

## A new family of Laniatores (Arachnida : Opiliones) from the Afrotropics

Prashant P. Sharma<sup>A,C</sup>, Carlos E. Prieto<sup>B</sup> and Gonzalo Giribet<sup>A</sup>

<sup>A</sup>Museum of Comparative Zoology, Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA.

<sup>B</sup>Department of Zoology and Cell Biology, Faculty of Science and Technology, University of the Basque Country, PO Box 644, 48080, Bilbao, Spain.

<sup>C</sup>Corresponding author. Email: psharma@fas.harvard.edu

**Abstract.** Among Opiliones, Afrotropical lineages constitute some of the least studied groups in comparison with those endemic to other biogeographic provinces. Based upon morphological evidence, we erect Pyramidopidae, fam. nov. to distinguish a group of Laniatores from the family Phalangodidae. We review evidence from recent molecular phylogenetic studies that corroborate the independence of Pyramidopidae, fam. nov. from previously described families and support its sister relationship to another largely Afrotropical group, the family Assamiidae. The monotypic genus *Maiorerus* Rambla, 1993 is transferred to Pyramidopidae, fam. nov. The new family comprises 12 genera geographically restricted to Africa and the adjacent Canary Islands. Interfamilial relationships of the derived Laniatores are discussed in the context of gross and genitalic morphology.

**Additional keywords:** Canary Islands, *Conomma*, Grassatores, *Maiorerus*, Pyramidopidae, *Pyramidops*.

### Introduction

Opiliones from the Afrotropics are poorly known or in need of extensive systematic revision. In the suborder Cyphophthalmi, the family Ogoveidae, endemic to West Africa, has long been absent from molecular phylogenies, in contrast with the remaining mite harvestman families. Eupnoi from Africa have largely been ignored for phylogenetic study. Within the suborder Laniatores, Assamiidae is peppered with monotypic genera (~250 genera, for ~500 species), Samoidae may not be monophyletic (Pérez González and Kury 2007), and a particular lineage long ascribed to Phalangodidae is a demonstrably separate family. Here we redress the last of these oversights by distinguishing this group of Laniatores as a new family.

The systematics of the derived Laniatores (the infraorder Grassatores, *sensu* Kury 2003) are complex and challenging, owing both to the diversity of this group and their frequently convoluted taxonomic history. Multiple family-level lineages were collapsed into Phalangodidae (Roewer 1912, 1923, 1949a), which has transiently harboured species of nearly all of the Grassatores families (as presently defined) at some point in the 20th century. In addition, new species were often described in a prolific, but insufficiently detailed, manner, and placed in myriad monotypic genera with minimal justification (e.g. Roewer 1949a, 1949b).

Subsequent to decades of taxonomic revision, Phalangodidae *sensu stricto* is presently limited to ~100 species in 20 genera, distributed mostly in temperate North America and Europe

(Ubick and Briggs 1992, 2002, 2004, 2008). However, one taxonomic oversight that has persisted is the case of the ‘African phalangodids,’ sometimes referred to as the ‘*Pyramidops* group’ or ‘Pyramidopidae’ (e.g. Kury 2006; Hallan 2008; Giribet *et al.* 2010; Santos and Prieto 2010). Staręga (1992) first recognised the distinction between this lineage (Fig. 1) and the true Phalangodidae, remarking, ‘[t]he African genera assigned to this family-complex belong to an undescribed family’ (Staręga 1992: 289).

Previous efforts towards a molecular phylogeny of Laniatores, however, reconstructed a *Pyramidops* group genus, *Maiorerus*, as sister to Phalangodidae, discouraging the removal of the African ‘phalangodids’ from Phalangodidae (Giribet *et al.* 1999, 2002; Fig. 2). These previous assessments undersampled several Grassatores lineages, specifically the Afrotropical family Assamiidae. A more recent molecular phylogeny based on five molecular loci (Giribet *et al.* 2010) tentatively separated the African ‘phalangodids’ from Phalangodidae, but with uncertain placement of the former (and without support in parsimony analysis; Fig. 2). The most recent assessment of Laniatores phylogeny, including all described families and based on ten genes, reconstructs the African ‘phalangodids’ as sister to Assamiidae with significant support (Sharma and Giribet 2011). These results corroborate morphological evidence favouring a family status for the African ‘phalangodids’. To redress this taxonomic oversight, we present a formal description of the new family Pyramidopidae.



**Fig. 1.** *Pyramidops pygmaea* Loman, 1902 (ZMHB-11532) Bismarckburg (Togo). Lectotype, male (selected herein) in (a) dorsal, (b) lateral, and (c) ventral view. Scale bar = 0.50 mm.

## Materials and methods

### Abbreviations

Examined specimens are lodged in the following institutions:

MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, MA (USA).

MHNG = Muséum d'histoire naturelle de la Ville de Genève (Switzerland).

SMF = Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt-am-Main (Germany).

ZMHB = Institut für Systematische Zoologie, Museum für Naturkunde der Humboldt-Universität, Berlin (Germany).

ZUPV = Departamento de Zoología y Biología Celular, Universidad del País Vasco, Bilbao (Spain).

### Material and examination of specimens

Material examined is indicated in Table 1.

Penes were removed from everted male genitalia or, more frequently, from inside the body. In the latter case, the last intersternal membrane was cut from side to side, and sternites and sternal plate were cut along a paraxial line and bent towards the opposite side while the penile complex was extracted with microforceps. The penis was revealed by careful tearing of the muscle sheath and temporarily mounted in glycerine within an ex-professo (semi-cylindrical) excavated microscopic slide to minimise undesired inclinations and to facilitate rotations of the penis for appropriate drawing views. Genitalic drawings were obtained with a drawing tube on a Nikon Optiphot-2 microscope and photos were taken with a Nikon DS 5M camera on a Nikon SMZ-1500 stereomicroscope. Drawings were traced using China ink on translucent paper and scanned to 600 dpi. Photo series taken at different focal planes were assembled with the free software Combine Z5 (<http://www.hadleyweb.pwp.blueyonder.co.uk/CZ5/combinez5.htm>, verified August 2011).

### Taxonomy

Order **OPILIONES** Sundevall, 1833

Suborder **LANIATORES** Thorell, 1876

Family **PYRAMIDOPIDAE**, fam. nov.

Type genus: *Pyramidops* Loman, 1902, by present designation and monotypy.

Type species: *Pyramidops pygmaea* Loman, 1902, by monotypy.

