Eutimesius simoni* ROEWER, 1913 – Stygnidae, Heterostygninae
59. *Flirtea picta* (PERTY, 1833) - Cosmetidae
60. *Geaya aenescens* ROEWER, 1953 – Sclerosomatidae, Gagrellinae
61. *Geaya atrolutea* ROEWER, 1910 – Sclerosomatidae, Gagrellinae
62. *Geaya aureolucens* ROEWER, 1910 – Sclerosomatidae, Gagrellinae (Manaus)
63. *Geaya bicornuta* MELLO-LEITÃO, 1939 – Sclerosomatidae, Gagrellinae
64. *Geaya centralis* ROEWER, 1953 – Sclerosomatidae, Gagrellinae (Manaus)
65. *Geaya crucicolorata* ROEWER, 1953 – Sclerosomatidae, Gagrellinae
66. *Geaya goodnighti* ROEWER, 1953 – Sclerosomatidae, Gagrellinae (Manaus)

67. *Geaya inermis* MELLO-LEITÃO, 1939 – Sclerosomatidae, Gagrellinae
68. *Geaya marginata* ROEWER, 1953 – Sclerosomatidae, Gagrellinae
69. *Geaya nigricoxa* ROEWER, 1910 – Sclerosomatidae, Gagrellinae
70. *Geaya tibialis* ROEWER, 1953 – Sclerosomatidae, Gagrellinae (Manaus)
71. *Geaya variegata* MELLO-LEITÃO, 1939 – Sclerosomatidae, Gagrellinae
72. *Gryne amazonica* ROEWER, 1947 – Cosmetidae (Manaus)
73. *Gryne leprosa* SØRENSEN, 1932 - Cosmetidae
74. *Gryne marginalis* (PERTY, 1833) - Cosmetidae
75. *Gryne orensis* (SØRENSEN, 1879) - Cosmetidae
76. *Gryne pustulata* ROEWER, 1927 – Cosmetidae (Manaus)
77. *Holcobunus tocaninus* ROEWER, 1953 – Sclerosomatidae, Gagrellinae
78. *Holcobunus trochanteralis* ROEWER, 1953 – Sclerosomatidae, Gagrellinae
79. *Huralxiooides hoeferi* KURY, 1995 – Gonyleptidae, Pachylinae (D)
80. *Huralxiooides paruensis* H. SOARES, 1970 – Gonyleptidae, Pachylinae
81. *Hutamaia caramaschii* SOARES & SOARES, 1977 – Gonyleptidae, undescribed subfamily
82. *Itequahy ensiferus* MELLO-LEITÃO, 1949 – Gonyleptidae, undescribed subfamily
83. *Krusa amazonica* ROEWER, 1953 – Sclerosomatidae, Gagrellinae (Manaus)
84. *Ladantola aspersa* ROEWER, 1932 – Cranidae, Cranainae
85. *Manaosbia scopulata* ROEWER, 1943 – Manaosbiidae (Manaus)
86. *Mecritta filipes* ROEWER, 1932 – Cranidae, Cranainae
87. *Metacynorta bimaculata* ROEWER, 1947 - Cosmetidae
88. *Metabitia fuscomaculata* H. SOARES, 1970 - Cosmetidae
89. *Metaogoea oviformis* MARTENS, 1969 – Neogoveidae (G)
90. *Metarhaucus ohausi* (ROEWER, 1912) - Cosmetidae
91. *Micrisaeus gracillimus* ROEWER, 1957 - Laniatores – family uncertain
92. *Minax tetraspinosus* PINTO-DA-ROCHA, 1997 – Stygnidae, Heterostygninae
93. *Neocynorta m-inscripta* MELLO-LEITÃO, 1939 - Cosmetidae
94. *Neogoea inmsi* HINTON, 1938 - Neogoveidae
95. *Neogoea microphaga* (MARTENS, 1969) – Neogoveidae (D)
96. *Ostracidium fuscum* PERTY, 1833 – Cranidae, Prostygninae
97. *Paecilaema amazonica* GONZÁLEZ-SPONGA, 1992 - Cosmetidae
