Opiliones are no longer the same—on suprafamilial groups in harvestmen (Arthropoda: Arachnida)

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Abstract

A review of the names used in the arachnid order Opiliones above superfamily level is presented. Many historical branching patterns of Opiliones (for five terminals), of Laniatores (for six terminals), and of Cyphophthalmi (for six terminals) are extrapolated, compared and graphically displayed. For the first time a historical review is made of the circumscriptions of those names and comparisons are drawn to current usage. Critical clades are used as terminals and represented by the oldest valid generic name of each. Comments are made on the variant usage for 25 suprafamilial names from the literature. Cladistic definitions are provided for these names under relevant hypotheses of phylogeny. It is noted that virtually all important suprafamilial names in Opiliones changed concept over time, and the purpose of this project is to clarify the original usage compared to current, and to add historical perspective. Two options are considered for higher-level nomenclature in Opiliones: (1) a circumscriptional option, sticking to the original inclusion of the names; (2) an inertial option, where no name has priority, and follows recent use in the literature. As there is no priority for names not regulated by ICZN, option 2 prevails, because it entails massive momentum. The following new names are introduced as unranked taxa to define clades under different hypotheses of phylogeny: Tricospilata (= Triaenonychidae + Grassatores), Lomaniatores (Laniatores in the restricted sense used by Loman/Pocock), and Eulaniatores (Laniatores excluding the bizarre Synthetonychiidae). Some of the hypotheses implied by these names are conflicting and mutually exclusive, but the state of knowledge of harvestman taxonomy is quickly changing, and no hypothesis that clearly supersedes the others can be detected.

Key words: Laniatores, Eupnoi, Dyspnoi, Cyphophthalmi, taxonomy, systematics, nomeclature, typification

Introduction

The names of larger groups in the arachnid order Opiliones have been confused throughout history and used in shifting concepts, including the name Opiliones itself. As the International Code of Zoological Nomenclature (ICZN) does not rule over names above superfamily rank (ICZN, 1999), ordinal and subordinal names are subject to tradition, subjective preference, and inertial usage. The increase in phylogenetic studies on the order is solidifying our knowledge of the relationships of major groups, which inexorably leads to a reevaluation of old classifications and, more than ever, names.

Cladistic hypotheses for subtaxa of Opiliones are starting to pile up. The first non-numeric cladistic morphological analysis of all Opiliones was conducted by Martens (1980) using morphological characters. The first numerical cladistic analysis was done by Shultz (1998) also using abundant morphological information. The first combined published morphological-molecular analysis was conducted by Giribet et al. (1999), and was derived from an analysis in an unpublished thesis (Giribet 1997).

In this paper, a review is presented of the suprafamilial names in Opiliones (meaning all names above superfamily rank), comparing original and current usage. Following the development of this work, the difference between typified and circumscriptional nomenclatures is discussed, and the use of typified names for suprafamilial taxa is discouraged (part 2). Additionally, generic names are used to stand for more inclusive taxa (parts 3 to 4), the hypotheses of relationship among them are shown (part 5), and original circumscription, current usage, and
phylogenetic definitions are provided for them (part 6). Finally, an attempt to propose classifications of the Opiliones is made (part 7).

Typified ordinal names

The Russian zoologist Nikita Kluge proposed a very thorough and interesting system of nomenclatural rules for superfamilial groups of arthropods (Kluge, 2000; 2004) that would be a complement to the ICZN (1999). Kluge’s system admits two basically different nomenclatures, which are based on two different and incompatible principles: one of them is typified and another is circumscriptional. The ICZN (1999) is based on the principle of typified nomenclature and regulates all names of the species-group, the genus-group, and the family-group. The ICZN does not now include rules about taxa that have ranks higher than superfamily. Kluge considers that such names should be used according to the same rules as family-group names. The names that are not formed from the valid generic name + suffix + ending do not fall under rules of ICZN. Kluge suggests applying to them the circumscriptional principle of nomenclature. Circumscriptional zoological nomenclature, as opposed to type-based nomenclature, gives each taxon a unique name, and the name-bearing type is the whole set of taxa listed in the original publication. He concludes that the best practice would be treating all non-typified names, except for ICZN’s genus- and species-group names, as circumscription-based, and keeping rank-based usage only for names having “generally accepted” types (including genus- and species-group names).

The use of a typified name for an order/suborder may bring some confusion as to authorship, because it often is based on the same genus as one of its families. The recognition that the use of a name as a family is confusing when the same is used as an order—so we speak simultaneously of a family Phalangidae Latreille 1802 and an order Phalangida Latreille 1802—but Latreille in 1802 effectively used this name only once, meaning only one thing. In typified nomenclature, one must accept simultaneously at least superfamily Phalangioida Latreille 1802, family Phalangiidae Latreille 1802, subfamily Phalangiinae Latreille 1802, tribe Phalangiini Latreille 1802, subtribe Phalangiina Latreille 1802 and intermediate taxa with the same authorship (see ICZN Article 36). To confuse matters still more, during the 18th century families were not generally in use in the Linnean scheme—genera were subordinated directly to orders. Therefore, varied authors may give different authorships to such a typified superfamilial name. This is the case in the suborder Oniscidea of isopod crustaceans, which includes the family Oniscidae. Carcinologists currently appear to agree (see Schmidt 2002: 276) that suborder Oniscidea is authored by Latreille (1829), while family Oniscidae was authored by Latreille (1802), an admittedly arbitrary decision, although Latreille himself did not seem to recognize any difference. Schmidt’s (2002) decision apparently depends on the recognition of the name “Oniscides” in 1829 as a superfamilial name (“section” under an “order”) as opposed to 1802 when it was explicitly called a family (“famille” under a “sous-classe”). There seems to be an older use of “Oniscoides” as a superfamilial group by Laicharting (1781), which would be the correct authorship to a hypothetical suborder Oniscidea in a typified nomenclature system.

In Table 1 a synopsis is made of early use of the name Phalangida, using the cited instances of Oniscidea as a comparison. The oldest example I could find of the use of an Oniscidea as a comparison. The oldest example I could find of the use of an “order” Phalangida is that of Billberg (1820), who cited a “natio Phalangides”, as opposed to the family Phalangiidae, which dates from Latreille (1802). It is clear from this example that using typified superfamilial names is a poor choice.

Comparing historical hypotheses

In Figs. 1 to 23, an appraisal of the classification schemes and “branching patterns” of harvestmen in the literature is presented. The “branching patterns” as used here are inferred from classification in those hypotheses prior to the recognition by Darwin in 1859 of the theory of descent. Before that time branching diagrams were never used to indicate relationships and relationships themselves were rarely, if ever, recognized since special creation was the dominant theory.

There is a difference between modern statistical phylogeny reconstructions and the “authoritative” reconstructions of the past. A preferred topology is usually an analytically optimal solution that is itself a
probabilistic statement. The disfavored topologies not presented as results also carry support, and it is the responsibility of each author to choose the preferred hypothesis, which thus has publication author and date.

These 23 hypotheses are here interpreted as phylogenetic trees and arranged into three groups: Opiliones (with cladograms drawn in yellow, Figs. 1–11), Laniatores (with cladograms drawn in red, Figs. 12–19) and Cyphophthalmi (with cladograms drawn in green, Figs. 20–23). In each figure, the names in green uppercase accompanying the bars above the icons are the names originally used by authors of the figured hypothesis. The names in blue lowercase and superimposed on the cladograms represent the modern usage names of clades adopted here, even if they were unknown/rejected at the time of the figured hypothesis. In the case in which different blue/green names are given to the same clade, this means that the green name has fallen into disuse (either resulting from workers’ ignoring it, forgetting it or replacing it with a synonym or the falsification of the hypothesis) and has been replaced by a more favored name. In short, the blue names are the names currently used in the literature and which are adopted here, even if they have not kept the original circumscription.

TABLE 1. Usage of the name Phalangida, compared to Oniscidea (see text for details).