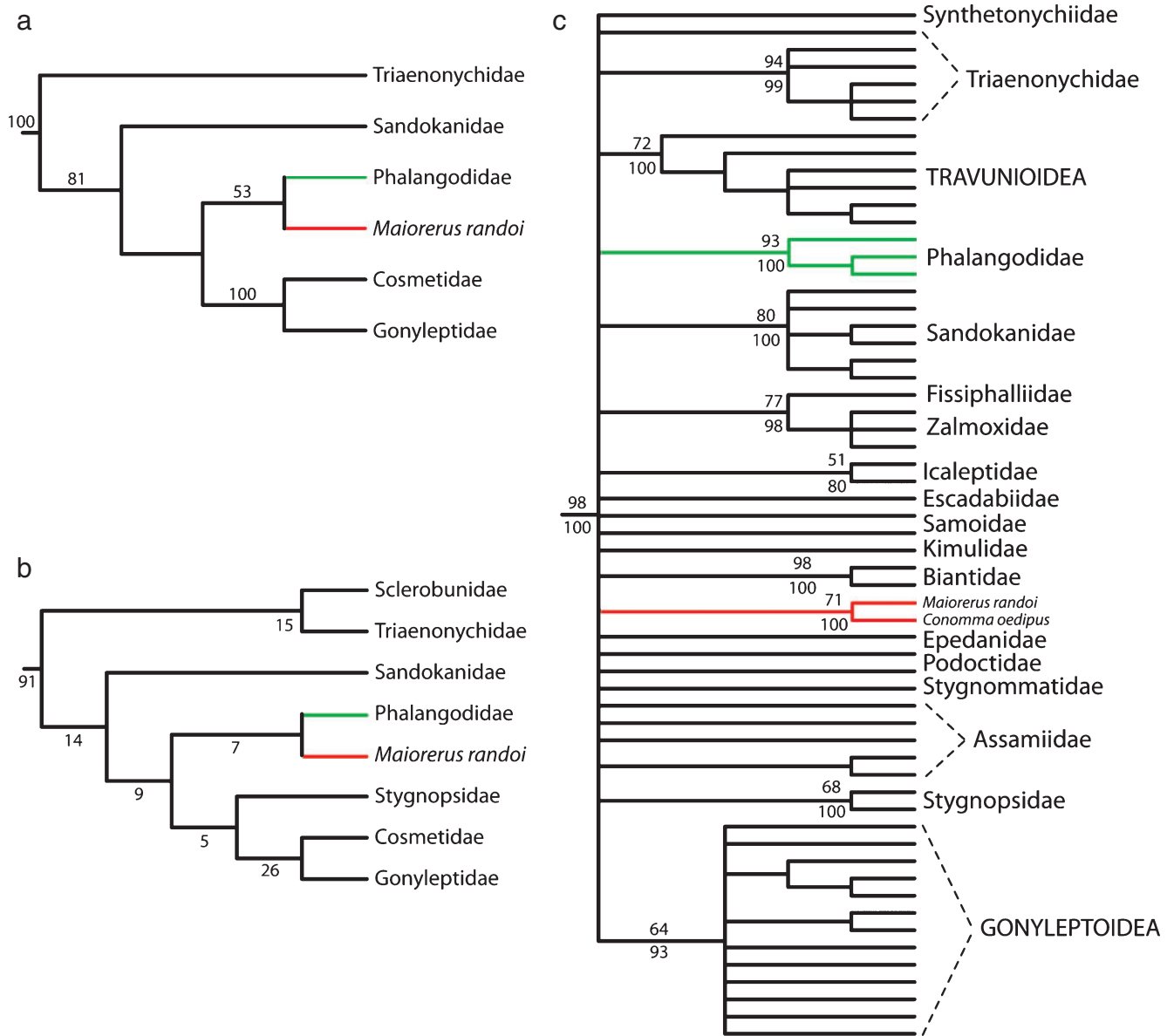
### Diagnosis

*Size.* Small to medium-sized Laniatores; body length: 1.5–5.5 mm.

*Dorsum.* Prosoma narrower than the dimorphic opisthosoma (usually maximum width at level of area I in males, at rear border of the scutum in females) and separated by a transverse groove. Ocularium large, conical or domed, at or very close to the frontal margin, entirely granular with conical tubercles or a single erect horn on top (posteriorly reclined in *Skufia parva* Roewer, 1949a). Opisthosomal portion of scutum (mesotergum) divided by transverse grooves into five areas, each with one or more rows of granules and, frequently, larger spines in some species.

*Venter.* Sternum narrowed and genital operculum enclosed by the oversized fourth coxae; opisthosoma with four free sternites, two fused sternites in a pre-anal plate and anal operculum. Spiracles hidden under the posterior margin of coxa IV.

*Chelicerae.* Not enlarged; basal segment with an inflated dorsodistal bulla.



**Fig. 2.** Hypotheses of relationships of Pyramidopidae (green) with respect to Phalangodidae (red). (a) Cladogram of Giribet *et al.* (1999), based on two molecular loci and morphology; numbers on nodes are bootstrap resampling frequencies. All terminals represented by one exemplar. (b) Cladogram from Giribet *et al.* (2002), based on two molecular loci and morphology; numbers on nodes are Bremer support values. Triaenonychidae, Sandokanidae and Phalangodidae represented by two exemplars each; all other lineages represented by one exemplar. (c) Strict consensus of two topologies (parsimony and maximum likelihood, unsupported nodes collapsed) from Giribet *et al.* (2010), based on five molecular loci; numbers on nodes are jackknife resampling frequencies (above; parsimony) and bootstrap resampling frequencies (below; maximum likelihood).

*Pedipalps.* Armed with megaspines. Trochanter with single ventral spine; femur with three large, and smaller interspersed, ventral spines, one to two mesodistal and a denticulate dorsal side; patella with two mesal spines; tibia with four spines; and tarsus with two to three spines on each side; pedipalpal claw stout.

*Legs.* Relatively short, with a leg II/scutum length ratio from 2 to 5; leg IV longer and stouter than leg II. Distitarsus I with two articles and II with three. Tarsal formula: commonly 4–5:5–14:5:6, but reduced to 3:5:4:5 in *Skufia parva* Roewer, 1949a; tarsus II with 16–18 articles in *Opconomma*

*hirsuta* Roewer, 1927 or 20 in *Conomma troglodytes* Lawrence, 1952 (Lawrence 1952). Tarsi III and IV with two simple claws; pseudonychium and scopula absent.

*Male genitalia.* Ventral plate undivided and highly variable (from linguiform to almost annular); dorsum and ventral plate of truncus typically with large paired setae (with exceptions); glans shape highly variable, lacking prominent parastylar conductors.

*Sexual dimorphism.* Apart from the stronger appearance of body and appendages in males, in addition to larger size, main secondary sexual characters are usually in leg II or leg IV. When in

**Table 1.** List of material examined, including accession numbers, type status, and collection localities

Species	Accession number	Specimens	Types	Locality
<i>Conomma</i> cf. <i>cassinium</i> Roewer, 1949a	ZUPV-2408	6 M, 7 F	Non-types	The Gambia
<i>Conomma feae</i> Roewer, 1927	SMF-RI/1414-4	2 M, 1 F	Syntypes	Príncipe Island, São Tomé and Príncipe
<i>Conomma feae</i> Roewer, 1927	SMF-RII/43/3-4	9 M, 8 F	Syntypes	Príncipe Island, São Tomé and Príncipe
<i>Conomma</i> cf. <i>forte</i> Loman, 1902	SMF-RI/230-4	1 M	Non-types	Sekondi, Ghana
<i>Conomma minimum</i> Roewer, 1912	SMF-RI/237-4	1 M, 1 F	Syntypes	Misahohe, Togo
<i>Conomma minimum</i> Roewer, 1912	MHNG-w/o number	1 M	Non-types	Yaoundé Mts, Cameroon
<i>Conomma oedipus</i> Roewer, 1949a	ZUPV-2306	6 M, 1 F	Non-types	Bioko Island, Equatorial Guinea
<i>Conomma princepeum</i> Roewer, 1949a	SMF-RII/84/20-4	HT + 10 M, 9 F	Holotype	Príncipe Island, São Tomé and Príncipe
<i>Opconomma hirsuta</i> Roewer, 1927	SMF-RII/42-4	9 M, 7 F	Syntypes	São Tomé Island, São Tomé and Príncipe
<i>Pyramidops albimana</i> Roewer, 1927	SMF-RII/58-4	1 M, 3 F	Syntypes	Bioko Island, Equatorial Guinea
<i>Pyramidops congonis</i> Roewer, 1949a	SMF-RII/5055-4	1 M	Holotype	Leopoldville (Kinshasa), DRC
<i>Pyramidops globipes</i> Roewer, 1927	SMF-RII/94/25-4	1 M	Holotype	Cameroon
<i>Pyramidops major</i> Roewer, 1949a	SMF-RII/8726-4	2 M	Holotype	Cameroon
<i>Pyramidops pygmaea</i> Loman, 1902	SMF-RII/5003/100-4	5 M, 8 F	Syntypes	Bismarckburg, Togo
<i>Pyramidops pygmaea</i> Loman, 1902	ZMHB-11532	13 M, 23 F	Syntypes	Bismarckburg, Togo

leg II, the tibia has a distoventral swelling of variable profile showing specialised bristles; when in leg IV, sexual characters may include trochanteral spurs, femoral tubercles and retrolateral and ventral rows (or isolate) tibial tubercles.

