

## PENIS MORPHOLOGY IN ONCOPODIDAE (OPILIONES, LANIATORES): EVOLUTIONARY TRENDS AND RELATIONSHIPS

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**ABSTRACT.** An interim report on our ongoing revisional study is given together with a short summary of the current knowledge on the systematics and distribution of the family Oncopodidae (Opiliones, Laniatores). An exceptionally high diversity in male genitalia is shown and its possible evolution is discussed. Four major penis types are distinguished in the Oncopodidae and compared with similar forms in other laniatorean families.

**Keywords:** Opiliones, Oncopodidae, penis types, Asia

The Oncopodidae is a family of obscure, soil-dwelling opilionids, which are easily recognizable by a general lack of spines and tubercles (which are otherwise typical for Laniatores), by a simple palp with a small claw, by fairly short, stout legs with few (1–3) tarsalia, and by a very large dorsal and ventral scutum (scutum completum), which leaves only the anal plate (tergite IX) free. These characters are probably plesiomorphic. Apomorphic traits defining the Oncopodidae as a monophyletic group are rather sparse. The most obvious one is a carapace-abdomen bridge formed by paired or unpaired cuticular processes on the posterior margin of the prosomal and on the anterior margin of the opisthosomal part of the dorsal scutum. The other apomorphies are less conspicuous, i.e. glans penis with paired lateral sclerites connected by an intermediate plate; ovipositor short and laterally compressed. Oncopodids were previously regarded as extremely rare, poor in species diversity, and morphologically uniform (Šilhavý 1961; Martens 1977, 1986). In the course of our taxonomic revision of this

family (Martens & Schwendinger 1998; Schwendinger & Martens 1999, 2002) several new taxa were described, but the truly remarkable discovery of this study is the surprisingly high diversity of penis forms present. This richness in genital morphology in described and yet undescribed species is shown and compared with similar penis forms in other opilionid families in the following provisional summary of our results.

### METHODS

The methods applied were described in Schwendinger & Martens (2002). Abbreviations used in the text are as follows: MAR = collection of J. Martens, Mainz ; MHNG = Muséum d'histoire naturelle, Genève; MSNG = Museo Civico di Storia Naturale, Genova.

### SYSTEMATICS

Family Oncopodidae Thorell 1876

Type genus: *Oncopus* Thorell 1876 by monotypy.

Genus *Oncopus* Thorell 1876

**Type species.**—*Oncopus doriae* Thorell 1876 by original designation (1 female and 1 juvenile syntype deposited in MSNG).

**Species account and distribution.**—Seven species; known from Thailand (doubtful record), peninsular Malaysia, Singapore, Sarawak and Sabah.

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**Main characteristics.**—Glans penis proximad-directed (Figs. 1–4); tarsal formula 1-1-1-1; body large; chelicerae massive, with ventral process on 2<sup>nd</sup> (sometimes also on 3<sup>rd</sup>) article; ventroproximal process on palpal tibia distinct; ventral process on palpal trochanter slightly distad-inclined.

Genus *Gnomulus* Thorell 1890

**Type species.**—*Gnomulus sumatranus* Thorell 1891 by ruling of the International Commission on Zoological Nomenclature (2001) (male lectotype, 3 female and 2 juvenile paralectotypes deposited in MSNG).

**Species account and distribution.**—48 species; known from the Himalayan region (central and east Nepal, NE-India), southern China, and from all over SE-Asia, as far east as Waigeo Island off the northwestern tip of New Guinea.

**Main characteristics.**—Glans penis proximad-directed, with a tendency for reduction and modification of different elements of the glans (Figs. 5–22); tarsal formula 2–2–3(2)–3(2); body small to large; chelicerae weak to massive, without ventral processes on 2<sup>nd</sup> and 3<sup>rd</sup> article; ventroproximal process on palpal tibia absent or developed as a low, rounded hump (distinct only in *G. sumatranus*); ventral process on palpal trochanter ventrad-directed, distad-directed or absent.

Genus *Caenoncopus* Martens & Schwendinger 1998

**Type species.**—*Oncopus cuspidatus* Schwendinger 1992 by original designation (male holotype and male paratype deposited in MHNG).

**Species account and distribution.**—Three species from Sumatra.

**Main characteristics.**—Glans penis hypertrophied, asymmetrical, proximad-directed (Figs. 23–28); tarsal formula 1–1–3(2)–3(2); body small; chelicerae weak, without processes on 2<sup>nd</sup> and 3<sup>rd</sup> article; no ventral process on palpal tibia; ventral process on palpal trochanter ventrad-directed.

Genus *Palaeoncopus* Martens & Schwendinger 1998

**Type species.**—*Palaeoncopus gunung* Martens & Schwendinger 1998 by original designation (male holotype and 3 female para-

types deposited in MHNG, 1 male and 1 female paratypes in MAR).

