

- **Genitalia:** Penis (Figures 4.19f,g) relatively short (about one-fourth to one-third of body length, maximally less than half), shaft stout, in general evenly narrowing from base, containing two muscles with short tendons. Glans simple, more or less asymmetrical, slightly movable; stylus not clearly distinct from glans. Ovipositor (Figure 4.19h) moderately short, corpus unsegmented, covered with setae elevated on conical protuberances containing gland sacs, furca with two segments.
- **Color:** Sclerotized parts brown to blackish, surface covered by soil incrustation. Overall coloration therefore influenced by substrate type.
- **Sexual dimorphism:** Only minor differences in dimensions. No pheromone glands on male chelicerae or pedipalps (Figures 4.19d,e).
- **Juvenile stages:** Differ much from adults: cuticle less sclerotized with paler coloration, lacking characteristic adult sculpture elements; the hood develops gradually; it does not totally hide the pedipalps at first, which are still visible on the outside.

**Distribution:** Western Palaearctic (Europe without northern and eastern regions, Mediterranean area with western North Africa and the Levant, in Southwest Asia to the Caucasus and northern Iran); *Trogulus tricarinatus* introduced in eastern North America.

**Relationships:** Though very different in external appearance from other phalangids, Trogulidae were placed, together with Dicranolasmatidae, Nipponopsalididae, and Nemastomatidae, in the superfamily Troguloidea, mainly on account of genital morphology and sternal structure (Martens, 1976). The relation to Dicranolasmatidae is somewhat controversial but supported in some molecular analyses (Giribet et al., 2002).

**Main references:**

- **Systematics:** Martens (1978b), Martens & Chemini (1988).
- **Natural history:** Pabst (1953), Martens (1978b).

## LANIATORES

### Historical systematic synopsis

Adriano B. Kury

Major changes in the systematics of Laniatores have been proposed by a great number of authors, writing in a diverse set of languages, including Latin, German, English, Portuguese, Spanish, and Italian, over a span of 170 years. Most family names were created in the nineteenth century, while a surge of activity can be detected at the end of the twentieth. The arrangement of families in larger groups is not yet stable.

In the late, eighteenth century, when the systematic study of Opiliones was mostly restricted to European researchers, the single genus *Phalangium* was recognized, being enough for the immediate post-Linnean scheme. Latreille (1802a) recognized the family Phalangides, which was in essence identical to the order Opiliones of today, but which was later equated only to the family Phalangiidae (Crawford, 1992). Kirby (1818) was the first to recognize the group Laniatores, erecting the new genus *Gonyleptes*, based on Brazilian material. Sundevall (1833) organized the five known genera and recognized three of the four current suborders of Opiliones in the following classification, which included an unjustified emendation for the genus name *Gonyleptes*:

Ordo Opiliones

Fam. 1. **Gonoleptides** new [= Laniatores]; genera *Gonoleptes* and **Mitobates** new.

Fam. 2. Phalangides [= Eupnoi]; genus *Phalangium*.

Fam. 3. **Trogulides** new [= Dyspnoi]; genera *Trogulus* and *Caeculus*.

Perty (1833), who focused on the Brazilian fauna, discovered many new Laniatores, erected six new genera, and offered a systematic arrangement with two divisions in which Cosmetidae were surprisingly grouped together with his concept of *Phalangium*, which corresponds to the present-day Eupnoi + Dyspnoi. Perty's classification was as follows:

Familia Trachearia Phalangida—Divisio Phalangiorum

Divisio Ima.

1. *Gonyleptes*
2. **Ostracidium** new
3. **Goniosoma** new
4. **Stygnus** new
5. **Eusarcus** new

Divisio IIda.

6. **Cosmetus** new
7. **Discosoma** new
8. *Phalangium*

Hope (1837) described a new genus "intermediate between *Gonyleptes* and *Phalangium*." The genus in question was later discovered to be a synonym of *Mitobates*, a gonyleptid with very long legs, rectangular body, and armature of femora/tibiae absent.

Thorell (1876b) proposed a major classification, organizing the order Opiliones into two suborders, which merged Cyphophthalmi with Palpatores. Laniatores were divided into two families, one including the European and American genera and the other the Australasian ones.