#### Included genera

***Aburiplus*** Roewer, 1949a. Monotypic for *Aburiplus trochanteralis* Roewer, 1949a, which was described based on a male (genitalia unknown) from Ghana.

***Conomma*** Loman, 1902. Erected for *Conomma forte* Loman, 1902, which was based on a single female; currently includes 20 species but the penis is known for two closely related species only (Kauri 1985). Penile disparity (Figs 4, 5) suggests that the current composition will be dismantled in future. Within the family, the geographical range is widest in this genus, crossing tropical Africa from the west (*Conomma cassinium* Roewer, 1949a) to the east (*Conomma orientale* Roewer, 1949a).

***Kwangonia*** Kauri, 1985. Monotypic for *Kwangonia feshiensis* Kauri, 1985, from the Feshi Territory and Kivu Province (Democratic Republic of Congo). Penis known from a rough sketch.

***Maiorerus*** Rambla, 1993. Monotypic for *Maiorerus randoi* Rambla, 1993 from a volcanic tube from Fuerteventura (Canary Islands). The only eyeless pyramidopid known.

#### Remarks

A handful of external morphological characters of *Maiorerus randoi* suggest a relationship to true Phalangodidae (e.g. *Banksula*, Ubick and Briggs 2002), such as the tarsal formula, the spination of the dorsal femur, and anophthalmy (absence of eyes). However, tarsal formula and spination have evolved convergently in Laniatores and may not be indicative of interfamilial relationships (Sharma and Giribet 2009; Giribet *et al.* 2010). Anophthalmy, though relatively rare in Laniatores, has also been acquired independently by multiple lineages, especially in cave-adapted species, as is the case of *Maiorerus* (e.g. Briggs 1971, 1974; Rambla 1993; Rambla and

Juberthie 1994; Ubick and Briggs 2002, 2008; Pinto-da-Rocha and Kury 2003; Hedin and Thomas 2010).

Examination of the genitalia of this species indicates gross differences from those of typical phalangodids. *Maiorerus* lacks the prominent parastylar lobes of typical Phalangodidae (Ubick and Briggs 1992, 2002, 2004, 2008) and the divided ventral plate characteristic of *Scotolemon* (Rambla 1993). The structure of the genitalia suggests inclusion within Pyramidopidae, but the relatively smaller genitalic setae suggest placement outside other described pyramidopid genera. Molecular sequence data from five molecular loci also support the inclusion of *Maiorerus* in Pyramidopidae, as this genus is consistently recovered sister to a pyramidopid (*Conomma oedipus*) in phylogenetic analyses (Giribet *et al.* 2010).

***Micronimba*** Roewer, 1953. Described from Mount Nimba (Ivory Coast) for *Micronimba bicurvata* Roewer, 1953, all the other three described species have the same geographical incidence. Genitalia of all species unknown.

***Neoconomma*** Özdikmen, 2006. Monotypic for *Metaconomma dentipes* Kauri, 1985, which was described based on a single female from the Feshi Territory (Democratic Republic of Congo).

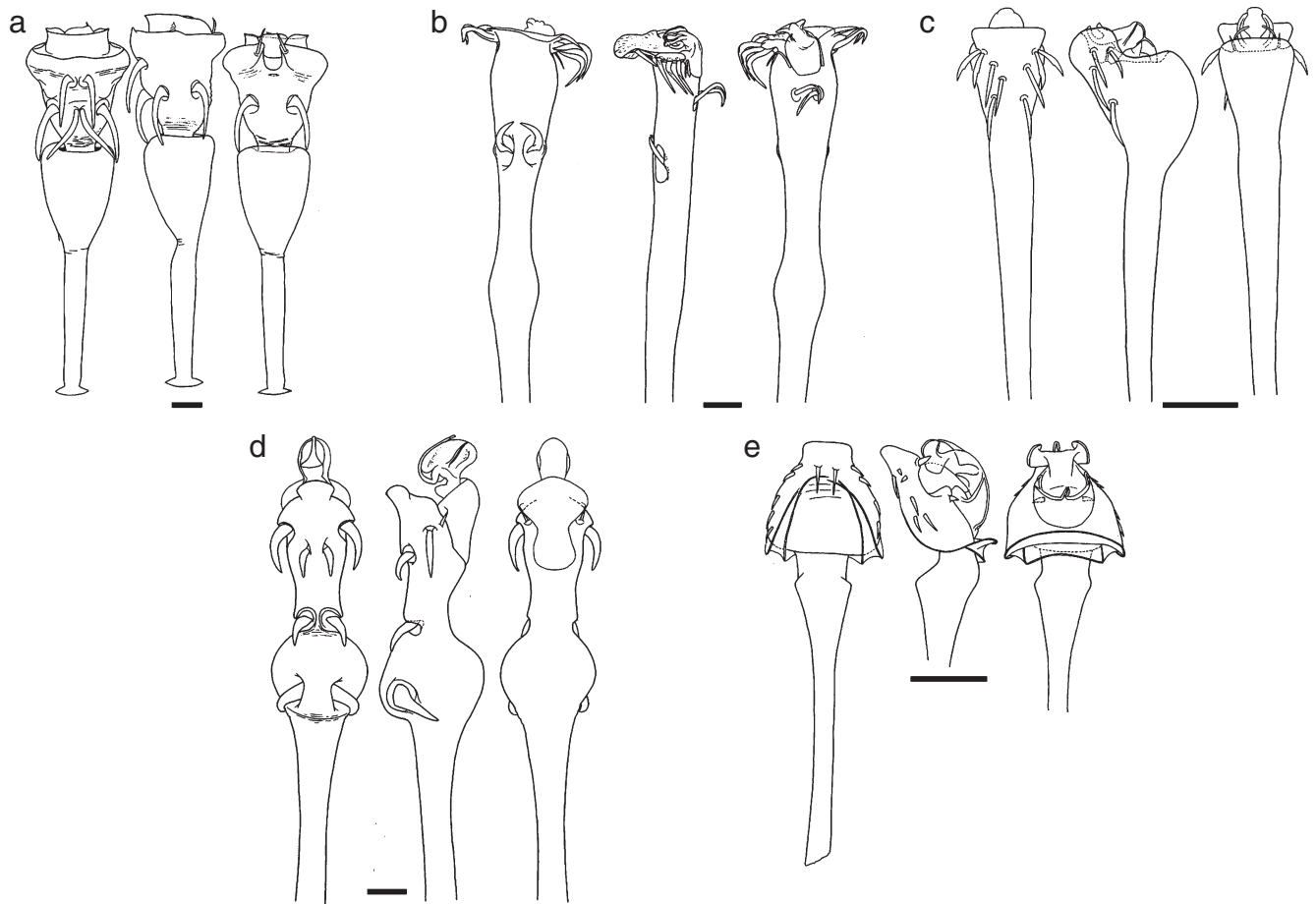
***Opconomma*** Roewer, 1927. Monotypic for *Opconomma hirsuta* Roewer, 1927, which was described from São Tomé. A drawing in Fig. 4 includes the first illustration of *Opconomma* genitalia.