**Species account and distribution.**—Three species from Sumatra.

**Main characteristics.**—Glans penis distad-directed, not expandible; membranous tubes of glans reduced or absent (Figs. 31–35); tarsal formula 1-1-3-3; palpal trochanter with prodorsal cone; body small; chelicerae weak, without processes on 2<sup>nd</sup> and 3<sup>rd</sup> article; no ventral process on palpal tibia; ventral process on palpal trochanter distad-directed.

Genus *Biantoncopus* Martens & Schwendinger 1998

**Type species.**—*Biantoncopus fuscus* Martens & Schwendinger 1998 by original designation and monotypy (male holotype, 2 male and 3 female paratypes deposited in MHNG, 1 male and 1 female paratypes in MAR).

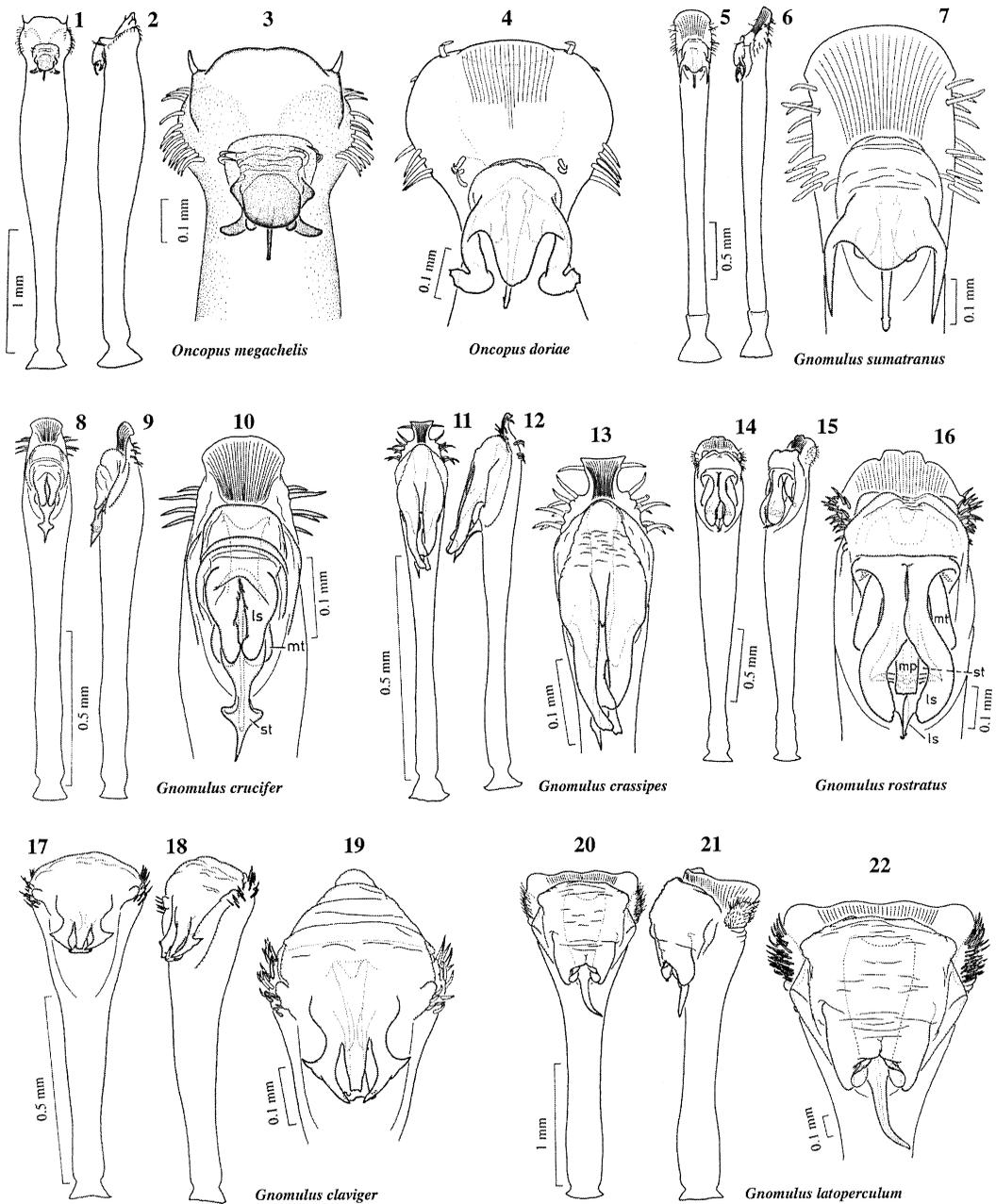
**Species account and distribution.**—One species from Leyte Island, the Philippines.