<table>
<thead>
<tr>
<th>Reference</th>
<th>original form</th>
<th>parent taxon</th>
<th>children taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Laicharting 1781</td>
<td>ordo Oniscoides</td>
<td>Insecten</td>
<td>1 genus?</td>
</tr>
<tr>
<td>Latreille 1802</td>
<td>FAMILLE SECONDE. Cloportides; oniscides.</td>
<td>SOUS-CLASSE PREMIÈRE. Tetracères; tetracera.</td>
<td>4 genera</td>
</tr>
<tr>
<td>Latreille 1829</td>
<td>sixième section (Cloportides, Oniscides, Lat.)</td>
<td>LE CINQUIÈME ORDRE DES CRUSTACÈS, Les Isopodes. (Isopoda.)</td>
<td>6 genera</td>
</tr>
<tr>
<td>Latreille 1802</td>
<td>FAMILLE TROISIÈME. Phalangiens; phalangita.</td>
<td>SOUS-CLASSE TROISIÈME. ACÈRES; acera. / ORDRE PREMIER. Chelodontes; chelodonta. / SECTION PREMIERE.</td>
<td>4 genera</td>
</tr>
<tr>
<td>Billberg 1820</td>
<td>nation Phalangides</td>
<td>Ordo Arachnoida / tribus Enarthrosoma</td>
<td>1 genus</td>
</tr>
<tr>
<td>MacLeay 1821</td>
<td>Phalangidea</td>
<td>Arachnida</td>
<td>1 genus?</td>
</tr>
<tr>
<td>Say 1821</td>
<td>FAMILY 2. PHALANGIDEÆ.</td>
<td>ORDER 3. DUOMEROSOMATA.</td>
<td>2 genera</td>
</tr>
<tr>
<td>Gerstaeker 1863</td>
<td>Zunft. Phalangita</td>
<td>Classis Arachnoidea / ordo Arthrogastra</td>
<td>1 family</td>
</tr>
<tr>
<td>Wood 1869</td>
<td>Suborder PHALANGIA.</td>
<td>Not cited, but coordinate taxon is Suborder PEDIPALPI.</td>
<td>2 families</td>
</tr>
</tbody>
</table>

To achieve the comparison among such different sources, three criteria were here used:

1) **Reduction to genus names.** All terminal names have been transformed into the correspondent genera. The generic names chosen were the oldest within each clade, and they are summarized in Table 2.

2) **Extrapolation.** Some unavoidable extrapolation must be done to allow comparison among hypotheses of phylogeny from the literature, which use different terminals. For example, the typical triaenonychids are represented by *Equitius* in some hypotheses and by *Adaeum* in others, while here *Equitius* and *Adaeum* are assumed to represent the same concept. This way, the following stand-ins are assumed here: *Equitius* (for *Adaeum*), *Erebomaster* (for *Holoscoletolemon, Peltonychia, Sclerobunus, Zuma*); *Gonyleptes* (for *Pachyloides*), *Phalangodes* (for *Scotolemon*), and *Siro* (for *Cyphophthalmus*).

3) **Simplification.** As some degree of simplification is needed, I decided to strip the hypotheses bare to the most meaningful components. Unnecessary complication would have produced too many trees to compare. Notable taxa left out of my figures are for example Nemastomatidae, which usually, but not always was grouped along with Trogulidae, but in Mello-Leitão (1944) it appears as a paraphylum with Ischyropsalididae. I have not included Acropsopilionidae, which since the beginning was said to combine features of Eupnoi and Dyspnoi, and was in Eupnoi since the 1970s, to be only recently stabilized in Dyspnoi (Groh & Giribet 2014). Also, the morphological analyses of Shultz (1998) and the molecular analysis of Shultz & Regier (2001) have been here combined into a complete single analysis, although the first lacked an equivalent to *Equitius* and the second to *Gnomulus*. 

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By comparing all those hypotheses, one can notice that three basic things change: 1) phylogenetic hypotheses (clades), reflecting different ideas on relationship; 2) names applied to a clade (that would be synonyms in a typified system) and 3) circumscription of a given name (taxa included). The latter surprisingly occurs very often in Opiliones, to the point that almost every major group name has changed circumscription over time.

**TABLE 2.** Reduction of family names to representative generic names. The names are the oldest valid names in each clade (see chapter 4 for details).

<table>
<thead>
<tr>
<th>Figures</th>
<th>Genus used</th>
<th>Represented families</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-2</td>
<td><em>Siro</em> Latreille, 1802</td>
<td>Neogoveidae, Ogoveidae, Pettalidae, Sironidae, Stylocellidae and Troglosironidae</td>
</tr>
<tr>
<td>1-2</td>
<td><em>Phalangium</em> Linnaeus, 1758</td>
<td>Caddidae, Monoscutidae, Neopilionidae, Phalangiidae and Sclerosomatidae</td>
</tr>
<tr>
<td>1-2</td>
<td><em>Ischyropsalis</em> C.L. Koch, 1839</td>
<td>Ceratolasmatidae, Ischyropsalidae and Sabaconidae</td>
</tr>
<tr>
<td>1-2</td>
<td><em>Trogulus</em> Latreille, 1802</td>
<td>Dicranolasmatidae, Nemastomatidae, Nipponopsalididae and Trogulidae</td>
</tr>
<tr>
<td>1-2</td>
<td><em>Gonyleptes</em> Kirby, 1819</td>
<td>All Laniatores (in Figs. 1-2)</td>
</tr>
<tr>
<td>3-4</td>
<td><em>Gonyleptes</em> Kirby, 1819</td>
<td>Agoristenidae, Assamiidae, Biantidae, Cosmetidae, Cranaidae, Epedanidae, Escadabiidae, Fissiphalidiidae, Gonyleptidae, Guasinidae, Icaleptidae, Kimulidae, Manaosbiidae, Podoctidae, Samoidae, Stygnidae, Stygnommatidae, Stygnopsidae, Trionyxxellidae and Zalmoxidae (in Figs. 3-4)</td>
</tr>
<tr>
<td>3-4</td>
<td><em>Erebomaster</em> Cope, 1872</td>
<td>Briggsidae, Cladonychiidae, Nippononychiidae, Paranychiidae (incl. Sclerobuninae) and Travunidae</td>
</tr>
<tr>
<td>3-4</td>
<td><em>Equitius</em> Simon, 1880</td>
<td>Synthetonychiidae and Triaenonychiidae</td>
</tr>
<tr>
<td>3-4</td>
<td><em>Phalangodes</em> Tellkampf 1844</td>
<td>Phalangodidae</td>
</tr>
<tr>
<td>3-4</td>
<td><em>Gnomulus</em> Thorell, 1890</td>
<td>Sandokanida</td>
</tr>
</tbody>
</table>

**Genera that define higher taxa in Opiliones**

Both for typified and non-typified names, the oldest genus-group names are used here to unequivocally refer to more inclusive taxa, as the circumscriptions of groups vary through time and with different authors. See Table 2 for a list of all families represented by each generic name.

CYPHOPHTHALMI, NEOGOVEIDAE: the oldest genus is *Parogovia* Hansen, 1921. OGOVEIDAE: the oldest genus is *Ogovea* Roewer, 1923. PETTALIDAE: the oldest genus is *Pettalus* Thorell, 1876. SIRONIDAE: the oldest genus is *Siro* Latreille, 1802. STYLOCELLIDAE: the oldest genus is *Stylocellus* Westwood, 1874.

EUPNOI: The oldest genus is *Phalangium* Linnaeus, 1758.

CADOIDEA and CADDIDAE: the oldest genus is *Caddo* Banks, 1892. PHALANGIOIDEA: the oldest genus is *Phalangium* Linnaeus, 1758. MONOSCUTIDAE: the oldest genus is *Pantopsalis* Simon, 1879. NEOPILIONIDAE: the oldest genus is *Thrasychirus* Simon, 1884. PHALANGIIDAE: the oldest genus is *Phalangium* Linnaeus, 1758. SCLEROSOMATIDAE: the oldest generic names are *Homalenotus* C.L.Koch, 1839 and *Leiobunum* C.L.Koch, 1839. NIPPONOPSALIDIDAE: the oldest genus is *Nipponopsalis* Martens & Suzuki, 1966.

LANIATORES: the oldest genus is *Gonyleptes* Kirby, 1819.

DYSPNOI: the oldest genus is *Trogulus* Latreille, 1802. ACROPSOPILIONIDAE: the oldest genus is *Acropsopilio* Silvestri, 1904. ISCHYROPALSIDOIDEA / ISCHYROPALSIDIDAE: the oldest genus is *Ischyropsalis* C.L. Koch, 1839. CERATOLASMATIDAE: the oldest genus is *Ceratolasma* Goodnight & Goodnight, 1942. SABACONIDA: the oldest genera are *Sabacon* Simon, 1879 and *Taracuas* Simon, 1879. TROGULOIDEA / TROGULIDAE: the oldest genus is *Trogulus* Latreille, 1802. DICRANOLASMATIDAE: the oldest genus is *Dicranolasma* Sørensen, 1873. NEMASTOMATIDAE: the oldest genus is *Nemastoma* C.L.Koch, 1836. NIPONOPSALIDIDAE: the oldest genus is *Nipponopsalis* Martens & Suzuki, 1966.