***Opconommula*** Roewer, 1949a. Monotypic for *Opconommula spinosa* (Roewer, 1927), which was described, contrary to what was originally stated, based on a single female (unpublished observation by C. E. P.) from Cameroon.

***Proconomma*** Roewer, 1961. Described for *Proconomma kahuzi* Roewer, 1961 (genitalia unknown), this and another species (based on a single female) are from Kivu Province.

***Pyramidops*** Loman, 1902. Described for *Pyramidops pygmaea* Loman, 1902 from a large series (almost 50 syntypes between SMF and ZMHB) from Bismarckburg (colonial name of





**Fig. 3.** Exemplars of male genitalia in *Pyramidops*, in ventral, lateral and dorsal views (left to right): (a) *Pyramidops albimana* Roewer, 1927; (b) *Pyramidops congonis* Roewer, 1949a; (c) *Pyramidops globipes* Roewer, 1927; (d) *Pyramidops major* Roewer, 1949a; (e) *Pyramidops pygmaea* Loman, 1902. Scale bar = 100  $\mu$ m.

Yegu , Togo), currently includes another 10 species ranging from Ghana to the south of the Democratic Republic of Congo. Rough sketches of the penis are known for two species only (Lawrence 1957, 1958). Penile disparity (Figs 3, 5) suggests that the current composition will be dismantled in future.

As per Article 30.1.4.3, all genus-group names ending in ‘-ops’ are to be treated as masculine, regardless of their treatment by the describing author. However, we follow do Amaral (1975), who contended that ‘-ops’ as suffix of generic names in zoology could not correspond to the ancient Greek form  $\omega\psi$  (-ops), since this form is a defective noun. Lexigenically, ‘-ops’ results from a contraction of ‘-opsis’ and all ‘opsis’, as well as other names ending in ‘-sis’ have always been considered feminine in Greek. We therefore maintain *Pyramidops* as feminine.

***Skufia*** Roewer, 1949a. Monotypic for *Skufia parva* Roewer, 1949a, which was described from a single male (genitalia unknown) from Misah he (Togo), it is the only member of this family with a reduced tarsomere number in legs III and IV.

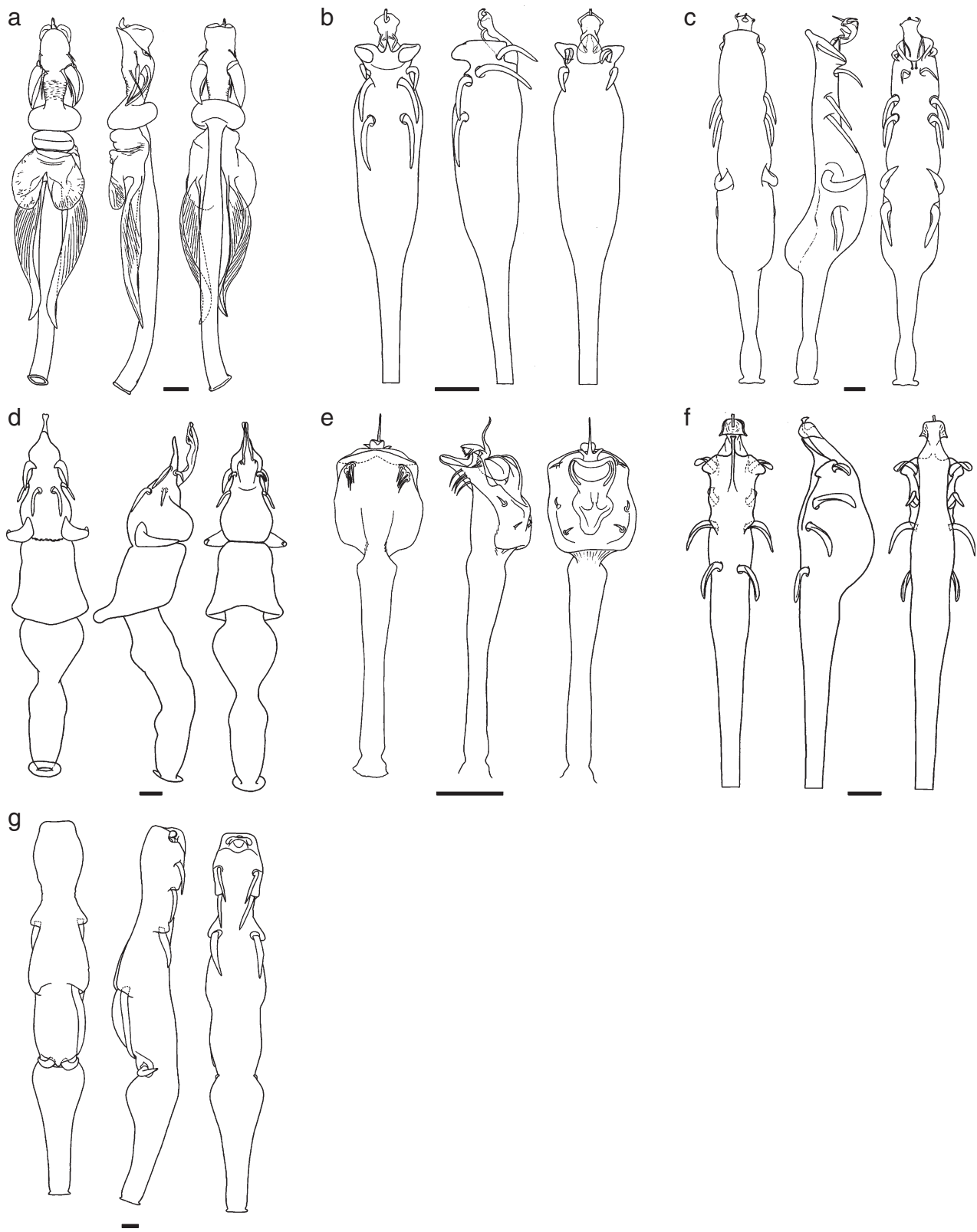
***Tonkouinatus*** Roewer, 1953. Monotypic for *Tonkouinatus magnituber* Roewer, 1953, which was described from a single male (genitalia unknown) from Mt Tonkoui (Ivory Coast).

Judging from external morphology, it seems to be a distantly related group.