## Ordo Opiliones

Sectio I. **Palpatores** new

Fam. Phalangioidae

Fam. Nemastomidae

Subfam. Nemastomatini

Subfam. Trogulini

Fam. Cyphophthalmidae

Sectio II. **Laniatores** new

Fam. Gonyleptoidea

Fam. Cosmetidae

That same year Thorell (1876a) reported the first Southeast Asian Laniatores for both of his families and created Oncopodidae as a subfamily of Cosmetidae. His classification of the Laniatores was as follows:

## Sectio Laniatores

Fam. Gonyleptoidea

Fam. Cosmetidae

[Fam. Cosmetinae]

Fam. **Oncopodinae** new

Simon (1879b) erected some new genera of Laniatores (for which he coined the term Mecostethi), mainly from South America. Important changes are the restriction of Cosmetidae to its present sense, explicitly excluding *Oncopus*, which was transferred to the newly created Phalangodidae, already in the sense later used by Roewer and followers. Another important change was the organization of Gonyleptidae into subfamilies. The planned part of his work including Coelopyginae/Caelopyginae never saw the light, and the name appeared only casually lost amid the text, making all subsequent authors (including Kury, 2003) assign this subfamily to Sørensen. His classification follows:

Sub-Ordo Opiliones **Mecostethi** new1. Familia—**Phalangodidae** new

2. Familia—Cosmetidae

3. Familia—Gonyleptidae

1. Sub-familia—**Stygninae** new2. Sub-familia—**Mitobatinae** new3. Sub-familia—**Coelopyginae** new

4. Sub-familia—Gonyleptinae

Karsch (1880) described the genus *Adaeum* (a triaenonychid) from South Africa and considered it to be an intermediate between the families Cosmetidae and Gonyleptidae.

Sørensen (1884) presented results of the study of diverse material, mainly from South America. He created several new families that were later mostly downgraded to subfamilies of Gonyleptidae. His classification of the Laniatores is as follows:

Subordo II: Laniatores

- I. Phalangodidae
- II. Cosmetoidae
- III. **Assamioidae** new
- IV. **Hernandaroidae** new
- V. Gonyleptoidae
- VI. **Coelopygoidae** "new" (in parallel with Simon)
- VII. Pachyloidae new

Following this classification, Sørensen (1886), in a book chapter dealing with Australasian fauna, presented important modifications by establishing new genera and as many as five of the currently accepted families. Interestingly, he recognized the affinity between his Dampetroidae from Australia and his own Assamioidae (described two years earlier) from India but failed to translate this into a classification. His classification (which was quickly adopted by Thorell) is as follows:

Ordo Opiliones

Subordo I. Palpatores

Phalangioidae

Subordo II. Laniatores

**Triaenonychoidae** new

Phalangodidae

**Zalmoxioidae** new

**Epedanoidae** new

Samoidae new

**Dampetroidae** new

Gonyleptoidae

Thorell (1889) created the family Biantoidae and later elevated Oncopodidae to family rank (Thorell, 1891). This change appeared in some of his works published in the 1890s and was promptly adopted by subsequent authors.

Loman (1900, 1902) created the new suborder Insidiatores to include only Triaenonychidae. Epedanidae still included many unrelated genera today placed in various families. The classification he presented is as follows:

Opiliones

Sub-ordo Laniatores

Fam. Oncopodidae

Fam. Cosmetidae

- Fam. Gonyleptidae
- Fam. Assamiidae
- Fam. Epedanidae
- Fam. Biantidae
- Sub-orde **Insidiatores** new
- Fam. Triaenonychidae
- Sub-orde Palpatores
- Fam. Phalangiidae
- Subfam. Phalangiini
- Subfam. Gagrellini

Pocock (1902b) criticized the Insidiatores of Loman, not in concept, but rather in degree, stating that there should be a group including Insidiatores + Laniatores. Within the same spirit of symmetry, he split the young family Triaenonychidae into three different ones, so that Insidiatores would have more than one family, namely, Adaeidae, Triaenobunidae, and Triaenonychidae. Pocock (1902a) created the superfluous family name Hinzuaniidae to replace Biantidae on the basis of the fact that the generic name *Hinzuanius* predated *Biantes* by five years. The International Commission on Zoological Nomenclature (ICZN) (1999) states that any generic name may be chosen as the type of a family, not necessarily the oldest.