LANIATOSES: the oldest genus is *Gonyleptes* Kirby, 1819.

TRAVUNIOIDEA: the oldest genus is *Erebomaster* Cope, 1872 (Cladonychiidae), and for the other families, *Sclerobuninae* Banks, 1893 (Paranychiidae), *Cytopus* Banks, 1905 (Paranychiidae), *Holoscotolemon* Roewer, 1915 (Cladonychiidae), *Travunia* Absolon, 1920 (Travunidae) and *Isolachus* Briggs, 1971 (Briggsidae). CLADONYCHIIDAE: the oldest genus is *Erebomaster* Cope, 1872, originally placed in Gonyleptidae. Simon
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(1879: 149) transferred Erebomaster to Phalangodinae (under synonymy of Phalangodes). Roewer (1923: 107) revalidated Erebomaster, keeping it in Phalangodinae. Hadži (1935) described the genus Cladonychium Hadži 1935 (p. 70) and the subfamily Cladonychiinae of Triaenonychidae (p. 69). Briggs (1969) made Erebomaster the type of family Erebomastridae and synonymized Cladonychium under Erebomaster. Cokendolpher (1985) discovered that Cladonychiidae is senior to Erebomastridae. Until the work of Briggs (1969), the family Cladonychiidae was not recognized, its genera being merged in the Phalangodidae. This affects the definition of many suprafamilial groups, which by definition include or exclude the Phalangodidae. TRAVUNIIDAE: the oldest genus Travunia was unknown until 1920, but we can extrapolate for dates before 1920, knowing that the first species which later would be Travunia—Pentonychia clavigera (Simon, 1879), Pentonychia leprieuri (Lucas, 1860), Pentonychia navarica (Simon, 1879), Pentonychia piochardi (Simon, 1872), Travunia troglodytes (Roewer, 1915)—have been all described under Phalangodes or Scoleoleon Lucas, 1860, a genus consistently included in Phalangodinae, in close proximity to Phalangodes.

TRIAENONYCHOIDEA / TRIAENONYCHIDAE: the oldest generic names are: Equitius Simon, 1880, Adaenium Karsch, 1880, the type genus is younger, Triaeonyx Sørensen, 1886.

ASSAMIOIDEA: the oldest genera are Epedamus Thorell, 1876 and Maracandus Simon, 1879. ASSAMIIIDAe: the oldest genera are Maracandus Simon, 1879 and Dampetrus Karsch, 1880, the type genus is younger, Assamia Sørensen, 1884. EPEDANIDAE: the oldest genus is Epedamus Thorell, 1876.

PYRAMIDOPIDAE: the oldest genera are Conomma Loman, 1902 and Pyramiopodes Loman, 1902.

STYGNOPSIS: the oldest genus is Hoplobunus Banks, 1900, the type genus is younger, Stygnopsis Sørensen, 1902.

PHALANGODOIDEA / PHALANGODIDAE: the oldest genus is Phalangodes Tellkampf 1844. SANDOKANIDAE: the oldest genus is Gnomulus Thorell, 1890. The homonymy of Oncopus Thorell, 1876 with a genus of butterflies and its replacement with Sandokan Özkikmen & Kury, 2007 (thus, making family Sandokanidae) should be kept in mind when perusing the tables below.

GONYLEPTOIDEA: the oldest genus is Gonyleptes Kirby, 1819. AGORISTENIDAe: the oldest genera are Vima Hirst, 1912 and Globibumus Roewer, 1912; the type genus is younger, Agoristenus Šilhavý, 1973. COSMETIDA: the oldest genus is Cosmetus Perty, 1833. CRANAIDAE: the oldest genus is Phalangodus Gervais, 1842; the type genus is younger, Cranopus Simon, 1879. GONYLEPTIDAE: the oldest genus is Gonyleptes Kirby, 1819.

MANOOSBIIDAE: the oldest genus is Cameliamus Roewer, 1912; the type genus is younger, Manaochia Roewer, 1943. STYGNIDAE: the oldest genus is Stygnus Perty, 1833.

SAMOOIDEA: the oldest genera are Feretius Simon, 1879 and Stenostygus Simon, 1879; the type genus is younger, Samoa Sørensen, 1886. BIANTEIDAE: the oldest genus is Stenostygus Simon, 1879 and Hinzuanius Karsch, 1880; the type genus is younger, Biantes Simon, 1885. PODOCTIDAE: the oldest genus is Ibalonius Karsch, 1880; the type genus is younger, Podoctis Thorell, 1891. SAMOIDEA: the oldest genus is Feretius Simon, 1879; the type genus is younger, Samoa Sørensen, 1886. STYGNOMMATIDAE: the oldest genus is Stygnomma Roewer, 1912.

ZALMOXOIDEA: the oldest genus is Zalmoxis Sørensen, 1886. ESCADABIIDAE: the oldest genus is Escadabius Roewer, 1949. KIMULIDAE: the oldest genus is Acanthominua Sørensen, 1932, Euminua Sørensen, 1932 and Micromina Sørensen, 1932. This family was originally called Minuidae Sørensen in Henriksen, 1932, but this was based on the generic name Minua Sørensen in Henriksen, 1932 invalid due to homonymy; the current type genus is younger. Kimula Goodnight & Goodnight, 1942. FISSIPHALIIIDAE: the oldest genus is Fissiphallius Martens, 1988. GUASINIDAE: the oldest genera are Guaiquinimia González-Sponga, 1997 and Guasinia González-Sponga, 1997. ICALIPEPIDAE: the oldest genera are Icaleptes Kury & Pérez, 2002 and Zalmopsylla Kury & Pérez, 2002. ZALMOXIDAE: the oldest genus is Zalmoxis Sørensen, 1886.

Phylogenetic hypotheses in Opiliones

Phylogeny of Opiliones

In Figs. 1 to 11, the most relevant hypotheses (or extrapolations) found in the literature concerning the branching pattern of the Opiliones are presented. The five following genera are here used to represent the major groups of Opiliones as currently understood: Siro (for the Cyphophthalmi), Gonyleptes (for the Laniatores), Phalangium (for
the Phalangioida), *Ischyropsalis* (for the Ischyropsalidoidea) and *Trogulus* (for the Troguloidea) (see also Table 2 for details).

The unity of Opiliones (Hypothesis O1, Fig. 1), as currently used, was established by Latreille (1802) and has never been seriously challenged except when Sundevall (1833) (and much later, Savory 1977) separated the Cyphophthalmi from the other Opiliones.

**FIGURE 1. Hypothesis O1 of phylogeny of the Opiliones (Latreille 1802).** The clade which is today called Opiliones (in blue, below) was originally called “Phalangiens” (in green, above). Members of the Laniatores and of the Ischyropsalidoidea were then unknown. The name Phalangida (as many others) has undergone a change of circumscription over time.
Hypothesis O2 (Fig. 2), by Sundevall (1833), was a step back from the work of Latreille (1802), who had included *Siro* in the Opiliones, under the name “Phalangiens”. The taxa within Opiliones were regarded as coordinate families, without resolution. A strange variation of this may be found in Perty (1833) and Gervais (1844), where part of the Laniatores (the Cosmetidae only) is included along with *Phalangium* among the non-gonyleptid Opiliones. These were the only attempts to challenge the monophyly of the Laniatores.

**FIGURE 2.** Hypothesis O2 of phylogeny of the Opiliones (Sundevall 1833). The original concept of the Opiliones (“Opiliones” in green) excluded the Cyphophthalmi (here represented by Siro). This group is currently called Phalangida (in blue). *Ischyropsalis* was still to be unknown for 6 years.
Hypothesis O3 (Fig. 3), by Thorell (1876), launched the Palpatores, a name that would frequently be used later with a different concept (equaled to the Plagiostethi, see below). At the same time, Thorell, following the then recent work of Sørensen (1873) united the groups that would be much later called the Dyspnoi, a concept that was widely disclaimed, but prevails today.

FIGURE 3. Hypothesis O3 of phylogeny of the Opiliones (Thorell 1876). Thorell created the name Palpatores (green) as opposed to the also new group Laniatores (here represented by Gonyleptes). Thorell’s Palpatores is currently called Cyphopalpatores Martens (blue), a name coined a century later, while the name Palpatores is used for another group (see Fig. 4 below). Thorell also recognized what later was to be known as Dyspnoi (blue), following Sørensen (1873).
Hypothesis O4 (Fig. 4), by Simon (1879), defined the Plagiostethi, a name that afterwards was extensively (and wrongly) regarded as a less-favored synonym of Palpatores. This concept is favored until now in recent analyses, although under the name “Palpatores hypothesis”.