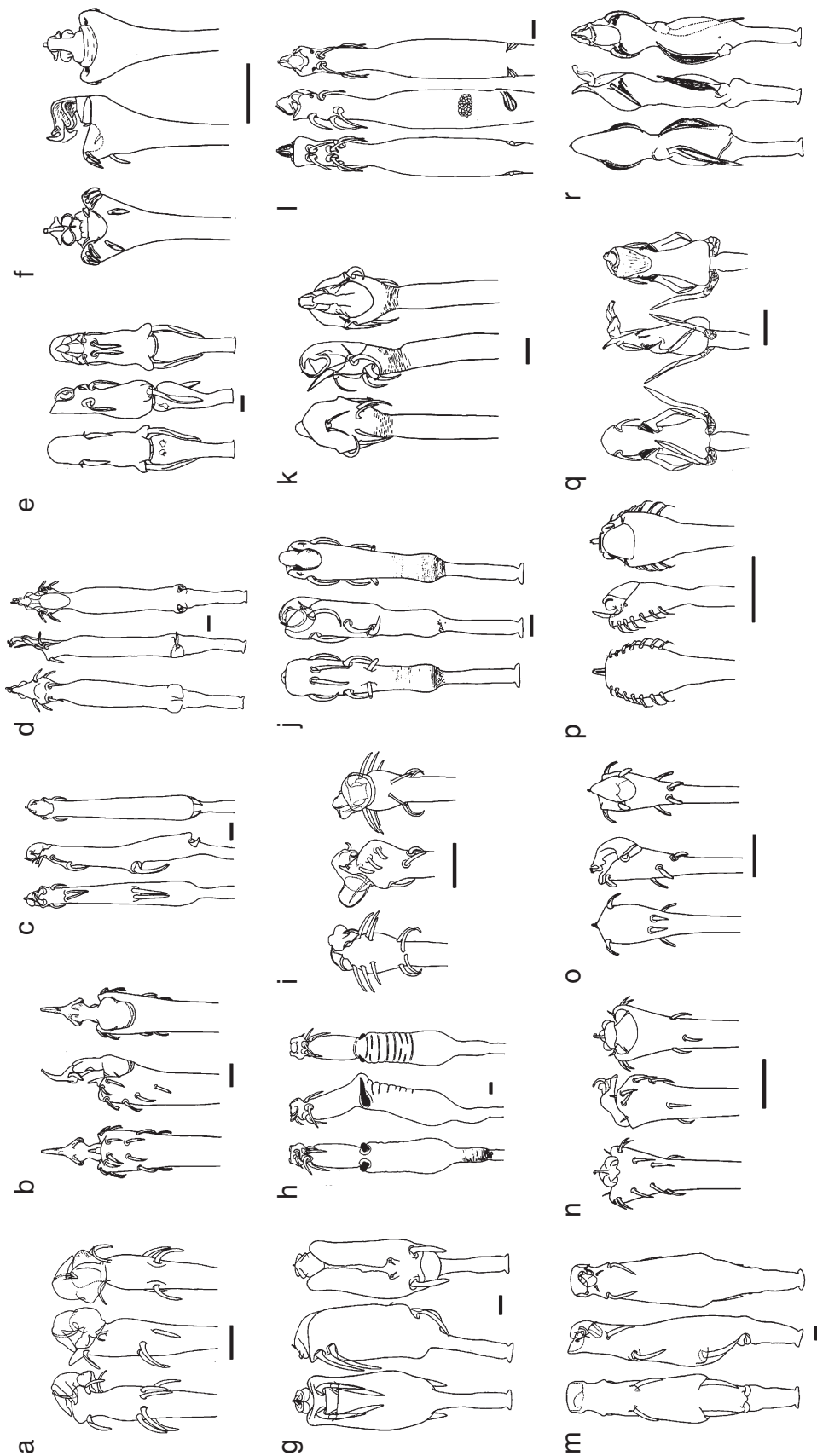
#### Excluded genera

***Hirstienus*** Roewer, 1949c (Biantidae, **new familial assignment**). Monotypic for *Phalangodes? nanus* Hirst, 1913 and described from a single female from Mah  (Seychelles Islands), it was considered to belong in Pyramidopidae by Star ga (1992). Judging from the description, tarsal formula and original figures, this species does not belong in this family. The most significant characters (size, frontal hump, size and position of the ocularium or palpal armature) match the description of *Samoa sechellana* Rambla, 1984, also described from female specimens (Rambla 1984). Although Hirst (1913) did not record the presence of scopulae on distitarsi III and IV, we believe the two are synonyms or very closely related species. In accordance with with P rez-Gonz lez (2006), who placed *Samoa sechellana* in Biantidae (Mitraceratinae), we consider *Hirstienus* to be another Malagasy–Seychellan biantid genus.

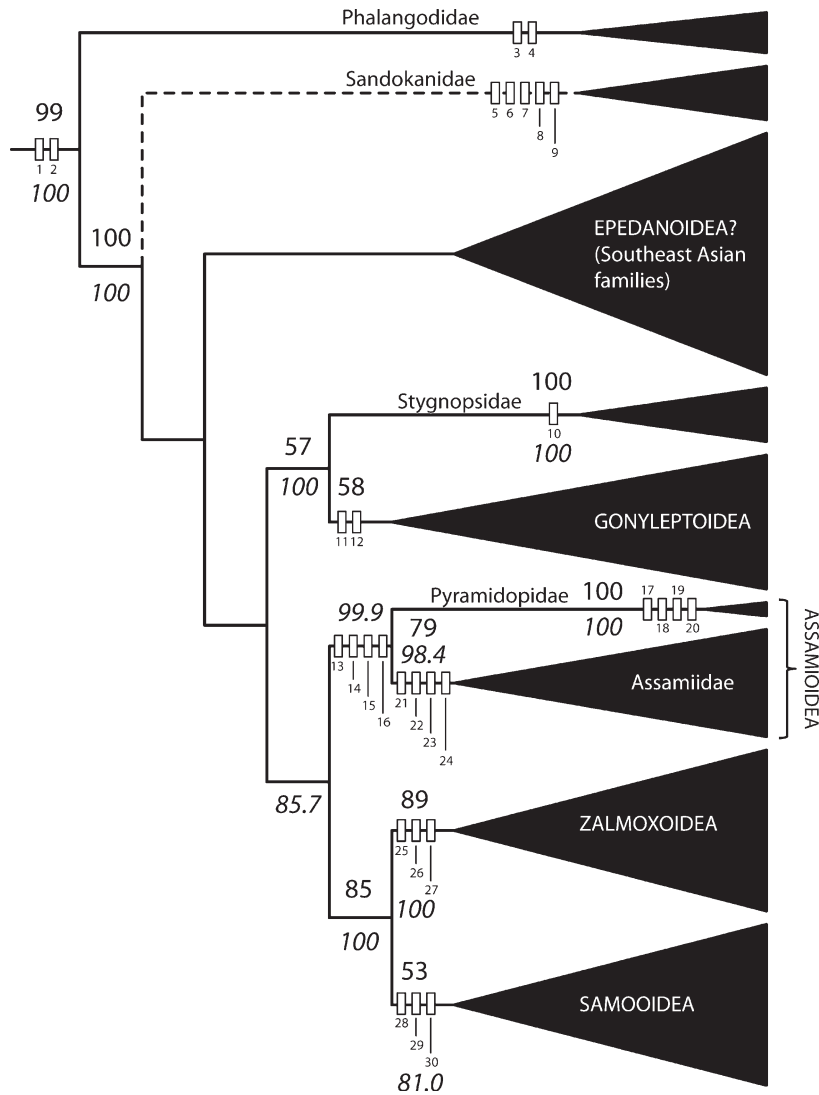
***Nimbadus*** Roewer, 1953 (*incertae sedis*). Monotypic for *Nimbadus femoralis* Roewer, 1953 from Mount Nimba (Ivory



**Fig. 4.** Exemplars of male genitalia in *Conomma* and *Opconomma*, in ventral, lateral and dorsal views (left to right): (a) *Conomma* cf. *cassinium* Roewer, 1949a; (b) *Conomma feae* Roewer, 1927; (c) *Conomma* cf. *forte* Loman, 1902; (d) *Conomma minimum* Roewer, 1912; (e) *Conomma oedipus* Roewer, 1949a; (f) *Conomma principeum* Roewer, 1949a; (g) *Opconomma hirsuta* Roewer, 1927. Scale bar = 100  $\mu$ m.