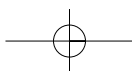
Loman (1903a), in view of the criticism of Insidiatores by Pocock, hastened to explain his views in more detail. His system recognized Dyspnoi (a mix of current members of Eupnoi and Dyspnoi) and was the first to claim a position for Oncopodidae within the group known today as Grassatores (the same hypothesis defended by Martens, 1980). His classification follows:

- Suborder I. Palpatores
- Suborder II. Laniatores
  - a. **Sterrhonoti** new (fam. Oncopodidae)
  - b. **Camptonoti** new (fam. Gonyleptidae, Epedanidae, Assamiidae)
- Suborder III. Insidiatores
- Suborder IV. (?) Cyphophthalmi (= Anepignathi of Thorell)

Roewer (1912b) promoted many changes in Assamiidae and Phalangodidae, such as creating many subfamilies, uniting the Australian Dampetridae with the African/Indian Assamiidae, and merging Zalmoxidae into Phalangodidae. He later summarized the taxonomy of the order Opiliones in a large volume (Roewer, 1923), complemented by a long series of addenda until the 1950s. His classification was immensely influential and persisted for many decades in spite of its numerous flaws. Many of the families of the former authors were downgraded to subfamilies:

1. Suborder Cyphophthalmi
2. Suborder Laniatores

1. Family Oncopodidae
2. Family Phalangodidae
  1. Subfam. Samoinae
  2. Subfam. Phalangodinae
  3. Subfam. Tricommatinae
  4. Subfam. Biantinae
  5. Subfam. **Stygnommatinae** new
  6. Subfam. Ibaloniinae
  7. Subfam. Podoctinae
  8. Subfam. Erecananinae
  9. Subfam. Acrobuninae
  10. Subfam. Sarasinicinae
  11. Subfam. Epedaninae
  12. Subfam. Dibuninae
3. Family Assamiidae
  1. Subfam. Trionyxellinae
  2. Subfam. Dampetrinae
  3. Subfam. Assamiinae
4. Family Cosmetidae
  1. Subfam. Cosmetinae
  2. Subfam. Discosomaticinae
5. Family Gonyleptidae
  1. Subfam. Pachylinae
  2. Subfam. Prostygninae
  3. Subfam. Phareinae
  4. Subfam. Stenostygninae
  5. Subfam. Gonyleptinae
  6. Subfam. Mitobatinae
  7. Subfam. Caelopyginae
  8. Subfam. Cranaina
  9. Subfam. Heterocranaina
  10. Subfam. Stygnocranaina [sic]
  11. Subfam. Stygninae
  12. Subfam. Heterostygninae
  13. Subfam. Hernandariinae
6. Family Triaenonychidae
  1. Subfam. Triaenonychinae
  2. Subfam. Adaeinae



3. Subfam. Triaenobuninae
3. Suborder Palpatores
  1. Tribe Dyspnoi
  2. Tribe Eupnoi

Sørensen, in an assembly of unpublished notes, published only posthumously by Henriksen sixteen years after his death (Sørensen, 1932), proceeded with the trend to create many smaller families, strongly contrasting with the then-widespread system by Roewer, which treated most of them as subfamilies. Henriksen tried hard to align Sørensen's system with Roewer's, even inserting the new families in Roewer's classification. The Sørensen/Henriksen scheme is as follows:

Opiliones Laniatores

Superfamilia Gonyleptoidea

- Familia Hernandariidae
- Familia Gonyleptidae
- Familia Stygnidae

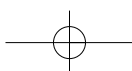
Superfamilia Phalangodoidea

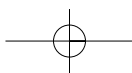
- Familia Acrobunidae
- Familia Dibunidae
- Familia Epedanidae
- Familia Erecananidae
- Familia Ibaloniidae
- Familia **Minuidae** new
- Familia Phalangodidae
- Familia Podoctidae
- Familia Samoidae
- Familia Saracinicidae [*sic*]
- Familia Stygnommatidae
- Familia **Stygnopsidae** new
- Familia Tricommatidae