**Main characteristics.**—Glans penis distad-directed, expandible (Figs. 39–46); tarsal formula 2-2-3-3; body small; chelicerae weak, without processes on 2<sup>nd</sup> and 3<sup>rd</sup> article; no ventral process on palpal tibia; ventral process on palpal trochanter distad-directed.

## PENIS MORPHOLOGY

The oncopodid penis is of the hemolymph-pressure type, i.e. the truncus penis lacks muscles and the complex of glans sclerites (Figs. 55–56) is agitated by internal pressure. The shape of the subterminal glans is highly species-specific (with considerable interspecific variation in the genus *Gnomulus*; see Figs. 5–22) and its orientation and functional morphology allow us to draw generic boundaries in most cases (except between *Oncopus* and *Gnomulus*). Four major penis types can be distinguished (see also Martens & Schwendinger 1998):

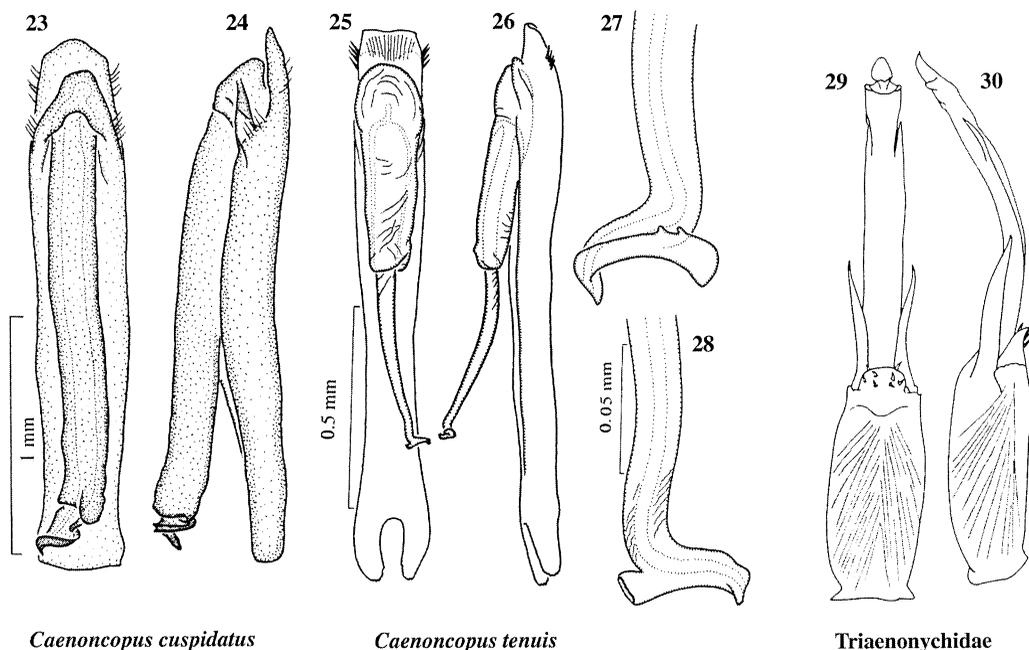
**Type 1.**—*Palaeoncopus* species possess a slender penis with a short, distad-directed glans (Figs. 31–35). Expansion of the glans in hot lactic acid causes the glans to spread away only slightly from the truncus without protruding the stylus (Fig. 34). Penes with a distad-directed glans are found in most laniatorean opilionids and therefore this type is probably plesiomorphic. A quite similar glans structure was illustrated for the phalangodid



Figures 1–22.—Penis type 3: 1–3. *Oncopus megachelis* Schwendinger; 4. *O. doriae* Thorell; 5–7. *Gnomulus sumatranus*; 8–10. *G. crucifer* Martens & Schwendinger; 11–13. *G. crassipes* Schwendinger & Martens; 14–16. *G. rostratus* Thorell; 17–19. *G. claviger* Schwendinger & Martens; 20–22. *G. latoperculum* Schwendinger & Martens. 1, 5, 8, 11, 14, 17, 20. Total penis, dorsal view; 2, 6, 9, 12, 15, 18, 21. Total penis, lateral view; 3, 4, 7, 10, 13, 16, 19, 22. Apex of penis, dorsal view.