**FIGURE 4.** Hypothesis O4 of phylogeny of the Opiliones (Simon 1879). Simon was the first to define a group that he called Plagiostethi (green), as opposed to the Mecostethi (here represented by Gonyleptes and identical to Thorell’s Laniatores). This name as of today has been abandoned in favor of a different usage of the name Palpatores Thorell.
Hypothesis O5 (Fig. 5), proposed by Pocock (1902) and espoused by Loman (1903), maintained Simon’s Plagiostethi, refining their inner relationships by creating the Apagosterni, a clade not supported by the most recent analyses (e.g., O10, O11).

FIGURE 5. Hypothesis O5 of phylogeny of the Opiliones (Pocock 1902). Pocock suggested a group formed by today’s Phalangioida + Ischyropsalidoidea, thus introducing the name and the concept of Apagosterni. Loman (1903) was the first to accept this clade, which alternately lost and regained favor, but endured for a century.
Hypothesis O6 (Fig. 6), proposed by Hansen & Sørensen (1904), also kept Plagiostethi, but changed their inner relationships by recovering (and for the first time naming) Thorell’s Dyspnoi. This classical hypothesis has been used during most of the 20th century.

**FIGURE 6. Hypothesis O6 of phylogeny of the Opiliones (Hansen & Sørensen 1904).** The Danes kept the solid Plagiostethi (= “Palpatores” in blue) and dismantled the Apagosterni resurrecting and firstly naming Thorell’s Dyspnoi as opposed to the Eupnoi. This hypothesis was also defended by Roewer (1923) and Shear (1975) and became the classic triad of the 20th century: Cyphophthalmi, Palpatores and Laniatores.
Hypothesis O7 (Fig. 7), proposed by Mello-Leitão (1944), was presented as a branching cactus instead of the standard “tree” (see reproduction in Giribet & Kury 2007). Mello-Leitão managed to combine the concepts of Cyphopalpatores, Palpatores and Apagosterni into a single hypothesis. It did not gain much favor.

**FIGURE 7. Hypothesis O7 of phylogeny of the Opiliones (Mello-Leitão 1944).** This author combined some older hypotheses such as the dichotomy Laniatores versus Palpatores (still using the original Thorell’s concept) and reintroduced the Apagosterni.
Hypothesis O8 (Fig. 8), proposed by Šilhavý (1961), was a large step back, because it did not contain any branching information besides keeping the Dyspnoi. For this reason, it was heavily criticized by Shear (1975).

**FIGURE 8. Hypothesis O8 of phylogeny of the Opiliones (Šilhavý 1961).** This author presented a hypothesis with very little information putting almost all groups as coordinate categories.
Hypothesis O9 (Fig. 9), proposed by Martens (1980), was the first cladistic analysis of Opiliones, representing a development of his earlier work (Martens 1976). It was non-numerical, used only a few morphological characters, and did not use real outgroups. However, it represented an immense advance in relation to the status quo and because of its solid scientific content, was target to many critics (see for example extended criticism in Shultz 1998: 257-258). Martens’ (1980) hypothesis resembled Mello-Leitão’s hypothesis O7 in that it retrieved the Palpatores (there called “Cyphopalpatores”, because Palpatores was then held as a synonym of Plagiostethi) and the Apagosterni.

**FIGURE 9.** Hypothesis O9 of phylogeny of the Opiliones (Martens 1980, morphological, non-numerical). By the end of the 20th century, the original concept of Palpatores was lost, so that a hypothesis recovering this clade received the new name Cyphopalpatores Martens. This was the first cladistic analysis of the Opiliones.
Hypothesis O10 (Fig. 10) is the classic molecular hypothesis, defended in Shultz & Regier (2001) and Giribet et al. (2010). Also supported by the purely morphological analysis by Shultz (1998), it resurrected the original Opiliones concept, by making the Cyphophthalmi the sister group of all other Opiliones (called “Phalangida” by Giribet et al. 1999). It also recovered the Palpatores and the Dyspnoi.

FIGURE 10. Hypothesis O10 of phylogeny of the Opiliones (Shultz 1998, morph). This analysis recovered the old Sundevall’s concept (Cyphophthalmi versus Phalangida), and Simon’s Plagiostethi (by then already universally called “Palpatores”). Within Palpatores, he recognized the Dyspnoi, burying the Apagosterni. Surprisingly, a molecular analysis by Shultz & Regier (2001, mol) recovered the same configuration. After some analyses which did not recover the Palpatores (see hypothesis K in Fig. 11 below), Giribet et al. (2010, mol) obtained the same pattern.
Hypothesis O11 (Fig. 11) is recovered by the two only combined molecular + morphological analyses conducted so far (Giribet et al. 1999; 2002), which recovered Lehtinen’s (1975) Phalangida (= Sundevall’s Opiliones), and for the first time proposed a sister group relationship of the Eupnoi against the rest of Phalangida (named Dyspnolaniatores by Giribet), something hinted at by Lehtinen (1975).

**FIGURE 11.** Hypothesis O11 of phylogeny of the Opiliones (Giribet et al. 1999, comb; 2002, comb). Following his 1997 thesis, Giribet recovered the early branching off for the Cyphophthalmi and resurrected the name Phalangida for its sister group. A new clade was also firstly proposed and named, causing the diphyly of the Palpatores—the Dyspnolaniatores. Both this hypothesis and J are the modern contrasting views of the deep relationships among Opiliones groups.

**Phylogeny of Laniatores**

The armored harvestmen (Laniatores) are here presented in more detail, separated from the rest of the Opiliones. In Figs. 12 to 19, the relevant hypotheses found in the literature concerning the branching pattern of the Laniatores are presented. The six following genera are here used to represent the major groups of Laniatores as currently
understood: *Erebomaster* (for the Travunioidea s.s.), *Equitus* (for the Triaenonychoidea), *Synthetonychia* (for the Synthetonychiidae), *Gnomulus* (for the Sandokanidae/Oncopodidae, consistently deemed to hold a special position), *Phalangodes* and *Gonyleptes*. See Table 4 for details.

The monophyly of this suborder has not been challenged since Perty (1833), who ranked the Cosmetidae together with the Eupnoi.

Hypothesis L1 (Fig. 12) was prevalent by the end of 19th century. The young Triaenonychidae and Oncopodidae did not have yet a separate placement, and the Cladonychiidae were not yet recognized, its species being merged along with Oncopodidae in the Phalangodidae.

**FIGURE 12. Hypothesis L1 of phylogeny of the Laniatores (Simon 1879).** The lineages which would cause greater disturbance in the future were still dormant inside the Phalangodidae. Karsch (1880) and Sørensen (1886) kept basically the same pattern.
Hypothesis L2 (Fig. 13) represented a major step forward, when Loman (1901; 1902) separated the Triaenonychidae as “sister” (a coordinate group) to the other Laniatores, calling it suborder Insidiatores. An expanded usage of the Insidiatores was later recovered by Kury (2003), also including Erebomaster, although formally this is not Loman’s original concept. Pocock (1902), in spite of his critics, followed this arrangement. Loman (1901) also separated Gnomulus from the Phalangodidae.

![Hypothesis L2 of phylogeny of the Laniatores (Loman 1901; 1902).](image)

FIGURE 13. Hypothesis L2 of phylogeny of the Laniatores (Loman 1901; 1902). This author proposed a sharp separation between the Triaenonychidae (which he called Insidiatores, here represented by Equitius) against all other Laniatores (which he called simply Laniatores [sensu stricto] and here called Lomaniatores). Pocock (1902) followed this hypothesis of phylogeny. The term Insidiatores was later reused in a broader sense.
Hypothesis L3 (Fig. 14) was a further refinement by Loman (1903), who created the names Sterrhonoti (for the Sandokanidae, then called Oncopodidae) and Camptonoti (for the rest of his Laniatores). Setting the Sandokanidae apart proved to be very popular, persisting in the literature for many decades. In the 1920s and early 1930s, a subdivision of the Laniatores became out of fashion. The families were simply listed as coordinate categories (e.g., Roewer 1923).