Not arranged in superfamilies

- Familia Assamiidae
- Familia Cosmetidae
- Familia Oncopodidae
- Familia Triaenonychidae

Absolon and Kratochvíl (1932a,b,c) created the family Travuniidae, of interest mostly to speleologists. Hadži (1935) created Cladonychiinae as a new subfamily of Triaenonychidae, which passed unnoticed until being resurrected by Cokendolpher (1985b). Mello-Leitão (1933a, 1938) reviewed Sørensen's (1932) Phalangodoidea





(= Roewer's Phalangodidae), adding important changes and breaking the large Phalangodidae into three separate families: Biantidae, Podoctidae, and Phalangodidae. He merged Sørensen's Minuidae and Stygnopsidae into Phalangodidae and created the new subfamilies Isaeinae and Minuidinae within Phalangodidae. Mello-Leitão's classification is as follows:

Laniatores

Assamiidae

**Biantidae** new

Biantinae

Stygnommatinae

Dibuninae

Cosmetidae

Gonyleptidae

Oncopodidae

Phalangodidae

Acrobuninae

Epedaninae

**Isaeinae** new

**Minuidinae** new

Minuinae

Phalangodinae

Sarasinicinae

Stygnopsinae

Tricommatinae

**Podoctidae** new

Erecananinae

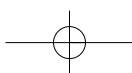
Ibaloniinae

Podoctinae

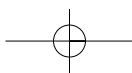
Stygnidae

Triaenonychidae

Roewer (1943) provided a synoptic table for the classification of Gonyleptidae, contributing a few new subfamilies and summarizing all his and Mello-Leitão's contributions to that family in the 1920s and 1930s. Mello-Leitão (1949), in his last article, provided a new general arrangement of Laniatores and explained at length his criteria of diagnosis. Phalangodidae was kept exactly as in his 1938 article. He recognized Travuniidae, absent from virtually all 1940s literature, separated Assamiidae with tarsal processes in a new family, Trionyxellidae, elevated the rank of Stygnommatinae (then in Biantidae) to family, and described a new subfamily of Gonyleptidae (Dasypoleptinae). In a review of Laniatores from New Zealand, Forster







(1954) described many new genera and created a very influential system for Triaenonychidae, separating the egg-guarding species from the non-egg-guarding as two subfamilies and downgrading Pocock's families to tribes. He also created the new family Synthetonychiidae, which he regarded as closely related to Triaenonychidae.

Kratochvíl (1958a), on the basis of posterior tarsal claw structure, proposed two superfamilies of Laniatores, **Oncopodoidea** and Travunoidea [*sic*], retrieving the system of Loman (1902) and Pocock (1902b) defended years later by Martens. He ignored the subdivisions proposed by Mello-Leitão (1938, 1949) and created the new family **Paralolidae** and another subfamily of Phalangodidae, **Lolinae**.

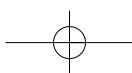
Lawrence (1959), while dealing with Biantidae from Madagascar, created Lacurbsinae, a name buried amid the text and forgotten by most subsequent authors. Šilhavý (1961), contradicting Kratochvíl (1958a), placed Oncopodidae in the suborder Oncopodomorphi as the sister group to all other Laniatores (= Gonyleptomorphi), which remained unchanged.

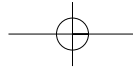
Later Šilhavý (1973), on the basis of material from the Antillean region and Trinidad, described Agoristenidae and Caribbiantinae (in Biantidae) and recognized the classification of Mello-Leitão (1938, 1949). Šilhavý (1974) recognized Stygnopsidae after some dubious inclusions and exclusions of its genera in Phalangodinae or Phalangodidae Stygnopsinae (e.g., Goodnight & Goodnight, 1944, 1946). Travunoidea were more intensely investigated in the 1970s; Briggs (1969) created the family Erebomastriidae and later (Briggs, 1971a,b) reviewed most North American species of Triaenonychidae and proposed a new subfamily. Suzuki (1975b, 1976e) followed Briggs and also proposed two new subfamilies of Japanese/Korean Triaenonychidae. Both Briggs (1974a) and Suzuki (1976d) devised a phylogenetic scheme based on the number of lateral prongs of the tarsal claws of adults and juveniles. Dumitrescu (1976), on the basis of his studies of the midgut diverticules, proposed a subfamily of Triaenonychidae ignored by all other authors.