*Haasus judaeus* Roewer 1949 (Figs. 37–38; see Martens 1976). The described species of *Palaeoncopus* all lack paired membranous tubes in their glans penis (Fig. 33), which is

certainly an apomorphic reduction, but an undescribed species from a cave on Sumatra still possesses a small pair of these tubes (Fig. 35). As the absence of this glans element was be-

*Caenoncopus cuspidatus**Caenoncopus tenuis*

Triaenonychidae

Figures 23–30.—23–28. Penis type 4: 23–24. *Caenoncopus cuspidatus*; 25–28. *C. tenuis* Martens & Schwendinger; 29, 30. *Cluniella minuta* Forster (Triaenonychidae) (from Hunt & Maury 1993). 23, 25, 29. Total penis, dorsal view; 24, 26, 30. Total penis, lateral view; 27, 28. Tip of stylus, different positions.

fore considered characteristic for *Palaeoncopus*, its diagnosis has to be changed.

A distad-directed, non-expandible glans with small membranous tubes was unexpectedly also found in an undescribed species from Nepal (Fig. 36), but we doubt if it is closely related to *Palaeoncopus*. Its stouter penis, different tarsal formula (2-2-3-3 instead of 1-1-3-3), larger body, and palpal trochanter with ventrad-directed ventral process but without prodorsal cone, rather indicate that the Nepalese species is a *Gnomulus* with reversal in its glans orientation.

**Type 2.**—The penis of *Biantoncopus fuscus* (Figs. 39–44) also has a distad-directed glans, but its structure is distinctly more complicated and—more importantly—it is expandible. In the resting position, the glans is retracted deeply into the truncus penis and during copulation (or artificially caused by hot lactic acid) internal pressure pushes the stylus forward and the membranous tubes are folded downwards (Figs. 41–42). This way the stylus can reach deeper into the female vagina during copulation.

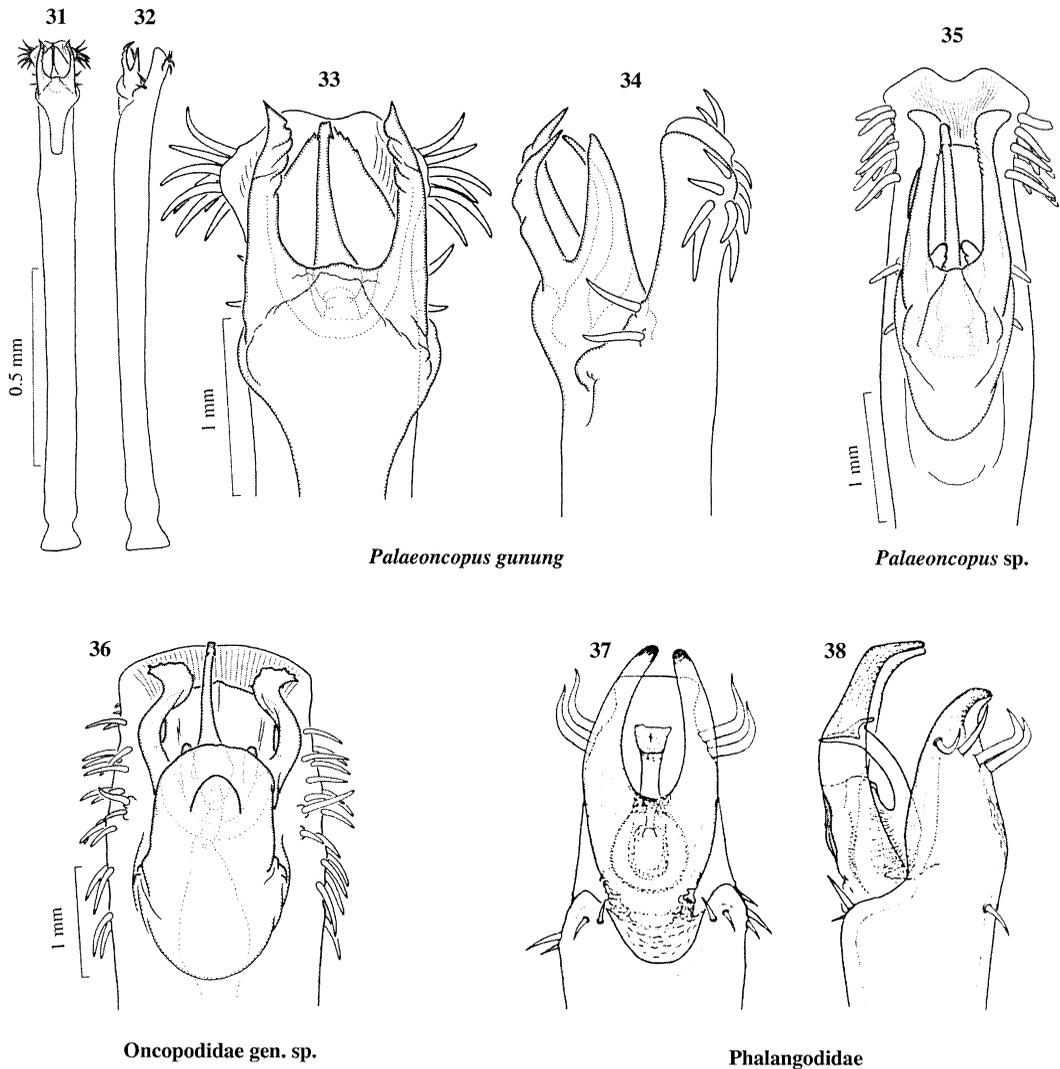
Penes with a distad-directed expandible glans are found in a number of laniatorean

families (e.g., Assamiidae, Podoctidae, Zalmoxidae, Biantidae), those of the Biantidae (Figs. 52–54; see also Martens 1986) are most comparable with *Biantoncopus*.