**FIGURE 14. Hypothesis L3 of phylogeny of the Laniatores (Loman 1903).** Only two years after creating the Insidiatores, Loman (1903) separated the Oncopodidae (which he called Sterrhonoti, here represented by *Gnomulus*) against the other Laniatores sensu stricto, called Camptonoti. This hypothesis lost support with the removal of the Cladonychiidae (here represented by *Erebomaster*) from the Phalangodidae by Briggs (1969).
Hypothesis L4 (Fig. 15): a major breakthrough happened in the mid-1930s, when Hadži (1935) recognized the close relationship between the southern hemisphere Triaenonychidae and the European Cladonychiinae. This group was later resurrected as Travunioidea (*Erebomaster + Equitius + Synthetonychia*) by Kratochvíl (1958) and as an “expanded” Insidiatores by Kury (2003), but it is currently widely regarded as a paraphylum. Kratochvíl (1958) put all remaining Laniatores as a monophylum (a hitherto unchallenged hypothesis, which he called “Oncopodoidea” and was later named Grassatores by Kury). Kratochvíl also combined Hadži’s group with Mello-Leitão’s special placement for Oncopodidae as sister group of the other Grassatores. Martens (1980) conserved exactly this arrangement, which also appeared in the combined molecular + morphological analyses by Giribet *et al.* (1999; 2002). This hypothesis was in the second half of the 20th century and at the turn of 21st century.

**FIGURE 15. Hypothesis L4 of phylogeny of the Laniatores Kratochvíl (1958).** After the work of Forster (1954), who created the Synthetonychiidae, this family went straight into the vicinity of the Triaenonychiidae in the views of all most authors. Kratochvíl proposed a symmetrical arrangement of the groups we now know as Insidiatores versus Grassatores (then respectively called Travunioidea and Oncopodoidea). The morphological cladistic analysis by Martens (1980) recovered this arrangement, as well as both combined analyses by Giribet *et al.* (1999; 2002). Kury in his catalogue (2003) resurrected and expanded the original concept of Loman’s Insidiatores, using this name for the same clade recognized by Kratochvíl as Travunioidea.
Hypothesis L5 (Fig. 16): Mello-Leitão (1944) led to an extreme version of Loman’s (1903) attempt to segregate the Oncopodidae and put it at the base of his tree of “oculariate” Laniatores. Hadži’s component *Erebomaster + Equitius* is ever present, although nested a node above. Šilhavý (1961), who seemed to hold Mello-Leitão’s views in high regard (see, for instance, Šilhavý 1973), followed this scheme, naming the Sandokanidae (then Oncopodidae) as Oncopodomorphi and all non-oncopodid Laniatores as Gonyleptomorphi. Bristowe (1976) did the same, separating the Sandokanidae from the rest, establishing a monofamilial suborder Oncopodines vs. the Laniatores s.s..

**FIGURE 16. Hypothesis L5 of phylogeny of the Laniatores Šilhavý (1961).** Šilhavý recognized the Travunioidea of Kratochvíl (here marked as “Insidiatores”, in blue) and made a change contraposing Oncopodidae against all other Laniatores, which has been anticipated by Mello-Leitão (1944), who had produced a surprisingly similar phylogeny (the famous cactus). This arrangement was conserved by Bristowe (1976).
Hypothesis L6 (Fig. 17): Shultz elaborated morphological (Shultz 1998) and molecular phylogenetic analyses (Shultz & Regier 2001) that agreed with the notion (Dumitrescu 1976 and Kury 1993) that the “expanded” Insidiatores were diphyletic. However, the branching pattern obtained was different from Kury-Dumitrescu scheme.

FIGURE 17. Hypothesis L6 of phylogeny of the Laniatores (Shultz 1998). Shultz morphological analysis (1998) and Shultz & Regier molecular analysis (2001) made a scarce sample of the Laniatores. The Insidiatores were dismantled, but the position of Synthetonychia was not made explicit, by not having been used in the analyses. The proximity of the Travuniidae with the Grassatores resembled Loman’s view of the Laniatores.
Hypothesis L7 (Fig. 18): supported by Kury (2002), Giribet & Kury (2007) and Mendes (2009), also has the Travunioidea and Triaenonychoidea as two clades, but with the sister group sequence inverted in relation to hypothesis O8. The special position for Sandokanidae is also refuted by this hypothesis; this taxon appears nested within the Grassatores.

Hypothesis L8 (Fig. 19): finally Giribet and collaborators (2010) and Sharma & Giribet (2011) in a molecular analysis also did not recover the “expanded” Insidiatores in full. They also found Sandokanidae nested within Grassatores, although in a different position from hypothesis L7. The need is clear to do a total evidence analysis to reconcile the molecular with the morphological view.
Phylogeny of Cyphophthalmi

The mite-harvestmen (Cyphophthalmi) are here presented in more detail, separated from the rest of the Opiliones. In Figs. 20 to 23, are presented relevant hypotheses found in the literature concerning the branching pattern of the Cyphophthalmi. The six following genera are here used to represent the major groups of Cyphophthalmi as currently understood, because they are the oldest in each family: Parogovia Hansen, 1921 (for Neogoveidae Shear, 1980), Ogovea Roewer, 1923 (for Ogoveidae Shear, 1980), Pettalus Thorell, 1876 (for Pettalidae Shear, 1980), Siro Latreille, 1796 (for Sironidae C.L. Koch, 1839), Stylocellus Westwood, 1874 (for Stylocellidae Hansen and Sørensen, 1904) and Troglosiro Juberthie, 1979 (for Troglosironidae Shear, 1993).
Hypothesis C1 (Fig. 20): Shear (1980) published the first cladistic analysis of the Cyphophthalmi, unfolding the group into five families, which resulted in a symmetrical arrangement. Shear called his two major clades Tropicophthalmi and Temperophthalmi. Later, Shear (1993) added a sixth family, Troglosironidae.

**FIGURE 20. Hypothesis C1 of phylogeny of the Cyphophthalmi (Shear 1980/1993, morph).** Shear (1980) was the first attempt ever of a cladistic analysis of the Cyphophthalmi. The analysis resulted in a symmetrical arrangement. Shear proposed the two infraorders Tropicophthalmi and Temperophthalmi. A sixth family was added in 1993. This graph is a combination of both works by Shear.
Hypothesis C2 (Fig. 21): Giribet & Boyer (2002) attempted both a morphological and a molecular analyses, which turned out very unresolved and it is not shown here. With a much expanded matrix, Boyer et al. (2007) made an important molecular analysis of the Cyphophthalmi, but failed to include Ogoveidae because of a lack of material for molecular study. This asymmetrical tree has Stylocellidae as sister group to the rest.

FIGURE 21. Hypothesis C2 of phylogeny of the Cyphophthalmi (Boyer et al. 2007, mol). An important analysis, which failed to include Ogoveidae by lack of material for molecular study. This asymmetrical tree has Stylocellidae as sister group to the rest. They have not recovered any of Shear’s clades. A previous work (Giribet & Boyer 2002) included both morphological and molecular analyses, but both are remarkably lacking in resolution, even for the monophyly of the families themselves.
Hypothesis C3 (Fig. 22): Clouse et. al. (2010) analyzed the Stylocellidae, including also the other Cyphophthalmi families. They used molecular data, and also did not include Ogoveidae. It was substantially different from Boyer’s analysis. They have not proposed any superfamilial names, but did recover the clade later known as Boreophthalmi.

FIGURE 22. Hypothesis C3 of phylogeny of the Cyphophthalmi (Clouse & Giribet 2010, mol; Clouse et. al. 2010, comb). Mostly molecular, which also did not include Ogoveidae. It was substantially different from Boyer’s analysis. They have not proposed any superfamilial names, but did recover the clade later known as Boreophthalmi.
Hypothesis C4 (Fig. 23): Giribet et al. (2011) finally obtained material of Ogoveidae for molecular study. The result showed Pettalidae as sister group of the rest as in Clouse et al. (2010) and some novel groups. They recovered only one of Shear’s clades, the Ogoveoidea. Three new infraordinal names were proposed.

**FIGURE 23.** Hypothesis C4 of phylogeny of the Cyphophthalmi (Giribet et al. 2011). Finally material of Ogoveidae was obtained for molecular study. The result was this asymmetrical tree, with Pettalidae as sister group of the rest as in Clouse et al. (2010). They recovered one of Shear’s clades, the Ogoveoidea. Three new infraordinal names were proposed.