98. *Paecilaema argentinoides* H. SOARES, 1970 - Cosmetidae
99. *Paecilaema carvalhoi* H. SOARES, 1970 - Cosmetidae
100. *Paecilaema graphicum* ROEWER, 1947 - Cosmetidae
101. *Paecilaema guttigerum* SØRENSEN, 1932 - Cosmetidae
102. *Paecilaema leucomelas* SIMON, 1880 - Cosmetidae
103. *Paecilaema limbatum* KOLLAR, in KOCH 1839 - Cosmetidae
104. *Paecilaema lobipictum* ROEWER, 1947 – Cosmetidae (Manaus)
105. *Paecilaema manifestum* ROEWER, 1927 – Cosmetidae (Manaus)
106. *Paecilaema marajoara* H. SOARES, 1970 - Cosmetidae
107. *Paecilaema paraense* H. SOARES, 1970 - Cosmetidae
108. *Paecilaema sigillatum* ROEWER, 1912 - Cosmetidae
109. *Paecilaema triseriatum* ROEWER, 1947 - Cosmetidae
110. *Paecilaema vittatum* (SØRENSEN, 1932) - Cosmetidae
111. *Paecilaema withi* HENRIKSEN, 1932 - Cosmetidae
112. *Parahuederwaldtia caramaschii* SOARES & SOARES, 1979 – Gonyleptidae, Pachylinae (Manaus)
113. *Paramicrocraneus difficilis* H. SOARES, 1970 - Manaosbiidae
114. *Paraphareus tatei* GOODNIGHT & GOODNIGHT, 1943 – Stygnidae, Stygninae
115. *Paraprotus quadripunctatus* ROEWER, 1947 – Cosmetidae (Manaus)
116. *Parkocraneus bimaculatus* MELLO-LEITÃO, 1949 – Cranidae, Cranainae (G)
117. *Paruleptes coronatus* H. SOARES, 1970 – Sclerosomatidae, Gagrellinae
118. *Pebasia singularis* ROEWER, 1947 - Cosmetidae
119. *Phalangodus poecilus* (ROEWER, 1943) – Cranidae, Cranainae
120. *Phareicraneus albigratus* ROEWER, 1932 – Cranidae, Cranainae

121. *Planophareus pallidus* GOODNIGHT & GOODNIGHT, 1943 – Stygnidae, Stygninae
122. *Poecilaemula peruviana* ROEWER, 1947 - Cosmetidae
123. *Prionostemma aureomaculatum* H. SOARES, 1970 – Sclerosomatidae, Gagrellinae
124. *Prionostemma aureum* ROEWER, 1928 – Sclerosomatidae, Gagrellinae
125. *Prionostemma bidens* ROEWER, 1953 – Sclerosomatidae, Gagrellinae (Manaus)
126. *Prionostemma fulvibrunneum* ROEWER, 1928 – Sclerosomatidae, Gagrellinae
127. *Prionostemma magnificum* ROEWER, 1953 – Sclerosomatidae, Gagrellinae (Manaus)
128. *Prionostemma richteri* ROEWER, 1953 – Sclerosomatidae, Gagrellinae (Manaus)
129. *Prionostemma transversale* ROEWER, 1953 – Sclerosomatidae, Gagrellinae (Manaus)
130. *Protimesius albilineatus* (ROEWER, 1957) – Stygnidae, Stygninae
131. *Protimesius amplichelis* (ROEWER, 1931) – Stygnidae, Stygninae
132. *Protimesius coxalis* (ROEWER, 1931) – Stygnidae, Stygninae
133. *Protimesius evelinae* (SOARES & SOARES, 1978) – Stygnidae, Stygninae
134. *Protimesius gracilis* ROEWER, 1913 – Stygnidae, Stygninae
135. *Protimesius laevis* (SØRENSEN, 1932) – Stygnidae, Stygninae