The penis of an undescribed oncopodid from Sarawak (Figs. 50–51) possesses a similar, expandible penis as *Biantoncopus fuscus*, but distinct differences in body shape and tarsal formula (1-1-2-2 instead of 2-2-3-3) place these two species generically apart.

An undescribed *Biantoncopus* sp. from the Philippines (Figs. 45–46) has its glans originating from far down the truncus penis and thus bears an additional resemblance with the penes of the Fissiphalliidae (Figs. 47–49; see also Martens 1988).

**Type 3.**—The species of *Gnomulus* and *Oncopus* show a penis form which was previously considered typical for the Oncopodidae. Here the glans is proximad-directed in its resting position (Figs. 1–22, 55, 56) and has to be folded upwards 180° for sperm transfer. This clearly presents an apomorphic situation. Considerable variation in the shape of penis and glans, with reduction of the median plate (Figs. 10, 13, 22) and enlargement of the stylus (Figs. 10, 13, 16, 22), exists within the



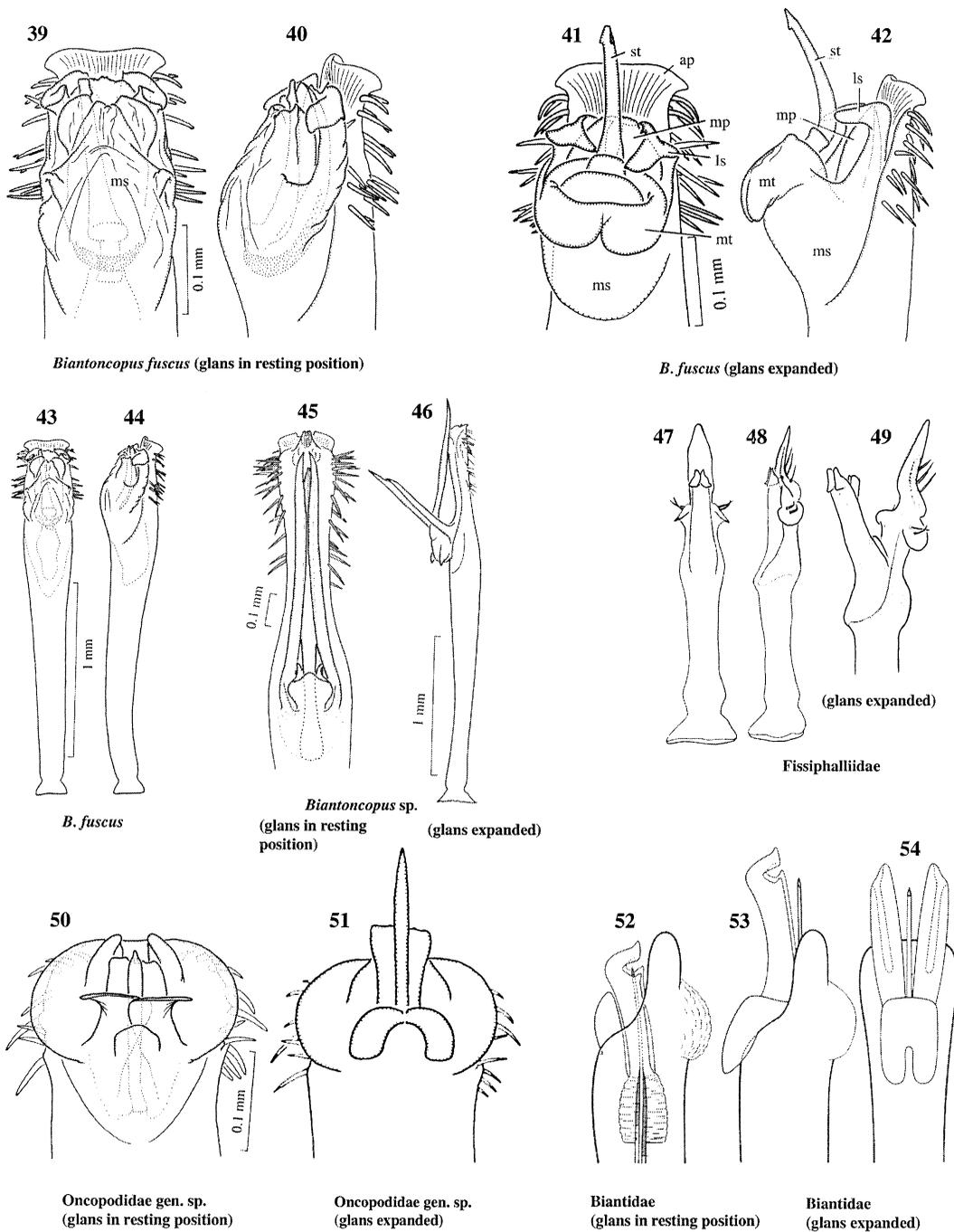
Figures 31–38.—31–36. Penis type 1: 31–34. *Palaeoncopus gunung*; 35. *Palaeoncopus* sp., an undescribed cave-dwelling species from northern Sumatra; 36. An undescribed oncopodid of uncertain relationships from Nepal; 37–38. *Haasus judaeus*, a phalangodid from Israel (from Martens 1976). 31. Total penis, dorsal view; 32. Total penis, lateral view (glans expanded); 33, 35–37. Apex of penis, dorsal view; 34 (glans expanded), 38. Apex of penis, lateral view.