**Fig. 5.** Exemplars of male genitalia of undescribed Pyramidopidae species, in ventral, lateral and dorsal views (left to right): (a) *Conomma* sp. from Mt Ngoa-Ekelé (Cameroon); (b) *Conomma* sp. from Ototomo Forest (Cameroon); (c) *Conomma* sp. from Buea (Cameroon); (d) *Conomma* sp. from Annobón Island (Equatorial Guinea); (e) *Conomma* sp. from Musola, Bioko Island (Equatorial Guinea); (f) *Pyramidops* sp. from Monte Alén National Park (Equatorial Guinea); (g) *Pyramidops* sp. from Alto de Nsork National Park (Equatorial Guinea); (h) *Pyramidops* sp. from Corisco River (Equatorial Guinea); (i) *Pyramidops* sp. from Alto de Nsork National Park (Equatorial Guinea); (j) *Pyramidops* sp. from Corisco Island (Equatorial Guinea); (k) *Pyramidops* sp. from Congie River (Equatorial Guinea); (l) *Pyramidops* sp. from Corisco Island (Equatorial Guinea); (m) *Opconomma* sp. from São Tomé Island (São Tomé and Príncipe); (n) Pyramidopidae, gen. sp. from Edyabe (Equatorial Guinea); (o) Pyramidopidae, gen. sp. from Acomibe (Equatorial Guinea); (p) Pyramidopidae, gen. sp. from Edyabe (Equatorial Guinea); (q) Pyramidopidae, gen. sp. from Edyabe (Equatorial Guinea); (r) Pyramidopidae, gen. sp. from Cogo (Equatorial Guinea). MHNG: a, b, m; MRAC: c; ZUPV: d, f–l, o–r; MNCN: e; SMF: n. Scale bar = 100 µm.



**Fig. 6.** Cladogram of Laniatores relationships, redrawn from Sharma and Giribet (2011). Infraorder Insidiatores (Triaenonychoidea, Travunioidea and Synthetonychiidae) not shown. Numbers on nodes are bootstrap resampling frequencies (above; maximum likelihood) and posterior probability values (below and italicised; Bayesian inference). Dashed line indicates ambiguity in the placement of Sandokanidae (alternatively placed as shown or as nested within 'Epedanoidea'). Morphological characters on nodes are as follows: (1) two tarsal claws on walking legs III and IV; (2) hydraulic penis; (3) telescoping or unfolding glans with prominent parastylar lobes (two or more); (4) megaspines on pedipalpal segments ventrally and ventrolaterally, with dorsal surface of pedipalpal femur smooth and unarmed; (5) scutum completum; (6) reduced tarsalia; (7) projections of carapace region bridging prosoma and opisthosomal tergite 1; (8) glans of penis composed of a membranous socket bearing a pair of lateral sclerites connected by a median plate; (9) ovipositor unsegmented and laterally compressed; (10) follis of penis multi-folded and partially eversible; (11) ventral plate of penis robustly defined; (12) simplified penis with glans free and subapical in the truncus; (13) Number of tarsomeres in distitarsus I (2–3) and II (3–4); (14) pedipalpi not subchelate; (15) mesotergum variably armed with tubercles or apophyses; (16) penis with poorly defined ventral plate and large paired setae; (17) bulbous ocularial horn at or close to anterior margin of carapace; (18) megaspines on pedipalpal segments ventrally and ventrolaterally, with dorsal surface of pedipalpal femur denticulate; (19) greatly enlarged and tumid pars distalis; (20) glans of penis with simple lobes and no eversible sac; (21) odd number of spines at anterior margin of carapace; (22) pedipalpal femur with a ventral row of tubercles and no megaspines; (23) pedipalpi crossed at rest; (24) glans with spined and eversible sac, and a gland at the base of the stylus; (25) incrassate leg IV segments, especially in males; (26) sexually dimorphic tegumental gland openings on tibia II; (27) small ocularium bearing eyes removed from anterior margin of carapace; (28) penis with capsula interna eversible and formed by a pair of conductors and a stylus; (29) sexually dimorphic and tumid metatarsus III; (30) scopulae on legs III and IV.





Fig. 7. Map of Africa showing known localities of Pyramidopidae species (red icons).

Coast), was placed among the pyramidopid genera by Starega (1992). But some features, such as tarsal formula (2:3:4:4), centred position of the ocularium, and armature of femur I (Roewer 1953) are strong evidence against its inclusion in Pyramidopidae. These features suggest a close relationship with the samoid *Microconomma* Roewer, 1915 and it is hypothesised that careful re-examination of types will show scopulae on distitarsi III and IV (a synapomorphy of Samoidae; Pérez González and Kury 2007).

## Discussion

### *Systematics of Pyramidopidae*

Monophyly of Pyramidopidae is supported by the bulbous, prominent, sexually monomorphic ocularial horn; denticulation on the dorsal surface of the pedipalpal femur, with ventral and ventrolateral spination on all other pedipalpal

segments; and unmodified tarsi (free of pseudonychia or scopulae). Moreover, while variable in shape, the genitalia of all Pyramidopidae are characterised by a tumid pars distalis adorned with large, paired setae; an undivided ventral plate; and a glans with simple lobes, but with no eversible sac.

However, genitalic diversity within the family Pyramidopidae is so great that it is difficult to delimit species groups. In particular, formally described species in *Conomma* or *Pyramidops* have such great genitalic disparity that we are unable to sort the undescribed species (Fig. 5) into these genera without ambiguity. Ongoing revision of Pyramidopidae will address the monophyly of constituent genera.

### *Inclusion in Assamiioidea*

Results of the most recent phylogenetic analysis of Laniatores (Sharma and Giribet 2011) support the sister relationship of Pyramidopidae and Assamiidae – constituents of the

superfamily Assamiioidea (*sensu* Sharma and Giribet 2011). The relationships recovered closely accord with the morphology of these two families (e.g. Bauer and Prieto 2009; Fig. 6). Pyramidopidae are united with Assamiidae by the number of tarsomeres in distitarsus I (two in Pyramidopidae, two or three in Assamiidae) and distitarsus II (three in Pyramidopidae, three or four in Assamiidae). Both lineages have pedipalpi that do not form a subchela. The mesotergum of both lineages is variably armed with tubercles or large apophyses. Finally, the genitalia of both lineages are characterised by an undivided ventral plate, several pairs of typically large setae that do not encircle the capsula interna (as in Epedanidae; Suzuki 1976, 1985), and a simplified glans with small lobes.

Upon morphological comparison, pyramidopids are unlikely to be related to other Laniatores families or superfamilies (Fig. 6). The lack of a *scutum completum* (fusion of all opisthosomal tergites with the prosoma), among many other characters, suggests no affinities to Sandokanidae. The absence of a telescoping/unfolding glans with prominent parastylar conductors indicates a distant relationship to Phalangodidae and some lineages of ‘Epedanoidea’<sup>1</sup> (Petrobunidae; Sharma and Giribet 2011). Similarly, the undivided ventral plate of the pyramidopid penis, as well as the absence of a ring of setae surrounding the glans, disfavors relationship to other lineages of Epedanoidea (Tithaeidae, Podoctidae and Epedanidae; Sharma and Giribet 2011). The absence of a well defined ventral plate or a multi-folded follis similarly excludes pyramidopids from the clade Gonyleptoidea + Stygnopsidae (Sharma and Giribet 2011). Pyramidopidae also lack (1) scopulae on legs III and IV, (2) sexually dimorphic metatarsi III, or (3) a penile calyx with a pair of conductors flanking the stylus – consistent with placement outside Samooidea. Finally, the absence of a capsula interna modified into a stragulum (articulated to the truncus like a jackknife) is dissuasive of a relationship to Zalmoxoidea.