136. *Protimesius longipalpis* (ROEWER, 1943) – Stygnidae, Stygninae (G)
137. *Protimesius palpalis* (ROEWER, 1931) – Stygnidae, Stygninae
138. *Protimesius trocaraincola* PINTO-DA-ROCHA, 1997 – Stygnidae, Stygninae
139. *Protus insolens* SIMON, 1879 - Cosmetidae
140. *Pucallpana pullex* AVRAM & SOARES, 1983 – Laniatores – family uncertain
141. *Rhopalocranaus apiculatus* ROEWER, 1932 - Manaosbiidae
142. *Rhopalocranaus aspersus* ROEWER, 1932 - Manaosbiidae
143. *Rhopalocranaus crulsi* MELLO-LEITÃO, 1932 - Manaosbiidae
144. *Rhopalocranaus marginatus* ROEWER, 1913 - Manaosbiidae
145. *Romerella punctata* GOODNIGHT & GOODNIGHT, 1943 – Sclerosomatidae, Gagrellinae
146. *Roquettea singularis* MELLO-LEITÃO, 1931 - Cosmetidae
147. *Santinezia manauara* PINTO-DA-ROCHA, 1994 – Cranidae, Cranainae
148. *Santinezia singularis* (H. SOARES, 1970) – Cranidae, Cranainae
149. *Saramacia annulata* (MELLO-LEITÃO, 1931) - Manaosbiidae
150. *Saramacia lucasae* (JIM & SOARES, 1991) - Manaosbiidae
151. *Sibollus margaritatus* ROEWER, 1929 – Gonyleptidae, undescribed subfamily
152. *Sickesia usta* (MELLO-LEITÃO, 1941) – Stygnidae, Stygninae
153. *Stenophareus roraimus* GOODNIGHT & GOODNIGHT, 1943 – Stygnidae, Stygninae
154. *Stenostygnus pusio* SIMON, 1879 - Biantidae
155. *Stygnus armatus* PERTY, 1833 – Stygnidae, Stygninae (?Manaus)
156. *Stygnus heliae* PINTO-DA-ROCHA, 1997 – Stygnidae, Stygninae
157. *Stygnus klugi* (GOODNIGHT & GOODNIGHT, 1943) – Stygnidae, Stygninae
158. *Stygnus lesserti* (ROEWER, 1943) – Stygnidae, Stygninae
159. *Stygnus luteus* (MELLO-LEITÃO, 1931) – Stygnidae, Stygninae
160. *Stygnus pectinipes* (ROEWER, 1943) – Stygnidae, Stygninae (D, F, G)
161. *Stygnus peruvianus* (ROEWER, 1957) – Stygnidae, Stygninae
162. *Stygnus simonis* (SØRENSEN, 1932) – Stygnidae, Stygninae
163. *Stygnus simplex* (ROEWER, 1913) – Stygnidae, Stygninae
164. *Stygnus tocantinensis* PINTO-DA-ROCHA, 1997 – Stygnidae, Stygninae
165. *Syncranaus cribrum* ROEWER, 1913 - Manaosbiidae
166. *Taperina nigripes* ROEWER, 1953 – Sclerosomatidae, Gagrellinae
167. *Tegyra cinnamomea* SØRENSEN, 1932 - Manaosbiidae
168. *Trinella bicoloripes* (ROEWER, 1949) – Agoristenidae, Leiosteninae
169. *Trinella glabrata* (GONZÁLEZ-SPONGA, 1998) – Agoristenidae, Leiosteninae
170. *Trinella matintaperera* PINTO-DA-ROCHA, 1996 – Agoristenidae, Leiosteninae (G)
171. *Trinella soaresorum* PINTO-DA-ROCHA, 1996 – Agoristenidae, Leiosteninae
172. *Verrucastygnus caliginosus* (PINTO-DA-ROCHA, 1990) – Stygnidae, Stygninae
173. *Yapacana tibialis* PINTO-DA-ROCHA, 1997 – Stygnidae, Stygninae