species-rich genus *Gnomulus* (Figs. 5–22). The species of *Oncopus*, on the other hand, appear to be much more uniform in their penis structure (Figs. 1–4).

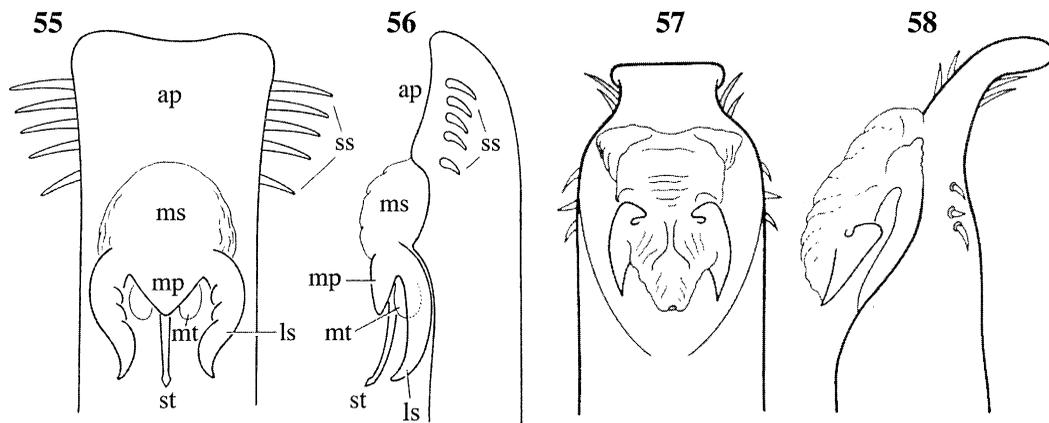
A comparable penis form with proximad-directed glans is found only in some species of the phalangodid genus *Scotolemon* Lucas 1860 in Europe (Figs. 57–58; see also Martens 1986).

**Type 4.**—*Caenoncopus* shows an extreme modification of the former penis type. Here

the stylus of the proximad-directed glans penis is asymmetrical and hypertrophied (Figs. 23–28), in one species almost reaching down to the base of the truncus (Figs. 23–24); the other elements of the glans are reduced (or fused with the stylus?). This penis type is highly apomorphic and truly unique among the Opiliones. Penes with a hypertrophied glans are elsewhere found in Triaenonychidae from Australia and South America (Figs. 29–30; see Hunt & Maury 1993), but there the



Figures 39–54.—39–46. Penis type 2: 39–44. *Biantoncopus fuscus*; 45–46. An undescribed *Biantoncopus* sp. from the Philippines; 50–51. An undescribed oncopodid from Sarawak; 47–49. *Fissiphallius sympatricus* Martens (Fissiphalliidae) (from Martens 1988); 52–54. Biantidae (from Martens 1986; generalized pattern). 43, 47. Total penis, dorsal view; 44, 46 (glans expanded), 48. Total penis, lateral view; 39, 41, 45, 50, 51, 54. Apex of penis, dorsal view (41, 51, 54 with glans expanded); 40, 42, 49, 53. Apex of penis, lateral view (42, 49, 53 with glans expanded). Abbreviations: ap = apex of truncus; ls = lateral sclerites; mp = median plate; ms = membranous socket; mt = membranous tubes; ss = subapical setae; st = stylus.