**Phylogenetic definitions of the larger groups in Opiliones**

Tables 3 and 4 summarize the original circumscription of each suprafamilial group in Opiliones, showing for example, that while Mecostethi is equal to Laniatores, Plagiostethi is not equal to Palpatores (which is in turn equivalent to Martens’ Cyphopalpatores), and could have been used instead of Martens’ name, to denote the clade Eupnoi + Dyspnoi.
A simple look at Table 3 makes clear that “Phalangita” (Phalangida) Latreille 1802 (originally including *Siro*, *Trogulus* and *Phalangium*), is a different group from Opiliones Sundevall 1833 (which explicitly excluded *Siro*). The proposal of Giribet *et al.* (1999; 2002) to use Opiliones for all members of the order and Phalangida for Opiliones excluding Cyphophthalmi follows recent tradition, but recovers the opposite notion to the original usage.

An attempt is made here to provide phylogenetic node-based or branch-based definitions of the larger groups in Opiliones, using the oldest generic names to refer to clades, in the same way as in Tables 3-4. For most of the discussion the prevailing competing hypotheses O10 and O11 are used.

A list of all names above the rank of superfamily used in the taxonomy of Opiliones is given below, in chronological order.

**TABLE 3.** Original concepts of suprafamilial names in Opiliones, tabulated against each oldest genus originally included. T = typified, NT = non-typified, + = originally included, - = originally excluded, (+) and (-) = originally not mentioned, but should be respectively included/excluded.

<table>
<thead>
<tr>
<th>SUPRAFAMILIAL NAME</th>
<th>Typified</th>
<th>Siro</th>
<th>Phalangium</th>
<th>Trogulus</th>
<th>Ischyropsalis</th>
<th>Gonyleptes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phalangita Latreille 1802</td>
<td>T</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>(+)</td>
<td>(+)</td>
</tr>
<tr>
<td>Opiliones Sundevall 1833</td>
<td>NT</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>(+)</td>
<td>+</td>
</tr>
<tr>
<td>Palpatores Thorell 1876</td>
<td>NT</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Cyphopalpatores Martens 1980</td>
<td>NT</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Plagiothelith Simon 1879</td>
<td>NT</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Cyphophthalmi Simon 1879</td>
<td>T</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Anepignathi Thorell 1882</td>
<td>NT</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Eupnoi Hansen &amp; Sørensen 1904</td>
<td>NT</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Dysplanothelenses Giribet <em>et al.</em> 2002</td>
<td>NT</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Eupagosterni Pocock 1902</td>
<td>NT</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Apagosterni Pocock 1902</td>
<td>NT</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Dyspnoi Hansen &amp; Sørensen 1904</td>
<td>NT</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Laniatores Thorell 1876</td>
<td>NT</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Mecostheti Simon 1879</td>
<td>NT</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

**TABLE 4.** Suprafamilial names used in Laniatores. T = typified, NT = non-typified, + = originally included, - = originally excluded, (+) and (-) = originally not mentioned, but should be respectively included/excluded.

<table>
<thead>
<tr>
<th>Suprafamilial name</th>
<th>Typified</th>
<th>Erebomaster</th>
<th>Equitius</th>
<th>Gnomulus</th>
<th>Phalangodes</th>
<th>Gonyleptes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Laniatores Thorell, 1876</td>
<td>NT</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Gonyleptomorphi Šilhavý 1961</td>
<td>T</td>
<td>(+)</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Laniatores (sensu Loman 1901; 1902), “Lomaniatores”</td>
<td>n/a</td>
<td>(+)</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Camptonoti Loman 1903</td>
<td>NT</td>
<td>(+)</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Sterrhonoti Loman 1903</td>
<td>N</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Oncopodomorphi Šilhavý 1961</td>
<td>T</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Oncopodines Bristowe 1976</td>
<td>T</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Oncopodoidea (sensu Martens 1980)</td>
<td>T</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Tricosipilata <em>new name</em></td>
<td>NT</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Grassatores Kury 2002</td>
<td>NT</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Gonyleptoidea (sensu Martens 1980)</td>
<td>T</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Travunioidea (sensu Kratochvíl 1958)</td>
<td>T</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>“expanded” Insidiatores (sensu Kury 2003)</td>
<td>n/a</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Insidiatores Loman 1901</td>
<td>NT</td>
<td>(-)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
Suprafamilial names in Opiliones

(1) Phalangida Latreille, 1802

**Original usage:** all harvestmen. Under hypotheses O10 or O11 (Figs. 10–11), the last common ancestor of *Siro* and *Phalangium*, and all descendants of that ancestor.

**Current usage:** all harvestmen, except the mite-harvestmen. Under hypotheses O10 or O11 (Figs. 10–11), the last common ancestor of *Phalangium* and *Gonyleptes*, and all descendants of that ancestor, as implicit in Giribet *et al.* (1999).

**Synonyms:** originally spelled Phalangiens (in French) and Phalangita (in Latin). Opiliones sensu Sundevall (1833), but not in the current sense.

**Comment:** the use proposed by Giribet *et al.* (1999) has a disadvantage of being contrary to the original usage of Latreille, who explicitly included *Siro*. A switch of the names Opiliones and Phalangida as used in Giribet *et al.* (1999) would solve the conflict, although, usage speaks against that. Sometimes it is difficult to establish if the name Phalangida refers to the whole order, because formerly all harvestmen were called a “family”. Besides Latreille (1802), another example of this pattern is the early use of “family” Phalangida (with “d”) by the Bavarian author Perty (1833). Although Sundevall’s name Opiliones was massively used for harvestmen from early times onward (notably in continental Europe, with Perty’s exception cited above), Latreille’s name also has found its way into the literature (especially in UK and the USA), having been variously rendered as Phalangideæ (Say 1821), Phalangia (Wood 1869), Phalangidea (Pickard-Cambridge 1890) and Phalangidia (Banks 1892). It was later standardized as Phalangida (e.g., Banks 1893), in a time when ordinal names were receiving the ending –ida.

(2) Opiliones Sundevall, 1833

**Original usage:** all harvestmen, excepted the mite-harvestmen. Under hypotheses O10 or O11 (Figs. 10–11), the last common ancestor of *Phalangium* and *Gonyleptes*, and all descendants of that ancestor.

**Current usage:** all harvestmen. Under hypotheses O10 or O11 (Figs. 10–11), the last common ancestor of *Siro* and *Phalangium*, and all descendants of that ancestor.

**Synonyms:** Phalangiens, only in the original sense of Latreille.

**Comment:** this has a disadvantage of being contrary to the original usage of Sundevall, who explicitly excluded *Siro*, placing it in the Solifugae. Massive usage in the literature through many decades speaks for the “expanded” Opiliones usage—the name Opiliones including the whole order.

(3) Laniatores Thorell, 1876

**Original usage:** the armored-harvestmen. Under hypotheses O3 and O10 (Figs. 3, 10), the first ancestor of *Gonyleptes* that is not an ancestor of *Phalangium*, and all descendants of that ancestor. Under hypothesis O11 (Fig. 11), the first ancestor of *Gonyleptes* that is not an ancestor of *Trogulus*, and all descendants of that ancestor.

**Current usage:** the same as original.

**Synonyms:** Mecostethi Simon 1879.

**Comment:** there are no challenges to the monophyly of this group. The circumscription of the name also remained constant, while Mecostethi fell in neglect.

(4) Palpatores Thorell, 1876

**Original usage:** all harvestmen, except the armored harvestmen. Under hypothesis O3 (Figs. 3), the first ancestor of *Phalangium* that is not an ancestor of *Gonyleptes*, and all descendants of that ancestor. This group is a paraphylum under hypotheses O10 and O11 (Figs. 10–11).

**Current usage:** all harvestmen, except the mite-harvestmen and the armored harvestmen, that is, daddy-
longlegs + dyspnoans. Under hypothesis O10 (Fig. 10), the first ancestor of *Phalangium* that is not an ancestor of *Gonyleptes*, and all descendants of that ancestor.

**Synonym:** Cyphopalpatores Martens 1980 is the same as the original usage. Modern usage may be exemplified by Fig. 10 (e.g., Giribet et al, 2010) and is the same as Simon’s Plagiostethi.

(5) **Mecostethi Simon, 1879**

**Original usage:** the armored -harvestmen. Same definition as for Laniatores. See Fig. 4.

**Current usage:** the same as original. Fallen into disuse. Pocock (1902), following Loman’s (1901) scheme, proposed a convenient system that would save the creation of new names: he considered the Mecostethi composed of Insidiatores + Laniatores, but no one used this proposal.