#### Exclusion from Assamiidae

The inclusion of Pyramidopidae in Assamiidae (i.e. as an early diverging lineage) is an alternative to the erection of a new family-level lineage. However, this treatment is undesirable because it obscures a clear diagnosis of the resulting Assamiidae, as Pyramidopidae violate many of the synapomorphies of assamiids. First, one of the readily apparent characteristics of African Assamiidae is an odd number of spines at the anterior margin of the carapace (Kury 2007). In contrast, the anterior carapacial margin of Pyramidopidae is smooth. Second, the pedipalpal femur of Assamiidae bears a single ventral row of tubercles and lacks megaspines altogether (the pedipalpi of Assamiidae are homogeneous in this respect). By contrast, the pedipalpal femur of Pyramidopidae is armed with megaspines on the ventral and/or ventrolateral surfaces; and a row of tubercles occurs on the dorsal surface of this segment. Third, the male genitalia of Assamiidae bears a glans mounted on a sac, the distal part of which is eversible and typically bears spines (‘spiny funnel’ or *Stacheltrichter*, *sensu* Martens, 1977). The stylus of

Assamiidae also bears a gland (*Drüsenkomplex*, *sensu* Martens, 1977) that rests inside the everted sac when the stylus is extruded. Pyramidopidae lack both these structures.

Though the inclusion of Pyramidopidae in Assamiidae would still result in a monophyletic taxon (Sharma and Giribet 2011), the resulting entity would be poorly defined and difficult to diagnose. As presently defined, both Pyramidopidae and Assamiidae are morphologically distinct entities that are readily recognisable and diagnosable, i.e. systems of utility for opilionologists, and promote the stability of a taxon already well delimited and recognised (e.g. Pinto-da-Rocha and Giribet 2007). For these reasons, we consider Pyramidopidae to be a family-level lineage independent of Assamiidae.

#### Geographic distribution

The geographic distribution of the family Pyramidopidae ranges from Guinea-Bissau and The Gambia (the far west of tropical Africa) to the Rift Valley and Katanga (east and south of the Democratic Republic of Congo, respectively), including the four islands of the Gulf of Guinea (Fig. 7). Outside this area, there are two records only, Fuerteventura (Canary Islands) for *Maiorerus randoi* and Moshi (Tanzania) for *Conomma orientale*. Both sites can certainly be considered relictual areas. Fuerteventura, which is 1800 km north of the tropical belt, has a sub-Saharan climate and is the oldest island in the archipelago, dating back 20.6 million years (Carracedo *et al.* 1998). Fossilised remnants of laurisilva ecosystems from the Miocene on neighbouring Gran Canaria suggest that Fuerteventura may once have been a high and lush island as well, but subsequently underwent erosion by trade winds (Anderson *et al.* 2009). Additionally, *Maiorerus randoi* does not occur in caves other than Cueva del Llano (Pedro Oromí, pers. comm.). The dynamics of arthropod diversity on another group of Atlantic islands, the Azores, suggests that the number of endemic cavernicolous species declines with the age of the island, due to erosive processes (Borges and Hortal 2009). If this phenomenon has occurred in the Canaries, *Maiorerus randoi* may represent the remnant of a formerly diverse lineage of Pyramidopidae that inhabited the erstwhile extensive cave systems of Fuerteventura.

Moshi is on the southern slopes of Mt Kilimanjaro, but this locality is within the Miocene range of tropical rainforest, as indicated by Herold *et al.* (2010). Inclusively, the range of the family roughly matches the range of the current tropical evergreen forest, and both could be related: pyramidopids are more abundant and diverse in undisturbed rainforests than in secondary growth forests, as demonstrated by Santos and Prieto (2010; Table 2).

#### Conclusion

The small size and leaf litter habitat of most Laniatores, in conjunction with their ancient age (Giribet *et al.* 2010) and understudied nature of African opiliofauna, engender the likelihood that entirely new lineages of Opiliones could be discovered in the Afrotropics, let alone a plentitude of new species. Studying this fauna is imperative to taxonomic and

<sup>1</sup>Sharma and Giribet (2011) recovered a clade comprised of four South-east Asian families in two topologies, and a clade comprised of these four as well as Sandokanidae in a third topology; in none of the three topologies were these clades supported. The inclusion of Epedanidae in this group of families led the authors to regard it tentatively as the superfamily Epedanoidea (at least in part), but few morphological characters support either grouping.

phylogenetic research of such diverse lineages as Assamiidae and Biantidae, and is required to address fundamental biogeographical questions, such as the ancestral range of the putative ancestor of all Laniatores and the significance of continental drift during the diversification of constituent lineages.