Martens's (1980) nonnumerical cladistic analysis combined the Loman-Kratochvíl concept of Insidiatores versus Laniatores *sensu stricto* with the Sterrhonoti versus Camptonoti of Loman (1903a). Soares and Soares (1984) revalidated Hernandariinae and later (1985) described Progonyleptoidellinae and Sodreaninae, all considered subfamilies of Gonyleptidae. Kauri (1985) focused on the Laniatores of central Africa and placed Dibuninae and Stygnommatinae among Biantidae, together with his new subfamily Zairebiantinae.

South America provided some new families of small, soil-dwelling Laniatores, all described within the last 20 years. Martens (1988) created Fissiphalliidae on the basis of Colombian material. González-Sponga (1997) erected Guasiniidae from Venezuela. Kury and Pérez G. (2002) described Icaleptidae on the basis of material from Ecuador and Colombia.

The 1990s and the twenty-first century saw many rearrangements in the established groups, partly due to the use of numerical cladistic analyses. Kury (1992a) removed Tricommatinae from Phalangodidae, an arrangement unquestioned for 80 years, and upgraded it to family level. Kury (1994a,b) studied the basal branches of





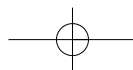
Gonyleptidae, described Cobaniinae, Metasarcinae, and Heteropachylinae within Gonyleptidae, and transferred Cranainae, Heterocranainae, Prostyginae, and Stygnicranainae to Cranidae. Pinto-da-Rocha (1995a) proposed the identity of Šilhavý's Caribbiantinae with Roewer's Stenostyginae. Kury (1997a) removed Manaosbiinae from Gonyleptidae, created the family Manaosbiidae, and transferred to it 26 genera that were previously in Gonyleptidae or Cranidae. In a cladistic analysis of Agoristenidae, Kury (1997b) described Zamorinae and synonymized Angelinae with Leiosteninae. Pinto-da-Rocha (2002) synonymized Dasypoleptinae with Caelopyginae. Kury (2002) offered evidence that the non-Grassatores Laniatores are a diphyletic group, but this has not yet been organized and properly documented for publication.

Kury (2003) published an annotated catalogue of the New World Laniatores, which contained the characterization of the new family Escadabiidae and Ampycinae, a new subfamily of Gonyleptidae. In this catalogue there is also a table with a classification of Laniatores as viewed by the author based on either published or unpublished data. Changes to the system include a definition of the family Epedanidae containing four subfamilies formerly in Phalangodidae and a formalization of Grassatores—recovering the concept of Loman (1903a) of Insidiatores versus Laniatores *sensu stricto*.

**Key to the families of Laniatores**

Ricardo Pinto-da-Rocha

- 1. Ocularium separated into two parts (Figure 4.22c) or absent (Figure 4.42a). . . . . 2
  - . Ocularium unique or with eminence between eyes. . . . . 9
- 2. Ocularium and eyes absent (except most troglobites). . . . . 3
  - . Ocularium and eyes present (Figure 4.22i). . . . . 5
- 3. Pedipalps without ventral setae on sockets or both much shorter than pedipalp length (Figure 4.27g); claws III–IV single or very branched on a stem (Figures 4.41e–g). . . . . 4
  - . Pedipalps with ventral setae on large sockets (longer than pedipalp length, Figure 4.42i); two single claws on legs III–IV. . . . . **Travuniidae**
- 4. Claws III–IV single. . . . . **Guasiniidae**
  - . Claws III–IV branched (Figures 4.41e–g). . . . . **Synthetonychiidae**
- 5. Male basichelecerite elongated, segment II with spines or conspicuous tubercles (Figure 4.39b); body outline pyriform to hourglass in dorsal view (Figure 4.38b). . . . . 6
  - . Male basichelecerite not elongated, segment II smooth or granulated; body outline rectangular-subrectangular in dorsal view (Figure 4.38d). . . . . 7
- 6. Dorsal surface covered with low tubercles; leg I small-tuberculate; pedipalp with moderate setae with low sockets on tibia-tarsus; without spine between eyes (Figures 4.39a,b). . . . . **Stygnommatidae**



S-  
O-  
1-