**Synonym:** Laniatores Thorell 1876.

(6) **Plagiostheti Simon, 1879**

**Original usage:** all harvestmen, except the mite-harvestmen and the armored –harvestmen, that is daddy-longlegs + dyspnoans. Under hypothesis O4 (Fig. 4), the last common ancestor of *Phalangium* and *Trogulus*, and all descendants of that ancestor. It holds under the hypothesis O10 (Fig. 10).

**Current usage:** the same as original. Fallen into disuse.

**Synonym:** this is the same as Palpatores Thorell 1876 but only in the current use.

**Comment:** this name has a disadvantage of being long since discarded in favor of Palpatores, although they are not the same. It is important to note, however, that this is the classical (although not the original) concept of Palpatores, as used by Hansen & Sørensen (1904).

(7) **Cyphophthalmi Simon, 1879**

**Original usage:** the mite-harvestmen only. Under hypotheses O10 or O11 (Figs. 10–11), the first ancestor of *Siro* which is not an ancestor of *Phalangium*, and all descendants of that ancestor.

**Current usage:** the same as original.

**Synonym:** Anepignathi Thorell 1882.

**Comment:** in a scenario of typified names being coordinately used for suprafamilial taxa (Kluge-style), this would be a typified-name, based on genus *Cyphophthalmus* Joseph 1869, synonym of a typified subordinal name based on *Siro* Latreille 1802 — Sironida Koch 1839.

(8) **Anepignathi Thorell, 1882**

**Original usage:** the mite-harvestmen only. Under hypotheses O10 or O11 (Figs. 10–11), the first ancestor of *Siro* which is not an ancestor of *Phalangium*, and all descendants of that ancestor.

**Current usage:** the same as original. Fallen into disuse.

**Synonym:** Cyphophthalmi Simon, 1879.

**Comment:** this is the oldest non-typified name for the group, thus it would not compete with the typified Cyphophthalmi in an eventual scenario of a Kluge-style classification.

(9) **Insidiatores Loman, 1901**

**Original usage:** armored harvestmen with trifid posterior claws (triaenonychids) as opposed to those with double claws (*Equitius* in Fig. 13). Under hypothesis L2 (Fig. 13), the first ancestor of *Equitius* that is not an ancestor of *Gonyleptes*, and all descendants of that ancestor.
**Current usage:** the name Insidiatores laid dormant for 100 years until Kury (2003) recovered it to use for the Travunioidea of the Czech authors and Martens. Kury stretched Loman’s concept to include also the Travuniidae and Cladonychiidae. Under hypotheses L5 and L6 (Figs. 15–16), the first ancestor of *Equitius* that is not an ancestor of *Gonyleptes*, and all descendants of that ancestor. Modern hypotheses (L6-8) do not recover the Insidiatores.

**Synonym:** as *Synhetonychia* was not to be described for another 50 years, it is especially difficult to extrapolate which would be the circumscription of Insidiatores.

**Comment:** all families of Laniatores with complex claws (peltonychium) that are currently associated with the Triaenonychidae were unknown at the time—although some double-clawed species that would become cladonychiids were then included in Phalangodidae under *Scotolemon* Lucas, 1860 (Palearctic) and *Erebomaster* Cope, 1872 (Nearctic). Loman (1901 p. 80) did not mention any genus, but only the family Triaenonychoidea, as opposed to the other Laniatores (that is, Laniatores stricto sensu), which were (Loman, 1901 p. 79): Gonyleptoidae, Cosmetoidae, Assamoidae, Epedanoidea, Biantoidae, Oncopodoidea, Samoidae and Zalmoxioidea. Loman refrained from formally including the Holarctic family Phalangodidae in this classification (both because he had not examined material and because he found it poorly sustained), although he commented (Loman 1901: 79) that Phalangodidae apparently should be included in the Laniatores (“Dem Anschein nach gehören auch die Phalangodidae hierher.”).

### (10) Eupagosterni Pocock, 1902

**Original usage:** the first ancestor of *Trogulus* that is not an ancestor of *Ischyropsalis*, and all descendants of that ancestor (see Fig. 5). This is the same as the typified name Troguloidea.

**Current usage:** the same as original. Fallen into disuse.

**Synonym:** *Troguloidea* Sundevall 1833.

### (11) Apagosterni Pocock, 1902

**Original usage:** under hypothesis O5 (Fig. 5), the last common ancestor of *Phalangium* and *Ischyropsalis*, and all descendants of that ancestor.

**Current usage:** the same as original. Fallen into disuse.

**Synonym:** none.

**Comment:** Pocock (1902: 504) strongly criticized Sørensen’s (1873) union of the Ischyropsalidoidea + Troguloidea (which is our modern concept of Dyspnoi) and proposed the Apagosterni concept, which was later reused by many authors, competing with Dyspnoi during most of the 20th century. Simon (1879) had avoided the problem leaving an unresolved trichotomy in his Plagiostethi (see Fig. 4). The Apagosterni appeared lastly in Martens’ (1980) phylogeny, but in the last 30 years the Dyspnoi hypothesis has predominated.

### (12) Camptonoti Loman, 1903

**Original usage:** under hypothesis L3 (Fig. 14), the first ancestor of *Gonyleptes* and *Erebomaster* that is not an ancestor of *Gnomulus*, and all descendants of that ancestor.

**Current usage:** the same as original. Fallen into disuse because the group was no longer supported.

**Synonym:** none.

**Comment:** having separated his Laniatores stricto sensu from the Insidiatores, Loman (1903) further divided the Laniatores into Oncopodidae (which he called Sterrhonoti) and the rest, the Camptonoti. This foreshadowed the Gonyleptoidea (*Gonyleptes* + *Phalangodes* of Figs. 15–16) of Šilhavý (1961) and Martens (1980), with the difference that it still included the Cladonychiidae indistinct amidst the Phalangodidae.
(13) Sterrhonoti Loman, 1903

**Original usage:** this group is coextensive with the Sandokanidae. Under hypothesis L3 (Fig. 14), the first ancestor of *Gnomulus* that is not an ancestor of *Gonyleptes*, and all descendants of that ancestor.

**Current usage:** the same as original. Fallen into disuse.

**Synonyms:** Oncopodomorpha Šilhavý, 1961; Oncopodines Bristowe, 1976 and Oncopodoidea Martens, 1980.

**Comment:** Loman (1903: 66) included only the family Sandokanidae (then Oncopodidae) in his [infraorder] Sterrhonoti, as opposed to all other non-Triaenonychidae Laniatores, which were placed in Camptonoti. This monofamilial group was also named as Šilhavý’s (1961) Oncopodomorpha, Bristowe’s (1976) Oncopodines and Martens’ (1980) Oncopodoidea, under different phylogenetic hypotheses, either as opposed to some or all Laniatores. This name is useless if Sandokanidae is nested amidst the other Grassatores (e.g., under hypothesis L8, Fig. 19), because it is the same as the family Sandokanidae, not defining any suprafamilial group. However, under hypothesis L7, Fig. 18, it becomes the same as Phalangodoidea (*Gnomulus + Phalangodes*).

(14) Eupnoi Hansen & Sørensen, 1904

**Original usage:** daddy longlegs and related species (Phalangioidea), big-eyed fast-moving harvestmen (Caddoidea). Under all hypotheses O6, O10, O11 (Figs. 6, 10, 11), the first ancestor of *Phalangium* that is not an ancestor of *Trogulus*, and all descendants of that ancestor.

**Current usage:** the same as original.

**Synonym:** none.

**Comment:** the Eupnoi are a well-established group, whose monophyly is universally accepted (but see Groh & Giribet 2014).

(15) Dyspnoi Hansen & Sørensen, 1904

**Original usage:** troglids/nemastomatids (Troguloidea) and ischyropsalidids/sabaconids/taracids (Ischyropsalidoidea). Under hypotheses O10 (Fig. 10) and O11 (Fig. 11), the last common ancestor of *Trogulus* and *Ischyropsalis*, and all descendants of that ancestor. Under J, the first ancestor of *Trogulus* that is not an ancestor of *Phalangium*, and all descendants of that ancestor and under K, the first ancestor of *Trogulus* that is not an ancestor of *Gonyleptes*.

**Current usage:** the same as original.

**Synonym:** none.

**Comment:** the Dyspnoi hypothesis of relationship, although first named by Hansen & Sørensen (1904), had been advanced earlier by Sørensen (1873) and Thorell (1876). This is in conflict with the Apagosterni hypothesis (see item 11 above), championed by Pocock (1902).

(16) Gonyleptomorphi Šilhavý, 1961

**Original usage:** all Laniatores except Sandokanidae. The last common ancestor of *Gonyleptes* and *Erebolomaster*, and all descendants of that ancestor. This definition only works under hypothesis L5 (Fig. 16), as this clade has never been recovered by most recent analyses.