*Oncopus / Gnomulus*

## Phalangodidae

Figures 55–58.—55–56. Penis type 3: generalized scheme of an oncopodid penis of the *Gnomulus/Oncopus* type in resting position; 57, 58. *Scotolemon lespesi* Lucas (Phalangodidae) (from Martens 1986). 55, 57. Apex of penis, dorsal view; 56, 58. Apex of penis, lateral view. Abbreviations: ap = apex of truncus; ls = lateral sclerites; mp = median plate; ms = membranous socket; mt = membranous tubes; ss = subapical setae; st = stylus.

glans is terminal, distad-directed and symmetrical, and the truncus possesses a muscle (muscle-tendon type of penis). No close relationship exists between these two opilionid groups.

The Oncopodidae thus show the greatest variability in penis forms among opilionids known at present. In other laniatorean families we usually find only one penis type, with the exception of the polyphyletic Phalangodidae (Figs. 37, 38, 57, 58), the different penis forms of which, after a thorough revision, will probably be assigned to different families. In other opilionid families (e.g., Phalangiidae and Nemastomatidae), penis structures are quite diverse as well, but due to the muscle-

tendon principle of their penes, the glans is strictly positioned at the end of the truncus. There the variability in forms is expressed in, e.g., wing-like structures at the end of the truncus, highly diverse spinations of the glans, and/or a system of sclerites and membranes of a bulbous glans (Martens 1978). These modifications often look less spectacular than freely movable and inflatable glans structures in many “hemolymph-pressure Laniatores”, but they nevertheless represent the outcome of rich radiation processes as well.

**Hypothetical evolution of penis types in the Oncopodidae.**—How could this richness of penis forms in Oncopodidae have developed? A preliminary interpretation of genital

Table 1.—The characters (and their polarization) currently considered to be most informative for identifying phylogenetic relationships in Oncopodidae.

Characters	Plesiomorphic state	Apomorphic state
Glans orientation	distad-directed	proximad-directed
Glans function	non-expandible	expandible
Stylus size	thin	widened, hypertrophied
Stylus form	symmetrical	asymmetrical
Median plate	present	absent
Membranous tubes	present	absent
Truncus penis	narrow	apex widened
Anterior tarsi	1 article	2 articles
Posterior tarsi	3 articles	1 or 2 articles