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## References

- Anderson, C. L., Channing, A., and Zamuner, A. B. (2009). Life, death and fossilization on Gran Canaria – implications for Macaronesian biogeography and molecular dating. *Journal of Biogeography* **36**, 2189–2201. doi:10.1111/j.1365-2699.2009.02222.x
- Bauer, C., and Prieto, C. E. (2009). Three new Assamiidae (Arachnida: Opiliones) from Cameroon, with a redescription of *Chilon robustus* and comments on related species. *Zootaxa* **2059**, 1–22.
- Borges, P. A. V., and Hortal, J. (2009). Time, area and isolation: factors driving the diversification of Azorean arthropods. *Journal of Biogeography* **36**, 178–191. doi:10.1111/j.1365-2699.2008.01980.x
- Briggs, T. S. (1971). The harvestman of the family Triaenonychidae in North America. *Occasional Papers of the California Academy of Sciences* **90**, 1–43.
- Briggs, T. S. (1974). Troglotic harvestmen recently discovered in North American lava tubes (Travuniidae, Erebomastriidae, Triaenonychidae: Opiliones). *The Journal of Arachnology* **1**, 205–214.
- Carracedo, J. C., Day, S., Guillou, H., Rodríguez Badiola, E., Canas, J. A., and Pérez Torrado, F. J. (1998). Hotspot volcanism close to a passive continental margin: the Canary Islands. *Geological Magazine* **135**, 591–604. doi:10.1017/S0016756898001447
- do Amaral, A. (1975). Complexidades nomenclaturais em biologia. Gênero de nomes genéricos terminados em *-ops*. *Memórias do Instituto Butantan* **39**, 27–36.
- Giribet, G., Rambla, M., Carranza, S., Baguñà, J., Riutort, M., and Ribera, C. (1999). Phylogeny of the arachnid order Opiliones (Arthropoda) inferred from a combined approach of complete 18S and partial 28S ribosomal DNA sequences and morphology. *Molecular Phylogenetics and Evolution* **11**, 296–307. doi:10.1006/mpev.1998.0583
- Giribet, G., Edgecombe, G. D., Wheeler, W. C., and Babbitt, C. (2002). Phylogeny and systematic position of Opiliones: A combined analysis of chelicerate relationships using morphological and molecular data. *Cladistics* **18**, 5–70.
- Giribet, G., Vogt, L., Pérez González, A., Sharma, P., and Kury, A. B. (2010). A multilocus approach to harvestman (Arachnida: Opiliones) phylogeny with emphasis on biogeography and the systematics of Laniatores. *Cladistics* **26**, 408–437.
- Hallan, J. (2008). Biology catalog. Section ‘Opiliones’. Available at <http://insects.tamu.edu/research/collection/hallan/> [Accessed 24 March 2008]
- Hedin, M., and Thomas, S. M. (2010). Molecular systematics of eastern North American Phalangodidae (Arachnida: Opiliones: Laniatores), demonstrating convergent morphological evolution in caves. *Molecular Phylogenetics and Evolution* **54**, 107–121. doi:10.1016/j.ympev.2009.08.020
- Herold, N., Müller, R. D., and Seton, M. (2010). Comparing early to middle Miocene terrestrial climate simulations with geological data. *Geosphere* **6**, 952–961. doi:10.1130/GES00544.1
- Hirst, A. S. (1913). The Percy Sladen Trust Expedition to the Indian Ocean in 1905 under the leadership of Mr. J. Stanley Gardiner. No. II. – Second report on the Arachnida – the scorpions, Pedipalpi, and supplementary notes on the Opiliones and Pseudoscorpions. *Transactions of the Linnean Society of London, Zoology, Series 2* **16**, 31–37. doi:10.1111/j.1096-3642.1914.tb00122.x
- Kauri, H. (1985). Opiliones from central Africa. *Annalen Zoologische Wissenschaften, Musée Royal de l’Afrique Centrale (Tervuren), (Sci. zool.)* **245**, 1–168.
- Kury, A. B. (2003). Annotated catalogue of the Laniatores of the New World (Arachnida, Opiliones). *Revista Ibérica de Aracnología Volumen especial monográfico* **1**, 1–337.
- Kury, A. B. (2006). Checklist of valid genera of Opiliones of the World, Museu Nacional/UFRJ. Available at <http://www.museunacional.ufrj.br/mndi/Aracnologia/checklaniator.htm/> [Accessed 1 February 2011].
- Kury, A. B. (2007). Assamiidae Sørensen, 1886. In ‘Harvestmen: The Biology of Opiliones’. (Eds R. Pinto-da-Rocha, G. Machado and G. Giribet.) pp. 173–176. (Harvard University Press: Cambridge, MA, USA.)
- Lawrence, R. F. (1952). A collection of carvenicolous and termitophilous Arachnida from the Belgian Congo. *Revue de Zoologie et de Botanique Africaines* **46**, 1–17.
- Lawrence, R. F. (1957). The Opiliones collected by Dr A. De Barros Machado in the Belgian Congo during 1953 and 1955. *Revue de Zoologie et de Botanique Africaines* **56**(1/2), 151–166.
- Lawrence, R. F. (1958). A collection of cavernicolous Arachnida from French Equatorial Africa. *Revue Suisse de Zoologie* **65**, 857–866.
- Martens, J. (1977). Opiliones aus dem Nepal-Himalaya III. Oncopodidae, Phalangodidae, Assamiidae (Arachnida). *Senckenbergiana* **57**(4–6), 295–340.
- Pérez-González, A. (2006). Revisão sistemática e análise filogenética de Stygnommatidae (Arachnida: Opiliones: Laniatores). Ph.D. Thesis, Universidade Federal do Rio de Janeiro, Museu Nacional, Programa de Pós-Graduação em Zoologia.
- Pérez González, A., and Kury, A. B. (2007). Samoidae Sørensen, 1886. In ‘Harvestmen: The Biology of Opiliones’. (Eds R. Pinto-da-Rocha, G. Machado and G. Giribet.) pp. 224–226. (Harvard University Press: Cambridge, MA, USA.)
- Pinto-da-Rocha, R., and Giribet, G. (2007). Taxonomy. In ‘Harvestmen: The Biology of Opiliones’. (Eds R. Pinto-da-Rocha, G. Machado and G. Giribet.) pp. 88–246. (Harvard University Press: Cambridge, MA, USA.)
- Pinto-da-Rocha, R., and Kury, A. B. (2003). Third species of Guasinidae (Opiliones: Laniatores) with comments on familial relationships. *The Journal of Arachnology* **31**, 394–399. doi:10.1636/H02-59
- Rambla, M. (1984). Contributions à l’étude de la faune terrestre des îles granitiques de l’archipel des Sechelles. *Annales du Musée Royale de l’Afrique Centrale – Sciences Zoologiques* **242**, 1–86.
- Rambla, M. (1993). *Maiorerus randoi* n. gen. n. sp., the first laniatorid from a Canary Island cave (Opiliones, Phalangodidae). *Memoires de Biospeologie* **20**, 177–182.
- Rambla, M., and Juberthie, C. (1994). Opiliones. In ‘Encyclopaedia Biospeologica’. (Eds C. Juberthie and V. Decu.) pp. 215–230. (Société de Biospéologie: Moulis, France & Boucares, Romania.)
- Roewer, C. F. (1912). Die Familien der Assamiiden und Phalangodiden der Opiliones-Laniatores (Assamiden, Dampetriden, Phalangodiden, Epedaniden, Biantiden, Zalmoxiden, Samoiden, Palpidediden anderer Autoren). *Archiv für Naturgeschichte, Berlin. Abteilung A* **78**(3), 1–242.
- Roewer, C. F. (1923). Die Weberknechte der Erde. In ‘Systematische Bearbeitung der bisher bekannten Opiliones’. (Ed. G. Fischer.) pp. 64–120 (Gustav Fischer: Jena, Germany.)

- Roewer, C. F. (1949a). Über Phalangodiden I: Subfam. Phalangodinae, Tricommatinae, Samoinae; weitere Weberknechte XIII. *Senckenbergiana* **30**(1–3), 11–61.
- Roewer, C. F. (1949b). Über Phalangodiden II: Weitere Weberknechte XIV. *Senckenbergiana* **30**(4–6), 247–289.
- Roewer, C. F. (1949c). Einige neue Gattungen der Phalangodidae (Opiliones). *Veröffentlichungen aus dem Museum für Natur-, Völker- u. Handelskunde in Bremen, Bremen, Reihe A. Naturwissenschaften* **1**, 143–144.
- Roewer, C. F. (1953). Opiliones aus Französisch-Westafrika, gesammelt durch Herrn Dr. A. Villiers. *Bulletin de l'Institut Français d'Afrique Noire* **15**(2), 610–630.
- Santos, R., and Prieto, C. E. (2010). Los Assamiidae (Opiliones: Assamiidae) de Río Muni (Guinea Ecuatorial), con la descripción de ocho nuevas especies. *Revista de Biología Tropical* **58**, 203–243.
- Sharma, P., and Giribet, G. (2009). Sandokanid phylogeny based on eight molecular markers – the evolution of a southeast Asian endemic family of Laniatores (Arachnida, Opiliones). *Molecular Phylogenetics and Evolution* **52**, 432–447. doi:10.1016/j.ympev.2009.03.013
- Sharma, P. P., and Giribet, G. (2011). The evolutionary and biogeographic history of the armoured harvestmen – Laniatores phylogeny based on ten molecular markers, with the description of two new families of Opiliones (Arachnida). *Invertebrate Systematics* **25**, 106–142. doi:10.1071/IS11002
- Starega, W. (1992). An annotated check-list of Afrotropical harvestmen, excluding the Phalangiidae (Opiliones). *Annals of the Natal Museum* **33**, 271–336.
- Suzuki, S. (1976). Report on a collection of Opilionids from Pasoh Forest Reserve, West Malaysia. *Nature and Life in Southeast Asia* **7**, 9–38.
- Suzuki, S. (1985). A synopsis of the Opiliones of Thailand (Arachnida) I. Cyphophthalmi and Laniatores. *Steenstrupia (Copenhagen)* **11**, 69–110.
- Ubick, D., and Briggs, T. C. (1992). The harvestman family Phalangodidae 3. Revision of *Texella* (Opiliones: Laniatores). *Texas Memorial Museum. Speleological Monographs* **3**, 155–240.
- Ubick, D., and Briggs, T. C. (2002). The harvestman family Phalangodidae 4. A review of the genus *Banksula* (Opiliones, Laniatores). *The Journal of Arachnology* **30**, 435–451. doi:10.1636/0161-8202(2002)030[0435:THFPAR]2.0.CO;2
- Ubick, D., and Briggs, T. C. (2004). The harvestman family Phalangodidae 5. New records and species of *Texella* Goodnight and Goodnight (Opiliones: Laniatores). *Texas Memorial Museum. Speleological Monographs* **6**, 101–141.
- Ubick, D., and Briggs, T. C. (2008). The harvestman family Phalangodidae 6. Revision of the *Sitalcina* complex (Opiliones, Laniatores). *Proceedings of the California Academy of Sciences* **59**, 1–108.

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