**Current usage:** the same as original. Fallen into disuse.

**Synonym:** none.

**Comment:** this was the first suprafamilial name to be proposed in more than half a century.

(17) Oncopodomorphi Šilhavý, 1961

**Original usage:** in Šilhavý’s scheme, the sister group to the Gonyleptomorphi, including only the Sandokanidae.
Current usage: the same as original. Fallen into disuse.
Synonym: Sterrhonoti Loman 1903.
Comment: this is a superfluous name for Sterrhonoti, even more because it includes only one family.

(18) Oncopodines Bristowe, 1976

Original usage: Sandokanidae.
Current usage: the same as original. Fallen into disuse.
Synonym: Sterrhonoti Loman 1903.
Comment: superfluous name.

(19) Temperophthalmi Shear, 1980

Original usage: under hypothesis C1 (Fig. 20) for Cyphophthalmi, the last common ancestor of Siro and Troglosiro, and all descendants of that ancestor, or the first ancestor of Siro which is not an ancestor of Stylocellus, and all descendants of that ancestor.
Current usage: the same as original. Fallen into disuse.
Synonym: none.
Comment: the dichotomy Temperophthalmi versus Tropicophthalmi was the first attempt of a cladistic phylogeny of the mite-harvestmen.

(20) Tropicophthalmi Shear, 1980

Original usage: under hypothesis C1 (Fig. 20) for Cyphophthalmi, the last common ancestor of Stylocellus and Parogovia, and all descendants of that ancestor, or the first ancestor of Stylocellus which is not an ancestor of Siro, and all descendants of that ancestor.
Current usage: the same as original. Fallen into disuse.
Synonym: none.
Comment: see item 19 above.

(21) Grassatores Kury, 2002

Original usage: under hypothesis L7 (Fig. 18), the first ancestor of Gonyleptes that is not an ancestor of Erebomaster, and all descendants of that ancestor. Under hypothesis L8 (Fig. 19), the first ancestor of Gonyleptes that is not an ancestor of Erebomaster, and all descendants of that ancestor. Under both hypotheses, and regardless of whether the Insidiatores are a clade or not, the last common ancestor of Gonyleptes and Phalangodes, and all descendants of that ancestor.
Current usage: the same as original.
Comment: this name appeared for the first time as “Grassatores Kury” in Giribet et al. (2002), but the hypothesis of the Grassatores may be tracked back to Kratochvíl (1958), widely corroborated by Martens (1980), Giribet et al. (1999; 2002; 2010), Shultz (1998), Shultz & Regier (2001), Giribet & Kury (2007), Mendes (2009), and Sharma & Giribet (2011).

(22) Dyspnolaniatores Giribet et al., 2002

Original usage: under hypothesis O11 (Fig. 11), the first common ancestor of Trogulus and Gonyleptes, and all descendants of that ancestor.
Current usage: the same as original.
Synonym: none.
Comment: this is a very recent concept put forward for the first time in the 21st century as a result of two total evidence analyses (Giribet et al., 1999; 2002). It conflicts with the Palpatores hypothesis (Fig. 10).

(23) Boreophthalmi Giribet et al., 2011

Original usage: under hypotheses C3 (Fig. 22) and C4 (Fig. 23), the last common ancestor of Stylocellus and Siro, and all descendants of that ancestor.
Current usage: the same as original.
Synonym: none.
Comment: this hypothesis had been advanced earlier by Clouse et al. (2010).

(24) Scopulophthalmi Giribet et al., 2011

Original usage: under hypothesis C4 (Fig. 23), the first ancestor of Pettalus that is not an ancestor of Siro, and all descendants of that ancestor.
Current usage: the same as original.
Synonym: none.
Comment: this unranked taxon is coextensive with family Pettalidae.

(25) Sternophthalmi Giribet et al., 2011

Original usage: under hypothesis C4 (Fig. 23), the last common ancestor of Troglosiro and Parogovia, and all descendants of that ancestor.
Current usage: the same as original.
Synonym: none.

(26) Lomaniatores new name

Original & current usage: this name refers to the Laniatores sensu Loman (1901 and 1903), which exclude the Triaenonychidae. Under hypothesis L6 (Fig. 17), the first ancestor of Gonyleptes which is not an ancestor of Equitius, and all descendants of that ancestor.
Comment: no hypothesis supporting this group is recovered by recent analyses, except hypothesis L6 of Shultz (Fig. 17). It was deemed useful to name such a group to facilitate reference in future discussions.

(27) Tricospilata new name

Original & current usage: under hypothesis L7 (Fig. 18), the last common ancestor of Gonyleptes and Equitius, and all descendants of that ancestor.
Comment: based on Dumitrescu (1976), the tripartition of diverticulum tertium in a ramus medianus, a ramus lateralis and a ramus exterior stands as derived character and putative synapomorphy of Triaenonychidae + Grassatores (hypothesis L7, Fig. 18). It is herein proposed to name this clade as Tricospilata from Greek τρίχα (threefold, in three parts) + σπίλη (string of gut). It is a paraphylum under hypothesis L8 (Fig. 19).
(28) Eulaniatores new name

Original & current usage: under hypothesis L8 (Fig. 19), the last common ancestor of Gonyleptes and Equitius, and all descendants of that ancestor.

Comment: supported by the molecular analyses of Giribet et al. 2010 and Sharma & Giribet (2011), this hypothesis and that of Tricospilata are mutually exclusive. Etymology. From Greek εὖ (rightful, proper, good) + Laniatores.

Conclusion

A Kluge-styled strict circumscriptional nomenclature (meaning that no typified names above superfamily are to be used), as appealing as the idea appears, is not practical now for Opiliones because of the strong inertia of recent practice. Such a classification would be strikingly at odds with current usage, especially in the name Opiliones itself. Two alternative classifications are proposed below for Opiliones, each of which is isomorphic with phylogenetic hypotheses O10 (Fig. 10) and O11 (Fig. 11). See also Table 5:

TABLE 5. Comparison of recent classifications of Opiliones.

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Opiliones: classification 1 (Fig. 10)
(morphological and molecular—Shultz, 1998; Shultz & Regier, 2001 and Giribet et al., 2010)

Opiliones Sundevall, 1833
   Cyphophthalmi Simon, 1879
   Phalangida Latreille, 1802
   Laniatores Thorell, 1876
   Palpatores Thorell, 1876
       Eupnoi Hansen & Sørensen, 1904
       Dyspnoi Hansen & Sørensen, 1904

Opiliones: classification 2 (Fig. 11)
(combined—Giribet et al. 1999; 2002)

Opiliones Sundevall 1833
   Cyphophthalmi Simon 1879
   Phalangida Latreille 1802
       Eupnoi Hansen & Sørensen 1904
       Dyspnolaniatores Giribet et al. 2002
       Dyspnoi Hansen & Sørensen 1904
       Laniatores Thorell 1876

Two alternative classifications are proposed below for Laniatores, each of which is isomorphic with phylogenetic hypotheses L7 (Fig. 18) and L8 (Fig. 19). See also Table 5:
Laniatores: classification 1 (Fig. 18)
(morphological—Kury 2002; Giribet & Kury 2007; Mendes 2009)

Laniatores Thorell 1876
   Travunioidea Absolon & Kratochvil, 1932
   Tricosopilata new name
      Triaenonychoidea Sørensen, 1886
      Grassatores Kury 2002

Laniatores: classification 2 (Fig. 19)
(molecular—Giribet et al. 2010; Sharma & Giribet 2011)

Laniatores Thorell 1876
   Synthetonychiidae Forster, 1954
   Eulaniatores new name
      Insidiatores Loman 1901 [stricto sensu]
      Grassatores Kury 2002

A single classification for Cyphophthalmi is outlined below, isomorphic with phylogenetic hypothesis C4 (Fig. 23).
See also Table 5:

Cyphophthalmi: classification (Fig. 23)
(molecular—Giribet et al. 2011)

Cyphophthalmi Simon 1879
   Scopulophthalmi Giribet et al. 2011
      Pettalidae Shear, 1980
   Unnamed clade
      Boreophthalmi Giribet et al. 2011
         Sironidae C.L. Koch, 1839
         Stylocellidae Hansen and Sørensen, 1904
      Sternophthalmi Giribet et al. 2011
         Troglosironidae Shear, 1993
         Ogoveoidea Shear, 1980
            Ogoveidae Shear, 1980
            Neogoveidae Shear, 1980

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