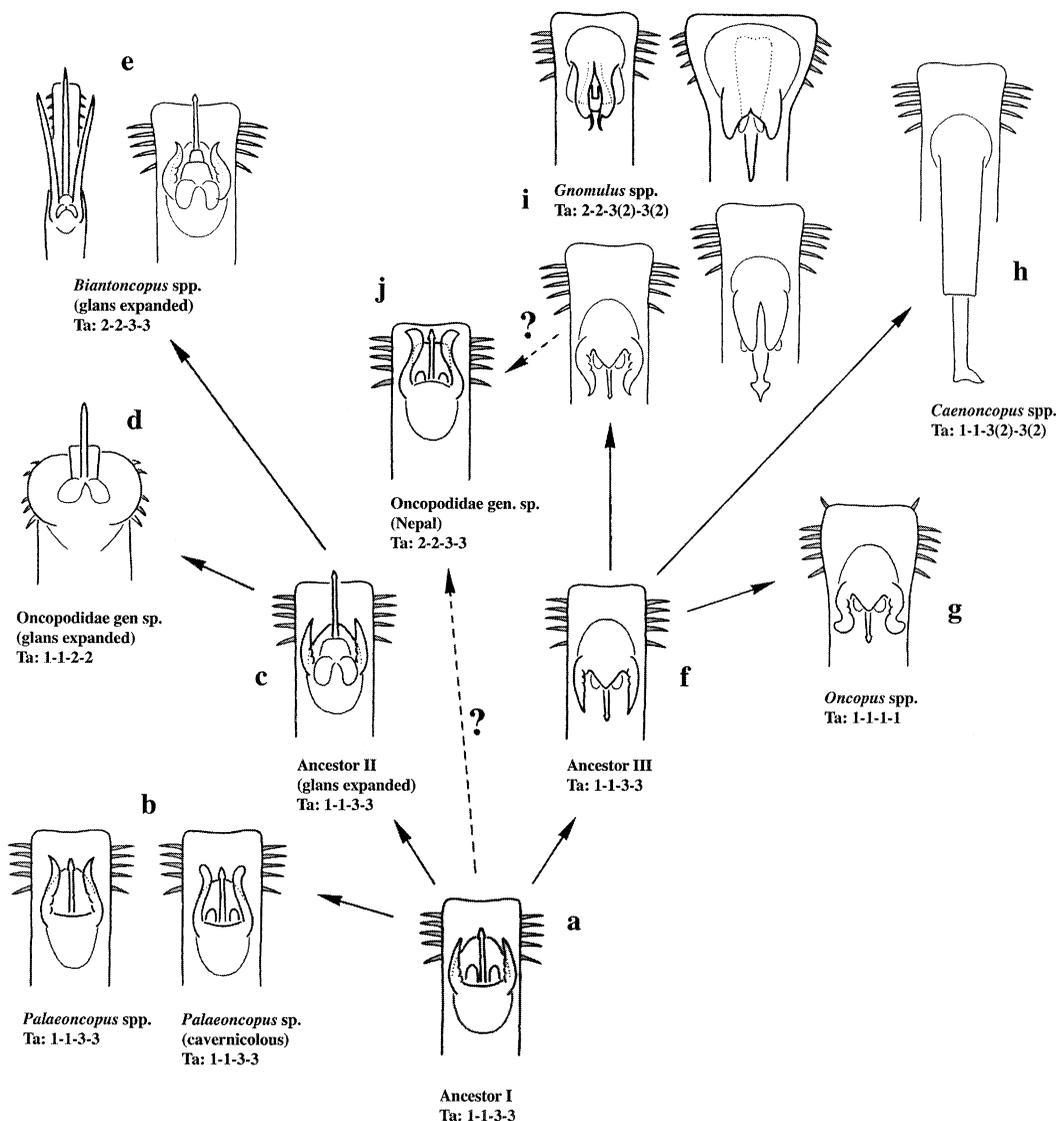


Figure 59.—Hypothetical evolution of the four penis types and presumed relationships in the Oncopodidae. Explanation given in the text (under "Hypothetical evolution of penis types in the Oncopodidae").

and external characters leads us to the following hypothetical evolution illustrated in Fig. 59 (modified after Martens & Schwendinger 1998: fig. 134). Shape of glans penis and tarsal formula are given as the most informative traits; character polarization is shown in Table 1.

From an ancestral taxon with a short, distad-directed, non-expandible glans and tarsal formula 1-1-3-3 (Fig. 59a), three phylogenetic lineages diverged. One development led to the basic *Palaeoncopus*, which remained quite

primitive apart from a reduction of the membranous tubes of the glans in 3 out of 4 species examined (Fig. 59b). A second lineage first acquired an expandable (still distad-directed) glans in a second, later ancestor (Fig. 59c) then split into terminal genera, one with a reduced number of tarsalia on posterior legs (Fig. 59d) and the other, *Biantoncopus*, with an increased number of tarsalia on anterior legs (Fig. 59e). The third lineage first had its glans transposed to a proximad-directed po-

sition in a third ancestral taxon (Fig. 59f) and then split into 3 extant genera: *Oncopus* with an unmodified glans and posterior tarsalia reduced to one article (Fig. 59g), *Caenoncopus* with a strongly modified glans (asymmetrical, hypertrophied stylus) and a primitive tarsal formula (posterior tarsalia apomorphically reduced to 2 in one species) (Fig. 59h) and *Gnomulus* with a primitive glans (but several modifications and reductions in individual species) and anterior tarsi increased to two (posterior tarsalia additionally reduced to 2 in a few species) (Fig. 59i).

The relationships of an undescribed species from Nepal are uncertain. Its distad-directed glans indicates a basic position within the Oncopodidae, whereas derived external characters (e.g., tarsal formula 2-2-3-3) point towards a more derived position (Fig. 59j). Due to striking resemblance in external morphology with species of the *Gnomulus aborensis*-group, we provisionally consider this undescribed taxon as an aberrant *Gnomulus*, which has undergone a reversal in its glans direction.

#### DISCUSSION

This interpretation of penis evolution also reflects our present view of relationships within the Oncopodidae. However, the picture that we draw is only preliminary and not the result of a thorough cladistic analysis. Some of the available but yet undescribed taxa have not yet been studied in great detail and further new oncopodids will probably be discovered in the near future, which may change the current picture considerably. A more detailed and thorough analysis of oncopodid relationships will thus be given at the end of our ongoing revision of this family.

At this stage, however, we feel safe to say that the Oncopodidae is, with respect to penis morphology, clearly the most diverse opilionid family. Penis forms range from quite primitive (in comparison with other Laniatores) to the most highly derived in opilionids, a range which in other Laniatores stretches over at least three different families.

Relationships with other families still remain unclear, but in view of primitive external morphology and a very wide range in penis morphology, the Oncopodidae can still be regarded as the sister group of the Gonyleptoidea, i.e. the remaining Laniatores with "hemolymph-pressure" penes. Consequently it

appears justified to claim superfamily rank for the Oncopodidae, as proposed by Martens (1976). This we have questioned in one of our preceding papers (Martens & Schwendinger 1998:502).

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